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SEED GERMINATION THEORY AND PRACTICE

SECOND EDITION

Norman C. Deno, Professor Emeritus of Chemistry

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Based on Experiments on 145 Families, 805 Genera, and about 2500 Species

Every species has some mechanism for delaying germination until after the seed has been dispersed. The Science of Seed Germination is the discovery and description of such mechanisms and the development of procedures for removing them so that the seeds can germinate.

To Plant a Seed Is a Noble Deed
Propagation Is Conservation

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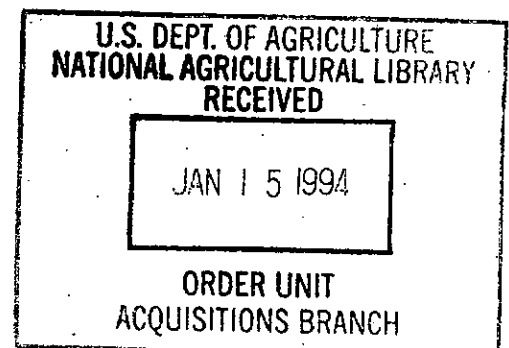
SEED GERMINATION, THEORY AND PRACTICE

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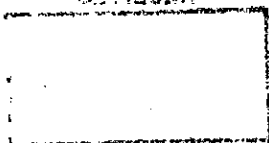
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FOREWORD TO THE SECOND PRINTING OF THE SECOND EDITION

This copy of the second edition of Seed Germination Theory and Practice is from a second printing which accounts for any delays. The experiments on seed germination are continuing and that had to take first priority. As compensation you will get the following brief update on some of the more significant observations made since the first printing in May 1993. Also the opportunity was taken to correct a few errors. The following update briefly summarizes some of the more significant results obtained since the first printing.

Alangium platanifolia seeds were washed and cleaned for seven days. Such seeds germinated over several weeks at 70 when treated with GA-3 and not otherwise. This is the first example of seeds in a fruit that had a GA-3 requirement for germination.

Adonis vernalis and its geographical variants continue to be a problem. Large amounts of seeds from two commercial houses have proven to be over 99% empty seed coats the same as seed from our own plantings and various other sources. There is need for someone to breed seed viability back into this species.

Several more cacti have been found to require GA-3 for germination. It is possible and even likely that the majority of cacti will be found to have this requirement. A definitive article has been written by myself and will appear in the *Journal of the Cactus and Succulent Society* early in 1994.

Caltha palustris required GA-3 for germination. Seeds rapidly die when held moist at 70, and all are dead in one month. This is one of the most rapid death rates yet observed for seeds held moist at 70.

Caulophyllum thalictroides and *Sanguinaria canadensis* self sow on our property yet fail to germinate under all conditions including treatment with GA-3. It is likely that these species have a gibberelin requirement for germination, but that some gibberelin(s) other than GA-3 are required. Note that it was already shown that different gibberelins initiate germination in *Shortia galacifolia* but in different patterns. The whole problem of gibberelin requirements for germination are obviously complex. It will be some time before they are completely understood.

Related to the gibberelin situation is the problem of germination in *Trillium*. *Trillium apetalon* and *Trillium pusillum* have now been shown to require GA-3 for the first step in germination, namely formation of the corm and root. Several other *Trillium* had this behavior, but others had more complex responses to GA-3. Needless to say the *Trillium* problem is under intensive study.

Plentiful supplies of seeds of *Lysochiton americanum* and *Symplocarpus foetidus* have now been obtained from our own plantings and the proper experiments were conducted. Both were found to require light for germination typical of most swamp plants. Germination occurs in several weeks in light at 70 and none in dark.

Seeds of four arctic willows (*Salix arctica*, *S. herbacea*, *S. lanata*, and *S. phylicifolia*) were collected by D. Haraldsson in Iceland and sent immediately. These germinated in two days at 70. Dry storage for two weeks at 70 completely killed the seed. However, the seeds can be stored moist at 40 for at least four weeks. Such seeds germinate in two days the same as fresh seed when shifted to 70. It is of interest that the seeds turn green when moist at 40, but do not develop further.

Sambucus pubens has been found to require GA-3 for germination the same as other *Sambucus*. This seems to be a general requirement in this genus.

Senecio aureus required light for germination. Further, exposure to moist conditions at 70 for just two months led to complete death of the seeds. *Vernonia altissima* also required light (or GA-3) for germination at 70. It is unusual for such light requirements in species of *Asteraceae*.

I am particularly indebted to Thomas Fischer, Senior Editor of *Horticulture*, for a charmingly written account of my work. As a result the first printing of the second edition sold out. Purchasers who are receiving the second printing will forgive a somewhat delayed shipment. I also wish to express my appreciation to the many amateur gardeners, seedsmen, and horticulturists who have cooperated by sending me seeds from every corner of the World. Further, it has been the utmost pleasure to see how nurseries and professional propagators have embraced my book with enthusiasm. Many kind letters were received for which I am most grateful.

In contrast, there has been little reaction from the academic community despite the fact that my work on seed germination applies techniques more sophisticated and analysis more profound than has been used in past work. There are reasons for this lack of response. The problem faced by departments of horticulture and other biologies is that they can no longer limit their research to bending over microscopes. To survive they are increasingly becoming pseudo-chemistry departments, because this is the direction that has the potential for large research grants. The previous head of the Department of Horticulture at Penn State had his Ph. D. in chemistry. The Department of Botany, Microbiology, and Zoology are gone. These are the signs of the times and indicative of the directions things are going.

The type of work described in this book is not the type that brings in big research money despite its importance to both theory and practice of horticulture. It will be interesting to see whether it ever gets much reaction from the academic community.

Finally to end on a note of humility, on recounting the number of species studied, the number is about 2500, not 4000 as given in the first printing. Further, gibberellin and gibberellic acid were misspelled throughout and should have an added letter l.

CHAPTER 1. (A) INTRODUCTION AND (B) PRINCIPLES

(A) INTRODUCTION

The initial concept of this book was to write a list of species with a one line description of the best method for germinating the seed. Such a book would be patterned after the The Seedlist Handbook of Bernard Harkness (ref. 1) and would supplement that book. After reading the six latest books on seed germination (refs. 2-7), it was evident that the book could not be constructed from data in the literature. The decision was made to embark on a broad program of studying seed germination. At this time the realization came that the germination of seeds is a chemical process, and seed germination should be studied with the same techniques and logic used to study chemical processes. Perhaps these techniques, which had so drastically changed our concepts of chemical processes, would have a similar effect on our concepts of seed germination.

Initially the studies were restricted to alpine and rock garden plants, but with each new discovery, the thrill of the hunt increased. Ultimately the studies were broadened to include trees and shrubs and finally tropical plants and the grasses. It became evident that the work was of importance not only to plant growers but also to research biologists and research chemists. The question arose whether to write separate books for each of these three audiences or to attempt a *tour de force* putting it all in one book. The *tour de force* was chosen, and this has necessitated some words of explanation directed at each of the three audiences.

For the **plant grower**, the directions for optimum germination of nearly 2500 species will be of the most interest. These directions are summarized in Chapter 20 and arranged in alphabetical order of the genera. A number of abbreviations are used in Chapter 20, and these are all explained at the beginning of that chapter. These directions for optimum germination can be followed without reference to any other part of the book. After the seed has been germinated, there is the problem of how to best handle the small seedlings. This subject is taken up in Chapter 14, and several highly efficient methods are described.

I can appreciate that the first reaction to the detailed recommendations and extensive data is that it is all too complicated. There will be the temptation to go back to old ways, to water long rows of pots twice a week for months on end, to expect only a small percentage to germinate, and to resort to growing the easy ones dismissing the rest as difficult and recalcitrant.

There are better ways with which you can expect success rates of 90% and better. Best of all it can be done with a fraction of the effort and expense and most of all a fraction of the space that are used in traditional methods. The procedures require the usual pots and media plus high wet strength paper towels and polyethylene sandwich bags called Baggies (both available at your grocery store) and permanent ink pens (available at any office supply store). The procedures are described in detail in Chapters 3 and 14. As you become more comfortable with these new techniques, you will have the confidence to try anything. Especially become familiar with germinating seeds in pots enclosed in polyethylene bags. Plants can be grown by this

procedure for six months to a year under fluorescent lights with watering reduced to less than once every two months. Also become familiar with germinating seeds in moist paper towels enclosed in Baggies. For seeds that require extended treatments, these lengthy periods of time can be spent in the moist paper towels. Watering is reduced to once every several months, the towels occupy very little space, and no light is needed. Be sure to read Chapters 3 and 14 to understand that the polyethylene bags must not be sealed too tightly and that thin polyethylene film is better than thick films. Aerobic conditions must be maintained.

Some species require gibberelic acid for germination, but do not let that frighten you. It is a natural requirement, and a highly efficient procedure has been developed for applying the gibberelic acid (see Chapters 3 and 12). The only additional materials that are needed are toothpicks and the gibberelic acid. No weighings or volume measurements are needed. The gibberelic acid is used so efficiently that one gram is sufficient for a thousand experiments since only one cubic millimeter is required for each experiment.

So now you have the program. Sit down on a cold winter's night with the list of seeds that have been ordered or perhaps have already arrived. Arrange them in alphabetical order. Then go through Chapter 20 looking up each one. Arrange them in groups that require similar treatments. Plan your strategies. Time the operations so that the seedlings started indoors are ready to be set outdoors at appropriate times. Use the highly efficient short cuts described in Chapter 3 and 14.

Let me encourage the plant grower to read the other chapters. The rate studies are framed in language that everyone can understand. A rate plot is simply a graph of the number or percent seeds germinated on the vertical axis against time on the horizontal axis. Such a plot with its induction time and rate curve contains much more information than percent germination and is a more sensitive way to determine the effect of variables. Everyone can understand the first principle of mechanistic chemistry. If a treatment A or conditions A are required to get germination under conditions B, critical processes were taking place during A and these were likely taking place at their optimum rates (greatest speeds). Thus if a period of three months at 40 deg F is required to get germination at 70, the period at 40 was a time when something was happening (typically destruction of germination inhibitors); and it is misleading to refer to this period as a period of dormancy or a period of breaking dormancy.

For **biologists** the rate studies and rate theory in Chapters 4 and 19 should encourage all biologists to make more use of rate studies. One of the principles of physical organic chemistry is that complex multiple step processes can obey simple rate laws. Generally in a complex sequence, one step will be the slow or rate determining step. This step not only dictates the overall rate, but it also dictates the rate law for the overall process. Chapter 19 shows the excellent fit of some germination rates to simple rate laws.

Biologists will also be interested in the special ability of biological systems to show enormous changes in rate with temperature. These can be (a) the result of configurational changes in proteins from enzymatically active configurations to inactive ones or (b) the result of structural changes in membranes that alter their permeability. These changes can be complete over a temperature range of as little as five degrees. Many examples of enormous rate changes are described in Chapters 6 and 7, and the

theory is discussed in Chapter 19. I find that biologists are quite familiar with the extreme sensitivity of metabolism to temperature changes, but they do not always look on these as rates and rates with enormous temperature coefficients.

For the **chemist** the ability of biological systems to show enormous changes in rate with temperature opens up new rate behaviors that are unknown in small molecule chemistry. Examples are the germinations that take place under conditions of oscillating temperatures. The theory of these is discussed in Chapter 19. Do not be put off by the simplicity of the experiments. At this stage the basic phenomena have to be discovered, and the simple experiments are best suited for this purpose. In my career we used every form of spectroscopy, and these were available. It will be for future workers to use these more sophisticated methods for determining the intricate chemistry involved.

This book depends on botanical taxonomy and the concept of a species. Linnaeus believed that species were immutable. Darwin and the principle of evolution (it is not a theory anymore) changed all that. Fortunately there is a solution to this conflict. The solution has been presented in its clearest form by Stephen Gould in his article What is a Species. His views are adopted and are described in Chapter 16.

The experiments, the writing, the publication, and the distribution of this book were done by myself. The book has been distributed below cost. The effort was pure pleasure as it allowed me to combine my career in chemistry where I had published one hundred and fifty papers with a secondary career in horticulture where I had published twenty papers.

This book and the experiments described would not have been possible without the contributions of seeds from over one hundred people, many botanic gardens, and the seed exchanges of horticultural societies. These are all acknowledged in Chapter 23. Since writing the first edition, many suggestions have been received (and some sharp criticisms). These have all been of value and all had some influence on this second edition. The people who sent these are acknowledged in Chapter 23. Also acknowledged are the many wonderful teachers that I had at all levels and the many wonderful colleagues and graduate students with whom I associated.

(B) PRINCIPLES

1. EVERY SPECIES OF PLANT HAS ONE OR MORE MECHANISMS FOR DELAYING GERMINATION UNTIL THE SEED IS DISPERSED

(Chapters 5-12). This principle pervades every aspect of seed germination. Without such mechanisms, seeds would germinate in the capsule or fruit and would never be dispersed. The challenge in germinating seeds is to overcome these delay mechanisms. It is proposed to call all treatments used to overcome delay mechanisms as conditioning. With 95% of the species studied, the delay mechanism is chemical. With the remaining 5% it is physical. Although some species have seeds that germinate quickly after dispersal such as *Oronticum*, *Populus*, and *Tussilago*; they still must have a mechanism to block germination before dispersal. A few species (the mangrove and *Polygonum viviparum*) germinate before dispersal, but the germination is so limited that in effect ungerminated seeds are being dispersed.

2. TEMPERATURES OF 40 OR 70 DEG. F WERE USED FOR BOTH GERMINATIONS AND CONDITIONING AND RARELY WAS ANY OTHER TEMPERATURE NEEDED (Chapter 3). A few species germinated better at temperatures in the range 90-100 or after brief exposures to even higher temperatures (Gomphrena, Kalmia, and Mimosa in Chapter 20). Such behaviors were rare. Although it is intended to conduct exploratory experiments on temperatures between 40 and 70, it is not expected that these will alter in any major way either the principles or the recommended procedures.

3. MEMBERS OF THE SAME FAMILY, THE SAME GENUS, AND EVEN CLOSELY RELATED SPECIES MAY HAVE DIFFERENT MECHANISMS FOR DELAYING GERMINATION. The data in Chapter 20 are arranged by genera, but this is not meant to imply any generalized behavior within each genus. While there are trends, behaviors are as much a result of adaptations to the environment in which the plant grows as by evolutionary associations.

4. FUNGAL PRODUCTS OF THE GIBBERELIN TYPE HAVE A MAJOR EFFECT ON GERMINATION OF AT LEAST 25% OF ALL SPECIES (Chapters 3 and 12). Some species have evolved gibberelins as a requisite for germination. This has important survival value, particularly for small plants in cold desert areas. With other species gibberelins may have a large effect on germination, but germination can be effected without it. It is remarkable that the species that required light for germination usually germinated in the dark with gibberelin. The reasons for this relation are not understood. Gibberelins can also be without effect or deleterious to germination so that gibberelins should not be conceived as some "cure all" for recalcitrant germination. The effects are complex and an example was found where gibberelic acid-3 affected the second step but not the first step in a two step germinator (*Lilium canadense*). Rarely germination with gibberelic acid-3 takes place at 40 (the rosulate violas) instead of at 70.

5. ABOUT 50% OF TEMPERATE ZONE PLANTS USE A DELAY MECHANISM THAT IS DESTROYED BY DRYING (Chapter 5). The prevalence of this mechanism leads to a common misconception that all seeds will germinate when exposed to warmth and moisture. The common practice of regarding such seeds as "immediate germinators" obscures the fact that a drying period is needed before the seed will germinate. The length of time needed for the drying is dependent on the species, the temperature, and the relative humidity. During the drying chemical changes take place that are amenable to rate analysis.

6. MOST SPECIES HAVE AT LEAST TWO DELAY MECHANISMS, ONE BEING IN THE NATURE OF A CHEMICAL TIME CLOCK (Chapter 4). Most seeds have an induction period of one to eleven weeks after moistening and before germination begins. This is true even after any requisite drying or any requisite cold or warm moist cycles. In the past such induction periods have been regarded as time required for physical transfer of oxygen and water or time required for growth of the embryo. However, such explanations would generate a rate plot where there was a gradual onset of germination. What is generally found is that there is a sudden onset of germination which is more typical of a chemical time clock.

7. IT IS COMMON FOR THE DELAY MECHANISM TO BE DESTROYED AT ONE TEMPERATURE FOLLOWED BY GERMINATION AT ANOTHER TEMPERATURE (Chapter 6). It has long been recognized that many seeds require a period around 40 deg. F followed by a shift to 70 deg. F before germination will occur. In the present work it was found that there were nearly as many examples of the reverse, namely a period of time at 70 followed by germination at 40. Both behaviors require that the processes involved in conditioning have enormous changes of rate with temperature.

8. SOME SPECIES HAVE SEVERAL DELAY MECHANISMS THAT MUST BE DESTROYED UNDER DIFFERENT CONDITIONS OF TEMPERATURE AND TIME AND IN SEQUENCE (Chapter 7).

9. SOME SPECIES GERMINATE UNDER CONDITIONS OF OSCILLATING TEMPERATURES (Chapter 10). Such seeds are programmed to germinate in the fall or spring when daily temperatures oscillate widely. Such oscillating temperatures were simulated in the laboratory with Cleome, and the same stimulation of germination resulted. The frequency of the temperature oscillations were varied with little effect on the rate plots. This was interpreted as showing that the results were due to the oscillating temperatures and not germination at some temperature intermediate between 40 and 70. Experiments are planned to investigate these intermediate temperatures and settle the question decisively.

10. LIGHT IS AN IMPORTANT VARIABLE AND IS A REQUIREMENT FOR GERMINATION IN SOME SPECIES (Chapter 11). The requirement of light for germination is characteristic of plants growing in swamps or woodland where the availability of light is more of a problem than the availability of water. The requirement of light for germination can usually (but not always) be replaced by treatment of the seeds with gibberelic acid-3 as mentioned in number 4 above. Rarely light can block germination, and the survival value of this is discussed. A photosynthesizing seed coat was a factor in one species (*Hymenocallis*) and a photosynthesizing seed capsule was a factor in another (*Zantedeschia*).

11. SEEDS IN FRUITS OFTEN HAVE CHEMICAL INHIBITORS IN THE FLESH OF THE FRUIT THAT BLOCK GERMINATION AND MUST BE REMOVED BY WASHING BEFORE GERMINATION WILL TAKE PLACE (Chapter 8). Usually these chemical inhibitors are water soluble so that soaking in water with daily rinsing for seven days is sufficient for their removal. Less commonly the inhibitors are oil soluble so that the washings must be conducted with aqueous detergents. The inhibitors are continually diffusing into the seed, and the seed is continually destroying the inhibitor. The rates of the destruction of inhibitors inside the seeds can be determined. Sometimes this rate is so fast that the seeds germinate in the third day of washing. Despite the physically hard nature of many seeds of this type, there is a cleft in the seed coat so that producing a hole in the seed coat has no favorable effect (*Prinsepia* is an exception). Although the above mechanism is often found in seeds in fruits, other mechanisms involving light and dry storage requirements are also found.

12. SOME SPECIES HAVE TWO STEP GERMINATIONS (Chapter 6). In the first step the radicle emerges, and a small bulb or corm with root is formed. In the second step a photosynthesizing leaf or leaves are formed. Usually the first step takes place at 70. Then a period of time at 40 is required followed by a return to 70. Sometimes simply an extended period of time at 70 or 40 serves to initiate the second step. The concept of two step germination should not be confused with epigeal and hypogeal germination. Epigeal (photosynthetic cotyledons) and hypogeal (aborted cotyledons) can be either one step or two step germinators.

13. SEEDS OF SPECIES FROM COLD DESERT AREAS GENERALLY GERMINATE AT LOW TEMPERATURES, TYPICALLY 35-40 DEG. F (Chapters 6 and 7). This is a principle of general validity. The survival value is obvious. Seeds of plants from cold desert areas have to get a quick start in spring when moisture is still available.

14. RATE DATA ARE LESS AMBIGUOUS THAN THE TRADITIONAL PERCENT GERMINATION AND ARE MORE SENSITIVE TO INTERNAL CHANGES IN THE SEEDS. The traditional percent germination can mean anything from the percent viable seeds that germinate to the percent of normal size seed coats that contain viable seeds. It will depend on the degree of sophistication used in detecting viable seeds from both non-viable seeds and empty seed coats.

15. SOME SPECIES PRODUCE QUANTITIES OF NORMAL SIZE SEED COATS WHICH ARE EMPTY (Chapter 3). This has survival value. The calculation of percent germinations is complicated by this factor, but rates of germination are not.

16. RESULTS THAT APPEAR TO BE INCONSISTENT CAN ARISE FROM SEVERAL CAUSES (Chapter 3). Causes include the presence or absence of gibberelin producing fungi in the media, variations in storage of the seed, uncertainties in the identification of the botanical species and subspecies, and possibly variations in the climate in different years or in different geographical localities. Pathogenic fungi were not a problem in the procedures used, and the evidence for this is presented in Chapter 3.

17. PARASITIC PLANTS MAY REQUIRE EXOGENOUS CHEMICALS FROM THE HOST FOR GERMINATION, BUT USUALLY THEY DO NOT (Chapter 12). Although exogenous chemicals may be required for the later development, the germination of the seed usually does not have such requirements.

18. GERMINATION OF SEEDS USUALLY FOLLOW ZERO ORDER OR FIRST ORDER KINETICS WITH GOOD PRECISION (Chapters 4 and 19). The reasons why complicated biological processes can follow simple mathematical equations is explained in Chapter 19.

19. SEEDS OF A SIGNIFICANT NUMBER OF SPECIES ARE SOLD AND DISTRIBUTED BY COMMERCIAL SEED COMPANIES IN A DOD (DEAD ON DELIVERY) STATE (Chapter 13). Many species have seeds that do not survive very long in dry storage even at 40. Ways to store and distribute seeds in moist states are described in Chapter 13.

20. THE CONCEPT OF DORMANCY AND REQUISITE COLD CYCLES HAS BEEN COMPLETELY REVISED (Chapter 19).

CHAPTER 2. GERMINATION, DEFINITION AND DESCRIPTION

In the rate studies described herein, germination was taken as the time when the radicle (or rarely the epicotyl) could first be detected breaking through the seed coat. In general the radicle elongates rapidly so that there was little ambiguity in deciding when a seed had germinated. Less common were confusing situations where the seed would expand 10-40% splitting the seed coat, but the radicle would not start development until after a significant period of time or after a shift to another temperature. In these situations germination was not recorded until the radicle began to develop. This latter behavior was found in *Cornus*, *Corydalis*, *Daphne*, *Euonymus*, *Prunus*, and *Taxus*.

An important distinction is now proposed. One-step germinators form the photosynthesizing leaves (cotyledons or true leaves) within a few weeks of germination and at the same temperature at which germination occurred. Two-step germinators form the radicle first. The radicle may or may not develop a bulb or corm with attached root. The photosynthesizing leaves do not form until (a) after a significant time gap of two or more months or (b) after one or two shifts of temperature. Examples of the first behavior are *Abeliophyllum distichum* and *Clematis lanuginosa* where simply keeping the seedlings for two to three months at the original germination temperature of 70 will initiate development of leaves. More often a shift in temperature is needed. Typical is the behavior of *Trillium* and about half of *Lilium*. With these a radicle and bulb or corm forms at 70. When this is complete the seedlings have to be shifted to temperatures around 35-40 for three months. On returning to 70 the photosynthesizing leaf (usually a single leaf) forms which is a cotyledon in *Trillium* and a true leaf in *Lilium*. The three months at 35-40 are a period where chemical changes are occurring, and these temperatures are the conditions where these chemical changes occur most rapidly. The resumption of growth usually occurs on a shift to warmer temperatures, but many examples were found where growth resumed at the low temperature after a period of time and after the inhibitors had been destroyed.

These chilling periods are termed conditioning or conditioning periods. Traditionally they have been described as dormancy or breaking dormancy. These traditional terms imply inactivity when in fact certain processes are occurring at their maximum metabolic rate. The chilling period has also been described as stratification, an archaic term derived from the old English process of placing seeds in layers in sand and placing them outdoors overwinter. This term is equally misleading as are terms like vernalization or winterization. It is best to get to the heart of the matter and call these periods conditioning periods in the sense that they get the seeds into a condition where they can germinate.

Flowering plants are divided into the monocotyledons with one germinating leaf and dicotyledons with a pair of germinating leaves. Even this most useful of divisions has an occasional exception. In the present work *Claytonia virginica*, a dicotyledon, developed only a single germinating leaf. This was discussed with Prof. Carl Keener at Penn State who said that *Ranunculus ficaria* also does this and that the phenomenon is known. Orchidaceae never develop any cotyledons. A description of their fascinating life cycle can be found in Summerhayes (ref. 8).

Flowering plants are also divided into epigeal and hypogeal germinators. In epigeal germination the cotyledon(s) are the first photosynthesizing leaves. In hypogeal germination the cotyledons wither within the seed coat, and the first photosynthesizing leaf or leaves are true leaves. Both monocotyledons and dicotyledons have species with both types of germination. Both types are found within the same family and even the same genus as in *Lilium*. In beans and peas the cotyledons do some photosynthesis, but are primarily storage organs. Thus the division into epigeal and hypogeal is not always clear and in any event does not seem fundamental to plant classification. Most important, epigeal and hypogeal must not be confused with one-step and two-step germinators. One-step germinators can be epigeal (most dicotyledons) or hypogeal (Iridaceae and Poaceae). Two-step germinators can likewise be either epigeal (*Trillium*) or hypogeal (many *Lilium*). All four combinations can be found in both monocotyledons and dicotyledons.

Before leaving germination it is appropriate to discuss percent germination and the difficulties that arise in determining this number. Percent germination is the number that has been used traditionally to measure germination and the effectiveness of germination procedures. It is defined as the number germinated x 100 divided by the total number of seeds. The number germinated can be determined with reasonable certainty using the definition of germination given above. It is the determination of the total number of seeds that causes the problem as illustrated by the following example. Anyone who has cracked open a number of pits of a stone fruit like plums will note that a number of the pits are hollow shells. Judging from external appearance these would have been counted as seeds. Suppose the investigation is more sophisticated and examines the seeds by X-rays and determines the number of such empty shells. It does not stop there. Techniques could be developed that would reveal that some of the seeds lacked embryos or had abnormal embryos. Thus the total number of seeds will depend on the technique used to determine the number of seeds.

For these reasons percent germination are best used in comparing sequential germination in a single sample or comparing results from different treatments of a single sample. It is of much less significance in an absolute sense.

CHAPTER 3. DESIGN OF THE EXPERIMENTS

Part A. Concepts and Variables

The overall plan of this work was to measure the rates of germination for a wide range of species and for a wide range of conditions. Plots or graphs were constructed with the number of seeds (or the percentage) on the vertical axis and time on the horizontal axis. These are rate plots, and they are the most sensitive way of detecting the effects of any treatments and conditioning of the seeds. It is emphasized that these rate plots can be used without any recourse to mathematical analysis. They can be treated as empirical plots and used simply as a delicate sensor to detect internal changes in the seeds that were caused by any prior treatments.

Work on seed germination in the past has been directed towards growing plants. The present work has a different philosophy. Seed germination is a science in itself and a fascinating one replete with a multitude of phenomena. An understanding of this science will best serve the goal of growing plants from seeds.

All seed bearing plants must have a delay mechanism as stated in Chapter 1. The 5% that use physical mechanisms are treated in Chapter 9. A question arises as to the nature of the chemical mechanisms used by the other 95%. The word chemical is used here in its broadest sense. It includes destruction of a specific chemical inhibitor, conformational changes in proteins to go from enzymatically active to inactive forms, restructuring of membranes to change their permeability, and possibly the formation of promoters.

Temperature is a major variable in seed germination. Virtually all of the experiments were conducted at either 40 or 70 deg. F. These two temperatures were chosen first for convenience. The temperature of 70 is the temperature at which most rooms are kept, and 40 is the temperature at which refrigerators are generally set. These two temperatures also roughly correspond to the temperatures of the winter and summer seasons. Also there has been much work done on the chilling periods required by fruit trees in order to prepare the buds for opening and growth in spring. It had been found that temperatures in the range 35-40 were most effective, and temperatures below freezing were ineffective.

As the work progressed it was found over and over that destruction of delay mechanisms would take place at either 40 or 70 but not both. This means that these processes undergo an enormous change in rate somewhere between 40 and 70. It is likely that nature has evolved these chemical processes to take place in just two temperature regions so that the plant has a well defined winter metabolism and a well defined summer metabolism. It is likely that 40 and 70 are near the center of these two temperature regions. It is proposed that temperature variations of the order of five to ten degrees centered around 40 or 70 have small effects on rates, but the jump from the region around 40 to the region around 70 causes enormous changes in rates. Much more work will be needed to firmly establish this principle.

Germinations also tend to take place either in the 40 region or the 70 region of temperatures. However, with germinations the division is not so complete. Examples were found where germination would take place at both 40 and 70.

There have been reports that temperatures in the 90-100 region are required for the germination of certain species and that short exposures of temperatures as high as 180 initiate germination (see *Gomphrena*, *Kalmia*, and *Mimosa* in Chapter 20). In the present work *Gomphrena haageana* and *Mimosa pudica* were the only species in which temperatures other than 40 or 70 were investigated. The generally successful germination of nearly 2500 species at 40 or 70 indicates that temperatures other than 40 and 70 are rarely needed.

Time is another critical variable. Nearly all the work was conducted using periods of three months at one temperature followed by a shift to the other temperature. This led to a series of alternating cycles each of three months duration. The three month period was chosen because it corresponds roughly to the length of the winter and summer seasons and because studies on fruit trees had shown that three months of chilling was about the amount required.

By using rate studies and rate techniques it was quite easy to show that the three month periods were a good choice. For example, *Eranthis hyemalis* has a delay mechanism that is destroyed at 70. Samples were held at 70 and portions periodically removed and shifted to 40 where germination took place. It was possible from rate plots of the germination at 40 to construct the rate plot for the destruction of the inhibitor system at 70 and to show that destruction of the inhibitor system was complete at the end of three months at 70.

Occasionally the rate plots showed that times longer than three months were needed. When this was the situation, longer times were investigated. Sometimes the rate plots showed that times shorter than three months could have been used.

Dry storage is a critical variable. All seeds are ultimately killed if dry storage is continued long enough (Chapter 13). The rates of dieing in dry storage vary widely and are a taxonomic character for each species. Some species cannot tolerate even a week or two of dry storage and others retain viability in dry storage for over a hundred years. These death rates follow a rate curve. There is no point where all the seeds suddenly die. These death rates depend on temperature and relative humidity, and even the best literature studies did not control these variables very well. There is some anecdotal evidence to indicate that seeds that have been stored too long and are near death will germinate, but the seedlings are weak and may not survive.

Some seeds require a period of dry storage to destroy inhibitors, and these are termed D-70 germinators (Chapter 5). The rates of the destruction processes vary widely and are a taxonomic character for each species. With these D-70 germinators there are opposing processes in dry storage. One is destroying inhibitors and favoring germination and the other is the dieing in dry storage which is unfavorable to germination. There will be an optimum time or range of times for the dry storage.

When fresh seeds were obtained, they were subjected to various treatments both in the fresh state and after dry storage. Six months was the usual time for the dry storage, but a few experiments were conducted for longer and shorter times where the data indicated that studies on other times would be of value.

Early in the work the seeds were subjected to dry storage at both 40 and 70. A number of experiments showed that there was little difference in viability between seeds dry stored at 40 relative to seeds dry stored at 70. As a result dry storage at 40 was abandoned, and all later experiments used only dry storage at 70. Where a difference occurred as in *Hyacinthus orientalis*, death rates at 40 were slower than at 70, but not by enough to be a solution to the problem of storing the seeds. This problem is discussed in more detail in Chapter 13.

Most of the samples of seeds were received in midwinter and had already been subjected to some dry storage at unknown temperatures and relative humidities. This introduced some uncertainty into the data in Chapter 20 and is a potential cause of results that appear to be inconsistent.

Light is an important variable (Chapter 11), and one that has often been poorly controlled in past work. Light stimulated the germination in many species. Where it stimulated germination, it was often an absolute requirement. This is contrary to past literature which generally regarded light as "favoring, not favoring, or having no effect" on germination.

In the present work only one light intensity was used and only one timing cycle (twelve hours on twelve hours off). A vast number of experiments could be constructed varying light intensity and timing cycles. It is expected that the results will not lead to improved germination procedures, but this will have to be tested.

Oscillating temperatures were required for germination by some species, and this behavior was totally unexpected (Chapters 10 and 19). It was found that some species would germinate under outdoor conditions, but not under the alternating three month cycles at 40 and 70. There are two explanations for this. One is that these are the first examples of chemical processes that proceed only under conditions of oscillating temperatures. Such an effect is theoretically possible, but has not been found to the best of my knowledge in small molecule chemistry. Experiments on germination of *Cleome* (Chapter 10) indicate that this is the correct explanation, but more work is needed. The other explanation is that germination is occurring at some temperature between 40 and 70 and not at 40 or 70. This is regarded as less likely, but the definitive experiments of conducting germination at 40, 50, 60, and 70 have not yet been done.

Gibberelins are a critical variable. Because of two recent papers (refs. 9 and 10, see Chapter 12) treatment with and without gibberelic acid-3 (GA-3) has become a standard treatment given to every sample of seeds. It is important to control this variable. It has been a cause of inconsistent results.

Disinfection of Seeds was not used in the present work. There was much evidence that pathogenic fungi were not a problem and that only dead seed and empty seed coats were attacked by fungi in the moist paper towels. First was the observations that fungal spots were generally few and isolated. Close examination with a lens showed that these were associated with empty seed coats or pieces of chaff and debris. Early evidence of fungal attack is sticking of the seed coat to the towel, appearance of a tiny droplet of white fluid at the apex of the seed, softness of the seed, and ultimately the fungus itself surrounding the seed coat. Such fungal spots and rotting seeds were removed by forceps or a toothpick. If they became too numerous, the unrotted seed was moved to a fresh towel. The remaining seeds stayed firm and in many cases germinated months later and sometimes years later, evidence that the fungi were not pathogenic and were not attacking live seed.

The second line of evidence was that the fungal attacks were spaced. They did not expand in concentric rings of growth nor did they progress along any front. Both would have happened if the fungi had been pathogenic. Third was the behavior of some species in Berberidaceae and Ranunculaceae. Certain of these do not survive dry storage although the seed shows no outward sign of having died. When such seed that has been dry stored for six months is placed in a moist towel, it is completely rotted in a week or two. In contrast fresh seed of the same species stayed firm and unrotted in the moist towels for months and even over a year until they finally germinated, and throughout this time there was no evidence of fungal attack. Fourth was the behavior of a few species, *Lindera benzoin* and *Skimmia japonica* for example, where about half the seed rotted within a week or two after encountering moisture while the rest of the seed ultimately germinated and produced vigorous seedlings. The seeds that rotted must have been internally infected for such rapid fungal attack.

Finally John Gyer has tried a number of methods for external disinfection of a strain of lima bean that he and his wife Janet market. None were effective and many were deleterious. Spraying the vines with fungicides at the time of blooming seemed to have some effect in lowering the percentage of internally infected seeds.

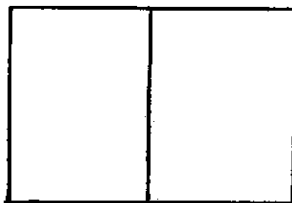
Several factors were found to have little importance despite reports in past literature. Soaking seeds in water has often been recommended. Of course seeds in fruits usually need to have the inhibitors removed by washing (Chapter 9), but that is something different than proposing that soaking alone is favorable. Table 8-1 in Chapter 8 gives some data comparing soaking for one week relative to soaking for four weeks. In general there was no advantage in the longer periods of soaking. It is concluded that the supposed favorable effects of soaking are largely a myth.

Removal of seed coats has been claimed to be beneficial for germination (ref. 11) because the seed coats were thought to be repositories for germination inhibitors. Not only is this unlikely from a chemical viewpoint, but no evidence of this could be found in the present work. From the chemical viewpoint the outer seed coat (the pericarp) and the inner seed coat (the testa) are lignaceous, insoluble, high polymers that are not suited to be repositories for water soluble or oil soluble germination inhibitors. From the experimental viewpoint a number of experiments were conducted on species of *Acer*, *Corylus*, *Prinsepia*, and *Quercus*. No evidence was found for seed coats as a repository for germination inhibitors and the claims for *Acer sacharum* and *Corylus avellana* were specifically tested. It is important to differentiate the claims of inhibitors in seed coats from the problem of an impervious seed coat. The latter can be readily detected by simply making a hole in the seed coat instead of total removal of the seed coat.

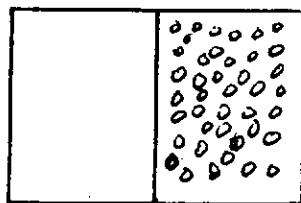
A minor problem involved empty seed coats. It is characteristic of some species to produce quantities of empty seed coats or produce empty seed coats some years and viable seeds other years. Some samples of seeds were found to contain up to 100% empty seed coats which cannot be detected by the outward appearance. Species of spruce, the beech nut, and *Adonis vernalis* are particularly prone to this behavior. It is proposed that this may have survival value. Seeds are eaten by many animals and insects. Suppose something eats the seeds, if it opens many seed coats only to find them empty, it will become discouraged and diminish efforts to eat the seeds. This survival technique is well known in certain fish such as grunions which spawn in great numbers in a highly localized area in a single night of the year.

Part B. Experimental Procedures

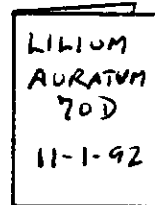
Basic Procedure. The only materials needed for the basic procedure are (A) ScotTowels, a high wet strength paper towel made by the Scott Paper Company; (B) Baggies, a polyethylene bag made by the Mobil Chemical Company; and (C) Pilot extra fine point permanent markers made by the Pilot Corporation of America. A perforated section of paper towel is torn off and folded in half three times in alternating directions to give a rectangular pad 2.5 x 4.5 inches. The name of the species and any other information is written on the outside of the pad with the Pilot marker. The final (third) fold is opened, and the towel is moistened with water. The seeds are sprinkled on the moist open pad. The third fold is closed and the whole placed in a Baggie. Fold the Baggie several times so that evaporation of water from the towel is inhibited, yet leaving ample access to air to insure aerobic conditions. The following drawings illustrate this procedure.



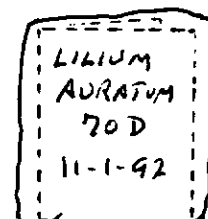
1. Moisten the folded towel



2. Sprinkle the seeds on one side



3. Fold the towel



4. Place in Baggie, fold loosely

A special warning is made about certain brands of paper towels that are advertised for their softness. These become mushy very quickly. It is important to use high wet strength paper towels, and the plain white type are preferred. Also a special warning against Ziploc bags and other polyethylene bags that are of thicker polyethylene film and are constructed to seal tightly. Polyethylene film is permeable to oxygen but not water (even though water is the smaller molecule) so that by using the thinner polyethylene, the permeability of the film to oxygen helps maintain aerobic conditions.

The paper towels remain moist for periods of months and only need to be remoistened at periods of two months or longer. The towels are inspected and the germinated seeds counted at least once every seven days and as often as each day if germination is occurring at a rapid rate. If there is debris or other material that starts to rot, the seeds are transferred to a new moist towel. Dead seeds rot in a month or two and are removed. It was usually necessary to transfer ungerminated seeds to a new towel about every three months as even the ScotTowels ultimately disintegrate. The edge of a dull knife blade was a particularly convenient instrument for transferring seeds from one towel to another. Samples of seeds were started at both 40 and 70 and shifted to the alternate temperature every three months.

This method of germinating seeds in moist paper towels was first described in a talk given by Margery Edgren at an annual meeting of the American Rock Garden Society, and I am much indebted to the inspiration of this talk. The procedure can be used to germinate seeds for growing on to plants as described in Chapter 14. It is a highly efficient procedure for seeds that have extended germinations since watering is minimal and little space is required. About twenty pads can be stacked in each Baggie, and about five hundred experiments can be conducted in one cubic foot. I dread to think of earlier investigators with rows and rows of pots or Petri dishes that needed almost daily attention.

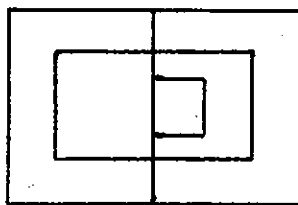
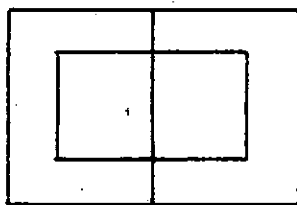
There was the possibility that chemicals used in processing the paper towels had an effect on germination. The fact that highly successful germination was achieved in all but perhaps five or less species out of the nearly 2500 examined indicates that this was not a factor.

Photoexperiments. The photoexperiments were started in the same way as the basic procedure except that the seeds were placed on top of the 2.5 x 4.5 inch pad of moist paper towel. Each moist pad was placed in its own Baggie, and the Baggie was folded several times as in the basic procedure. These were placed at a distance of eight inches under two fluorescent lights. These lights were daylight type, four foot long, and forty watts each. The lights were timed to provide alternating twelve hours of light and twelve hours of dark. The effects of light were sometimes complex and changed by prior treatment as discussed in Chapter 11.

Outdoor Treatment. The outdoor conditions simply consisted of placing the polyethylene bags containing the towels and seeds outdoors in a shed. The only important precaution is to prevent any direct sunlight from striking the polyethylene bags as that would lead to overheating.

Gibberelic Acid-3 (GA-3). The GA-3 experiments started with the same basic procedure. After opening the third fold and moistening the towel, two inserts were made before sowing the seeds. The first was a 3 x 3 inch piece of polyethylene cut from a Baggie. The second was a small piece (2.5 x 2.5 inches) of ScotTowel folded three times to give a rectangular pad 0.5 x 1.0 inches. This is moistened and placed on top of the polyethylene. The seeds are placed on top of this inner pad and one cubic millimeter of 95% GA-3 is sprinkled on top of the seeds. This amount of GA-3 is about the amount that can be balanced on the 0.5 mm tip of a toothpick using a type of toothpick that is pointed at both ends. The whole is folded once and placed inside a Baggie as in the basic procedure. These steps are illustrated below.

ROMNEYA
COULTERI
70 GA-3
1-1-93



Sow seed, add
GA-3, fold, insert
in Baggie, and
loosely fold as
before

1. Towel
folded

2. Towel with poly-
ethylene insert

3. Inner pad inserted,
moistened, and ready
for seed

It was important to adopt reasonably hygienic techniques since some species such as *Evodia danielli* were very sensitive to GA-3, and it would not do to contaminate the work area with GA-3. Everything used to handle the GA-3 was washed after use.

The beauty of the above procedure is that it does not require any weighing, volume measurements, or filtering. The experiments take up very little space, and they can be set up rapidly and examined rapidly. The size of the inner pad is such that it takes about six drops of water to moisten it and with the one cubic millimeter of GA-3 this works out to be a concentration of about 1000 ppm, the concentrations found to be about optimum in other work (refs. 9 and 10). By applying the GA-3 to only the inner pad, the GA-3 is used most efficiently. The moist outer pad serves as a water reservoir maintaining 100% relative humidity so that the small inner pad does not dry out. The amount of GA-3 can be reduced or increased and the time of exposure varied by simply transferring the seeds from the GA-3 experiment to a fresh moist paper towel. A further advantage is that there are no solutions of GA-3 that have to be discarded. Note that reuse of GA-3 solution would lead to uncertainties because of varying absorption of GA-3 by seed coats as well as the seeds.

A further beauty of the above procedure is that it can be used by every home gardener, and it can be used for the growing of plants. As soon as a seed germinates, it is removed and planted as described in Chapter 14. If there are problems with the seedlings being weakened by etiolation, the dosages and times of contact can be adjusted as described in Chapter 12.

Washing Seeds in Fruits and Berries. Seeds in fruits and berries generally contain germination inhibitors in the pulp and these seeds were always washed and cleaned. The abbreviation WC is used to indicate that the seeds were washed and cleaned. Some fruits such as those of *Euonymus* contain inhibitors that are oil soluble rather than the usual water soluble, and such seeds must be washed with detergents. This subject is covered in Chapter 8. Generally seeds in fruits have a channel through the seed coat so that impervious seed coats are virtually never found although *Prinsepia* is an exception. Thus germination is not benefitted by physical treatments of the seed coat. Fruits of a number of *Ericaceae* such as *Vaccinium* use another delay mechanism so that washing is more for convenience than necessity.

Impervious Seed Coats. Certain species use the mechanism of an impervious seed coat to prevent germination before dispersal of the seed (Chapter 9). Many treatments have been recommended for such seed, but the only treatment that gives reliable and reproducible (and usually dramatic) effects is to physically produce a hole in the seed coat.

Such holes in the seed coats were made in several ways. Large seeds could be rubbed against a file or sandpaper until the endosperm showed. It is advisable to make this hole away from the embryo to avoid physical injury. With bean shaped seeds of *Fabaceae*, this means making the hole on the convex edge of the seed. Every attempt was made to use this reliable method of making a hole. However, there were some seeds that were so small that recourse was made to rubbing them between sandpaper.

Soaking in sulfuric acid has often been recommended for seeds with impervious seed coats, but I advise against it. First of all the temperatures, concentrations of sulfuric acid, and times of exposure all have to be worked out for each separate species. More important sulfuric acid is dangerous to use. Many years ago there were tragic accidents involving loss of eyesight using sulfuric acid, and this is one of the principal reasons for requiring safety goggles in all chemistry laboratories. This is no trivial caution from someone outside the field as I was internationally known for my work and publications on rates and equilibria in sulfuric acid.

Part C. Results that Appear to be Inconsistent

There will be the temptation for readers to cite some anecdote that appears to be inconsistent with the results herein, and the experiments themselves occasionally gave the appearance of being inconsistent. Five factors were identified that could lead to such apparent inconsistencies.

Seeds are stored under a variety of conditions. To cite an extreme example, seeds could be stored in a sealed polyethylene bag. Since polyethylene films do not transmit water, seeds stored in this way are in effect being stored under conditions of 100% relative humidity or close to it. Such seed is in effect being stored moist and the behavior will be that of seeds stored moist not dry.

The dieing of seeds in dry storage is a chemical rate process. It is like radioactive decomposition. A certain amount dies in each time period. Even after extended dry storage there may remain a few viable seeds.

A most serious problem is the presence or absence of gibberelin producing fungi in the medium in which the seeds are planted. Since gibberelins such as GA-3 can have a dramatic effect on germination, this factor must be rigidly controlled to get consistent results. Fortunately in the present work aseptic conditions were used and the factor was controlled. Much of the past work reported in the literature used soils and composts and this factor was not controlled. The uncertainties caused by this factor places much of the past work under a cloud of uncertainty. An interesting anecdotal example involves the rosulate violas of the Andes. English collectors had brought back seeds of these, but germinations were only rarely observed, and such germinations could not be correlated with any particular treatment. The presence or absence of gibberelins was probably the unknown factor.

A minor problem relates to variations in the seeds produced. Rarely species produce two kinds of seed with different behaviors. There have also been reports that seeds of a particular species differed when produced from different geographical areas or from years with different weather patterns. This problem was not actively investigated, but there were many times that two or more samples of seeds of a species were obtained from widely different areas and sources. Generally the same pattern of germination was observed so I am inclined not to attach much importance to this factor as a cause of apparent inconsistencies.

The fifth factor is the problem of defining a species. Different strains of a species could have different germination behavior. In the limit two strains could be identical in all respects except the nature of their seed germination.

The results herein show that many seeds can be stored for six months or more in a moist state by careful choice of the temperature for storage. For example *Eranthis hyemalis* and *Fritillaria acmopetala* germinate only at 40 deg. F so that the seeds can be stored moist for many months at 70. Conversely species that germinate at 70 (and not 40) could be stored for many months in a moist state at 40. For the many seeds that cannot tolerate dry storage, it is necessary to develop procedures for storing the seeds in a moist state.

Seeds can be stored moist by placing them in the moist paper towels, placing the towel in a polyethylene Baggie, and folding loosely. Commercial seed houses are urged to start storing and distributing seeds of certain species in the moist state.

A question that has not been investigated is whether the moist storage could be conducted in sealed systems. It may vary from species to species. If it worked, the seeds could be sealed in polyethylene packets containing a drop of water. Already some seed houses distribute some of their seeds in sealed packets (Thompson and Morgan) so that they are already set up for such procedures. Again it is emphasized that the feasibility of such distributions in the moist state will have to be established for each species. Note that thin polyethylene films will transmit oxygen. It may well be that sealed packets will work with polyethylene films but not other plastic films.

CHAPTER 4. RATES OF GERMINATION

Although the focus on rates of germination was a unique feature of the present work, most horticulturists and botanists will be interested only in the gross aspects of such rates. These gross aspects are now presented, and the correlation with theory is placed in Chapter 19. In the rate experiments the numbers of seeds that germinated each day were counted, and the data plotted with the number germinated on the vertical coordinate and the time in days on the horizontal coordinate. Four types of plots were observed and these are shown in Figures 1-4. The plots apply only to the cycle in which most of the germination occurred. This was sometimes a 70 cycle and sometimes a 40 cycle, and it was often preceded by a 3 m cycle at the other temperature. Sometimes it was preceded by several cycles in a multicycle pattern, but this was less common.

Figure 1 is characterized by an induction period followed by a linear plot in which a constant percentage of the original sample germinates each day. The induction period is a chemical time clock during which some critical chemical process takes place. The linear rate plot is that of a zero order rate process, and the rate can be conveniently expressed as the percentage that germinates each day (%/d). Typically the linear plot held until 80-90% germination after which a tailing off occurred as shown by the dotted line. Figure 1 was the commonest pattern observed. The tailing off is theoretically required, and is not an aberration.

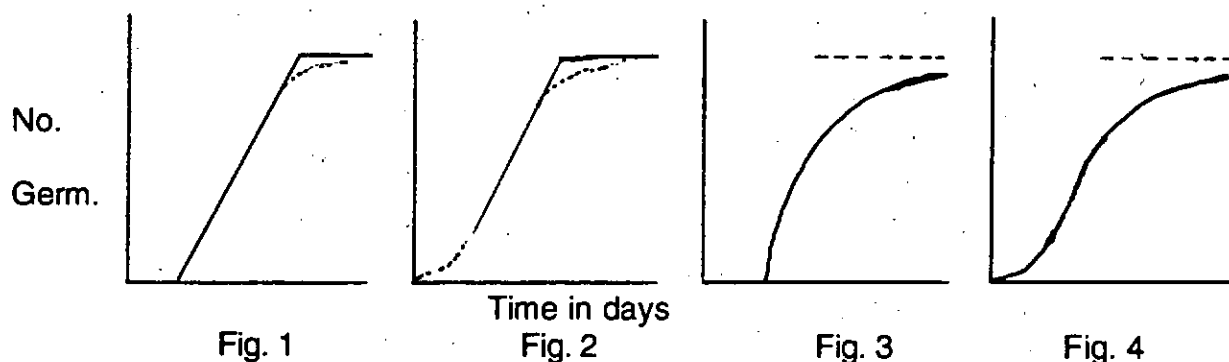


Figure 2 is like Figure 1 except that there is no induction period. Germination starts in the first or second day. In the early stages the rate of germination is slowed down by a deficiencies of water and oxygen in the embryo so that in the first few days the overall rate depends not only on the rate of the chemical process, but also on the rates of diffusion of water and oxygen through the seed coat. Within several days the diffusion rate is no longer a factor, and the linear plot develops. Figure 2 is typical of many common garden annuals and vegetables. The curve is like an S-shaped curve at the beginning and at the end and can be mistaken for a true S-shaped curve.

Figures 3 and 4 are analogous to Figures 1 and 2 except that the plot is a rounded curve and of the type where in each time period, a day for example, a constant fraction of the remaining sample germinates. This type of curve is that of a first order rate process, and the rate is conveniently expressed as the half time, the time for half of the seeds to germinate. Thus a half time or half life of five days would

mean that half of the seeds germinated in five days. This first order type of rate should be familiar because it is the rate law for radioactive decomposition.

Even in the species that required light for germination (Chapter 11), germinations often followed zero or first order rate laws because of the exact timing and constant intensity of the light. Even where precise data were not recorded, it was still possible to record induction times and the range of days or weeks over which 80-90% of the germination took place. Thus major changes in rates and induction time could still be detected. These rates of germination and induction times as well as other features of the germination have taxonomic significance and serve to characterize taxa just as much as gross morphology. It was possible in a few examples to detect two kinds of seeds in the sample by showing that the rate plot was a composite of two separate rates (see Chapter 19).

Three important generalizations emerged from the rate data. First was the prevalence of induction periods. Second was the extremely large changes in rates with temperature which were found for the reactions involving conditioning of the seeds (see Chapter 6). Third was the numerous examples of chemical processes that increased in rate as the temperature was lowered (negative temperature coefficients).

The induction periods shown in Figures 1 and 3 are interpreted as chemical time clocks involving destruction of germination inhibitors. The phenomenon of an induction period followed by an abrupt onset of germination (or any chemical reaction) is diagnostic for a chemical clock reaction and the destruction of an inhibitor. It is unlikely that the patterns in Figures 1 and 3 can be due to delays in diffusion of water and oxygen through the seed coat, formation of germination promoters, or time required for an embryo to grow. All of these would lead to a gradual onset of germination.

It might help in understanding chemical time clocks to give an example from everyday life. Rubber bands can sit in a drawer for a year or more without any apparent change in outward appearance or any change in their elasticity. One day cracks start to develop and the rubber band is soon easily ruptured and ultimately crumbles. The explanation is that raw rubber is rapidly oxidized by oxygen in air in a complex chain reaction which results in cleavage of the polymeric chains and crumbling of the rubber to a powder. In the manufacture of rubber chemical inhibitors are introduced into the rubber which block the chain reaction and preserve the rubber. Ultimately these chemical inhibitors are used up whereupon the oxidative degradation of the rubber abruptly begins and proceeds rapidly.

It may seem surprising to persons outside the field of physical organic chemistry that chemical processes of multistep and complex nature can still follow simple rate laws such as those of a zero order or first order process. The reason has been understood for some years in physical organic chemistry in terms of a rate determining (r.d.) step. Generally in a process consisting of a number of steps, one step will be the slowest. Not only will it limit the rate of the overall process, but it will dictate the rate law.

One might wonder why seeds that appear to be identical germinate over a period of time and not all at once. The same question arises for radioactive disintegration and in fact all chemical processes. It was one of the great triumphs of science when Boltzmann worked out the theory of this (Boltzmann statistics). The answer using seeds as an example is that germination requires a particular conformation of the molecular motion and a particular concentration of energies. The chance of achieving this for any seed at any moment is statistically determined. To add a brief personal note, the Noble Laureate George Uhlenbeck gave a course at the University of Michigan in which he traced the course of Boltzmann's life and the development of his theories. My wife Virginia was taking the course so I sat in. It was a wonderful experience, and it gave an invaluable insight into this field.

Incidentally for young people starting out in any career. Take time to broaden your viewpoints by attending lectures in areas outside of your own. Considerable selectivity must be exercised to avoid wasting time hearing endless garbage, but the rewards can be great. It is the cross fertilization of fields that leads to innovation.

CHAPTER 5. INHIBITOR DESTRUCTION BY DRY STORAGE

A common misconception is that seeds will germinate if given a little moisture and a little warmth. This misconception arises because the seeds of about 50% of all temperate zone plants can be collected, put in an envelope on the shelf, and germinated months later when given moisture and warmth. What is often overlooked is that the period of dry storage on the shelf was essential to the germination. What happens is that chemical inhibition systems are present initially and these are destroyed by the drying. This is the commonest mechanism for preventing germination of the seed before it is dispersed. It is convenient to call these D-70 germinators. Germinators of the D-70 type are predominant in Asteraceae (daisies), Brassicaceae (mustards), Campanulaceae (bellflowers), and Poaceae (grasses). They also predominate in species of agricultural importance, because it was important to early man to be able to dry store the seed over winter. What evolved in agriculture was an efficient selection for this type. Most of the common garden annuals are also of this type. The 50% of all temperate zone plants that are not D-70 germinators tend to be avoided and regarded as recalcitrant germinators. The use of the term immediate germinators for these of the D-70 type is objectionable because they will not immediately germinate unless given a prior dry storage.

The processes involved in the destruction of germination inhibitors have not been examined from a chemical standpoint, and in fact have hardly been recognized as chemical processes in the literature on seed germination. It is planned to determine if oxygen is required by testing whether these processes can be conducted in sealed envelopes and anaerobic atmospheres. It will be an exciting area of research in the future to elucidate the nature of these chemical processes. They may prove to not be simple destruction of a chemical compound, but rather changes in protein conformations and changes in membrane structure. These are regarded as ultimately chemical in nature.

The dry storage requirement and the dramatic effects of dry storage are shown by some representative data in Table 5-1. The effect of dry storage can be overlooked if seed is collected from seed capsules in which sufficient drying has already occurred, particularly in species requiring only a short dry storage period. Dry storage times have been reported to range from three weeks for barley to sixty months for *Rumex crispus* (ref. 12). These times must depend on temperature and relative humidity. However, in the experiments reported these variables were not precisely controlled.

Fresh seed of many D-70 germinators show two curious behaviors. The more important one is that if fresh seed is placed in moisture at 70, it seems to be permanently injured and fails to give significant germination thereafter no matter what the treatment. This was found to be true for the species in Table 5-1. The second curious behavior was shown by the *Armeria*, the five *Draba*, and the *Doronicum* in Table 5-1. Although fresh seed germinated poorly if at all at 70, it germinated fairly well at 40 albeit slowly. It is as if the germination inhibitors that are so effective at 70 are either not so effective at 40 or are partially destroyed at 40.

The percent germinations in Table 5-1 were calculated on the basis that the number of seeds was the number that germinated under the optimum conditions. This was always at least 60% and usually 80-90% of the normal size seed coats.

Many species of the D-70 type grow well and set abundant seed in climates with moist summers, but few seedlings appear. The explanation is that the seed is shed in midsummer and encounters summer moisture before the seed has had a chance to dry. This injures the seed irreversibly. The solution is to collect the seed, dry store it, and sow after drying. In this way colonies can be maintained.

There are some seeds that seem to germinate immediately at 70 both fresh and dry stored. An example is *Eunomia oppositifolia*. It is possible that these are D-70 germinators in which the requisite dry storage time is very short. Another species with a related behavior is *Centaurea maculosa*. The seed germinates immediately at 70 on being placed in a moist towel so the question arises as to why the seed does not germinate in the seed capsule, particularly since the ripe seed is held in the seed capsule for months. An explanation is given in Chapter 9 and involves a tight receptacle that protects the seed from moisture.

Table 5-1. Comparison of Germination of Fresh Seed Relative to Seed Dry Stored for Six Months at 70

Species	% Germ. in one month at 70		Species	% Germ. in one month at 70	
	fresh	dry stored		fresh	dry stored
<i>Anemone cylindrica</i>	4	98	<i>Draba densifolia</i>	0	100
<i>Armeria caespitosa</i>	15	90	<i>Draba lasiocarpa</i>	1	100
<i>Aster coloradoensis</i>	0	100	<i>Draba parnassica</i>	5	100
<i>Campanula carpathica</i>	2	85	<i>Draba sartori</i>	5	100
<i>Doronicum caucasicum</i>	10	100	<i>Hesperis matronalis</i>	0	50
<i>Draba aizoon</i>	0	100	<i>Penstemon grandiflorus</i>	0	50
<i>Draba compacta</i>	2	100	<i>Townsendia parryi</i>	5	100
<i>Draba dedeana</i>	0	100			

For species of the D-70 type, two competing chemical reactions are taking place during the dry storage. One is the destruction of germination inhibitors discussed above. The second is steady dieing of the seeds. Ultimately all seeds die if dry storage is prolonged far enough. The situation is best pictured as the superposition of two plots. Both plots have time on the horizontal coordinate. One plot proceeds upwards from the zero-zero point as time progresses, and this represents the number of seeds that have become ready for germination due to destruction of the germination inhibitor. The second plot also starts from zero and is the number of seeds that have died. The true number of germinatable seeds is the first plot minus the second plot. The resulting curve will go through a maximum so that there is some time when the number of germinatable seeds maximizes. Fortunately the maximum will be a broad one as there will be a considerable time period when the two processes approximately compensate for each other.

In principle it is also possible to have D-40 germinators. That is the seed requires drying to destroy inhibitors but then germinates at 40. In such species everything is like the D-70 germinators except that the rate of germination is much

faster at 40 than at 70. However, species that germinated at 40 after dry storage generally had induction periods of at least six weeks at 40 suggesting that further germination inhibitors were present that had to be destroyed at 40 in moisture. Thus the germination patterns were more complex. This type is discussed in Chapter 6.

Most garden annual and vegetables are D-70 germinators. A representative selection were examined and these are presented here rather than in the data summary in Chapter 20. Germinations were rapid. Celosia, marigold, portulaca, radish, and zinnia showed emergence of the radicle in two days. Tomato, bean, cucumber, watermelon, squash, swiss chard, corn, sweet pea, sweet william, and candytuft showed emergence of the radicle in three days. Four to five day induction periods were shown by alyssum, lobelia, nasturtium, and carrot. The rates were approximately first order for marigold, radish, squash, sweet william, swiss chard, watermelon, and zinnia with half lives of one to two days. The rates were approximately zero order for candytuft, carrot, and sweet pea with rates of 25-50%/d. In general the germination rates were negligible at 40, but alyssum germinated at the same rate and ind. t at 40 as at 70 and with candytuft, carrot, nasturtium, radish, sweet william, and swiss chard the germination rate was the same but the ind. t was two to three times longer.

The number of genera studied could have been much increased by including studies on numerous garden annuals and Asteraceae. However, these are almost invariably D-70 germinators (Vernonia in Asteraceae is an exception), and were not studied unless there was some reason for anticipating unusual behavior.

CHAPTER 6. INHIBITOR DESTRUCTION BY MOIST CONDITIONS

Destruction of the inhibiting system takes place at 40. In many species the germination inhibitors are destroyed simply by exposure to moisture. There is an induction period before germination begins. After the induction period there is a sudden onset of germination. This pattern can occur at either 40 or 70. Some examples of this behavior for species germinating at 40 are shown in Table 6-1. This group is a problem only because it has not been generally recognized that many species germinate exclusively at 40.

A pattern that requires somewhat more planning to achieve germination are those in which the inhibiting system is destroyed by exposure to three months moist at 40 followed by germination on a shift to 70. These will be termed 40-70 germinators. Some examples of these are given in Table 6-2. This pattern is well known, but the period at 40 has traditionally been spoken of as a period required to "break dormancy." It should be clear from the discussion in Chapters 1 and 2 that this is a conditioning period and a period of maximum metabolic activity for those chemical processes that destroy the inhibiting system. It is only a dormant period in respect to vegetative growth.

The destructions of the inhibitor systems at 40 are rate processes and will be different for each species. Minimum times for the low temperature cycle for seeds have been reported to be twelve hours for wheat, seven days for *Poa annua*, fourteen days for *Delphinium ambiguum*, and six months for *Crataegus mollis* (ref. 13). Data given below in Table 6-3 for *Nemastylis acuta* shows that the time for this species is about three months.

The destructions of germination inhibitors in seeds at 40 are clearly related to the destruction of growth inhibitors which occurs during winter in vegetatively dormant flower buds and vegetative buds of deciduous trees and shrubs as well as vegetatively dormant bulbs and tubers. A similar period of about three months at temperatures around 35-42 degrees F is needed in order for vegetative growth to occur on shifting to warmer temperatures. The similarity or possible identity with the chemical processes in seeds remains for future investigators to determine. In any event such periods should be called conditioning periods and not breaking dormancy unless one specifies that one is speaking of dormancy only in regard to vegetative growth.

The fact that these inhibitor destruction reactions occur at 40 but not 70 requires that the rates of the processes increase enormously in lowering the temperature from 70 to 40. Enzyme reactions and protein and membrane restructuring have a special capacity for these unusual negative temperature coefficients, and the theory of this is explained in Chapter 19.

The data in Tables 6-1 and 6-2 represent two limiting situations. The inhibitors are destroyed at 40 in both, but in the examples in Table 6-1 germination occurs at 40 whereas in the examples in Table 6-2 germination is so slow at 40 relative to the germination rate at 70 that a shift to 70 is necessary to achieve germination.

There are intermediate situations where the rate of germination at 40 is significant, but the rate at 70 is much faster. *Nemastylis acuta* illustrates this situation and the data appear in Table 6-3. The inhibitor destruction requires about three

months at 40. At this time there is the option for either allowing a slower germination to proceed at 40 or a faster germination to proceed at 70 by shifting the seed to 70. Analysis of the data shows that the germination rate at 70 is 2.3 times faster than at 40. This temperature coefficient is in the range typical for most chemical processes. Note that the grower will fail if the seeds are kept moist at 40 in the dark, because after three months they will start to germinate and die for lack of light. Incidentally, *Nemastylis acuta* has beautiful two inch wide sky blue flowers with Tigridia-like pleated foliage. It is one of the most beautiful of hardy bulbs and is little known in horticulture.

Destruction of the inhibiting system takes place at 70. This situation also generates two limiting germination patterns. In one pattern there is a long induction period at 70 followed ultimately by germination at 70. The interpretation is that inhibitors are destroyed at 70 and that the germination itself is faster at 70. In the other limiting pattern the germination inhibitors are destroyed at 70, but germination occurs only at 40 so that after the inhibitors have been destroyed at 70, the seeds must be shifted to 40 in order for germination to occur. Species with this pattern are called 70-40 germinators. This type of pattern has not been explicitly recognized in the literature, and it was a surprise to find that there were comparable numbers of 70-40 and 40-70 germinators.

Following is a list of species in which germination occurs at 70, but only after an induction period. This list is restricted to species where the induction time at 70 was two weeks or longer since this length of time makes it reasonably certain that germination inhibitors were present. The induction is given in weeks (w) in parentheses after the name of each species. *Aucuba japonica* (5 w), *Centaureum erythrosa* (2.5 w), *Clematis integrifolia* (6 w), *Clematis pitcheri* (4 w), *Clematis recta* (8 w), *Clematis viorna* (8 w), *Cortusa matthioli* (3 w), *Cortusa turkestanica* (3 w), *Delosperma cooperi* (4 w), *Eritrichum howardi* (4 w), *Haberlea rhodopensis* (4 w), *Jankaea heldrichii* (4 w), *Leucojum vernum* (8 w), *Lilium auratum* (3 w), *Lilium canadense editorum* (7 w), *Lilium canadense flavum* (7 w), *Lilium cernuum* (6 w), *Lilium concolor* (8 w), *Lilium davidi* (8 w), *Lilium maximowiczii* (8 w), *Paeonia officinalis* (12 w), *Paeonia suffruticosa* (12 w), *Podophyllum emodi* (5 w), *Prunus armenica* (5 w), *Silene polypetala* (12 w), *Silene regia* (12 w), *Thlaspi bulbosum* (6 w), *Thlaspi montanum* (6 w), and *Thlaspi rotundifolia* (6 w).

Table 6-4 lists those species that were straightforward 70-40 germinators. Examples that had additional complexities are not listed here, but are of course described in Chapter 20. Note that usually the germination was completed rapidly over a time span of one to three weeks and this was shorter than the induction times. There was a minor difference in the species that germinated at 70 relative to the species that germinated at 40. Where germination occurred at 70, development of photosynthesizing cotyledons or leaves soon followed. Where germination occurred at 40, sometimes cotyledons or leaves developed at 40 as in *Brodiaea congesta* and *Eranthis hyemalis*, but more commonly only the radicle developed at 40, and a shift to 70 was required for leaf development.

In rare examples either dry storage of the seed for six months at 70 or subjecting the seed to three months moist at 40 were equally effective in destroying the germination inhibitors. In *Eupatorium urticaefolium* germination at 70 was 95%

complete in 2-5 days after the three months at 40 and 95% complete in 5-10 days after the dry storage. The slightly longer times in the latter were due to time required for water transport in the freshly moistened seed.

Up to now it has been emphasized that inhibitor destruction under moist conditions virtually never occurred at both 40 and 70. *Anemone baldensis* is a possible exception in that germination occurred at both 40 and 70 and with significant induction times. Seed sown at 40 had an induction time of 44 days and a rate of germination of 4.0%/d. Seed sown at 70 had an induction time of 18 days and a germination rate of 5.1%/d. These values are for fresh seed. As with *Eupatorium urticaefolium*, dry storage removed most of the inhibition so that germination at 70 was speeded up and was 95% complete in 10-15 days.

A major difference was present between the 40-70 germinators and the 70-40 germinators. In the 40-70 germinators germination took place immediately after the shift to 70 so that there was usually no significant induction period at 70. In the 70-40 germinators germination took place at 40 usually after a significant induction period, and this induction period was followed by relatively rapid germination over a period of two to three weeks. This is interpreted to mean that there was a second set of germination inhibitors that had to be destroyed at 40. This leads us into the concept of two or more sets of germination inhibitors which is the subject of the next Chapter.

Table 6-1. Inhibitor Destruction at 40 Followed by Germination at 40 (a,b)

Species	Induction time	Germination rate
<i>Allium albopilosum</i>	5 weeks	85% in 5-13 weeks
<i>Allium moly</i>	9 weeks	90% in 9-11 weeks
<i>Calandrinia caespitosa</i>	7 weeks	40(33%)-70(29% in 6-10 days)(c)
<i>Camassia leichtlinii</i>	5 weeks	100% in 5-14 weeks
<i>Chaenomeles japonica</i>	7 weeks	86%, 5%/d
<i>Disporum lanuginosum</i>	7 weeks	100% in 8th week
<i>Erythronium citrinum</i>	10 weeks	40(65%)-70(35% in 1-2 days)(c)
<i>Erythronium hendersoni</i>	8 weeks	93% in 8-12 weeks
<i>Euonymus bungeana</i>	5 weeks	90% in 6th week
<i>Fritillaria acmopetala</i>	9 weeks	40(45%)-70(23% in 2-6 days)(c)
<i>Fritillaria persica</i>	8 weeks	97%, ind. t 54 days, 8%/d
<i>Gladiolus anatolicus</i>	7 weeks	90% in 7-9 weeks
<i>Gladiolus imbricata</i>	7 weeks	90% in 7-9 weeks
<i>Gladiolus kotschyanus</i>	6 weeks	90% in 6-12 weeks
<i>Hebe guthreana</i>	7 weeks	96%, ind. t 48 days, 4%/d
<i>Iris bracteata</i>	8 weeks	90% in 9th week
<i>Iris germanica</i>	7 weeks	40(31%)-70(31% in 1-6 days)(c)
<i>Iris magnifica</i>	10 weeks	30-100% in 10-12 weeks
<i>Kirengoshima palmata</i>	12 weeks	90% in 12-16 weeks
<i>Lonicera sempervirens</i>	7 weeks	100%, ind. t 50 days, 3%/d
<i>Parrotia persica</i>	11 weeks	90% in 12th week
<i>Penstemon glabrescens</i>	5 weeks	84% in 5-12 weeks
<i>Rosa multiflora</i>	5 weeks	26% in 5-7 weeks
<i>Saponaria caespitosa</i>	9 weeks	87% in 9-12 weeks (dry stored seed)
<i>Scilla hispanica</i>	9 weeks	32% in 10th week
<i>Zigadenus fremonti</i>	6 weeks	92% in 6-9 weeks

(a) It is important to remember that these species gave no germination when sown at 70 and kept at 70. Where the percent germination was low, it was because of a predominance of empty seed coats and not because there was further germination at a later date.

(b) The Table includes only those species where the induction time was five weeks or longer since it was felt that these were the clearest examples of an induction period.

(c) Probably germination would have been completed at 40 if more time had been given. These are examples where the germination rate is much faster at 70 than at 40.

Table 6-2. Inhibitor Destruction at 40 Followed by Rapid Germination on Shifting to 70

Species	Germination rate after the shift to 70
<i>Aesculus hippocasteanum</i> (a)	100% in 1-7 days
<i>Aesculus pavia</i>	100% in 1-7 days
<i>Allium tricoccum</i>	95%, largely in 10-13 weeks
<i>Aquilegia formosa</i>	50% in 14-42 days
<i>Asclepias tuberosa</i>	100% in 2-7 days
<i>Asimina triloba</i>	76% in 2-35 days
<i>Aureolaria virginica</i>	30% in 5-24 days
<i>Campanula altaica</i>	68% in 4-14 days
<i>Ceanothus americana</i>	28% in 1-21 days
<i>Cercidiphyllum japonicum</i>	50%, ind. t 2 days, 10%/d
<i>Cornus nuttallii</i>	40% in 8-10 days
<i>Diospyros virginiana</i>	60% in 7-28 days
<i>Dodecatheon jeffreyi</i>	90% in 1-5 days
<i>Dodecatheon media</i>	92% in 1-3 days
<i>Eupatorium purpureum</i>	90% in 3-5 days
<i>Ilex japonica</i>	87% in 90% in 1-2 days
<i>Myrica pennsylvanica</i>	85% in 1-2 days if wax was removed from seed
<i>Phytolacca americana</i>	80% in 5-16 days if seed was washed and dry stored
<i>Primula intercedens</i>	43% in 6-10 days if seed was dry stored
<i>Primula japonica</i>	100% in 2-4 days if seed was dry stored one month
<i>Primula parryi</i>	32% in 4-42 days
<i>Rhamnus caroliniana</i>	98% in 4-7 days
<i>Ruellia humilis</i>	33% in 3-9 days (rest of the seed rots quickly)
<i>Trillium albidum</i>	100% in 2-4 days
<i>Trollius acaulis</i>	70% in 6-10 days
<i>Vernonia novaboracensis</i>	100% in 2-4 days
<i>Viburnum tomentosum</i>	50% in 1-26 days
<i>Vitis vulpina</i>	76% in 4-6 days

(a) With large fleshy seeds like this species, there is apparently sufficient moisture in the seed itself so that dry storage at 40 destroys the inhibitors as effectively as 3 m moist at 40. Although 6 m dry storage at 40 was used, it is likely that 3 m would have been equally effective.

Table 6-3. Inhibitor Destruction at 40 Followed by Germination at Either 40 or 70 for *Nemastylis Acuta*

Time in months (at 40)	1	2	3	4	4.5	5
Percent germination						
seed kept at 40	0	0	0	38%	58%	72%
seed shifted to 70 (a)	0	0	44%	92%	90%(b)	90%(b)
seed kept at 70	0	0	0	0	0	0

(a) The shift to 70 was made after the time at the head of the column. The germination at 70 was rapid and was completed in 2-7 days. The value of 44% at the end of the three months at 40 is very sensitive to the exact conditions, and values ranging from 40-80% were observed. This is because the inhibitor destruction reaction is just at the point of being completed.

(b) These values include the seeds that had germinated earlier at 40.

Table 6-4. Inhibitor Destruction at 70 Followed by Germination at 40 (a)

Species	Germination rate at 40 after 3 months at 70	Species	Germination rate at 40 after 3 months at 70
<i>Actaea pachypoda</i>	85% in 5-8 w	<i>Fritillaria thunbergii</i>	50% in 5-7 w
<i>Actaea spicata</i>	88% in 4-7 w	<i>Galanthus elwesii</i>	45% in 5th w
<i>Anemone blanda</i>	75%, ind. t 63 d, 3%/d	<i>Galanthus nivalis</i>	45% in 2-5 w
<i>Chionodoxa luciliae</i>	50% in 12th w	<i>Helleborus niger</i>	93% in 9th w
<i>Cimicifuga racemosa</i>	100% in 3-6 w	<i>Helleborus orientalis</i>	100% in 5-10 w
<i>Claytonia virginica</i>	79% in 7th w	<i>Hyacinthus orientalis</i>	100% in 6-8 w
<i>Clematis alpina</i>	80% in 5-11 w	<i>Iris albomarginata</i>	50% in 7-12 w
<i>Clematis maculata</i>	100% in 4-8 w	<i>Isopyrum bitematum</i>	25% in 8-11 w
<i>Colchicum autumnale</i>	33% in 6th w	<i>Ligustrum obtusifolium</i>	84% in 2-12 w
<i>Colchicum luteum</i>	58% in 0-3 w	<i>Lilium pardalinum</i>	90% in 2nd w
<i>Corydalis lutea</i>	70% in 10-12 w	<i>Lilium parvum</i>	90% in 2nd w
<i>Crocus speciosus</i>	86% in 3-5 w	<i>Lilium shastense</i>	90% in 2nd w
<i>Delphinium glaucum</i>	25% in 4-6 w	<i>Lilium washingtonianum</i>	61% in 3-12 w
<i>Eranthis hyemalis</i>	100% in 8-9 w	<i>Melampyrum lineare</i>	55% in 4-8 w
<i>Erythronium americanum</i>	60% in 10-12 w (b)	<i>Scilla campanulata</i>	75% in 3-11 w
<i>Erythronium revolutum</i>	33% in 12th w	<i>Scilla tubergeniana</i>	100% in 3-5 w

(a) No further germination occurred unless noted.

(b) Germination was 100% after six cycles.

CHAPTER 7. TWO OR MORE INHIBITING SYSTEMS

Many examples were found where there were two or possibly more sets of inhibiting systems, and each set required different conditions for destruction. *Eranthis hyemalis* is an excellent example of this and was studied in detail. *Eranthis* has to be one of the great horticultural treats. In late March great drifts of the yellow buttercups carpet the woods and field, and the air is filled with their intense honey fragrance. On warm days the honey bees and butterflies that have hibernated come for their first feast after the long winter. As a result there is always a rich crop of seed that ripens in the first week of May.

Eranthis hyemalis has one inhibiting system that is destroyed at 70 and another that is destroyed at 40, and they must be destroyed in that order. The seeds are placed in moist towels at 70 as soon as they are ripe in May. After 3 m at 70, the seeds are shifted to 40. After an induction period of exactly 55 days (note the length), germination begins and proceeds at a rate of 25%/d (note the high rate) so that germination is over 90% complete in four days. Over the following month the radicle develops and the cotyledons start to open. The seedlings have to grow under relatively cool conditions as this species is programmed to go dormant if temperatures above 70 persist. As a result shifting the seedlings directly to 70 leads to their dieing off. Of course the simplest procedure for a gardener is to broadcast the seed as soon as collected and in a few years large colonies will develop.

If the seed is subjected to a three cycle pattern starting at 40, the results are 40-70-40(90% in 55-59 d). The first three months at 40 have absolutely no effect on the percent germination, the induction period, or the rate of germination and is truly a dormant state with little or no metabolic activity. The three months at 70 in either the 70-40 or 40-70-40 pattern is again a time of metabolic activity inside the seed despite the absence of any outward signs, and chemical reactions are occurring that are absolutely essential for the germination in the following cycle at 40.

The importance of low temperature metabolism has been a dominant theme in this book. In *Eranthis hyemalis* the germination, development of radicle, and expansion of cotyledons takes place rapidly at 40 and will not occur at 70. It is evident that in the plant kingdom neither germination inhibitor destruction nor growth of roots and leaves are restricted to either high (70) or low (40) temperatures.

A number of experiments were conducted on the seeds of *Eranthis hyemalis* to better understand the chemical reactions and metabolism in the three months at 70. If the period at 70 is shortened from three months to two months, germination at 40 is seriously affected. The induction time lengthens to 60-70 days and the germination rate drastically slows down. It is evident that two months is not long enough for the requisite chemical changes to be completed. If the time at 70 is lengthened from three months to six months, the germination behavior at 40 is identical to seeds given three months at 70 showing that the additional three months were a period of inactivity. However as the time at 70 is further increased, the induction period starts to lengthen and the germination rate declines showing that irreversible injury and death is beginning to occur. Although it was not examined, it is likely that seedlings from non-optimum conditions for germination will be weaker and perhaps fail to develop. In the 40-70-40 treatment the effect of lengthening the first three months period at 40 was not

examined. Presumably it could be lengthened to a point where irreversible injury appeared.

Seed of *Eranthis hyemalis* will not tolerate dry storage for six months at either 70 or 40 and seed so treated is dead. In the future if seeds of *Eranthis* are to be stored and distributed, it is recommended that they be stored in moist towels at 70 or 40 and distributed in this state. As it stands now, all the seed distributed commercially or by seed exchanges is DOD (dead on delivery).

Eranthis hyemalis produces only the pair of cotyledons in the first year of growth. Among dicotyledons this behavior is uncommon, but it has been found in *Oxytropis williamsii* in Fabaceae; *Anemonastrum*, *Clematis albicoma*, and *Eranthis* in Ranunculaceae; *Dodecatheon amethystinum* and *Dodecatheon media* in Primulaceae; and *Skimmia japonica* in Rutaceae.

Suppose that in *Eranthis hyemalis* the germination had been fast at 70 and zero at 40. The seed would then have required three months at 70, three months at 40, and finally germination after a shift to 70. Now *Eranthis* does not do this, but it illustrates that the inhibitor destruction pattern for 70-40 germinators can be the same as for 70-40-70 germinators, and this introduces us to the world of multicycle germinators.

Many species did not germinate until after two or more alternating three month cycles. These are termed multicycle germinators. While more work is needed to conclusively demonstrate that two or more sets of inhibitors were present, this is the most likely interpretation (although it is not readily distinguished from situations where the rate of germination is very slow at the temperature of the second cycle). These multicycle germinators were of two types. In the simpler type germination was reasonably confined to three or four cycles. *Actaea rubra* and *Iris graeberiana* were 40-70-40 germinator and *Cercis chinensis* and *Erythronium mesochorum* were largely 70-40-70 germinators. *Delphinium tricornis* was a 70-40-70-40 germinator. In others the germination dragged on cycle after cycle, usually with a little germination in the first two cycles with the majority in subsequent cycles.

There is always the question as to whether longer cycle times, different temperatures, or some other untried factor would have speeded up the process. In fact some species that were initially observed to have long drawn out germination over many cycles were later found to germinate readily in outdoor treatment, in various phototreatments, or when treated with gibberelins. Some *Iris* have these long drawn out germinations, particularly the *Juno* and *Oncocyclis*. Attempts were made to speed up germination by subjecting the seeds to month long soakings in water, by removing the brown seed coats, by light, and by treatment with gibberelin, all without effect. Combinations of wet and dry cycles and temperatures over 100 were not tried, and these merit exploration since these species come from regions with hot desiccating summers.

Table 7-1 summarizes the data on some three cycle germinators. Table 7-2 lists some species with even longer drawn out germinations. Sometimes these long drawn out germinations were associated with stepwise germination in which the radicle developed in one cycle and the leaves in a following cycle as in *Jeffersonia diphylla* and *dubia*. One obvious survival advantage of such long drawn out germinations is that if a particular year had inclement weather, there would be new seedlings for the following years. However, the way *Oncocyclis Iris* seed will remain in a firm and

healthy condition for years suggests that some key factor needed for germination is as yet undiscovered.

Table 7-1. Species Whose Germination Is Predominantly in the Third or Fourth Cycle
70-40-70 Germination

<i>Acer spicatum</i>	70-40-70(28% in 3-8 weeks) 40-70-40-70(9%)
<i>Chionanthus virginica</i>	70-40-70(54% in 5-9 weeks)-40-70(29% in 5-7 weeks) 40-70(7%)-40-70(54% in 4-8 weeks)
<i>Corylus cornuta</i>	70-40-70(86% in 1-3 weeks) 40-70(14%)-40-70(57% in 1-6 weeks)
<i>Dicentra spectabilis</i>	70-40(12%)-70(28% in 3-9 days) 40(21%)-70(5%)-40(12%)-70(1%)
<i>Dionysia involucrata</i>	70-40-70(50%)
<i>Iris hookeri</i>	70-40-70(100% in 2nd week)
<i>Lilium chalcedonicum</i>	70-40-70(100% in 5-7 weeks)
<i>Paris quadrifolia</i>	70(6%)-40-70(69% in 7-12 weeks) 40-70-40-70(66% in 7th week)
<i>Passiflora edulis</i>	70-40-70(81% in 4-6 weeks) 40-70-40-70 none
40-70-40 Germination	
<i>Iris graeberiana</i>	40-70-40(90% in 6-11 weeks) 70-40(45% in 10th week)-70-40(18% in 9-12 weeks)
40-70-40-70 Germination	
<i>Stylophorum diphyllum</i>	40-70-40(4%)-70(69% in 1-15 days)
70-40-70-40 Germination	
<i>Viburnum dilitatum</i>	70-40-70-40(70% in 2-5 weeks)
<i>Viburnum opulis</i>	70-40(3%)-70-40(62% in 2-8 weeks) 40-70-40(18% in 4-7 weeks)-70(3%)-40(16%)-70-40(14%)

Table 7-2. Examples of Extended Multicycle Germinations

<i>Allium karataviense</i>	70-40-70(6%)-40(30%)-70(10%)-40(14%)-70(6%) 40-70-40(3%)-70(14%)-40(2%)-70(14%)
<i>Eleagnus umbellata</i>	70-40(24%)-70(25%)-40(6%)-70(18%)
<i>Fritillaria pallida</i>	40-70-40-70(20%)-40(60%)
<i>Iris acutiloba</i>	70-40-70(10%)40-70-40-70(70%)
<i>Jeffersonia dubia</i>	70-40(4%)-70-40(2%)-70(4%)-40(14%)-70(24%)-40(6%)
<i>Rhodotypos tetrapetala</i>	70-40(44%)-70(16%)-40(12%) 40(14%)-70(24%)-40-70(14%)-40(11%)-70(3%)
<i>Taxus baccata</i>	70-40-70(1%)-40-70(28% in 5-15 days)-40-70 40-70-40-70(11% in 1-16 days)-40-70(26%)-40-70(10%)- 40-70(8%)

CHAPTER 8. SEEDS EMBEDDED IN FRUITS

Many plants produce their seeds embedded in a fruit. The natural cycle is for a bird or animal to eat the fruit and to excrete the seed or to carry the fruit off and eat off the pulp in a secluded spot. This is an effective mechanism for seed dispersal. It also introduces a new mechanism for preventing germination of the seed before the seed is dispersed. This mechanism is to have the pulp contain powerful germination inhibitors and to have a water channel through the seed coat to allow the inhibitor to continuously diffuse into the embryo. When the pulp is removed, the embryo soon destroys the remaining inhibitors and germination begins. Before going further, it is important to point out that not all seeds in fruits use this mechanism, and the other behaviors will be taken up later in this Chapter.

The presence of an inhibitor in the fruit is clearly the situation with *Actinidia chinensis* (Kiwi fruit), *Asparagus officinalis*, *Celastrus scandens* (bittersweet), *Lycopersicon esculentum* (the tomato), and *Morus alba*. Germination begins after several days of washing with water using daily rinsing. From the viewpoint of chemical kinetics these results shows that the inhibitor is continuously diffusing into the embryo, that the embryo rapidly destroys the inhibitors by a chemical reaction, and that the half-life of the inhibitors after diffusing into the seed must be less than one day.

A variation of the above is shown by *Berberis thunbergii*, *Lonicera maacki* and *sempervirens*, and several *Malus* hybrids. After washing and cleaning for seven days, the seed germinates at 40, but only after a significant induction period indicating that the half-life of the inhibitors in the seed is longer so that more time is needed for their complete destruction. Incidentally these species do not germinate at 70.

All the evidence shows that the inhibition is due to specific chemical compounds. The acidity can be neutralized and the osmotic pressure varied with no effect on the inhibition (ref.14). The juice of fruits such as apple, grape, and lemon will inhibit the germination of seeds that normally are immediate germinators (ref. 15). Observant readers will have noticed that the seeds inside of citrus fruits and tomatoes sometimes germinate if the fruit has been stored for a lengthy period. Rather than being an exception, these situations further support the picture presented above. After lengthy periods the supply of inhibitor finally becomes exhausted and germination begins.

Seeds of sweet peppers (*Capsicum*) and squash (*Cucurbita*) germinated 100% in 4-6 days after rinsing the seeds in water for just ten minutes. Not only was the requisite washing period so short, but the seeds do not seem to be in contact with the juices in the interior of the fruit. The seeds are attached by a thin filament. It is possible that the germination inhibitors are continuously transmitted through this filament. As soon as this filament is broken the seeds germinate.

The question arises as to whether simple water washing is enough or whether surfactants and other chemicals in the digestive tract of birds and animals play a positive role in germinating the seed. It was found that *Euonymus alatus* and *Euonymus europaeus* germinated only if washed with aqueous detergents so that the inhibitor must be an oil soluble chemical compound. These two *Euonymus* have oily fruits so that it is not surprising that the germination inhibitors are oil soluble.

The examples of seeds that germinate immediately after washing are the exception. More often seeds from fruits have extended multicycle germinations. This is found in *Cornus*, *Cotoneaster*, *Ilex*, *Prunus*, and *Viburnum* for example. With these species the pulp may or may not have germination inhibitors since the seed already has another mechanism for delaying germination until after seed is dispersed such as the mechanisms described in Chapters 5-7. The question arises as to whether grinding a hole through the seed coats would promote germination, particularly since such seeds have hard and even bony seed coats and since the acid and enzymes in the digestive tracts of birds and animals might weaken such seed coats, make them more permeable, and promote germination. This subject of impervious seed coats is treated in the following chapter, Chapter 9, but it is noted here that impervious seed coats in seeds embedded in fruits are certainly rare. *Prinsepia* is the one clear example of a seed embedded in a fleshy fruit that has an impervious seed coat.

Generally treatment with gibberelic acid did not initiate germination in the seeds from fruits. A notable exception was *Viburnum trilobum*. Its behavior is described in Chapter 20.

All seeds embedded in fruits were washed and cleaned before the germination experiments were started as explained in Chapter 3. This included species of *Cactaceae* and *Trillium*. Although these are not usually thought of as fruits, I have (cautiously) tasted a number of these fruits and found them to be sweet and of an acceptable flavor. It is most probable that these depend on animals, birds, or insects who eat the fruits and are responsible for dispersal of the seed. Claude Barr told me that fox eat *Opuntia* fruits.

Some seeds have a fleshy appendage called an aril. Examples are seeds of *Chionodoxa*, *Jeffersonia*, *Trillium*, and *Oncocyclus* and *Regelia Iris*. It is convenient to remove the arils as this reduces the mold in the towels, however, there is a more fundamental question. The aril is designed to attract ants and other insects who carry off the seed with the attached aril. They eat the aril at their leisure in a sort of insect picnic. Two questions arise. Does the aril have to be removed for germination, and do the ants and other insects secrete any chemicals that facilitate germination. Experiments were performed to see whether removal of the aril affected germination. Generally there was little if any effect. An exception was *Chionodoxa lucilliae* where germination occurred only with seed in which the aril had been soaked off.

Seed from botanical expeditions, seed exchanges, and commercial houses are usually distributed in the dried fruit. Just as with fresh fruit, the seed must be soaked, washed, and cleaned. A few experiments were performed in which a comparison was made between storing the seeds in the dried fruit relative to storing the seed in a washed and cleaned state. Generally no differences were detected, and storing the seed in the washed state gives less trouble from mold. Where there was a difference as in *Arisaema dracontium*, storage in the dried fruit gave better storage life.

With all seeds in berries and fruits there is the possibility that the washing and cleaning were not carried out for enough time. Some experiments were conducted comparing washing and cleaning for seven days with washing and cleaning for four weeks. The results are summarized in Table 8-1. The results can be complicated if the germination inhibitors are oil soluble chemical species as in some *Euonymus*.

Table 8-1. Comparison of Washing and Cleaning for Seven Days Versus Four Weeks

Species	Germination after washing and cleaning	
	Seven days	Four weeks
<i>Physalis alkekengi</i> (a)	70L(43%) 40-70L(65%)	70L(33%) 40-70L(68%)
<i>Solanum dulcamara</i> (a)	70L(93%) 70D none 40-70L(100%) 40-70D(23%)	70L(97%) 70D none 40-70L(100%) 40-70D(60%)
(a) The symbols L and D refer to light and dark. The specific conditions of light are described in Chapter 3. There was no germination of <i>Physalis</i> in dark.		
<i>Iris douglasiana</i> DS 3 y	70(1/3)-40(2/3) 40(2/5)-70	70(14/17) 40(13/13)
<i>Iris lactea</i> DS 2 y	70-40-70-40 40-70-40-70(9%)	70-40-70(5%) 40-70(3%)-40
	sown outdoors in Nov., 60% germ. in April-Sept.	sown outdoors in Nov., 89% germ. in April-May
<i>Iris latifolia</i> DS	70(10%)-40(80%) 40-70-40(80%)	70-40(90%) 40(50%)-70-40(17%)
<i>Iris magnifica</i> DS 2 y	70-40(1/8)-70-40-70(1/8) 40(93%)	70-40(15%) 40(43%)-70-40(17%)
	sown outdoors (30%)	sown outdoors (30%)
<i>Iris magnifica</i> DS 9 y	70, all rotted 40(100%)	70-40(5%)-70-40(5%) 40-70(17%)-40-70(4%)
	sown outdoors (15%)	sown outdoors (50%)
<i>Iris reticulata</i> DS	70-40-70-40(2/5) 40-70-40-70	70-40-70-40(2/7) 40-70-40-70
<i>Iris setosa</i> DS 2 y	70(16%)-40 40(4%)-70(71%)	70(12%)-40 40(2%)-70
	sown outdoors in Nov., 97% germ. in March	sown outdoors in Nov., 87% germ. in March and April
<i>Iris subbiflora</i> DS 3 y	70(2/12)-40-70 40(2/8)-70(1/8)	70(1/10)-40 40-70

The reason for applying extended washing to so many *Iris* was that it had been suggested that germination of *Iris*, particularly seed that had been dry stored for years might benefit from extended soaking before sowing. In general the extended washing had little effect except with *Iris douglasiana* and *Iris tenax* where some increase in percent germination and rate of germination occurred. The extended soaking actually reduced germination at 40 in *Iris magnifica* that had been dry stored for nine years.

Many Ericaceae have the seeds embedded in fruits, but the fruit does not appear to contain inhibitors. These seeds depend on exposure to light to destroy the inhibitor systems. Careful examination of the fruit of the common cranberry, *Vaccinium macrocarpum*, will show that the seed is in a locule inside the fruit. It can actually rattle around inside this locule and has no direct contact with the juice of the fruit.

CHAPTER 9. PHYSICAL MECHANISMS FOR INHIBITING GERMINATION

Many Fabaceae (legumes), a few Malvaceae, and a few other species use impervious seed coats as the mechanism for preventing germination before the seed is dispersed. It is not clear whether the mechanism operates by excluding water or oxygen or both, but what is clear is that grinding a hole through the seed coat produces a dramatic effect with the seeds germinating in a few days after puncturing the seed coats and placing in moist media. With seeds large enough to be held in pliers, the seed is held against a grinding wheel until the interior of the seed just shows. Alternatively the seeds can be filed or sawed with a hacksaw until the endosperm shows. The seeds can also be held in pliers or tweezers and ground against sandpaper or a file. It was best to grind against the convex side of the seed to avoid any mechanical damage to the undeveloped radicle. The dramatic effects of such pretreatment of the seed is shown in Table 9-1 at the end of this Chapter.

The favorable effects on germination induced by various grinding and abrasion procedures has long been known. This subject is treated in recent books under the title scarification. This term should be promptly abandoned because producing a scar on the seed coat surface has no effect. Only the formation of a true water channel and hole through the seed coat will reliably and reproducibly give immediate germination. Thompson and Morgan use the words nicking, pricking, and filing in their catalog. Puncturing has been used herein. Obviously we are searching for a suitable word.

It has often been recommended to soak seeds of this type in hot water or to pour hot or boiling water over the seeds. An example taken from the Thompson and Morgan catalog is to immerse seeds of *Mimosa pudica* in 140 deg. F water for twenty minutes. I have verified the effectiveness of this procedure. Prof. Roger Koide at Pennsylvania State University has found that ten minutes in water at 140 is effective for *Abutilon theophrasti*. The Thompson and Morgan catalog recommends soaking in hot water for a number of species, and it can be inferred that these have impervious seed coats. There are two problems with these hot water treatments. The optimum conditions vary with each species and have to be determined, and the results are generally less effective than physically producing the hole in the seed coat as shown below by the results with *Gymnocladus dioica*.

The hot water treatments work because the heat causes expansion of the seed coats. This causes microfissures to form and in effect a hole has been produced in the seed coat. The extensive studies described below on *Gymnocladus dioica* are all in accord with this interpretation. Inferences in the literature that the soaking softens the seed coat are incorrect, although the seed coats often soften in a day or two due to enzymes secreted by the activated seed.

Gymnocladus dioica seeds were treated for five and ten minutes at ten degree temperature intervals ranging from 120 to 180 deg F. Eight seeds were used at each condition. The number germinated in the five minute treatments were 3, 4, and 4 at 120, 130, and 140. The number germinated in the ten minute treatments were 2, 4, and 2 at 120, 130, and 140. The seeds were all killed at 150-180. Increasing the time from five minutes to ten minutes increases the number of seeds killed with no added stimulation of germination. Samples of eight seeds were then given fifteen second treatments at 150, 160, and 170. The numbers of seeds germinated were 4, 1, and 1.

Clearly the fifteen seconds at 150 was just enough to expand the seed coat without cooking the seed inside. However, none of these treatments gave over 50% germination which is less effective than the 100% germination effected by physically producing a hole in the seed coat. All germinations were in two to ten days.

Freezing and thawing have often been recommended for inducing germination of seeds. In general the effect of freezing and thawing is a myth, and true freezing and formation of ice crystals within the seed would be fatal. However, temperature oscillations generally serve to open microfissures. *Albizia julibrissin* exemplifies this effect. Seed subjected to outdoor treatment over one winter gave 24% germination in the following April and first week of May showing that microfissures had been opened in 24% of the seeds. There was additional germination after a second winter. There was no germination in controls held at 40 or 70. In nature it may take several years for a significant number of seeds to form the requisite microfissures, and it has been observed in the garden here that Kentucky Coffee Tree (*Gymnocladus*) seeds do not germinate for several years after falling. Drying can also induce fissures in the seed coats, and this was evident in Honey Locust and Kentucky Coffee Tree, Table 9-1.

Many other treatments have been recommended, but all of them suffer in that they give results that lack uniformity and reproducibility, and they require extensive study to define optimum conditions. These methods include rubbing between sandpaper, heating until a few seeds pop, centrifugal devices that throw the seed against abrasive surfaces, and immersion in concentrated sulfuric acid. This last procedure is particularly hazardous as was described in Chapter 3.

Although impervious seed coats are characteristic of Fabaceae, many species in this genus have microfissures already present in varying degrees. Peas and beans of the vegetable garden germinate readily enough without pretreatment. *Hedysarum cephrolotes*, *Lathyrus latifolius*, *Lespedeza bicolor*, and *Wisteria chinensis* germinated immediately at 70. *Baptisia australis*, *Cercis canadensis*, *Cercis chinensis*, and *Indigofera heteranthera* showed some increase in rate of germination with pretreatment but the minor gain in rate was overbalanced by the increase in rotting which lowered the overall percent germination (Chapter 20). *Coronilla varia*, *Genista subcapitata*, *Lotus corniculatus*, and a number of *Astragalus* and *Oxytropis* would probably have benefitted from a hole in the seed coat, but the experiments were not conducted and modest amounts of germination were achieved without puncturing.

Finally some species with impervious seed coats produce a significant percentage of seeds that are imperfect in that they already have a microfissure. These germinate immediately, but the remaining will not germinate until a hole is produced in the seed coat. The data on *Melilotus alba* are an excellent example of this effect.

As might be expected it is species with impervious seed coats that have the longest life in dry storage. This is discussed in Chapter 13.

The presence of a hard bony seed coat does not indicate the need for mechanical pretreatment, and in fact a number of very hard and bony seeds have a water channel through the seed coat. Examples are *Cornus*, *Prunus*, and *Rosa multiflora*. Careful examination of these seeds will reveal the cleavage between the two halves, and producing a hole in the seed coats does not initiate germination. Conversely a soft pliable seed coat can be an impervious seed coat as in *Acer negundo*.

The dispersal of seeds with impervious seed coats is interesting. Often the seed is embedded in a pod containing sweet edible material as in the Kentucky Coffee Tree pods. Animals carry away these pods and eat the contents thus dispersing the seed.

There have been repeated reports in the literature that physically hard seed coats serve as a mechanical constraint on germination. I know of no convincing evidence that seed coats significantly inhibit germination by mechanically preventing expansion of the seed. Three examples from my own work illustrate how seeds germinate despite very hard seed coats. In stone fruits like many *Prunus* the seed is disk shaped with a cleft along the keel. Not only does this cleft allow access by water and oxygen, but it is a weak point which breaks when the seed starts to expand. In *Gymnocladus dioica* the seed coats are very hard and impervious. When a hole is made in this seed coat, water is rapidly imbibed and the seed secretes powerful enzymes that soften the seed coat. Thus in 1-3 days the seed coat has become soft and rubbery and the seed has expanded to 2-3 times its original volume without rupturing the seed coat. The radicle has no difficulty in penetrating such a soft seed coat. Many legumes (*Fabaceae*) exhibit this phenomenon. In *Halesia caroliniana* the seed coat is very hard, but when the seed finally decides to germinate the radicle bursts through the side in a particularly constructed thin spot and the radicle and cotyledons develop within a week.

There were several unusual examples of delay mechanisms that could be classified as physical mechanisms. In *Centaurea maculosa* the seeds remain in the receptacle until late into the winter. If removed from the receptacle they germinate immediately on encountering moisture at 70. Close examination shows that the apex of the receptacle is constricted, and tightly filled with pappus. This prevents the entrance of moisture. In the winds of winter these receptacle are blown off, dispersed, and mechanically broken apart. The seeds falls on the ground and are ready to germinate as soon as warm weather arrives.

Populus, *Salix*, and *Tussilago farfara* are a bit of a puzzle. There is no question that the capsules suddenly open, the seeds rapidly disperse by wind, and the seeds quickly germinate on encountering moisture. The seeds rapidly die on drying. This could be regarded as a physical mechanism for delaying germination until dispersal.

Several grasses, *Pennisetum villosum* for example, have the seed in the center of a cluster of spiny bristles. These could inhibit contact of the seed with moist ground and delay germination.

The question of green seed and induced dormancies is taken up here because the only examples of such effects from my work were with seeds with impervious seed coats. The horticultural literature contains suggestions that immature (green) seed will sometimes germinate immediately whereas ripe seed will not. While it is possible that germination inhibitors could be produced at the very last stages of seed ripening, this is unlikely and has certainly not been demonstrated. What was found was that seeds of *Sophora japonica* hang on the tree in a green state for weeks in late fall. If this seed is removed and washed, it will germinate immediately. However, if this seed is dry stored for just three months at 70, the seed coat hardens and becomes impervious. Now the seed coat must be punctured to get the immediate germination recorded in Table 9-1. These effects are described in detail under *Sophora* in Chapter 20. It is

likely that this same effect could be found in other legumes. It is particularly easy to demonstrate with *Sophora japonica* because the seed hangs on the tree in a green but fully sized state for weeks. Attempts to duplicate this effect with *Gymnocladus* were unsuccessful as all green seed rotted on contacting moisture.

Table 9-1. Dramatic Initiation of Germination from Making a Hole in the Seed Coat

Species	Germination at 70	
	with pretreatment	without pretreatment
Fabaceae		
<i>Albizzia julibrissin</i> (Mimosa Tree)	100% in 2-4 days (a)	zero in 6 months
<i>Colutea arborescens</i> (Bladder Senna)	100% in 3-5 days (a)	zero in 6 months
<i>Cytisus scoparius</i> (Scotch Broom)	100% in 4-7 days	zero in 2 months
<i>Gleditsia triacanthos</i> (Honey Locust)	100% in 3-6 days	14% in 2 months (b)
<i>Gymnocladus dioica</i> (Kentucky Coffee T.)	100% in 2-4 days	zero in 6 months (c)
<i>Laburnum vossii</i> (Golden Chain Tree)	100% in 5-10 days	zero in 6 months
<i>Robinia pseudoacacia</i> (Black Locust T.)	100% in 4-6 days	10% in 3 months
<i>Sophora japonica</i> (DS seed only)	100% in 3-6 days	zero in 2 months
<i>Tephrosia virginiana</i>	100% in 4-6 days	zero in one month
<i>Thermopsis alpina</i>	100% in 2-3 days	zero in one month
<i>Vicia americana</i>	100% in 2-4 days	65% in 3 months(d)
Malvaceae		
<i>Abutilon theophrasti</i>	100% in 2-3 days	10% in 2 months(e)
<i>Spharalcea parvifolia</i>	100% in 2-3 days	zero in 4 months
Anacardiaceae		
<i>Rhus typhina</i>	100% in 10-12 days	zero in 6 months

- (a) If the pretreated seed is placed in a wet towel at 40 instead of 70, all rotted.
- (b) This was increased to 40-50% if the seed was dry stored at 70 for one year.
- (c) Dry storage at 70 for six months gave 25% germination in 2-4 days.
- (d) This was reduced by six months of dry storage. The percent germinations were 6% for seed dry stored at 70 and 55% for seed dry stored at 40. The seeds with a hole in the seed coat still germinated 100% in 2-4 days.
- (e) Dry storage for six months at 70 gave 25% germination in 1-8 weeks.

CHAPTER 10. OUTDOOR EXPOSURE AND OSCILLATING TEMPERATURES

A time honored procedure in horticulture and gardening has been to sow seeds in pots and place them outdoors in the fall. Germination often takes place in the spring. In light of the discussions up to here it is easy to see why this procedure is so often successful. It provides the low temperatures at which some species germinate and the low temperatures where some inhibitor systems are destroyed. It is also moderately successful with seeds with impervious seed coats as described in the previous chapter. However, there is much more to it.

A number of species were found which gave good germination when placed outdoors whereas germination was low or none in all other treatments. The following list gives some idea of the variety of species that showed this effect: *Acer pennsylvanicum*, *Agalinis setacea*, *Aquilegia flavescens*, *Aquilegia juncunda*, *Aquilegia olympica*, *Arisaema dracontium*, *Arisaema quinquefolium*, *Arisaema triphyllum*, *Asarum canadensis*, *Collinsonia canadensis*, *Cornus alternifolia*, *Cornus amomum*, *Cornus sibirica*, *Echinocystis lobata*, *Fritillaria pudica*, *Juglans cinerea*, *Juglans nigra*, *Impatiens biflora*, *Iris forrestii*, *Iris lactea*, *Iris setosa*, *Linum capitatum*, *Myrrhis odorata*, *Phellodendron amurense*, *Phlox paniculata*, *Sanguinaria canadensis*, *Trollium laxus*, and *Xerophyllum asphodeloides*.

Now there is nothing magical about being outdoors, and there must be some explanation in terms of chemical rate theory. One explanation is that the oscillating temperatures themselves are required. This explanation has been proposed before for the germination of *Agrostis alba* and *Lycopus europaeus* (ref. 16) based on limited data. The other explanation is that germination occurs at some temperature intermediate between 40 and 70. The oscillating temperatures pass through this intermediate temperature and provide enough residence time at the intermediate temperature to achieve germination. The results described below for *Cleome serrulata* favor the first explanation, namely that the oscillating temperatures themselves are required. The theory of this is discussed in Chapter 19.

It had already been found with *Cleome serrulata* that seeds collected in September and placed outdoors germinated in October whereas controls held at either 40 or 70 failed to germinate a single seed. Specifically, seeds were collected on September 27, 1990. Portions were placed in moist towels at 70, 40, and in outdoor conditions. On October 12, fifteen days later 125/125 (100%) of the seeds placed outdoor had germinated vigorously. In this period outdoor temperatures had ranged from 30 to 70 with large daily oscillations. There was absolutely no germination in either 70 or 40 in the dark. The experiment was repeated on a sample of seed collected October 23, 1990. The outdoor treatment germinated 36% on November 11, 7% on November 15, and 11% on December 3. At that time temperatures dropped below freezing each day and germination ceased. Again there was not a single germination in the samples in the dark at 70 and 40.

The experiment was now repeated in a more controlled manner using exactly controlled oscillating temperatures. The *Cleome* seeds were subjected to alternating twelve hours at 70 and twelve hours at 40 starting one sample at 40 and the other at 70. Both samples of seeds germinated following a zero order rate law with a rate of 6% per day and an induction time of four days.

The experiment was now made more elegant by subjecting the seeds to six hour, twelve hour, and twenty four hour periods alternating between temperatures of 70 and 40 and starting at either 40 or 70. Germination started after four days in all six experiments. Although the rate was somewhat faster at the start for the six hour alternations, at the end of a week the rate curves were virtually coincident. The experiment in which the temperature shifts were every six hours spent more time at intermediate temperatures. Since its rate was about the same as the others, it indicates that the oscillating temperatures themselves are responsible for the germination. Obviously experiments should be conducted at constant temperatures of 40, 50, 60, and 70. These are planned, and these will decisively settle the question. Germination of the *Cleome* seeds is also promoted by light as described in Chapter 20. Why light and oscillating temperatures should have comparable efficacy in initiating germination is a chemical mystery that will someday be solved.

With most examples of germination in outdoor treatment, the seeds were placed outdoors in the fall with germination occurring in spring. However, with a few such as *Cleome serrulata* and *Trillium flexipes* germination occurred in September or October before anything like winter conditions had begun. It was the results with these two species that indicated that the temperature oscillations themselves were the key factor. Where seeds were placed outdoors in early fall but did not germinate until spring, the interpretation is that a chilling period around 40 was needed first in order to destroy germination inhibitors followed by the period of oscillating temperatures.

Corydalis nobile has an interesting pattern. The seeds do not tolerate dry storage so they must be placed in the moist towels when they ripen in June. In the oscillating temperatures of fall about half of them expand enough to split the seed coats. Only these split seeds germinate in the oscillating temperatures of the following spring. The oscillating temperatures of both fall and spring are required.

With the discovery of the effect of oscillating temperatures, outdoor treatment became one of the standard procedures. It was found that many of the species that had previously given low and much extended germinations gave high germination in the outdoor treatment.

CHAPTER 11. PHOTOEFFECTS

The literature on photoeffects is dominated by two publications. First was a book by Kinzel which reported studies on 970 species (ref. 17). These were grouped into those in which germination was favored by light, those in which germination was not favored by light, and those in which light had no effect. The second publication was Borkwith and coworkers (ref. 18) which demonstrated that the effects of light were reversible in lettuce with implications that photoeffects in germination of seeds were related to the phytochrome equilibrium. A brief review of these two publications is given at the end of this Chapter.

The responses of germination to light were complex. Usually light was either required for germination, had no effect, or blocked germination. This differs from the past literature which described the germinations as "favored or unfavored" by light. It is suspected that in the past the presence or absence of light was not rigidly controlled. An entirely unexpected result was that many of the species that required light for germination would also germinate in the dark if treated with gibberelic acid-3. This subject is deferred until the next chapter.

The requirement of light for germination was characteristic of swamp plants. It also occurred frequently in woodland plants and in many Ericaceae and Solanaceae. In swamps and woodlands light is more apt to be a limiting factor than moisture so the requirement of light for germination has survival value. The response to light was sometimes affected by prior treatments such as dry storage or three months moist at 40, but in some species pretreatments had no effect on the response to light. When seed catalogs say surface sow, it can be inferred that light is required.

The genus *Asclepias* demonstrates a range of behaviors in a single genus. Light has no effect on the germination of dry land species such as *Asclepias tuberosa* whereas it is an absolute requirement for germination in a swamp species such as *Asclepias incarnata*. Species from an intermediate environment such as *Asclepias syriacus* have an intermediate behavior. The example of *Asclepias* illustrates the general trend that photorequirements are more associated with the environment in which the species grows than with the family or genera. Thus the photorequirement was found in both monocotyledons and dicotyledons and in both epigeal and hypogeal germinators. This suggests that the mechanism of the photorequirement must be very old in an evolutionary sense and that all families have some common chemical system that can be activated to generate a photorequirement for germination. The responses to light can be divided into seven categories, and each are now discussed.

It was convenient to divide the behaviors into seven categories. The first category consists of species which germinated only in light at 70 and the germination rates and percent germinations were relatively insensitive to prior treatments. Thus six months of dry storage or up to a year of alternating moist cycles at 40 and 70 had little or no effect. This group uses the photorequirement as the only mechanism for preventing germination of the seeds before they are dispersed. A complete set of experiments were conducted in most, but not all, of the following so that future experiments may lead to some revision. Some members of this category are listed in Table 11-1.

Table 11-1. Species That Use Only a Photorequirement to Delay Germination

Aconitum heterophyllum	Iris sibirica	Penstemon hirsutus pygmaea
Aletris farinosa	Iris spuria	Penstemon smallii
Angelica grayi	Iris tectorum	Physalis alkekengi
Asclepias phytolaccoides	Iris tectorum alba	Physalis virginiana
Astilbe chinensis	Kalmia angustifolia	Pinguicula macroceras
Campanula takesimana	Kalmia latifolia	Polemonium grayanum
Campsis radicans	Lamium maculatum	Polemonium vanbruntiae
Cephalanthus occidentalis	Lobelia cardinalis	Ranunculus repens
Chelone glabra	Lobelia syphilitica	Rhexia mariana
Clematis verticillata	Lyonia mariana	Rhexia virginica
Clematis virginiana	Macleaya cordata	Rhododendron lepidotum
Diplacus bifidus	Meconopsis aculeata	Spirea betulaeifolia
Dipsacus sylvestris	Mimulus primuloides	Spirea japonica
Epigea repens	Mimulus ringens	Telesonix jamesii
Gaultheria trichophylla	Monarda fistulosa	Tiarella cordifolia
Gentiana saponaria	Nepeta cataria	Tiarella wherryi
Geum coccineum	Oenothera biennis	Tricyrtis affinis
Helonias bullata	Peltoboykinia tellimoides	Tricyrtis dilitata
Hydrangea quercifolia	Penstemon digitalis	Verbascum blattaria
Iris milesii	Penstemon frutescens	Viola tricolor
Iris pseudoacorus	Penstemon hirsutus	

The second category consists of species which not only require light to germinate but also a prior pretreatment. *Leucothoe racemosa* and *Primula kisoana* required six months dry storage at 70 before they would germinate in light. *Asclepias incarnata*, *Campanula americana*, and *Verbena hastata* required three months moist at 40 before they would germinate in light.

The third category consists of species whose germination was totally blocked by light. A prior three months at 40 or a prior three months in light at 70 had little or no effect. On shifting to the dark at 70, germination began. The induction time, the germination rate, and the percent germination were the same as if the prior treatment had not occurred. Examples of such species are *Convallaria majalis*, *Cyclamen persicum*, *Ophiopogon japonicus*, and *Poncirus trifoliata*. *Schizanthus* approximated this behavior. The earlier experiments were not designed to recognize this behavior, and there may be more examples of this behavior than the meagre list would suggest.

The fourth category consists of species that absolutely require light for germination of fresh seed at 70, but various pretreatments remove this photorequirement. In some such as *Paulownia tomentosum* and *Silene armeria* the photorequirement is eliminated by six months dry storage at 70. The *Paulownia* was particularly interesting because fresh seed germinated nearly 100% in 70L and gave not a single germination in 70D in samples of 500 seeds. After two years of dry storage at 70, the seed germinated in either 70L or 70D. The induction times and germination rates and the percent germination (100%) were identical in either the light (70L) or the dark (70D). It is possible that more species were in this category, but were

not recognized because only DS seed was available for study.

The behaviors of *Ailanthus altissima*, *Gentiana scabra*, and *Solanum dulcamara* were more complex, but the essence was that the photorequirement was eliminated by either three months at 40 or by dry storage. The effects of the chilling period and of the dry storage were additive suggesting that both are destroying the same chemical inhibitor(s) and that these are the same inhibitor(s) destroyed by light.

The fifth group consists of species that required light for germination at 70, but they also germinated in the dark at 40. The percent germination at 40 is lower and the germination rates are slower, but percent germination is enough to constitute satisfactory germination. Some examples are *Calyptidium umbellatum*, *Centaurium scilloides*, *Cynoglossum amabile*, *Gentiana autumnalis*, *Geum montanum*, *Tricyrtis hirta*, *Tricyrtis hirta alba*, and *Tricyrtis macrantha*.

The sixth category consists of species that germinate in either light at 70 (70L) or in outdoor conditions. Germination fails in all other treatments.

The seventh category consists of species whose germination is promoted by light, but some germination occurs in the dark. Members of this group are listed in Table 11-2. This category fits the "favored" by light description of Kinzel (ref. 17). It is possible that these actually have an absolute photorequirement, but only a very short exposure to light is required. Thus the short exposure to light that occurs in making the observations might have been enough to trigger some germination. It is also possible that some of this group showed a slightly higher germination in light at 70 because absorption of light caused the temperature of the experiment in light to be slightly above the temperature of the dark experiments. This possibility was tested with *Gomphrena* and found to be the explanation (see *Gomphrena* in Chapter 20). This possibility was also examined by placing seeds of *Lobelia cardinalis* on different colored paper and placing under the lights. The idea was that the darker the paper the higher the effective temperature with the black paper being the warmest and the white paper the closest to the room temperature. The seeds gave the same germination on all papers.

Table 11-2. Species Whose Germination Is Increased by Light
but Light Is Not Essential

<i>Campanula punctata</i>	<i>Itea virginica</i>	<i>Primula pamirica</i>
<i>Campanula ramosissima</i>	<i>Lisianthus russelianum</i>	<i>Primula warshenewskiana</i>
<i>Campanula rapunculoides</i>	<i>Lychnis wilfordii</i>	<i>Ranunculus adoneus</i>
<i>Catalpa bignonioides</i>	<i>Lythrum salicaria</i>	<i>Rhododendron cawtawbiense</i>
<i>Cichorium intybus</i>	<i>Parnassia fimbriata</i>	<i>Sedum pulchellum</i>
<i>Clematis connata</i>	<i>Parnassia glauca</i>	<i>Spraguea umbellata</i>
<i>Clematis grata</i>	<i>Pieris japonica</i>	<i>Symplocarpus foetidus</i>
<i>Datura stramonium</i>	<i>Platanus occidentalis</i>	<i>Trichostema setaceum</i>
<i>Hypericum perforatum</i>		

Two curious effects were observed with the aquatic *Hymenocallis occidentalis* and *Zantedeschia aethiopica*. The *Hymenocallis* has a thick green seed coat. It is necessary to keep this on and to keep it photosynthesizing in light in order to get germination several months later. Presumably the photosynthesis of the seed coat produces chemicals essential for the ultimate germination. In the *Zantedeschia* there is a green photosynthesizing seed capsule, and this must be removed and the seeds washed to give germination. Presumably the seed capsule is producing an inhibitor by its photosynthesis.

This brings us to commenting on the past literature. The Kinzel work (ref. 17) is always summarized (refs. 2-7) in terms of germination being favored or not favored. Perhaps Kinzel is being misquoted or perhaps something is lost in translation or perhaps Kinzel conducted the experiments in media where the variable of light was not well controlled. In any event the word favored suggests minor effects. Unfortunately, I have not been able as yet to get a copy of Kinzel's book (it was published in German in 1926), and the summaries of his work are so qualitative as to make one wonder if the reviewers had read the original work. At least no critical analysis has appeared. In the present work, although the term favored is possibly applicable to the species in Table 11-2, it was more common for light to be an absolute requirement for germination or to absolutely block germination.

The Borkwith work (ref. 18) is cited (refs. 1-6) as the classic demonstration of photoeffects and the demonstration that such effects can be reversible. Specifically fresh seeds of Grand Rapids lettuce were irradiated with alternating cycles of one minute of red light and three minutes of infrared light. Germination was 10% for the dark blank, 90% if the seed had been last exposed to red light, and 50% if the seeds had been last exposed to infrared light. The Borkwith paper led to many studies designed to determine whether or not the phytochrome photoequilibria, so important in photosynthesis, was responsible for the effects in seed germination. A recent book on phytochrome (ref. 19) has a chapter by J. D. Smith on seed germination, and the author concludes that the question is still unsettled. The Borkwith papers also inspired studies on varying light periods. It has been reported that different strains of *Zea* may have different responses to light (ref. 20) and that differing light cycles had different effects on germination of *Kalanchoe* (ref. 21). None of this seems of much practical importance for the successful germination of seeds.

The experiments and conclusions of Borkwith and his coworkers disturb me. First, measurement of induction periods and rates would have shown more than the percent germinations that were reported. Second, my experiments with *Paulownia* show that several days of exposure to light were required to reach the maximum germination (see *Paulownia* in Chapter 20). Third, in my view light is acting by destruction of an inhibitor system. If so, the effects will be largely governed by the wave lengths of the light, the intensity of the light, and the duration of exposure. Fourth, the difference of 50% and 90% is minor compared to the absolute light requirements and absolute blocks of germination by light which were characteristic of my own work. Finally I have heard that the light effects on Grand Rapids lettuce rapidly disappears on dry storage.

CHAPTER 12. EXOGENOUS CHEMICAL EFFECTS AND THE STIMULATION OF GERMINATION BY GIBBERELINS

This Chapter is divided into four parts: Stimulation of Germination by Gibberelins, Parasitic Plants, Stimulation of Germination by Nitrogen Compounds, and Stimulation by Anaerobic Conditions.

Stimulation of Germination by Gibberelins. The work reported herein and two recent papers (refs. 9 and 10) leave no doubt that gibberelins and particularly Gibberelic Acid-3 (GA-3) will from now on play an important role in growing plants from seeds. The reaction of the seeds of various species to GA-3 varies from dramatic stimulation of germination to little effect to killing the seeds. Among the species exhibiting dramatic stimulation of germination, the effect varies from producing normal healthy seedlings to producing seedlings so badly etiolated that they soon die. Concentrations and exposures can be varied, and it is possible with some species to optimize these variables and get healthy seedlings. This was found for *Gentiana verna* (ref. 9, confirmed in present work) and for *Linum capitatum* and *Ribes cereum*. It has been reported that cytokinins are helpful in reducing the etiolation (ref. 9). However, there is no certainty that satisfactory conditions can be found with all of the species that show stimulation, and most growers will prefer to avoid the use of GA-3 and other gibberelins unless necessary such as in the following circumstance.

It is now proposed that gibberelins are natural stimulators of germination in certain species and that the evolution of this requirement is critical to the survival of those species. The recognition of this came about when it was found that germination in *Echinocereus pectinatus* hybrids was less than 1% and germination in the rosulate *Violas* was zero without the use of GA-3. Both of these species are relatively tiny plants growing in harsh dry environments, The *Echinocereus* from the dry windswept deserts of Southwestern United States and the rosulate *Violas* from high in the dry windswept Chilean Andes. For these tiny seedlings with their tiny root systems to survive, the seeds must fall into crevices in rocks or deep into coarse gravel where there is a small pocket of moist leaf mold. The fungal action in this leaf mold produces gibberelins which trigger the germination. In this way germination is triggered in the only place where the seedlings could survive. Some other species that give significant germination only with GA-3 are *Evodia danielli*, some *Gentiana*, *Physoplexis comosum*, *Ranunculus lyallii*, *Ribes cereum*, *Romneya coulteri*, *Rubus parviflorum*, most *Thalictrum*, *Trillidium*, and most *Trillium*.

A brief personal note may interest the reader. Claude Barr (author of Jewels of the Plains) had always cautioned me that Cactus seedlings cannot take direct sun and dessicating conditions and that he had killed many cactus seedlings before he recognized this. It now becomes clear how they have developed a clever detection system for germinating in the one place in which they could survive.

The dosages and times of exposure can be regulated. For example with the three species studied in detail (*Gentiana verna*, *Linum capitatum*, and *Ribes cereum*), one-tenth as much (0.1 cubic millimeter) of GA-3 can be used, and the seeds can be removed each day, washed, and placed in clean moist towels. While all of this may be somewhat qualitative and unscientific, the usual procedure of making up exact

concentrations and soaking the seeds for exact time periods is not as precise as might be thought. There is selective absorption of the Gibberelin on the seed coats which alters the effective concentrations, and the solutions cannot really be used again.

A totally unexpected result was that most of the species that required light to germinate would germinate in the dark if treated with GA-3. This obviously has important implications in regard to the chemistry involved in the stimulation of germination by both light and GA-3. It would be tempting to speculate, but for the moment the examples are all documented in Chapter 20 under each species, and it is best left at that.

About half of all *Lilium* are two step germinators in that they form a small bulb and root at 70, but then need about three months at 40 before the true leaf will form on returning to 70. Three of these (*L. canadense*, *L. martagon*, and *L. szovitsianum*) were subjected to treatment with GA-3. The first step was unaffected both in respect to the rate characteristics of the germination and the appearance of the seedlings. However, about three weeks after the initial germination and after the bulb and root had formed, the true leaf emerged in about half of the *L. canadense*. This effect is of some value because it much reduces the time required to get a photosynthesizing leaf.

Trillium are also two step germinators. The GA-3 treatment was tried on several species as described in Chapter 20. With Trillium the rates of both steps increased with the GA-3 treatment, and most Trillium germinated only when treated with GA-3.

The results with *Shortia galacifolia* are now described in detail because they illustrate the intricate complexities and interactions. In the first edition it was reported that *Shortia galacifolia* required New Jersey Pine Barren Sand plus light in order to germinate (discovered by John Gyer). This was clearly an example of an exogenous chemical requirement for germination and was only the second such example at the time (the other was *Striga*, discussed further on). Further work has shown that *Shortia* is a particularly interesting example. It is now found that GA-3 stimulates the germination in either 70L or 70D whereas the New Jersey Pine Barren Sand stimulated the germination only in 70L. Clearly the chemical in the Sand is not GA-3, although it is likely that it is a fungal product of the gibberelin type.

When sown on the surface of wet New Jersey Pine Barren Sand under the fluorescent lights, germination was 60-70% at a rate of 6-7% per day with an induction time of eight days. When a single layer of paper towel was placed between the seed and the sand, germination occurred at the same rate and percentage. When four layers of towel were placed between the seed and the sand, germination was reduced to 30%. The induction time was the same, and the rate was the same providing it was calculated on the basis of the reduced number of seeds germinating instead of the total number of seeds. When the seed was sown on the sand in the dark and shifted to light after seventeen days, germination was only 20% showing that a time in the dark as short as seventeen days caused severe injury. The above treatments were the only ones that gave germination.

The following procedures failed to give a single germination. The seed was placed on moist towels in dark and light. The seeds were placed on towels in light, and the towels were moistened with 1% aqueous acetic acid, 5% aqueous acetic acid, or 1% aqueous iron sequestrene. The seed was sown in light on sphagnum peat. The seed was shifted from the towels to the sand after two weeks. The seed was dry stored at 70 for four weeks and then sown on the New Jersey sand in light.

There is another situation that could be interpreted as an exogenous chemical requirement. In growing orchids from seed in agar gel, many components are needed in the gel, and this is discussed under Orchidaceae in Chapter 21. However, it is not clear whether these exogenous chemical requirements are needed for the germination itself or for the development of the seedling. The two aspects become intertwined in Orchidaceae where the seed is so small and carries barely any store of nutrient.

One is hesitant to add an anecdotal observation, but it relates to *Fraxinus* and *Liriodendron*, which have been singularly difficult to germinate, and it relates to fungal action and the possibility of a gibberelin requirement for germination. A number of truck loads of leaves and chopped branches were placed on our property to make a great compost pile. Three years later there appeared a dozen seedlings of *Fraxinus americana* and about one hundred seedlings of *Liriodendron tulipifera*. No germination of these two species had occurred in the towel experiments. Related to this is the report that embedding *Crataegus* seed in peat speeds up germination (ref. 22).

Before leaving this subject, the two most useful papers (refs. 9 and 10) will be summarized, and the history of gibberelins briefly reviewed. Stewart and Presley (ref. 9) found marked stimulation of germination in *Aquilegia jonesii* x *saximontana*, several *Campanula*, several *Gentiana*, *Lewisia tweedyi*, and *Primula parryi*. Nikolaeva and coworkers (ref. 10) reported stimulation in *Campanula latifolia*, *Lunaria rediviva*, *Polygonum bistorta*, *Primula veris*, and ten species of *Trollius*. Ten of these *Trollius* germ. in 5-20 days if the seeds were soaked for two days in 500-1000 mg/l (equivalent to ppm) of GA-3, and *Trollius asiaticus* germ. in 30-50 d after treatment. Normally these species require 3-5 months of chilling before they will germinate in warmth, and *Trollius asiaticus* require eleven months of chilling. In addition Prof. Roger Koide at Pennsylvania State University found that germination of dry stored seed of *Plantago erecta* was increased from the 2-5% range to 80% by one hour immersion of the seed in 300 ppm aqueous solution of gibberelic acid.

The history of gibberelins is exhaustively reviewed in Gibberelins (ref. 23). Briefly, a Japanese chemist in 1926 showed that the "crazy rice" disease was caused by a chemical secreted by a *Gibberelus* fungus growing on the rice. This chemical was named gibberelin after the fungus from which it was derived. In 1936 another Japanese chemist crystallized the active principle. In the years that followed many chemicals were tested for growth promoting activity by applying a solution of the compound to be tested in a block of gel to the side of an oat coleoptile. The degree of bending and the concentration of the compound defined a quantitative measure of activity. By the time the book Gibberelins was published, 67 different gibberelins had been isolated and their chemical structure proven.

My information at present is that Gibberelic Acid-3 (GA-3) is marketed by several companies. They buy it from Abbott Laboratories, North Chicago, Illinois, who are the actual producer. Generally orders for GA-3 will not be honored unless originating from an academic institution or some formally recognized research group so that it is not available to the general public.

Up to two years ago, although there was a general consensus in the literature that gibberelins were the most promising group for stimulating germination of seeds, the reports were so fragmentary that the subject was only briefly mentioned in the first edition of this book and the book Gibberelins (ref. 23) did not have any Chapter or hardly any mention of this subject. All of this changed with the two recent publications (refs. 9 and 10).

Related to the initiation of germination by gibberelins is the blockage of germination by abscisic acid. This is elegantly reviewed in the book Abscisic Acid (ref. 24). It is tempting to regard the whole subject of promotion and blockage of germination as due to the ratio of gibberelin to abscisic acid, but I believe the matter to be far more complex. Incidentally auxins did not stimulate germination (ref. 25).

Parasitic Plants. Although the literature gives the general impression that parasitic and semiparasitic plants require proximity to the host for germination, this has not been found to be true in the present work. *Aureolaria*, several *Castillejas*, and *Phoradendron* (Mistletoe) all germinated on paper towels moistened only with water. The *Aureolaria* and the *Castillejas* developed the two cotyledons and several true leaves before dieing off because of lack of host. The *Phoradendron* developed only a 2-4 mm. green leaf like shoot. A dramatic exception to the above comes from the work of David Lynn and others (reviewed in ref. 26) where it was unequivocally demonstrated that *Striga asiatica* requires a specific hydroquinone (exuded from the host) in order for germination to occur.

Striga asiatica is a serious parasite of grasses. It has been much studied because it reduces grain production in Asia and there is the potential for this problem to become serious in this country. Most of the studies have been conducted with sorghum. Briefly, sorghum exudes droplets along the entire length of the roots. These droplets are 95% a single chemical whose structure has been determined. Suffice to say that it is a hydroquinone (HQ) with a structure resembling phytol. This HQ is readily oxidized to the quinone form Q which is inactive. The droplets of exudate contain an oxidation inhibitor as a minor constituent and this inhibitor does slows down the oxidative destruction of the HQ. The inhibitor resembles the well known antioxidant di-t-butyl-p-cresol and undoubtedly acts in the manner well documented for the cresol. Even with the oxidation inhibitor, the HQ does not survive beyond 5-10 mm. from the sorghum root so that the seeds of *Striga* must be that close to the sorghum root for germination to occur. Incidentally, the HQ is also required for formation of the haustoria, and the seedling has just five days to develop the haustoria and attach it to the host or the seedlings dies. It is possible that there are further levels of response by the seedlings to the chemicals exuded from the host so that there is much complexity.

Other chemical compounds can initiate the germination of *Striga*. Among these are ethylene, gibberelins, cytokinins, NaOCl, and sulfuric acid. It would appear that the initiation of germination is the result of the destruction of some specific germination inhibitor. Most interesting is the fact that cotton secretes a substance similar to HQ named strigol which also initiates germination of *Striga*, but cotton is not a suitable host. Thus cotton can be planted in a field infested with *Striga* seed as a trap plant. It initiates germination, but the seedlings perish and the infestation is reduced. The seeds of *Striga* can survive over twenty years in soils and remain viable so that destruction of *Striga* seed is important agriculturally.

Stimulation of Germination by Nitrogen Compounds. There have been many fragmentary reports that compounds of nitrogen stimulate germination. The most quantitative study was on germination of red rice (refs. 2-7, 27, and 28) where it was shown that nitrite stimulated germination and the stimulation was measured as function of the pH. The curve resembles the curve for the equilibrium between nitrous acid and nitrite anion suggesting that nitrous acid is attacking some inhibitor.

This speculation would also explain various reports that nitrate, hydroxylamine, ammonia, and thiourea (refs. 2-7, 27, and 28) sometimes stimulate germination. All three are well known to be converted to nitrite in soils, nitrate by reduction and the other two by oxidation.

Related to the question of exogenous chemical effects are situations like the black walnut whose roots secrete a substance, juglone, which inhibits the growth of many species. This could give the appearance of inhibiting germination, although the action might be described as killing the seedling as the radicle emerges. It would be difficult to distinguish the two effects, and in fact it merges into a semantic argument.

Seedlings have been raised from excised embryos, and some *Iris* and *Lilium* hybrids require such treatment. This field has been omitted in this book, but obviously the excised embryos need exogenous nutrient and perhaps other materials.

Stimulation by Anaerobic Conditions. Several reports in the literature can be interpreted to suggest that germinations of *Nymphaea*, *Typha latifolia*, and other aquatic species are stimulated by mildly anaerobic conditions. Germination of *Nymphaea* and *Typha* has been reexamined. It was found that *Nymphaea tetragona* germinated best in a 40-70 pattern and *Typha latifolia* required light for germination, both in aerobic conditions. However, a mild stimulation of germination was observed in *Nymphaea tetragona* and in *Butomus umbellatus* using mildly anaerobic conditions.

Seeds of *Butomus umbellatus*, *Nymphaea tetragona*, and *Typha latifolia* were placed in the moist towels in a polyethylene bag. The bag was blown full by my exhaling into it several times. The bag was collapsed and the processes repeated two more times. In this simple way a mildly anaerobic atmosphere was created in which the oxygen was reduced and the carbon dioxide increased. Germination was mildly stimulated at 70 for both *Butomus umbellatus* and *Nymphaea tetragona* but not *Typha*.

My conclusion is that mildly anaerobic conditions may play some role in the germination of aquatic species under natural conditions, but it is not an absolute requirement. For the pragmatic horticulturist aerobic conditions can be found that give better results, at least for the three species cited above.

The literature reports are now briefly reviewed. *Typha latifolia* was reported to germinate only under water, and it was proposed that the reduction in oxygen pressure induced the germination (ref. 29). *Nymphaea* germination has been studied by two groups. Else and Riemer found that crowding of *Nymphaea odorata* seeds stimulated germination and that aeration inhibited germination. They attributed these effects to ethylene formation (ref. 30). Roberta and Fred Case of Saginaw, Michigan, also found that crowding of seeds of *Nymphaea* stimulated germination. An effective procedure was to place 1-2 inches of mud in a small glass jar, place the seeds on the mud, add 2-3 inches of water, and close with a screw cap. Of course some oxygen is required for the germination metabolism, so that oxygen cannot be completely excluded, but only reduced.

A number of aquatic plants have been reported to require daily oscillations of water temperature to achieve germination (ref. 31). It is possible that the temperature oscillations develop mildly anaerobic conditions. As the temperature rises oxygen is forced out of the water because the solubility of oxygen is lower at the higher temperature. When the temperature drops the oxygen is slow to reestablish the equilibrium solubility at the lower temperature so that mild anaerobic conditions develop. Finally, the cocklebur (*Xanthium canadense*) contains two seeds in each capsule. The upper one germinates in completely aerated media. The lower seed require partially anaerobic conditions for germination (refs. 31 and 32).

CHAPTER 13. DRY STORAGE AND LONGEVITY OF SEEDS

Ultimately dry storage is fatal to all seeds including those of the D-70 type even though these require dry storage in order to germinate. The dieing of seeds in dry storage is a rate process so that no single time can be given for the retention of viability. It will also depend on temperature and relative humidity. There is also the problem that dry stored seeds may still germinate, but the seedlings may be weak and unable to survive because of internal deterioration in the seeds.

The longevity of seeds in dry storage has been the subject of much interest (refs. 2-7), and an entire book has been devoted to this subject (ref. 6). There are studies on the viability of seeds in dry storage that have been conducted continuously since the 1850-1860 period (refs. 6 and 33). The results can be summarized succinctly. A few species have seed that retain viability for only days such as *Populus*, *Salix*, and *Tussilago*. Most species retain viability for a year or two. Some species retain viability for 10-50 years. Some species of *Fabaceae* have seeds that are still viable after 100-150 years in dry storage and a few *Malvaceae* are also long lived (ref. 33). The seeds with long lives are invariably seeds with impervious seed coats.

Tabloid stories claiming viability of ancient seeds are false, even though they have been repeated in reputable journals. Examples of such stories are reports of viable seeds of grains being found clutched in the hands of Egyptian mummies, viable seeds of lotus that are ten thousand years old being dug up in ancient peat beds in China, and viable seeds that are thousands of years old being found in the caches of Arctic rodents. All of these have been disproven (refs. 2-6).

In the first few years of the program it was the standard procedure to compare the behavior of fresh seeds with seeds dry stored for six months at 40 and seeds dry stored for six months at 70. When it was found that differences were small, the experiments on dry storage at 40 were discontinued. The data in Table 13-1 illustrate these small differences. The practice of storing seeds in the refrigerator is overrated.

Table 13-1. Percent Germinations for Seeds Dry Stored (DS) for Six Months at 40 Relative To 70

Species	Fresh Seed	DS at 40	DS at 70
<i>Hyacinthus orientalis</i>	70-40(100%)	70(85% rotted)-40-70-40-70-40(11%)	70(100% rotted)
<i>Scilla sibirica</i>	70(22%)-40(65%)	70-40(53%)-70(12%)	70(100% rotted)
<i>Trillium albidum</i>	70(74%)-40(11%)	70-40(20%)	70(100% rotted)

Seeds of many species are totally killed by dry storage for six months at either 40 or 70. Some examples are *Anemonella thalictroides*, *Chelidonium majus*, *Claytonia virginica*, *Corydalis cheilanthifolia*, *Delphinium tricorne*, *Dentaria laciniata*, *Dicentra cucullaria* and *spectabilis*, *Jeffersonia diphylla* and *dubia*, *Leucojum vernum*, *Meconopsis cambrica*, *Populus tremuloides*, *Ranunculus hispidulus*, *Salix*, *Sanguinaria canadensis*, *Stylophorum diphyllum*, *Tiarella cordifolia*, *Trillium grandiflorum*, and *Tussilago farfara*.

Dry storage is not the only way to store seeds. The germination pattern of many species offers the opportunity for storing the seeds in a moist condition, and this is the answer for seeds that cannot tolerate dry storage. For example, a 40-70 germinator such as *Nemastylis acuta* could be stored moist at 70 for many months and possibly a year or more. This period of time in moisture at 70 is a true dormant period, and destruction of the germination inhibitors will not begin until the shift to 40.

With a 70-40 germinator like *Eranthis hyemalis*, the seeds could be stored moist at 40 for many months and possibly a year or more. This period of time in moisture at 40 is a true dormant period and destruction of the germination inhibitors will not begin until a shift to 70. Alternatively seeds of *Eranthis* could be stored moist at 70 for at least six months because even though inhibitors are being destroyed in the first three months under these conditions, germination will not take place until the shift to 40.

Storing seeds in moist towels in polyethylene bags is nearly as convenient as storing seeds in paper envelopes, and seeds stored in this manner can be shipped anywhere. I can confidently predict that such a practice will become widespread. The information presented in Chapter 20 is sufficient to select the species which have germination patterns adapted to such procedures.

A major question is whether the inhibitor destruction reactions require oxygen. Using *Eranthis hyemalis* as an example, if the inhibitor destruction reactions did not require oxygen, the seeds could be stored and distributed at 70 in sealed polyethylene packets containing a drop of water. If the reactions required only small amounts of oxygen, possibly the diffusion of oxygen through the polyethylene would be sufficient, and again the seeds could be placed in sealed packets. However, if the inhibitor destruction reactions consumed large amounts of oxygen, some provision would have to be made for keeping the packet of moist seeds aerated. Perhaps a small hole in the polyethylene would be sufficient. All of these questions could be readily answered with a few direct experiments, but the answers might well vary from species to species.

Another possibility that deserves more study is the storage of seeds moist in the presence of germination inhibitors. Seeds in fruits are a natural example. The procedures could be refined by adding preservatives to stop fermentation and by refrigeration. Abscicic acid blocks the germination in many species (ref. 24), and perhaps this could be used to delay germination in seeds being stored moist.

There have been frequent reports that seeds stored in the presence of drying agents such as silica gel retain viability better than seed stored under conditions of higher humidity (ref. 34). This would only apply to seeds that survive dry storage. To do this sort of work correctly, the phenomena have to be treated as rates and the rate characteristics measured. Reports that seeds store better in sealed containers appears to be only due to lower humidity (ref. 35). Experiments were conducted on dry storage of seeds at 40 in and out of polyethylene bags. These were discontinued when no differences were found.

There have been studies on the preservation of seeds in liquid nitrogen (ref. 36). Special precautions were necessary to get the moisture content of the seed unusually low. At best this type of storage would be suitable only for seed that can be dry stored, and inferences that it has general applicability are false.

CHAPTER 14. GROWING PLANTS FROM SEEDS

Chapters 5-12 describe the various delay mechanisms and the means of overcoming them. In general the healthiest seedlings were obtained when the seeds were germinated under the optimum conditions. It was found with *Hastingsia alba* and *Lilium canadense* that although germination could be accomplished under several conditions, only the seedlings from the optimum conditions of germination were healthy and went on to produce adult plants. Seedlings from other conditions showed a strong propensity to rot at the tip of the root or radicle and to ultimately die. Related to this are seeds which have been in dry storage long enough to have a significant percentage die. The remaining seeds may germinate, but the seedlings are often weak and soon die.

Even after the optimum germination pattern has been found, there are still decisions that must be made in regard to the handling of the seedlings and growing them on to adult plants. Each of these decisions is now taken up in turn with a discussion of the advantages and disadvantages of each alternative.

Should the seeds be sown in open ground, pots, or paper towels?

This question can be answered with illustrative examples. Sowing in open ground is the method used for *Eranthis hyemalis*. The seeds ripen in early May and are sown immediately as they do not tolerate dry storage. The seeds receive the requisite three months at 70 during the summer and the requisite fifty-five days around 40 during the fall. They germinate during late fall, winter, and early spring. Growth is completed during the cool and cold days of spring. The seedlings are programmed to grow at temperatures around 40. If the temperature rises to 70 for any length of time, the seedlings cease growth. If they have not had time to build up a tuber, they perish. Since it is troublesome to provide bright sunlight at 40 indoors, the sowing in open ground is the easiest and simplest method for growing *Eranthis* from seed.

Sowing in open ground is convenient for other species where the seedlings need cool conditions for growth. Examples are *Actaea*, *Asarum*, *Chionodoxa*, *Eranthis*, *Hepatica*, *Puschkinia*, *Trillium*, and *Tulipa*. Like *Eranthis*, if seedlings of these species are moved too quickly to 70 as they might if kept indoors, the tip of the root starts to rot and the seedlings dies.

Haberlea rhodopensis illustrates a species where sowing directly in a pot is a necessity in the climate of Central Pennsylvania. The seeds are tiny and the seedlings have a root system that penetrates the medium for less than a centimeter. Even the adult plants have shallow root systems. If the seeds are sown directly outdoors, dry soil conditions (at least at the surface) are sure to arise and certain to kill the young seedlings. Sowing the seeds on towels is ruled out because the seedlings are tiny and inconvenient to handle. Even sowing in open pots is ruled out because overwatering and underwatering of the surface layer is inevitable. The answer is to sow *Haberlea* seeds directly in pots on top of surface sterilized soil and enclose immediately in polyethylene Baggies as described in more detail in following sections. This insures constant and lightly moist conditions.

Sowing in paper towels is the method of choice for species with multistep and extended germinations. *Lilium canadense* seeds are collected in October and immediately placed in moist paper towels at 70. During the next four months a small bulb and attached root forms. The seedlings are now shifted to 40 for three months. It is now April and the seedlings are ready to form their true leaf on shifting to 70. The seedlings are treated like small plants and can either be planted directly outdoors or in pots. Conducting the first two cycles in moist towels (as described in Chapter 3) effects an enormous saving of space, time, and effort. The seedlings need to be checked no more than once every two months to see that moisture is sufficient. The paper towels should be placed upright so that the root extends vertically along the face of the towel.

Another example where the paper towel method would be chosen is *Iris graeberiana*. The seeds are collected in late June. They are put in the moist towels and placed at 40 in the refrigerator. In October the towels are shifted to 70 for three months followed by a shift back to 40 in January. Over the next three months a corm and root forms. It is now late March, and the small corm and root can be planted outdoors treating it like a small plant. The true leaf will form in April. This is another species that must have cool to cold growing conditions for the young seedling. Of course the seedlings could be planted in a pot in late March and placed outdoors if the grower wants to keep careful watch over them. By keeping the seedling in the aseptic paper towels as long as possible, attack by insects and fungi are avoided and space and effort are minimized.

A final example where the paper towel method would be used is *Cardiocrinum giganteum*. This is mentioned because there have been so many reports of failure with this species. Fresh seeds germinated in a 40-70-40-70(2%)-40(97% in 5-11 w) pattern. If one had sown the seeds in pots outdoors, there would have been several years before any seedlings appeared. During that time the grower would have become exhausted with constant watering and maintenance. The pots would have been shunted aside and underwatered, and all chance of success lost. By using paper towels the long requisite conditioning takes place in the the towels wrapped in Baggies. Little space is required and no maintenance. The grower knows when germination will begin from the above pattern and begin weekly checks in the fifth cycle. It was found that shifting the germinated seedlings directly to 70 led to healthy plants contrary to the remarks in the first printing of the second edition.

Should the pots of seeds or seedlings be kept in polyethylene Baggies? For the seedlings of many species, growing the seedling in pots enclosed in a polyethylene bag is virtually a necessity. I call this technique bagging. The commercial product Baggies is ideal because the polyethylene film is thin and allow significant diffusion of oxygen into the bag. The Baggie is closed at the top with a wire Twistem, but not so tightly as to totally seal the bag since aerobic conditions must be maintained. Moisture conditions are constant inside the Baggie, and there is none of the alternate overwatering and drying out that plagues open pots. Before sowing the seeds, it is important to **surface sterilize** (ref. 37) the medium by pouring boiling water over the medium three times allowing to drain each time. Allow the pot and

medium to cool, sow the seeds on the surface, and enclose the pot and contents in the Baggie. The surface sterilization destroy insects and other life injurious to the seedlings, and it inhibits the growth of moss and algae.

Pots enclosed in a Baggie must always be kept under fluorescent lights and never exposed to direct sunlight. It is a question of the wave-length of the light. Suffice to say that direct sunlight will heat up the Baggies and cook the seedlings even in time periods as short as thirty minutes. Under the fluorescent lights the bagged pots will remain cool and at room temperature. Tungsten filament lights are not suitable. The tungsten filament gives off infrared radiation which heats up the bulb. This indirectly heats up nearby bagged pots. Using four foot forty watt fluorescent bulbs as described in Chapter 3, the surface of the medium can be as close as four inches to the fluorescent light bulbs without any heating up of the contents of the bagged pot.

Fluorescent lights are marketed in several types. Some have been developed specifically for use in growing plants. These have various trade names such as "Gro-lite." Perhaps they have some small advantage. In the present work the plain daylight reading type fluorescent lights were used.

The fluorescent lights are connected through a timer. The timers used here were purchased from a Sears Roebuck store and have proved to be most serviceable. The timers were always set to give twelve hours of light and twelve hours of dark. It is possible that other cycle times would give somewhat better growth and that this would vary from species to species. The timers can be readily set to give any combination of hours of light and hours of dark. Growers may wish to experiment with this.

Haberlea rhodopensis has tiny seeds and tiny seedlings. By enclosing the pot in the polyethylene Baggie, the seedlings are protected from drying at the soil surface. Seedlings of *Haberlea* have been kept growing in the Baggies for a year. At the end of a year one has a potfull of healthy seedlings without having to do any watering or other maintenance for the whole year. The Baggies are opened once every two months to check on moisture conditions. Rarely a Baggie will develop a tear that causes the contents to dry out faster than usual, and this is the reason for the two month check. The bagging technique is an incredibly easy and efficient method of growing *Haberlea* and other Gesneriads such as *Briggsia*, *Jankae*, and *Ramonda*. You can go on your two week or month vacation confident that the seedlings are in great condition and growing at their optimum rate.

Echinocereus pectinatus hybrids germinate significantly only when treated with gibberelic acid-3 (GA-3). Seedlings of this species are very small with shallow root systems. As soon as a seed germinates in the paper towel (GA-3 treated), it is transferred to a pot, and the pot enclosed in a Baggie. As the seeds germinate, every other day a new batch is lined into the pot until the pot contains about fifty. A pot of these seedlings all lined in little rows is entrancing. The process is so easy that everyone should have all they want. It may surprise many that cacti seedlings need constant moisture and light free of ultraviolet radiation for the first year of their life. The reasons for this were discussed in Chapter 12.

Lobelia cardinalis requires light to germinate. At the same time the seed is small and requires high humidity. The answer is to sow the seeds directly in a pot, enclose the pot in a Baggie, and place under fluorescent lights. The seeds get light

and even moisture conditions. This is an incredibly easy way to raise seedlings of many swamp plants since they generally require light for germination along with constant moisture.

Even large seedlings with a four inch radicle such as *Podophyllum hexandrum* or readily germinated annuals such as petunias and tomatoes benefit from keeping the pots of seeds in a Baggie until germination starts and until the seedlings have a true leaf. In this way no attention has to be paid to watering until the seedlings are well under way. The pots enclosed in Baggies have to be kept under fluorescent lights.

In today's economic environment it may be cheaper and more convenient to put the seedlings under fluorescent lights than to construct greenhouses, lath houses, and other structures. This is certainly true for the amateur grower who is growing something of the order of one hundred pots of seedlings a year. Even commercial growers will want to investigate the economics of this. Eliminating the daily watering and reducing maintenance to a check at two month intervals are enormous advantages in today's situation with the high cost of labor.

There are three groups that are not so well adapted to the bagging technique. One are those species that require outdoor conditions and oscillating temperatures for germination. The bagged pots can be placed on the north side (in the northern hemisphere) of a house or building where they receive only indirect (reflected) north light. As the seeds germinate, the bag is opened and the seedlings given increasing amounts of direct sunlight. This is the traditional "hardening off" procedure. With these species the bagging procedure does eliminate watering until the seeds germinate, and this is of some help.

The second are species whose seedlings need to grow in cool or cold temperatures. A list of these was given earlier. The discussion in the previous paragraph applies equally to this group. Again the bagging technique gives some reduction in the effort of the grower, but the bagging technique is not so overwhelmingly advantageous.

The third are those species requiring gibberelins for germination. The methods for handling them are discussed later on in a section on GA-3.

What type of pots should be used? There has been a long standing argument between those who use the old traditional clay pots and those that use plastic pots. The simple truth is that the porosity of the clay pots allows one to get away with overwatering. However, the bagging technique plus the use of modern high porosity media (see next section) obviates all this so that there is no question that plastic pots should be used. They have the advantage of being cheaper, much lighter in weight, and easier to clean. Here we use pots that are 3.5 x 3.5 inches square at the top. After bagging these are placed in 12 x 18 inch trays that holds twelve such pots. These are then placed on shelves under the fluorescent lights. The shelves can be spaced as little as fourteen inches apart so that banks of these can be lined up from the floor to the ceiling.

What medium should be used in the pots? The choice of medium depends on the growing requirements of each species. The medium used most frequently here is composed of equal parts peat moss, leaf mold, and Perlite. This medium has a high water holding capacity, around 15%, due to the Perlite. This helps prevent drying out. It also has a high free air space of around 20%. This gives high aeration and insures that the medium stays aerobic. This is particularly important with seedlings because they have actively growing roots which consume oxygen rapidly. Few growers will want to measure water holding capacity or free air space, but they are easily measured as described at the end of this chapter.

The medium is mixed in a wheelbarrow and stored in plastic bags or large plastic containers of the type used so much these days for waste disposal. Peat moss is tamped over the bottom of each pot. This is permanent enough since the seedlings will be removed from the pots in 6-12 months. The pots are filled with medium, tamped down, and surface sterilized just before use.

It has often been recommended to sterilize the whole medium, but there are studies that indicate that this is overall harmful. In principle a fungicide such as Benelate could be used, but I have not heard favorable reports of such procedures. More specifically John Gyer has tried a number of disinfectant procedures on lima beans in attempts to reduce rotting of the seeds. None has been effective. However, orchid seeds are regularly disinfected before planting, see Chapter 21. Finally the germination of the seeds in moist paper towels gives some help in avoiding fungal attack.

There is the problem of acid or alkaline media. Suffice to say that some species such as azaleas, rhododendrons, and most Ericaceae require acid media in the pH range of 4-5 and quickly become chlorotic and die in alkaline media. Other species such as most Campanula require neutral to slightly alkaline conditions in the pH range 7-8. Of course the best answer is to grow only those species suitable to your soil. It is quite futile to imagine that one can permanently change the soil. A local tragedy is a real estate development in an acid sandy area. This used to have marvelous colonies of trailing arbutus, *Lilium philadelphicum*, *Rhododendron roseum*, *Phlox ovata*, *Cypripedium acaule*, and other acid lovers. When the homes were built and people moved in, they felt that nothing would do but to have a Kentucky blue grass lawn. Great amounts of limestone and lime has been poured onto these properties. In some places neither the blue grass or the acid lovers will grow very well because the soil is so lacking in uniformity.

On a small scale acid conditions can be created. As emphasized in James Wells's book Plant Propagation Practice, the only way to increase acidity is to use finely powdered sulfur. In transplanting azaleas and rhododendrons, Wells recommends lining the hole with a light dusting of sulfur and then applying another coating on the surface. Wells says that he never saw any damage from use of excess sulfur in all of his years as chief propagator at one of the largest nurseries. I have personally followed his recommendations with excellent results. It is particularly effective if your soil is already at a pH of around six, and it just needs a little more acidification. Leaf mold and other media with a high capacity for ion exchange also replace to some extent the need for an acidic medium. Finally application of dilute

aqueous solutions of iron sequestrene will replace acidity to a certain extent.

For species needing neutral to alkaline media, the application of ground limestone has been used for centuries and is effective. The use of lime itself is a bit drastic and is usually not needed.

It is appropriate here to clarify one of the most pernicious misconceptions in the horticultural literature, namely the subject of drainage. Growing roots are actively consuming oxygen. It is easy for them to be asphyxiated if the oxygen pressure is reduced below the 0.2 atmospheres that is present in the air. The susceptibility varies in different species. This subject is misunderstood to an incredible degree in the horticulture literature. The word drainage is like a drumbeat punctuating every paragraph. In fact a plant cannot possible care whether water drains fast or slow over the roots. What is critical is the supply or more precisely the pressure of oxygen. The word **drainage** should be crossed out throughout the horticultural literature and replaced by the word **aeration**. The misunderstanding arose because media that drain well usually are porous with 10-30% free air space so that they remain aerobic. What has happened in the horticultural literature is that an aeration requirement became misinterpreted as a drainage requirement. It can be added that if drainage were essential, plants could never be grown by hydroponics.

Should any special precautions be taken against insects and other creatures? Generally insects were not a problem. Sooner or later aphids appear. Some species are more susceptible than others and this varies with the species of aphid. The tiny grub of a fungal fly has been particularly troublesome with seedlings of *Tricyrtis*. Usually the grub eats only dead tissue, but it is able to eat live *Tricyrtis*. This has not been seen on the seedlings of any other genera. Snails and slugs are always a potential problem.

All of the above problems are eliminated by surface sterilization of the medium and enclosing the pots in Baggies. Both procedures were described earlier. These two procedures will make growing plants from seeds so easy and effortless that I make no apology for having repeatedly promoted their use in this book.

Should treatment with gibberelic acid-3 (GA-3) be one of my procedures? The answer is an absolute yes, however, it is a method of last resort since there is often the problem that the seedlings are weak and etiolated and have difficulty surviving. Some species have GA-3 as a natural requirement for germination as discussed in Chapter 12. For these GA-3 is essential. The seeds are germinated by the procedure described in Chapter 3. As soon as they have germinated they are transferred to pots. Sometimes the seedlings from GA-3 treatment are weakened by etiolation and are more sensitive to low humidity and drying. Enclosing the pots in Baggies as described above will help in combating this problem. Treatment with cytokinins has been recommended to combat the etiolation, but this has not been tried here.

For small seeds or large batches of seeds, the procedure of germinating the seeds in paper towels would be inconvenient. The following procedure is suggested as an alternative way of applying GA-3 that should work although it has not been

tested as yet. The seeds would be lightly dusted with GA-3 and then planted. This dusting could be accomplished either by stirring the seeds with GA-3 in a small container or shaking the seeds with GA-3 in a paper envelope. Such procedures would be applicable to commercial production. Such methods have to be used with those species that require gibberelins for germination.

How can I naturalize wild flowers? The highway department in Pennsylvania and private groups have taken to broadcasting seed of flowers in patches in the median strip in our four lane divided highways and in the plots enclosed in clover leaf intersections. This has been most successful, but it should be remembered that it only works if the area is first sprayed with an herbicide of the glycoposphate type such as RoundUp. The seeds can be planted in a day or two after the spraying. Using this technique we maintain sizable beds of *Dianthus barbatus*, *Delphinium grandiflorum*, and *Primula japonica* with minimum effort. The glycoposphate type of herbicide is rapidly degraded in soils to glycine and phosphates which are plant nutrients and are both beneficial to plants. The above point is emphasized because there is much promotional literature appearing that infers that one can just throw the wildflower seed anywhere. This simply will not work if there is a thick sod of grass or a thick growth of other plants.

Many growers are frightened of chemicals. It is true that some older herbicides such as simazine and arsenicals should not be used because they leave residues in the soil that are detrimental to life. It is also true that herbicides of the Paraquat type are dangerously toxic to humans. However, glycoposphate herbicides such as RoundUp and its congeners quickly degrade in soils to glycine and phosphates. Glycine is a natural amino acid and a component of every protein in your body and phosphates are a plant nutrient. No harmful residues are left, and seeds can be planted minutes after spraying. These glycoposphate herbicides are the basis for no-tillage farming which is the way that much corn is raised today as well as many other crops.

Avoiding the use of RoundUp because it is a chemical reminds me of a bumper sticker that I saw on a pick up truck on a desolate back road in the outback of Wyoming. "If you think education is costly, try ignorance."

The Measurement of Free Air Space and Water Holding Capacity.

The only thing required is a graduated cylinder or a kitchen measuring cup for measuring volumes. A container is selected which has a small hole in the bottom which can be temporarily closed with a stopper or a piece of plastic tape. A measured volume of the dry media is placed in the container. A measuring cup is filled with water to the top mark, and water is slowly poured into the container until the water level just reaches the level of the medium. The volume of water added is V-1. The stopper covering the hole at the base of the container is now removed and the water that drains through is run into the measuring cup. This is V-2 and is the volume of free air space. The volume of held water is (V-1)-(V-2). These can be converted to percentages in the usual way.

Many species require 15-20% free air space in the media to grow well. An example are the marvelous *Kabschia saxifrage* grown by Doonan and Pearson at the Grand Ridge Nursery in WA.

CHAPTER 15. COLLECTION OF SEEDS

Not all seeds are as easy to collect as *Aquilegia* and *Jeffersonia* where the seed capsule need only to be turned over and the seeds pour out. Seeds of *Penstemon* are enclosed in a hard capsule with a sharp beak. The procedure with these is to lightly crush the capsules with pliers after which the seed falls out with some mechanical manipulation. Separation of the seed from the capsule debris is accomplished by shaking the mixture lightly in a cupped sheet of smooth paper. The debris rises to the top and the seed settles to the bottom. The sheet of paper is laid flat and the debris brushed to one side and off the paper using a half inch wide soft brush. The process is repeated several times. This brushing procedure has been much more effective with small samples of seeds than any version of blowing or the ancient art of threshing and winnowing.

Seeds of *Campanulaceae* and *Lobelia* are shed from pores in the sides of the seed capsule. Shaking the seed capsules vigorously in a paper bag will form a pool of seed at the bottom. These can be given a final cleaning by the brushing technique described above. Seeds of *Acantholimon* and *Asteraceae* are easy enough to collect, but there is much voluminous chaff and empty seed coats. These are not easily removed in the dry state, but after placing on the wet towels, the debris starts to rot and stick to the towel. At this time they are more easily recognized and removed along with a change of towel for the good seeds. Actually *Acantholimon* and most *Asteraceae* germinate quickly at 70 so it is all over in a few weeks.

If the seed pods of *Asclepias* (milkweeds) are picked just before splitting, they can be opened without fluffing up the silky parachutes attached to each seed. Running the cylinder of seeds between the thumb and forefinger will allow (with luck) the seed to be stripped of the silk to give seeds that are completely free of silk.

Seeds of *Corydalis* and *Eranthis* are shed from the capsule while the capsule is still green. Close attention is needed to catch the seed before it falls. Seed of *Echinocereus* (*Cactaceae*) is also shed from rather green fruit and need to be watched closely. Seed of *Violaceae* has been some of the most difficult to collect. The capsule is green one day with soft immature seed and only a few days later the capsule suddenly splits and sends the seed flying. One solution is to wrap the immature capsules in aluminum foil in a manner that catches the seed in the aluminum foil envelope some days later. This was used with *Adonis vernalis*, *Lathyrus vernus*, and many *Violas*.

Seeds of *Buddleia* and *Weigelia* are best collected by placing the stems lined with the small seed capsules in a paper bag. They will open on drying and shed there seeds whereas attempting to extract the seeds from the unopened capsules is most difficult.

Seed of *Phlox* is frustrating to collect because just as it is ripe it rolls off the receptacle, usually just as one is about to grab it. Also there are so few seeds per

recepticle. As a result seed of Phlox is usually scarce.

Seeds in fruits were washed as described in Chapter 8. After several days washing and after most of the pulp had been mechanically removed, the seeds were placed each day in a small strainer. By placing ones hands over the bottom of the screen, the strainer was allowed to half fill and then drain by removing ones hand. This was so efficient that 10-20 rinses per minute could be accomplished. The seeds can then be transferred back to the soaking dish by inverting the strainer and using a squirt bottle of the type used in chemistry laboratories.

One problem arises because nurserymen tend to propagate clones on the basis of larger flowers, more fruit, and better foliage, and these are propagated vegetatively. Gardeners also tend to plant a sort of Noah's Ark garden with one plant of each species instead of self sowing colonies. In fact many gardeners look upon myriads of self sown seedlings as disrupting their perfect picture. All of this leads to situations that are not conducive to the production of viable seed in quantity. In our area plantings of *Pyracantha lalandi* (firethorn) and *Sorbus aucuparia* (mountain ash) are often composed entirely of a vegetatively propagated sterile clone. Abundant fruit is set which makes a great display but the fruits are seedless. Even more frustrating are the trees of *Photinia villosa* on the Penn State Campus that are laden with fruit filled with normal size seed coats, but alas in many years all are empty shells. Beech trees do the same and only occasionally is there a set of viable seeds. The only viable seed of *Pyracantha lalandi* was found in a nearby junkyard where the birds had undoubtedly roosted and sown the seed. Some species seem to be losing the ability to set viable seed, clearly the case with *Ceratostigma plumbaginoides* and *Franklinia*.

The notion that all good seed sinks in water and bad seed floats is just not always true. All the *Iris setosa* seed floats even after a month in water. In fact it starts to germinate after a couple of weeks floating. *Iris pseudoacorus* seed floats for a few days and then sinks. Large sample of seed of *Cornus amomum* were collected from our own colonies and after thorough washing and cleaning, about half the seed floats and half sinks. Both types gave about the same germination both in percent germination and in the rates and other germination characters.

In some species much of the seed is infected with the eggs of certain insects such as weevils. *Ipomoea leptophylla*, the bush morning glory of the midwest U.S., is particularly prone to this problem. One midwinter day I was working at my desk, and I kept hearing a rattling and scraping sound. It was the weevils in a sack of the *Ipomoea* seeds. Certain beans have the same problem and one of our childhood playthings were "Mexican Jumping Beans." Perhaps some carefully controlled heat treatment or treatment with a toxic gas would kill the insects without damaging the seeds.

A disturbing problem is that due to extensive public spraying for gypsy moths and oak leaf roller moths along with much private spraying of insecticides, the population of moths and butterflies has been much depleted. I have not seen the cocoon of one of the silk worm moths in years. In my childhood they were commonplace. Of course the silkworm moths are not pollinators, but they reflect the general decline in population of moths. Since the noctuid moths and the sphinx moths are major pollinators of many flowers, the result is an absence of natural pollinators. Fortunately the humming bird clear wing moth still is abundant and the hummingbird

itself is common and active, but the decline in population of insect pollinators has to be a factor in reducing the seed set.

It was possible to obtain seeds from about 2500 species. Much of this seed was personally collected. Our own plantings include woods, cliff, marsh, stream, and spring and contain breeding colonies of over 400 species. The Penn State University has a wide diversity of trees and shrubs on the campus, and the Borough of State College employs a full time arborist and there are street plantings of interesting trees.

Most of the seeds were obtained from outside sources. The listing of these in Chapter 23 may be helpful to gardeners. Foremost are the seed exchanges run by the American Rock Garden Society, the British Alpine Society, and the Scottish Rock Garden Club. These contain up to 6000 entries each year, and the Seedlist Handbook (1) was written to sort out this plethora of names. Botanical Gardens were important contributors with Khorag and Tbilisi in USSR, Beijing in China, and Denver in US being particularly helpful. Many individuals took time to collect seeds and send them to me and the list of over 100 are listed in Chapter 23. Finally there have been botanical collecting expeditions that sent a wide variety of seeds. Notable were Jim and Jenny Archibald in the Rockies and Turkey, Chris Chadwell in Kashmir and Ladakh, Sonia and Jim Collins in Arizona, Jim Forrest in Australia and New Zealand, Leon Glicenstein in California, Doris Goldman in Pennsylvania, Josef Halda in Turkey and USSR, Gwen and Panayoti Kelaidis in the Rockies, Vaclav Plestl in Czechoslovakia, Ron Ratko in Washington, and Sally Walker in Southwestern US and Mexico.

CHAPTER 16. PLANT NOMENCLATURE

Following are some explanations of how taxonomy has been handled in this book and some suggestions as to how taxonomy can be made more effective. The Linnaeus binomial system of classifying plants was based on the morphology of the sexual parts of plants. One of its triumphs was that it led to a classification of plants that was in accord with their evolutionary development. This accord was not only at the macroscopic level but also at the molecular level. For example the alkaloid berberine is characteristic of Berberidaceae, and there are many other examples of particular chemicals and chemistries that are characteristic of plant families and genera.

However, the Linnaeus system had two misconceptions. At the time of Linnaeus academic institutions still clung to latin as an emblem of intellectualism. This is now archaic. A name like *Eranthis hyemalis* is an internationally recognized name for a plant and belongs to no specific language. It is not a foreign word and is specifically not a latin word so that to italicize it is grammatically incorrect. Plant names have not been italicized throughout this book, and it is anticipated that this practice will become more prevalent with time. Plant names are not italicized in our local newspaper or in ref. 1, and names are not italicized in other fields of science.

The second misconception was that plant species are immutable. The work of Darwin and Darwinian Evolution showed the error in this. The problem is then how can the Linnaean system be so successful when its very premise is wrong. Recently

Gould has discussed this problem in a publication entitled "What is a Species" (ref. 48). The answer is that species differentiate over a relatively short period of geological time and remain distinct over long periods of geologic time. This means that at any instant only a relatively few plants are undergoing species differentiation. Examples of such active species differentiation at this present time would be the some of the small Mediterranean orchids and the Phlox of Southeastern U.S. that center around *Phlox pulchra* and *Phlox glaberrima*.

Plant families and genera have separated so far in an evolutionary sense that they can be regarded as immutable. Thus a lily and a rose will never interbreed nor exchange genetic information, and in effect Liliaceae and Rosaceae are for all practical purposes permanent and immutable.

Species can then be defined by the principle that members of a species can breed with others in the same species but not with individuals belonging to a different species. The most obvious reason for lack of interbreeding is incompatibility (intersterility) and the failure of crosses to set viable progeny. It also can be the result of different flowering times and other differences in habits. Gould excludes geographical separation as a failure to interbreed. These definitions are adopted in this book. Genus can then be defined as a group that are interfertile but do not normally interbreed. This definition is laborious to test, so that genera have been delineated largely by inference. Yet it is remarkable that so few examples of intergeneric hybrids have ever been made, and these few exceptions could be eliminated by coalescing the genera involved. I can think of only one example at the moment, and that is the hybrid of *Belamcanda chinensis* and *Iris dichotoma*.

All of the above seems clear, yet there are serious problems in taxonomy. The most important function of taxonomy is to facilitate communication. This is more important than taxonomy as a field in itself. Several practices have impeded this objective. The principle that priority is given to the first given name seems simple at first, but in fact has led to mischief. As one goes back in time the descriptions of plants become more vague and ambiguous. At the present time and the present stage of the situation, efforts to find an earlier description with a concomitant name change is science at its worst, and such efforts should be ended right now. To resurrect some earlier name at this stage hurts communication badly and serves no purpose other than to get a cheap and trivial publication. In chemistry an international conference was convened in Geneva in 1892, and an end was put to further frivolous name changes. Botanical taxonomy would be well advised to follow a similar route.

Names of plants should be changed only with the greatest reluctance and when overpowering arguments favor such a change. This has recently come to the fore in regard to the names of plant families. Nearly all the plant families have names derived from a particular genus within the family, and the name ends in ceae. However, there are seven families in which the name has been derived from a characteristic of the family and the name ends in ae. New names have been proposed for these seven families which conform with more general practice. These new names and the old name in parenthesis are Apiaceae (Umbelliferae), Asteraceae (Compositae), Brassicaceae (Cruciferae), Fabaceae (Leguminosae), Hypericaceae (Clusiasceae, Guttiferae), Lamiaceae (Labiatae), and Poaceae (Graminae). These new names have

been adopted in this book primarily because it makes the ending of the name diagnostic for a plant family, and thus further reduces any need for italics.

In virtually all fields of science the principle of Occam's razor is given first priority. Applied to plant taxonomy this would state that no more plant names should be invoked than are necessary for unambiguous and efficient communication. In the past the practice of taxonomists in commemorating each other in plant names and the desire for publications has often led to a needless proliferation of names. Fortunately recent trends towards coalescing plant names is a step in the right direction. A name like *Paris quadrifolia* conveys much more information than a commemorative name like *Tricyrtis bakeri*. It is unfortunate that commemorative names ever got started. It is obvious that commemorating influential people by naming a plant after them has been used for financial and political benefit and to further ones career. All of this introduces subjectivity and political influence into what should be an objective science.

CHAPTER 17. ENDANGERED SPECIES AND CONSERVATION

After all, in the course of evolution, countless species have appeared and disappeared so that the extinction of a single species cannot be the tragedy that some would portray. Yet there is an atmosphere of sadness when a pretty plant such as *Primula kisoana* nears extinction in the wild. It is here that the amateur and professional grower can make a contribution. The grower can accumulate every clone available and can increase the genetic pool and evolutionary health of the species by a program of cross pollination, propagation, and distribution. In part this book is dedicated to such programs.

Such propagation programs compliment programs directed towards preserving natural habitats. The Nature Conservancy has done a magnificent job in studying the needs of species, both plants and animals, and setting up sanctuaries by land purchases and other means. But this is not enough. Even now a number of species are more plentiful in cultivation than in the wild; Ginkgo, Metasequoia, and *Primula kisoana* for examples. With the present density of human population in the world it is futile to think that nature preserves of such magnitude can be established that would insure the survival of the above three species by natural propagation. The possibility that they are naturally dying out cannot be overlooked.

The United States government and State governments have published lists of endangered species. It is illegal to distribute these plants or seeds of these plants. This policy and the laws designed to enforce this policy can only serve to **speed up the extinction of the species by discouraging propagation.** Further, many of the species on the present list are only minor variants of common species. The law can be easily circumvented by distributing the variant under the name of the species, particularly since the variants are marginally distinct, or by distributing under a new name since there is no final authority at present on names of species. It is felt that the laws should be more specifically directed towards preventing commercial collecting. The laws could also be rewritten to encourage propagation, especially by seed.

Two groups oppose propagation programs. One group places their force behind saving plants as if plants were static objects. In their view it becomes more important to save plants than to grow plants. In other words a plant saved is better than a plant grown. A second group has the view that raising large numbers from seed, introducing the species into new and suitable habitats, and other actions which promote and accelerate evolution are looked upon at best as causing taxonomic grief. This book takes the view that these oppositions to propagation are in error. Our society already propagates, manages, and distributes animals and fish with much success. Now we must manage plants the same way. This is the way to preserve endangered species and serve conservation, and most of all, to express our love of plants.

CHAPTER 18. LIST OF GENERA STUDIED ARRANGED BY THEIR PLANT FAMILIES

At the beginning it was thought that there might be sufficient similarity in germination behavior within families that the data could be organized by families. In fact there proved to be not only much diversity within families, but sometimes within genera. Nevertheless, some general comments about the larger families may be helpful. The following list of families studied also provides an opportunity for listing the genera in each family for which data was recorded.

- ACANTHACEAE.** Ruellia
- ACERACEAE.** Acer
- AIZOACEAE.** Delosperma, Mesembryanthemum
- ALISMACEAE.** Alisma
- AMARYLLIDACEAE.** Alstroemeria, Galanthus, Habranthus, Hymenocallis, Hypoxis, Ixolirion, Leucojum, Lycoris, Narcissus, Rhodolirion, Rhodophiala, Ungernia, Zephyranthes. - Many species germinate only at 40. Photorequirements were never found.
- AMERANTHACEAE.** Gomphrena
- ANACARDIACEAE.** Rhus
- ANNONACEAE.** Asimina
- APIACEAE (UMBELLIFERAE).** Aciphylla, Anethum, Angelica, Anisotome, Anthriscus, Astrantia, Athamanta, Bupleurum, Coriandrum, Cymopterus, Daucus, Erigenia, Eryngium, Ferula, Heracleum, Levisticum, Lomatium, Meum, Myrrhis, Pimpinella, Pseudotaenidia, Selinus, Zizia. - Germinations were complex with many germinating at 40, some requiring light and being stimulated by GA-3, and oscillating temperatures being required for Myrrhis.
- APOCYANACEAE.** Adenum, Amsonia, Nerium
- AQUIFOLIACEAE.** Ilex
- ARACEAE.** Arisaema, Arum, Eminium, Lysichitum, Orontium, Pinellia, Symplocarpus
- ARALIACEAE.** Aralia, Panax
- ARISTOLOCHIACEAE.** Aristolochia, Asarum
- ASCLEPIADACEAE.** Asclepias, Matelea, Periploca
- ASTERACEAE (COMPOSITAE).** Achillea, Ajania, Anacyclus, Anaphalis, Andryala, Antennaria, Anthemis, Arnica, Artemisia, Aster, Asteromoa, Balsamorhiza, Carlina, Carthamus, Celmisia, Centaurea, Chaenactis, Chamaechaenactis, Cremanthodium, Chrysanthemum, Chrysopsis, Cichorium, Coreopsis, Dimorphotheca, Doronicum, Enceliopsis, Erigeron, Eriophyllum, Eupatorium, Gaillardia, Gutierrizia, Haplopappus, Helianthus, Helichrysum, Heterotheca, Hippolytica, Hymenoxys, Inula, Leontopodium, Liatris, Ligularia, Lygodesmia, Machaeranthera, Marshallia, Melampodium, Mutisia, Pachystegia, Psychrogeton, Rudbeckia, Saussurea, Senecio, Solidago, Stokesia, Tanacetopsis, Tanacetum, Taraxacum, Townsendia, Tussilago, Vernonia, Waldheimia, Wyethia, Xeranthemum, Xylanthemum. - These are predominantly D-70 germinators. One species of Aster, two Eupatorium, and one Vernonia were 40-70 germinators. Centaurea has an interesting physical mechanism for delaying germination.

BALSAMINACEAE. Impatiens

BEGONIACEAE. Begonia

BERBERIDACEAE. Berberis, Bongardia, Caulophyllum, Epimedum, Gymnospermium, Jeffersonia, Leontice, Mahonia, Nandina, Podophyllum. - These have complex and multicycle germinations. Photoeffects, oscillating temperature effects, and the common D-70 pattern were all absent.

BETULACEAE. Alnus, Betula, Corylus, Ostrya

BIGNONIACEAE. Argylia, Campsis, Catalpa, Chilopsis, Incarvillea, Jacaranda. - Photorequirements were found in Campsis and Catalpa.

BIXACEAE. Bixa

BORAGINACEAE. Anchusa, Arnebia, Borago, Cryptantha, Cynoglossum, Echioides, Eritrichum, Lindelofia, Lithospermum, Mertensia, Myosotis, Onosma, Pseudomertensia, Pulmonaria. - While many are simple D-70 germinators, photorequirements and oscillating temperature requirements are present.

BRASSICACEAE (CRUCIFERAE). Aethionema, Alyssoides, Alyssum, Arabis, Aubrieta, Brassica, Cheiranthus, Cochlearia, Degenia, Dentaria, Draba, Erysimum, Eunomia, Fibigia, Hesperis, Hutchinsia, Iberis, Lepidium, Lesquerella, Lunaria, Mathiola, Nasturtium, Parrya, Petrocallis, Physaria, Ptilotrichum, Stanleya, Thlaspi. - All are D-70 germinators except Dentaria which requires oscillating temperatures and germinates in a hypogeal manner whereas all other genera are epigeal germinators.

BUTOMACEAE. Butomus

BUXACEAE. Sarcococca

CACTACEAE. Coryphantha, Echinocereus, Ferocactus, Neobessya, Opuntia, Pediocactus, Rebutia, Sclerocactus. - Some species germinate readily at 70. However, the discovery that *E. pectinatus* hybrids required gibberelins for germination means that GA-3 treatment needs to be tried on the reluctant germinators.

CALYCANTHACEAE. Calycanthus

CAMPANULACEAE. Adenophora, Campanula, Codonopsis, Cyananthus, Edraianthus, Jasiona, Michauxia, Ostrowskia, Physoplexis, Phyteuma, Platycodon, Symphyandra, Trachelium. - Most are D-70 germinators, but photorequirements are found in some Campanula, and a GA-3 requirement was found in a few.

CANNACEAE. Canna

CAPPARIDACEAE. Capparis, Cleome

CAPRIFOLIACEAE. Kolkwitzia, Lonicera, Sambucus, Symphoricarpos, Viburnum, Weigelia. - These exhibit a variety of germination patterns with many germinating exclusively at 40 whereas 40 is fatal to Kolkowitzia. Some germinations are multistep. Photoeffects were not found.

CARICACEAE. Carica. - Light was required.

CARYOPHYLLACEAE. Acanthophyllum, Arenaria, Cerastium, Dianthus, Gypsophila, Lychnis, Melandrium, Minuartia, Paronychia, Petrocoptis, Saponaria, Silene. - All are D-70 germinators except for Silene where photoeffects and other complexities were found.

CELASTRACEAE. Celastrus, Euonymus. - Some Euonymus require oscillating temperatures, extended multicycles, and washing the seeds with detergents.

- CERCIDIPHYLLACEAE.** Cercidiphyllum.
- CHENOPODIACEAE.** Chenopodium, Morocarpus
- CHLORANTHACEAE.** Chloranthus
- CISTACEAE.** Cistus, Fumana, Helianthemum, Hudsonia
- CLETHRACEAE.** Clethra
- COMMELINACEAE.** Commelina, Tradescantia
- CONVOLVULACEAE.** Convolvulus, Ipomoea
- CORIARIACEAE.** Coriaria
- CORNACEAE.** Aucuba, Cornus. - Cornus generally require oscillating temperatures.
- CRASSULACEAE.** Chastophyllum, Dudleya, Kalanchoe, Rhodiola, Sedum, Sempervivum. - Light and GA-3 requirements were found.
- CUCURBITACEAE.** Citrullus, Cucumis, Cucurbita, Echinocystis, Sicyos, Trichosanthes. - The temperate zone species require oscillating temperatures. The germination behaviors are complex and interesting.
- CUPRESSACEAE.** Umbilicus
- DIAPENSIACEAE.** Pyxidantha, Shortia. - Shortia requires light and exogenous chemicals.
- DILLENACEAE.** Actinidia
- DIOSCOREACEAE.** Dioscorea, Tamus
- DIPSACEAE.** Cephalaria, Dipsacus, Jurinella, Scabiosa. - Dipsacus requires light.
- DROSERACEAE.** Dionea
- EBENACEAE.** Diospyros
- ELAEAGNACEAE.** Eleagnus, Hippophae
- EPHEDRACEAE.** Ephedra
- ERICACEAE.** Arbutus, Arctostaphylos, Bruckenthalia, Cassiope, Enkianthus, Epigaea, Gaultheria, Kalmia, Ledum, Leiophyllum, Leucothoe, Lyonia, Oxydendrum, Pernettya, Phyllodoce, Pieris, Rhododendron, Vaccinium. - The majority more or less require light.
- EUPHORBIACEAE.** Euphorbia, Securinega.
- FABACEAE (LEGUMINOSAE).** Acacia, Albizzia, Anthyllis, Astragalus, Baptisia, Bauhinia, Cercis, Chamaecytisus, Cladastris, Clanthus, Colutea, Coronilla, Cytisus, Dalea, Dorycnium, Genista, Gleditsia, Gymnocladus, Hardenburgia, Hedysarum, Indigofera, Laburnum, Lathyrus, Lespedeza, Lotus, Lupinus, Oxytropis, Piptanthus, Robinia, Sophora, Tephrosia, Thermopsis, Trifolium, Vicia, Wisteria. - Impervious seed coats are present in most species.
- FAGACEAE.** Quercus
- FUMARIACEAE.** Adlumia, Corydalis, Dicentra. - These have some of the most complex and extended germination patterns in the plant kingdom.
- GENTIANACEAE.** Blackstonia, Centaurium, Eustoma, Frasera, Gentiana, Gentianella, Gentianopsis, Lisianthus, Lomatogonum, Sabatia, Swertia. - Photorequirements and GA-3 requirements are present in some genera.
- GERANIACEAE.** Geranium

GESNERIACEAE. Briggsia, Haberlea, Jankae, Opithandra, Ramonda. - All are D-70 germinators. The pots of seedlings must be kept in high humidity for at least a year as the seedlings are sensitive to desiccation. This is readily accomplished by keeping the pots in polyethylene bags which are loosely tied at the top with a wire.

GINGKOACEAE. Ginkgo

GLOBULARIACEAE. Globularia

HALORAGIDACEAE. Gunnera

HAMAMELIDACEAE. Corylopsis, Hamamelis, Liquidambar, Parrotia, Parrotiopsis. - Germinations are usually multicycle.

HIPPOCASTANACEAE. Aesculus

HYDRANGACEAE. Deinanthe

HYDROPHYLLACEAE. Nemophila, Phacelia, Romanzoffia. - Oscillating temperatures are required in some species.

HYPERICACEAE (CLUSIACEAE). Hypericum. - Light is usually required.

IRIDACEAE. Acidanthera, Belamcanda, Crocosmia, Crocus, Dierama, Freesia, Gladiolus, Hermodactylus, Iris, Lapeirousia, Melasphaerula, Moraea, Nemastylis, Romulea, Sisyrinchium, Tigridia. - A large variety of behaviors are found including photorequirements and extended multicycle germinations.

JUGLANDACEAE. Juglans

LAMIACEAE. Agastache, Ajuga, Ballota, Collinsonia, Dracocephalum, Eremostachys, Horminum, Hymenocrater, Hyssopus, Lallemantia, Lamium, Lavandula, Majorana, Mentha, Monarda, Monardella, Nepeta, Rosmarinus, Ocimum, Origanum, Pelkovia, Petroselinum, Phlomis, Physostegia, Prunella, Salvia, Satureia, Scutellaria, Sideritis, Stachys, Teucrium, Thymus, Trichostema, Ziziphora. - Photorequirements are found in several of the genera.

LARDIZABALACEAE. Decaisnea

LAURACEAE. Lindera, Sassafras

LENTIBULARIACEAE. Pinguicula

LILIACEAE. Agave, Allium, Androcymbium, Androstephium, Anthericum, Arthropodium, Asphodeline, Asphodelus, Asparagus, Bellevalia, Brimeura, Brodiaea, Bulbinella, Bulbocodium, Calochortus, Caloscordum, Camassia, Cardiocrinum, Chionodoxa, Chlorogalum, Clintonia, Colchicum, Convallaria, Disporum, Eremurus, Erythronium, Fritillaria, Gagea, Galtonia, Hastingsia, Helonias, Hemerocallis, Hosta, Hyacinthus, Ixolirion, Kniphofia, Korolkowia, Leucocrinum, Lilium, Liriope, Lloydia, Maianthemum, Manfreda (Agave), Merendera, Muscari, Nothoscordum, Ophiopogon, Ornithogalum, Paradisea, Paris, Polygonatum, Puschkinia, Rhinopetalum, Sandersonia, Schoenolirion, Scilla, Scoliopus, Smilacina, Smilax, Strangweia, Theropogon, Tricyrtis, Trillidium, Trillium, Tritoleia, Tulipa, Uvularia, Veratrum, Xeronema, Xerophyllum, Yucca, Zygadenus. - Convallaria and Ophiopogon provided the two clearest examples of blockage of germination by light. Tricyrtis generally require light. Many species germinate only at 40. Multistep and multicycle germinations are common. Oscillating temperature requirements are also found. Every conceivable germination pattern is present.

LIMNANTHACEAE. Limnantes

LINACEAE. Linum

LOASACEAE. Cajophora, Loasa, Mentzelia

- LOBELIACEAE.** Lobelia
LOGANIACEAE. Buddleia, Spigelia
LORANTHACEAE. Phoradendron
LYTHRACEAE. Cuphea, Lythrum
MAGNOLIACEAE. Magnolia
MALESHERBIACEAE. Malesherbia
MALVACEAE. Abutilon, Hibiscus, Illiamna, Malva, Sidalcea, Sphaeralcea. - Impervious seed coats were found in some species.
MELASTOMACEAE. Osbeckia, Rhexia. - Light was more or less required in all species.
MESEMBRYANTHEMACEAE. Delosperma
MORACEAE. Maclura, Morus. - Germination is rapid if the inhibitors in the fruit are removed.
MYRICACEAE. Myrica
MYRTACEAE. Callistemon, Calothamnus, Eucalyptus, Kunzea, Melaleuca
NYCTAGINACEAE. Abronia, Mirabilis
NYMPHAEACEAE. Nelumbo, Nymphaea
NYSSACEAE. Nyssa
OLEACEAE. Abeliophyllum, Chionanthus, Forsythia, Fraxinus, Jasminum, Ligustrum, Menodora, Syringa. - Multistep and multicycle germinations were found.
ONAGRACEAE. Circaea, Clarkia, Epilobium, Fuschia, Gaura, Oenothera, Zauschneria. -- Photorequirements were found in a few species.
ORCHIDACEAE. See Chapter 21
OXALIDACEAE. Oxalis
PALMACEAE. Phoenix, Sabal, Washingtonia
PAPAVERACEAE. Argemone, Chelidonium, Glaucium, Macleaya, Meconopsis, Papaver, Romneya, Sanguinaria, Stylophorum. - A variety of patterns were found including photorequirements and multicycle and multistep patterns.
PARNASSIACEAE. Parnassia
PASSIFLORACEAE. Passiflora
PHYTOLACCACEAE. Phytolacca
PINACEAE. Abies, Cedrus, Cunninghamia, Cupressus, Juniperus, Larix, Libocedrus, Picea, Pinus, Pseudotsuga, Sciadopitys, Sequoia, Sequoiadendron, Taxodium, Thuja, Tsuga
PLATANACEAE. Platanus
PLUMBAGINACEAE. Acantholimon, Armeria, Dictyolimon, Goniolimon, Ikonnikovia, Limonium, Popoviolimon. - These are generally D-70 germinators.
POACEAE (GRAMINAE). Andropogon, Bouteloua, Briza, Bromus, Calamagrostis, Eleusine, Festuca, Hystrich, Koeleria, Lagarus, Melica, Miscanthus, Panicum, Pennisetum, Scleria, Stipa. - See Chapter 22.
POLEMONIACEAE. Collomia, Gilia, Ipomopsis, Leptodactylon, Leptosiphon, Linanthrastum, Linanthus, Phlox, Polemonium. - Germinations were varied and complex. It is of much value to know the exact pattern.
POLYGALACEAE. Polygala
POLYGONACEAE. Eriogonum, Polygonum, Rheum, Rumex

PORTULACACEAE. Calandrinia, Calyptridium, Claytonia, Lewisia, Montia, Portulaca, Spraguea, Talinum. - A variety of patterns were found including photorequirements and low temperatures for germination.

PRIMULACEAE. Androsace, Cortusa, Cyclamen, Dionysia, Dodecatheon, Douglasia, Primula, Soldanella. - It is of much value to know the exact pattern as low temperature germination, complex photoeffects, multicycle germinations, and sensitivity to dry storage were all present.

PROTEACEAE. Dryandra

PUNICEAE. Punica

PYROLACEAE. Pyrola

RANUNCULACEAE. Aconitum, Actaea, Adonis, Anemone, Anemonastrum, Anemonella, Anemonopsis, Aquilegia, Callianthemum, Caltha, Cimicifuga, Clematis, Delphinium, Eranthis, Glaucidium, Helleborus, Hepatica, Hydrastis, Isopyrum, Paeonia, Paraquilegia, Ranunculus, Thalictrum, Trollius. - Low temperature, delayed, and multicycle germination patterns were all present. Also found were photorequirements, oscillating temperature requirements, and impervious seed coats. Is it any wonder that this family has long been regarded as difficult to germinate. They are really not difficult if the exact pattern is known.

RHAMNACEAE. Ceanothus, Rhamnus

ROSACEAE. Acaena, Alchemilla, Amelanchier, Armenaica, Aruncus, Cercocarpus, Chaenomeles, Cotoneaster, Crataegus, Dryas, Exochorda, Filipendula, Geum, Gillenia, Holodiscus, Ivesia, Malus, Petrophytum, Photinia, Potentilla, Prinsepia, Prunus, Pyracantha, Pyrus, Rhodotypos, Rosa, Rubus, Sanguisorba, Sibbaldia, Sorbus, Spiraea, Stephanandra, Waldsteinia. - Low temperature and multicycle germinations were found.

RUBIACEAE. Asperula, Cephalanthus, Cruckshanksia, Hedyotis, Houstonia, Mitchella, Mussaenda. - An absolute photorequirement is found in several genera.

RUTACEAE. Citrus, Crowea, Dictamnus, Evodia, Phellodendron, Poncirus, Ptelea, Skimmia. - Germinations are sometimes extended in multicycle patterns.

SALICACEAE. Populus, Salix

SAPINDACEAE. Cardiospermum, Koelreuteria

SARRACENIACEAE. Sarracenia

SAXIFRAGACEAE. Astelboides, Astilbe, Bensoniella, Bergenia, Deutzia, Elmera, Heuchera, Hydrangea, Itea, Kirengeshoma, Leptarrhena, Mitella, Parnassia, Peltoboykinia, Philadelphus, Ribes, Rodgersia, Saxifraga, Telesonix, Tellima, Tiarella. - Photorequirements were frequent.

SCHISANDRACEAE. Schisandra

SCROPHULARIACEAE. Agalinis, Alonsoa, Antirrhinum, Asarina, Aureolaria, Calceolaria, Castilleja, Chaenorrhinum, Chelone, Digitalis, Diplacus, Erinus, Gerardia, Hebe, Lagotis, Libanotis, Linaria, Melampyrum, Mimulus, Nemesia, Ourisia, Paulownia, Pedicularis, Penstemon, Striga, Synthyris, Verbascum, Veronica, Wulfenia, Zaluzianskya. - Photorequirements were frequent and sometimes complex.

SIMAROUBACEAE. Ailanthus

SOLANACEAE. Atropa, Capsicum, Datura, Lycopersicon, Petunia, Physalis, Salpiglossis, Schizanthus, Solanum. - Photorequirements and stimulation by GA-3 were frequent.

STYRACACEAE. Halesia, Styrax. - These are truly recalcitrant germinators. Although all species gave some germination, the critical factors are not yet understood.

SYMPLOCACEAE. Symplocos

TAXACEAE. Taxus. - Germinations were extended.

TECOPHILIACEAE. Conanthera

THEACEAE. Franklinia, Stewartia

THYMELAEACEAE. Daphne, Pimelea, Stellaria. - Germinations were extended.

TILIACEAE. Tilia. - Germinations were extended.

TROPAEOLACEAE. Tropaeolum

TYPHACEAE. Typha

ULMACEAE. Aphananthe, Celtis, Ulmus

VALERIANACEAE. Centranthus

VERBENACEAE. Callicarpa, Caryopteris, Pleuroginella, Verbena. - Photorequirements were found and they were sometimes complex.

VIOLACEAE. Viola. - Photorequirements and stimulation by GA-3 were frequent.

VITACEAE. Parthenocissus, Vitis

ZYGOPHYLLACEAE. Larrea

NAME IN DOUBT: GRUMOLO

CHAPTER 19. RATE THEORY IN MORE DETAIL

This Chapter is organized into five sections. The first involves a revision of the traditional concepts of dormancy and particularly "breaking dormancy." The other four involve different aspects of rates of seed germination.

Dormancy and "Breaking Dormancy" In Seeds and Plants

It has been known for many years that deciduous trees and shrubs as well as corms and bulbs require a period of time at temperatures around 32-45 during winter in order for stem and leaf growth to resume in spring. The same chilling period is needed for the flowering of deciduous trees and shrubs in spring. Times and temperatures for such chilling periods have been determined in detail for important commercial crops such as cherries and other fruit trees. As already noted in Chapter 5, these chilling requirements are analogous to the chilling requirements for the germination of certain seeds.

A cardinal principle of physical organic chemistry is that if condition A is required in order for a process to proceed under conditions B, critical chemistry must have been taking place in conditions A. Applying this principle to the chilling requirements described above, it means that during the chilling period critical chemical reactions were occurring. These chemical reactions are the destruction of growth blocking systems whether this be the destruction of a specific inhibitor or something more subtle such as the restructuring of a membrane or a protein. In either situation it is a chemical change that is taking place.

Not only must these chemical changes be taking place, but they are taking place at their **maximum metabolic rate**. Clearly they are taking place at temperatures around 40, and their rates must be in effect zero at temperatures around 70. This is again an example of the enormous rate changes found in certain biological processes, and this phenomenon in terms of rate theory is discussed in the fourth section of this Chapter.

The traditional view that trees and shrubs are dormant in late fall, winter, and early spring is at best misleading and completely wrong in terms of the destruction of growth inhibitors. In terms of the latter the trees and shrubs are at their **maximum metabolic activity** in late fall, winter, and spring. It is of course true that in respect to vegetative growth the trees and shrubs are dormant, and in this sense they are dormant. The problem is that the dormancy in respect to vegetative growth has misled biologists into thinking that all metabolic activity has ceased or at least fallen to a low level. It cannot be emphasized enough that it is not just a matter of the blocking systems being slowly destroyed in winter. They are being destroyed at what for them is their optimum and maximum rate.

First Order and Zero Order Rates of Germination

One of the principles that came out of physical organic chemistry in the 1940-1960 era was that complex chemical processes involving a number of individual chemical steps could still follow simple rate laws. Generally one step in the sequence will be significantly slower than the rest. This step is called the rate determining (r. d.) step. It not only limits the rate of the overall process, but the rate law of this rate determining step becomes the rate law for the whole process. This discovery does not seem to be appreciated by horticulturists and biologists. The old idea still prevails that biological processes are so complex that they are not amenable to precise mathematical treatment.

In the present work all data were treated as rate data. When sufficient data were available, rate plots were constructed. The number or percent germination was on the vertical coordinate and the time in days on the horizontal coordinate. Generally these plots approached one of the four types illustrated by Figures 4-1 to 4-4 in Chapter 4 for at least 60-80% of the germination in any single cycle. These plots can be expressed more concisely in tabular form. Tables 19-1 through 19-6 illustrate how exact these fits can be to simple zero order and first order kinetics. Tables 19-1, 19-2, and 19-3 show a fit with zero order kinetics, $dn/dt = k$. Tables 19-4, 19-5, and 19-6 show a fit with first order kinetics, $dn/dt = kn$. The closeness of the fit is shown by closeness of the values in columns 2 and 3.

The examples in these Tables were chosen to show a wide range of conditions. Table 19-1, 19-3, and 19-4 are for germinations taking place at 70. Table 19-2 is for a germination taking place at 40. Table 19-5 is for a germination that takes place only in light using alternating cycles of twelve hours dark and twelve hours light. Table 19-6 is for a germination that requires gibberelic acid-3 (GA-3).

The good fits in Tables 19-1 through 19-6 could be dismissed as further examples of a rate-determining step dictating a simple rate law in a complex process. These are well known in mechanistic chemistry, but there we are dealing with homogeneous systems which exchange energy continuously between the component molecules. In contrast seeds are isolated systems and even their component cells may be relatively isolated insofar as they exchange only small molecules such as water and oxygen.

A limiting situation can be envisioned in which the seeds behave like radioactive atomic nuclei which are similarly isolated. When the internal dynamics achieve a certain configuration and distribution of energies, reaction takes place. This would be germination with seeds and radioactive decomposition with atomic nuclei. The rates of achievement of such reactive states are governed by Boltzmann statistics. A certain percentage reacts in each time period generating first order kinetics.

To explain zero order kinetics for germination is more of a challenge. The following is proposed. In a complex series of steps there are two slow steps. For convenience let us regard them as consecutive and represent them as A to B to C. Both are first order processes and both have about the same rate constant. It can be shown mathematically that for the time period in which 20-90% of A is being destroyed, the amount of B remains roughly constant. During this period the formation of B from A is roughly compensated by the conversion of B to C. This approximate

constancy of the amount of B means that C will be produced at a constant (zero order) rate. Now if germination were to depend on the concentration of C or the concentration of C reaching a critical level, the overall rate of germination would approach zero order. This explanation is a bit too superficial. It will be for others to provide more insight into the kinetics of germination, and in fact the kinetics of all biological processes.

At the beginning of the work it was thought that there would be so much genetic variation in seeds even from a single capsule that the rates of germination would follow the laws of chemical kinetics in only an approximate fashion at best. In fact the data fit zero order rates quite exactly in most experiments suggesting that most species produce seeds that are genetically homogeneous, at least in respect to rates of germination. In fact pure species generally produce seedlings that are indistinguishable from each other, and the appearance of a mutation is relatively rare.

Table 19-1. Rate of Germination of *Mimulus luteus* at 70, zero order rate, ind. t 1.2 days, rate 17% per day

Time (days)	% Germ. (a)	
	Found	Calculated
1	0	0
2	14	14
3	31	34
4	49	48
5	64	65
6	79	82
7	97	99

Table 19-2. Rate of Germination of *Lilium pumilum* at 40, zero order rate, ind. t 33 days, rate 5.5% per day

Time (days)	% Germ. (a)	
	Found	Calculated
0-33	0	0
34	8	8
38	26	26
42	50	47
46	60	63
50	87	87
53	93	100

Table 19-3. Rate of Germination of *Pulsatilla vulgaris* at 70, first order rate, ind. t 13 days, half life 7 days.

Time (days)	% Germ.	
	Found	Calculated
0-13	0	0
14	2	0
16	32	33
19	57	57
24	68	70
26	75	76
38	92	91

Table 19-4. Rate of Germination of *Primula cortusoides* at 70, first order rate, ind. t 10 days, half life 5 days.

Time (days)	% Germ.	
	Found	Calculated
0-10	0	0
11	10	13
13	40	33
18	66	65
27	87	89
32	93	94
63	99	100

Table 19-5. Rate of Germination of *Aruncus sylvestris* in light at 70, zero order rate, ind. t 20 days, rate 7.5% per

Time (days)	% Germinated	
	Found	Calculated
0-20	0	0
22	17	15
24	30	30
26	46	45
28	63	60
30	76	75
32	89	90

Table 19-6. Rate of Germination of *Echinocereus pectinatus* with GA-3 at 70, first order rate, ind. t 6 days, half life 4.9 days

Time (days)	% Germinated	
	Found (a)	Calculated
0-5	0	0
9.9	52	50
14.8	76	75
19.7	87.5	87.5
24.6	93.8	93.8
29.5	97.0	96.9
34.4	98.3	98.4

(a) The precision expressed is real as a sample of 1200 seeds was used.

Rate data can be used to detect situations where two kinds of seeds are present. An example was in the germination at 40 of a large sample of seed from a colony of hybrids of *Primulas* of the Vernales section. The rate plot was a composite of two zero order rate plots. One had a rate of 6%/d and an ind. t of 16 d. The other was much slower with a rate of 1%/d but with the same ind. t of 16 d.

Induction Periods and Chemical Time Clocks

Most of the rate plots were characterized by an induction period. The induction times ranged generally from five days to fifty-five days. As discussed in Chapter 1 and 3, a significant induction period followed by an abrupt onset of germination is typical of a chemical time clock and the destruction of a chemical inhibitor. They cannot be due to time required for diffusion of water and/or oxygen since these would produce a gradual onset of germination. From the viewpoint of survival, time clocks are another mechanism for delaying germination until the seed is dispersed.

A word of explanation about chemical clock reactions is appropriate. These are not common, but are familiar to most chemistry students as they are usually demonstrated in the first course in college chemistry. The one most often chosen for demonstration involves the near instantaneous change of a colorless solution to a dark brown solution because of the formation of iodine. The induction time (delay period) required for this change can be varied from seconds to minutes by varying the concentrations of the reagents. Another and more common example of a chemical time clock is present in all the articles made of rubber that surround us everywhere as described in Chapter 4. All clock reactions involve the destruction of a critical block or inhibitor. When this block is finally reduced below a critical level, the chemical process starts up and quickly runs to completion. The chemical nature of these clock reactions in plants have not been studied.

Low Temperature Metabolism and Large and Negative Temperature Coefficients for Rates of Metabolic Processes

It has long been known that warm blooded animals control their temperature and operate at essentially a constant temperature. When body temperature moves above or below this temperature, rates of body reactions undergo large changes. It is also known that arctic marine animals require low temperatures to live and that these low temperatures must be within narrow limits. What has not been recognized is that the chemical processes in plants often have equally enormous changes in rate with temperature.

It has been found in the present work that where a cold cycle or a warm cycle is required to destroy germination inhibitors, such processes take place either around 40 or around 70, but never at both temperatures. This means that the change in rates between 40 and 70 are very large, essentially infinite. The survival value of this is apparent. Plants have evolved a winter metabolism and a summer metabolism, and generally these are kept separate and distinct. Nature plays no favorites here, and there are about as many species in which the germination inhibitors are destroyed at 70 as at 40. Thus about as many undergo an enormous increase in rate on raising temperature (positive temperature coefficient) as those that undergo an enormous increase in rate on lowering temperature (negative temperature coefficient).

The above situation in biological systems is markedly different from the situation in small molecule chemistry and in the usual chemistry laboratory. In small molecule chemistry, rates of chemical reactions typically change by the order of 2-3 for each ten degree change in temperature. Further, although reactions with negative temperature coefficients are known, they are rare and arise in a different way. The explanation of negative temperature coefficients in small molecule chemistry is shown in the following sequence of steps 1 to 3.

- (1) $A + B = \text{Intermediate}$
- (2) $\text{Intermediate} = \text{Inactive Species}$
- (3) $\text{Reactant} + \text{Intermediate} = \text{Product(s)}$

All three steps have positive temperature coefficients which is true of all single step chemical processes. It might seem impossible to combine three steps with positive temperature coefficients and get an overall process with a negative temperature coefficient, but watch closely. What if step 2 slows down with falling temperature much more than steps 1 and 3, and what if this factor is so large as to dwarf the others. Now the concentration of the Intermediate increases and builds up. This causes step 3 to go faster leading to an overall increase in rate for the overall combination of steps 1-3.

The fact that enormous temperature coefficients and negative temperature coefficients, which are so rare in small molecule reactions, become so common in biological processes means that biological systems have some special way to generate these situations. The explanation almost certainly involves changes in the configurations of enzymatic proteins. Many examples are known where proteins change conformation over a very narrow range of temperatures (refs. 41 and 42), and

such changes can be reversible. If on lowering the temperature a critical protein changes its conformation to form either an enzymatically active form or a form that allows some critical diffusion, this would explain the large temperature coefficients, and one that can be either positive or negative.

Although chemical processes can exhibit a negative temperature coefficient over a limited range of temperatures, this cannot persist indefinitely. Ultimately a temperature is reached where further decreases in temperature slows down the process. Thus low temperature metabolism will always exhibit an optimum temperature in a plot of rate versus temperature. This has been demonstrated in arctic animals. It has now been demonstrated in the inhibitor destruction reactions in seed germination. Although further work is needed to settle the matter conclusively, it is suspected that somewhere between 40 and 70 the rates of inhibitor destruction reactions undergo an enormous change in rate over a few degrees of temperature.

The rates of germination may go faster at 40 than 70 or the reverse. In this respect they are like inhibitor destruction reactions. However, the change in rate between 40 and 70 may or may not be large. Examples were found where the rates of germination were identical at 40 and 70 or differed by only small amounts. In other examples there was a large difference in rate of germination between 40 and 70.

Optimum Rates Under Conditions of Oscillating Temperatures

In Chapter 10 data was presented showing that some species give significant germination only under outdoor conditions. The significant feature of these outdoor conditions that set them apart from indoor treatments was the oscillating temperatures that occurred each day. Although I know of no prior reports where a chemical process was recognized to maximize its rate under conditions of oscillating temperatures, the phenomenon is theoretically possible. Suppose that in a complex series of reactions there is a critical step that takes place only at 70 and another critical step that takes place only at 40. In order for the overall process to take place the system must oscillate between 70 and 40. Part of the time is spent at 70 to let the first process function and part of the time must be spent at 40 to let the second process function. Only in this way can the overall process take place.

We can only surmise at this time that biological processes offer more opportunity for the above phenomenon, because of the prevalence of reactions that have enormous changes in rates over narrow ranges of temperature.

CHAPTER 20. SUMMARY OF DATA ARRANGED BY GENERA

The data are arranged alphabetically under each genus. The orchids (Orchidaceae, Chapter 21) and the grasses (Poaceae, Chapter 22) are in separate chapters. Data on some summer annuals are given at the end of Chapter 5. Sedges were not studied. Many more D-70 germinators (Asteraceae, Caryophyllaceae, summer annuals, and common vegetables) could have been studied, but their germination does not present a problem. More Fabaceae could have been studied, but they usually have impervious seed coats (see Chapter 9). A few tropical plants have been studied with interesting results.

A number of abbreviations are used. Seeds were subjected to three months at 70 (or 40) followed by a shift to 40 (or 70). Every three months the temperature was shifted. It is convenient to represent these alternating cycles as 70-40-70 etc. with each number standing for a period of three months at the temperature given. If germination took place in a particular three month period, the details of the germination in that period are given in parentheses following the number. Occasionally longer or shorter time periods were used, and these are specifically stated when used.

The following abbreviations are used: germ. for germinated, d for day, w for week, m for month, y for year, T for temperature (degrees Fahrenheit used throughout), ind. t for induction time, DS for dry storage, and WC for washing and cleaning as described in Chapter 8. Where light and dark experiments were conducted, 70L means 70 in light and 70D means 70 in dark. The term 70D GA-3 means that the seeds were treated with GA-3 as described in Chapter 3 and placed at 70 in dark. Terms like 50% germ. in 2-4 w means that 50% germ. with germination taking place between the end of the second week and the end of the fourth week and is equivalent to saying that germination occurred in the third and fourth weeks.

When seeds embedded in fruits were subjected to washing and cleaning (WC) for seven days, time was regarded as starting at the end of the seven day washing period. In rare instances the seeds began to germinate during the WC period. When this happened, it is clearly stated.

It is convenient to categorize the type of germination in an abbreviated way. A D-70 germinator is one that requires dry storage followed by germination at 70 as described in Chapter 5. A 40-70 germinator is one that requires three months at 40 followed by germination at 70 as described in Chapter 6. This system can be extended indefinitely so that for example a 40-70-40-70 germinator is one that required three alternating three month cycles starting at 40 before germination finally occurred at 70.

Percent germinations were calculated on the basis that the total number of seeds were the number of normal size seed coats. Efforts were made to discard undersize seed coats, seed coats that obviously lacked endosperm, seed coats that readily crushed and were empty, and seeds lacking an embryo which is evident in *Lilium* and *Fritillaria*. Where the supplies of seeds were small, expressions like 5/10 were used which means 5 out of 10 germ. Rates are described in qualitative terms giving the time period in which the germination occurred. Where the sample was of sufficient size and the data followed a zero order or first order rate law with good

precision, the rates are described in quantitative terms using the terminology of chemical kinetics as explained in Chapters 4 and 19.

Initially it was intended to present only work conducted by myself. However, two authors have done work of sufficient quality that it has been included in the following tables and are appropriately referenced. One is Nikolaeva (ref. 7). The other is L. V. Barton who worked for many years at the Boyce Thompson Institute for Plant Research, and who has summarized much of this work in references 28 and 31. I am indebted to Prof. John White at Penn State Univ. for allowing me to use his personal copies of these two references as they are not generally available. I am also particularly indebted to Dr. Norma Pfeiffer of the Boyce Thompson Institute who many years ago gave talks and wrote papers on germination of lily seeds in connection with the North American Lily Society. These had a strong influence in choosing the times and temperatures of the cold cycles.

Also included are a few directions for germination taken from the catalog of the Thompson and Morgan Company (T & M) and the catalog of J. L. Hudson of Redwood City CA (J H). Also included are some data from James Forrest in Tauranga, New Zealand, that were communicated by letter.

Experiments are in progress so that some of the following data are incomplete. It is intended to issue a Supplement in 2-3 years.

Abeliophyllum (Oleaceae). *A. distichum* seed germ. 85-95% by collecting the seed in November, separating the seed from the round wings and capsule, and sowing directly at 70. The ind. t is 25 d, and the rate is 7%/d. If the seed is sown at 40, germination does not take place until the shift to 70 after which it germ. at the same rate as if it had been sown directly at 70, but the percent germ. is lowered to 70%. Seed collected in November has already undergone some DS, nevertheless DS at 40 or 70 for 6 m lowered the percent germination to 60%. There is also a small reduction in percent germination if the seeds are sown while still in the seed capsules. In all of these treatments the ind. t and rate are still 25 d and 7%/d. After the radicle emerges, it takes about a month to complete its development. There is a further two month delay between when the radicle development is complete and when stem and leaves appear (hypogean). The development of stem and leaves is not hastened by a shift to 40, and in fact shifting to 40 after radicle development was complete caused all the seedlings to rot.

Abies (Pinaceae). The cause of the low germinations is not known.

A. amabilis germ. 70(2/11 in 2-5 w)-40-70-40 and 40-70(4/12 in 1-3 w)-40-70.

A. arizonica (ref. 44, Ch. 7) and *A. concolor* (ref. 43, Ch. 10) were reported to be 40-70 germinators.

A. koreana germ. 70D(1/7 in 8th w) and 40-70D(2/14 in 2nd and 4th w).

A. nordmanniana germ. 70D(1/8 in 5th w) and 40-70D(1/11 on 6th d).

A. veitchii germ. 70D(15% in 2nd w) and 40-70D(3%). Light had no effect, and a five minute wash with detergent had no effect. Seeds rotted if treated with GA-3.

Abronia (Nyctaginaceae).

A. fragrans germ. 70(2% in 8-10 d). Light or a prior 3 m at 40 had no effect. The percent germination could not be accurately determined because of the abundance of chaff and empty seed coats.

A. villosa germ. 40% in 4-6 d in 70D or 70L and 40% in 3rd w at 40.

Abutilon (Malvaceae). *A. theophrasti* germ. 100% in 2 d at 70 if an opening is ground through the seed coat. If the opening is not made, germination ranges from 5-25% and takes place erratically over 1-10 w whether sown at 70 (with or without a prior 3 m at 40) or in outdoor treatment. Prof. Roger Koide of Penn State Univ. found that germination is immediate if the seed is immersed in water at 140 for 10 minutes.

Acacia (Fabaceae). *A. iteophylla* has an impervious seed coat. It germ. 70(6/11 in 2-13 d, hole in seed coat) and 70(1/13 on 4th d, control).

Acaena (Rosaceae). There is much debris in the bur like seed capsules so that estimates of the number of seeds were not always possible.

A. anserinifolia germ. only one seed in eight samples received over the years. Germination occurred in the 3rd m at 70. The seedling developed normally.

A. inermis germ. 70D-40-70D(30% in 4-6 w). GA-3 had no effect.

A. splendens germ. a single seed on the 4th d at 70.

Acantholimon (Plumbaginaceae). Good seed always germ. in 1-4 w at 70, and any seed not germ. by this time can be discarded. Of fifteen samples from Russian Botanical Gardens, twelve germ. Of eight samples collected in the wild by the Archibalds, four germ. Of four samples from the ARGS seed exchange, three germ. Of ten samples from a commercial seed house where the seed is believed to have been stored for several years, only one germ. This suggests some loss of viability on extended dry storage, although D-70 is the likely pattern for the genus. Viable seed is rarely set on plants grown in gardens in the U. S. and England, but it is not known whether this is a self-sterility problem, a pollination problem, or a weather problem. The following species germ. in 1-4 w at 70: *A. araxanum*, *armenum*, *bracteatum*, *caryophyllaceum*, *diapensoides*, *glumaceum*, *hedinum*, *hilariae*, *litvinovii*, *pamiricum*, *parviflorum*, *pterostegium*, *reflexifolium*, *spirizianum*, *vedicum*, and *venustum*. Seed of *A. puberulum*, *pulchellum*, *raddeanum*, *ulcinum*, and *velutinum* failed to germinate. It is of interest that Flora USSR lists about 150 species of this attractive and little grown genus. The plants look like a tufted *Dianthus* but are as spiny as a cactus and equally dangerous to handle.

Acanthophyllum (Caryophyllaceae). One sample of each of six species were received from Russian Botanical Gardens. *A. shugnanicum* was received in February and sown outdoors with germination taking place at the end of March. *A. gypsophiloides* and *pungens* were received in July. They did not germinate immediately at 70, but when left outdoors until January 1 and then brought into 70, germination took place in 3-5 w. *A. glandulosum*, *macrocephalum*, and *sordidum* were treated the same as *A. shugnanicum* but failed to germinate. These studies on *Acanthophyllum* were conducted in soil and before procedures were standardized. The species are probably 40-70 germinators.

Acer (Aceraceae). The three dominant themes in this genus are the diversity of germination behaviors, the presence of impervious seed coats in about half of the species, and the large percentages (90% or more) of empty seed coats in some of the samples even though the seeds were collected from thriving natural colonies. The genus divides into three groups. (a) Seeds ripen in late spring, germinate immediately at 70 (and 40), and do not survive dry storage. (b) Seeds ripen in fall, tolerate dry storage, and usually germinate at 40. (c) Seeds ripen in fall, usually tolerate dry

storage, have an impervious seed coat, and may or may not have inhibitors. The discovery of an impervious seed coat in *A. negundo* showed that impervious seed coats can be present even in seeds that have soft and pliable seed coats.

The seed coats are sometimes easily removed. With others the seed coats are removed only with considerable difficulty. Generally it was helpful to soak the seeds for several days. Seed coats were removed with thumbnails, vices, pliers, and scissors in various combinations. Seeds that have had the seed coats removed are termed opened seeds.

Acer germination has been extensively studied, and the results reviewed (ref. 6, p. 41). The literature reports that *A. saccharinum* germ. in a few days at 70 and rapidly lost viability on DS. Eight other species (*A. ginnala*, *monspessulanum*, *palmatum*, *pennsylvanicum*, *platanoides*, *pseudoplatanus*, *semenovii*, and *tataricum*) germ. at low T over extended periods. My results show that the extended germinations that have been reported would have been eliminated if the seed coats had been opened.

A. buergerianum germ. 40(82% in 6-8 w), 70-40(89% in 10-16 w), and outdoor treatment (59% in March and April). The preliminary 3 m at 70 slowed down the germination at 40, but did not affect the overall percent germination. Removing the seed coats or producing a hole in the seed coats only increased the percentage that rotted (presumably due to mechanical injury). Although the seeds were obtained from an isolated specimen, all contained endosperm and 80-90% were viable.

A. crataegifolium germ. 40-70(10-20% in 3rd w) providing the seed coats were removed. The seed coats can be removed at the start or after the shift to 70. The latter is preferred since the seed coats are difficult to remove, and they are easier to remove after the 3 m moist at 40. The preliminary 3 m at 40 was necessary. The interpretation is that in addition to the impervious seed coat there is a germination inhibitor system that is destroyed at 40, and that the unopened seeds have enough moisture in them for the inhibitor destruction reactions to take place. The final conclusive demonstration of the impervious seed coats was to take the 40-70 control and after 5 w at 70, remove the seed coats. This gave 10% germination. Seeds that had been DS 6 m at 70 were all dead and soon rotted on opening and contacting moisture. The seeds were obtained from an isolated tree, and 70-80% of the seed coats were empty shells. These were not counted in calculating the percent germination.

A. ginnala v. *aidzense* germ. best with fresh seed at 40(95% in 5-7 w). It also germ. 94% in March in outdoor treatment which is effectively equivalent to the germination at 40. There was no germination at 70. In computing the percent germination, the 30-50% of the seed coats that were hollow shells were not included. Seeds DS 6 m at 70 germ. 40(47% in 3-12 w) and 70(3% in 2nd w) showing that there was some deterioration on DS. Removal of the seed coats has no effect.

A. griseum has a hard impervious seed coat. The seeds germ. 70(25% in 2nd w) and 40(30% in 4-9 w)-70(15% in 2nd w) if the seed coats are removed at the start and 40-70(50% in 2nd w)-40-70(30% in 2nd w) if the seed coats were removed after the first 3 m at 40. It is likely that the higher percent germination in this latter treatment was because the seed coats were easier to remove without mechanical injury after the 3 m moist at 40. The 60% of empty shells were not counted.

A. heldreichii seeds had been DS for several years and all rotted showing intolerance to DS.

A. japonicum germ. 40-70(100% in 2nd w) if the seed coats were cracked on the shift to 70. A preliminary 3 m at 70 before the 3 m at 40 had no effect. This is another Acer that has both an impervious seed coat and an inhibitor system. The latter is destroyed at 40 even in the unopened seeds. There was no advantage in removing or cracking the seed coats before the shift to 70. About 80% of the seed coats are empty shells, and these were not counted.

A. negundo has an impervious seed coat despite the seed coat being soft and pliable. Germination is 50-100% in 1-4 w if a hole is produced in the seed coat. This hole can be produced either by cutting off the tip with a scissors or by peeling off the seed coat. The presence of an impervious seed coat was confirmed by opening some of the controls after 3 and 6 w at 70 whereupon 80% germ. in 1-4 w. The results were the same for slightly green seed collected in September and for seed collected in January. Many empty seed coats are produced. A sample collected in fall 1990 had 95% empty, and a sample collected in fall 1991 had 50% empty.

A. nikoense was received as a sample that had been DS for 5 y and most of the seeds were dead. This species has an impervious seed coat (at least after the 5 y DS), and the seed coats must be removed to get any germination. The seed coats were best removed after the seeds had been soaked in water for 3 w with a change of water each day. On opening 16% of the seed coats were found to be empty, and these have not been counted. In the first month 86% of the seeds rotted. These were dead and have not been counted. Seeds opened initially at 70 germ. 70-40-70(2%)-40-70(4%). Seeds opened after the shift to 40 germ. 70-40(2.5%). Despite the low percent germinations, the seedlings were healthy and developed true leaves. Treatment with GA-3 did not initiate germination. Data is needed on fresh seeds.

A. pennsylvanicum has an impervious seed coat. If the seed coats are removed, seeds germ. 40(40% in 4-12 w), 70(2%), and outdoor treatment (40% in March and early April). Germination in unopened seeds was 40(2%)-70(4%), 70(none), and 2% in outdoor treatment. A preliminary 3 m at 70 had no effect. Cracking the seed coats was not as effective as removing the seed coats. Seeds can be stored moist or dry for at least a year. Samples that had been subjected to 1-2 y of moist cycles gave 40-80% germination at 40 upon removal of the seed coats.

A. platanoides germ. at 40, and fresh seeds should be sown immediately at either 40 or outdoors as exposure to moist conditions at 70 is deleterious. Fresh seed germ. 40(41% in 12th w)-70(23% in 2-3 d), 70-40(13% in 10-12 w)-70(4% on 2nd d), and 93% in outdoor treatment with germination taking place in late winter and early spring. Germination would have been greater at 40 if the time at 40 had been extended beyond 3 m. Opening the seed coats has no effect. Seeds collected in December gave the same results as seeds collected in October showing that some DS at 40 is tolerated. However, there is significant deterioration of the seeds and hardening of the seed coats when DS for 6 m at 70. The DS seeds germ. 38% in 4-7 w at 40 but only if the seed coats were removed. The seedlings were weak and did not survive. DS should be avoided.

A. pseudosieboldiana seeds germ. 40(3% in 12th w)-70(7% in 1-8 w) and 70-40(none). Cracking the small hard nutlet did not stimulate germination. Opening the nutlets showed that over 90% were either entirely empty or had a tiny undersized endosperm. It is possible that germination was nearly 100% in the viable seeds.

A. rubrum ripens its seeds in May. Fresh seeds germ. 70(100% in 4-13 d, first order rate, ind. t of 3 d, and half time one d) and 40(79%, first order rate, ind. t of 15 d, half time of 4 d). Seeds DS for only 2 m at 70 were all dead.

A. semenovii germ. 40(3/4 in 8-10 w). The sample sown at 70 all rotted. The behavior is much like that of *A. platanoides* to which it is closely related, and like *A. platanoides*, sowing at 70 is to be avoided.

A. saccharum ripens its seeds the 3rd w in May, and germ. 70(75% in 3-7 d) and 40(75% in 3rd w). Removing the seed coats had no effect, and light had no effect. Seeds DS 6 m at 70 were dead.

A. spicatum germ. 70D-40-70D(26% in 3-8 w). After the seed had been in alternating cycles for 12 m, the seed coats were removed from half of the seeds. Such seed germ. 8/9 in the 2nd w and none in the control. It is likely that this species has an impervious seed coat and would have germ. better if the seed coats had been removed. Neither light nor a preliminary 3 m at 40 had any effect. Outdoor treatment is of no advantage and leads to long extended germinations. The seed had been collected at the end of January indicating that DS is tolerated.

A. tataricum has an impervious seed coat and an inhibitor system that must be destroyed at 40. Seeds germ. 40-70(82% in 1-3 w) if the seed coats were removed on the shift to 70. Germination was lower if the seed coats were removed at the start of the cycle at 40, were cracked instead of total removal, or were started at 70. Outdoor treatment germ. 68% in March with either opened or unopened seeds. This germination in unopened seeds is attributed to the opening of microfissures in the seed coats under the oscillating temperatures of outdoor conditions. Seeds DS for 6 m at 70 germ. in the same pattern as fresh seed, but germination was reduced to 60% indicating deterioration.

Achillea (Asteraceae). *A. millefolium* is D-70 like most composites.

Acidanthera (Iridaceae). *A. bicolor* germ. 70 (60% in 2-11 w), 40-70(10%)-40-70(30%), and 45% in May in outdoor treatment starting March 1. Starting the seeds at 40 caused the germination to extend over four cycles. This could be one of the rare examples of an inhibitor being formed in the initial cycle at 40, but more work is needed to establish this interpretation. Light and GA-3 had no effect on the rate of germination. Germination was hypogeal.

Aciphylla (Apiaceae). The three species studied require GA-3 for germination. With GA-3 at 70 germination was 3/3 in 3rd w for *A. aurea*, 2/3 in 3rd w for *A. dobsonii*, and 1/3 in 4th w for *A. hectori*. None germ. in the controls. A preliminary 3 m at 40 had little effect. Despite the small samples, the results are dramatic, and the seedlings were healthy. GA-3 treatment is strongly recommended for this difficult group. Many samples had failed to germinate in earlier work without the GA-3.

Aconitum (Ranunculaceae). Seed of *A. ajanense*, *apetalum*, *ferrox*, *firmum*, *macrostynchium*, *napellus*, *nasutum*, *orientale*, *pubiceps*, *raddeanum*, *variagatum*, *volubile*, *vulparia*, and two unidentified species were received in midwinter, and all soon rotted on contacting moisture showing that DS is not tolerated

in accord with the results on *A. wilsoni*. Helen Sykes of Sudbury MA communicated that *A. ferox* and *A. lycoctorum* received in January, given 4 w at 40, and placed at 55 germ. 65% 3 m later. Three other species were dead showing intolerance to DS.

A. heterophyllum germ. best in 70L(8/9 in 3-5 w) and none in 70D. The photorequirement in this *Aconitum* contrasts with *A. wilsoni* where light has no effect. Sowing at 40 gave 40-70(1/18). It is not known whether this is a rare species of *Aconitum* that can survive DS or whether the seed was received shortly after collection. The seed was received July 1.

A. wilsoni seed ripens late in November, and the seed is killed by freezing in some years. It is prudent to collect the stems and place them inside in water if the the temperature threatens to go below 25. The seed will ripen satisfactorily if the seed capsules have reached full size. *A. wilsoni* is strictly a 40 germinator. The overall germination at 40 over 10 w was 82%. The rate plot was composed of two separate zero order plots indicating that two kinds of seed were present. The ind. t was 30 d. Two-thirds of the seed had a germ. rate of 7%/d and one-third had a rate of 1.8%/d. Outdoor treatment gave 52% germination, all occurring in February and March again showing the exclusive germination at cold temperatures. Germination was low in 70L(7%)-40(15% in 5-7 w)-70(1%) and 70D-40(12% in 5-10 w) and germination of all DS seed was less than 2% showing that DS is not tolerated. This raises a question as to how to store the seed, and this is one of the few species for which there is no simple solution to the problem of storage.

Actaea (Ranunculaceae). The seeds are enclosed in a berry and were given an initial WC for 7 d. Germination took place at 40, but only after one or more prior cycles. The radicle develops at 40 to a length of 2-3 inches after which growth stops. It was found that an immediate shift to 70 when the 3 m cycle at 40 was over led to total rotting of the radicles and death of the seedlings. Some success was achieved in getting the cotyledon to develop in *A. pachypoda* and *A. rubra* by keeping the seedlings for 4 m at 40 after radicle development was complete. A shift to 70 now gave cotyledon development with about half of the seedlings. It is suspected that in order to get efficient development of the cotyledons it would have been better to raise the T from 40 to 70 gradually.

A. erythrocarpa seed was received in April, sown outdoors, and brought into 70 on January 1. The seed had presumably germ. by this time since true leaves were produced in the 4th w after the shift to 70.

A. pachypoda germ. 40-70-40(85-90% in 3-6 w, zero order with ind. t 20 d and 5%/d) using fresh seeds and 70-40(85-90% with same ind. t and rate) using seeds that had been DS for 6 m at 70 or 40. It is curious that 3 m moist at 40 and 6 m DS at 70 had the same effect, and either one or the other were necessary for germination in the 70-40 pattern. Other treatments gave more extended germination as shown by 70-40(52%)-70-40(46%) for fresh seed. After the radicle has completed its development, the seedlings must be kept an additional 4 m at 40 before being shifted to 70. Even then only 50% of the seedlings develop their cotyledon normally, and it is suspected that a more gradual increase in T would have given better development of the cotyledons. Treatment with GA-3 had little effect. Seeds placed outdoors in August germ. 25% in November and in March and April.

A. rubra germ. 40-70-40-70-40-70-40(24% in 5-7 w) for fresh seed, 40-70-40(18% in 4-6 w) for seed DS 6 m at 40, and 40-70-40(4%) for seed DS 6 m at 70. When started at 70, germination did not start until the 3rd to 6th cycle and was overall only 4% for both fresh and DS seed. All seed that did not germinate ultimately rotted. Difficulties were encountered in getting the cotyledons to develop. The discussion under *A. pachypoda* applies here.

A. spicata germ. best in 70-40(88% in 4-7 w) using seed that had been WC and DS 6 m at 70 in the WC state. Germination was more extended with fresh WC seed as shown by 70-40(53%)-70-40(31%) and 40-70-40(55%)-70-40. The seedlings formed a 2-3 inch radicle at 40. If the seedlings were planted outdoors in early spring, they ultimately sent up cotyledons and a true leaf, but if shifted directly to 70, all rotted.

Actinidia (Dilleniaceae). *A. chinensis* is the commercial fruit called kiwi. Seed WC 7 d germ. 70D(41%), 70L(96%), and 70D GA-3(96%) all in the 3rd w. A 3 m period at 40 was fatal, and only 1% of the seeds survived.

Adenium (Apocyanaceae). *A. obesum* germ. 40% in 12-15 d in either 70D or 70L. All seeds rotted when treated with GA-3 or when started at 40.

Adenophora (Campanulaceae). Four species germ. in the 2nd w in soil in the percentages indicated: *A. farreri* (44%), *A. lilifolia* (44%), *A. potanini* (92%), and *A. tashiroi* (8%). Light and GA-3 should have been studied in view of the following data.

A. koreana germ. 70L (87% in 1-3 w), 70D GA-3(100% in 12-15 d), 70D(5%), 40(2%)-70L(70% in 4-13 d), and 40(2%)-70D(56% in 8-13 d).

A. kurilensis germ. 70L(17% in 2nd w), 70D GA-3(46% in 3rd w), and 70D(none).

Adlumia (Fumariaceae). *A. fungosa* germ. in the 7th d at 70.

Adonis (Ranunculaceae). *Adonis* divides into two groups. *A. aestivalis* is an annual with red flowers and a D-70 germination pattern. The rest are a collection of names that can be treated as a single circumpolar species which has evolved into variants in each geographical region. All have perennial character, much divided foliage, and large beautiful yellow flowers. More seed of these have been planted without success than any other genus. Over thirty samples of *A. amurensis*, *brevistylis*, *chrysocyathus*, *pyrenaica*, *turkestanica*, and *vernalis* combined have been total failures. The main problem is that a high proportion of normal size seed coats are empty shells. Three samples of *A. turkestanica* and one sample of *A. wolgensis* that had been collected in the wild by Josef Halda were found to be 100% empty shells. Samples of *A. chrysocyathus* collected in the wild by Chris Chadwell were largely empty shells. This is not the fault of the collectors as such empty shells are normal in size and resemble normal seeds externally. Seeds of *A. vernalis* from my own plantings are largely empty shells despite the most vigorous and persistent hand pollination of the flowers. John Gyer has examined this problem by microscopic examination of pollen and pistils with staining techniques and feels that it is not a self sterility problem but rather genetic defects that lead to defective pollen and pistils. Of six clones of *A. amurensis* in gardens in Eastern U.S., only the one in the National Arboretum in Washington DC sets viable seeds.

A. chrysocyathus seed that had been collected in the wild in Kashmir was tried repeatedly. One sample after two years of alternating cycles was placed outdoors whereupon 1/15 germ. in April.

A. vernalis gives a rare self sown seedling here. The two examples of germination to date were 40(3% in 10-16 w) with fresh seed and 70-40(1/41 in 8th w) in a sample DS 6 m at 70. Three samples were crushed and found to be 80%, 96%, and 98% empty seed coats.

Aesculus (Hippocastanaeae). *A. hippocasteanum* and *A. pavia* behaved identically and germ. 40-70 (100% in 1-7 d). The first 3 m at 40 can be conducted either moist or dry. Apparently there is enough moisture in these large seeds so that DS at 40 has the same effect as placing in moisture at 40. If sown at 70, 20-30% germ. in 1-2 m, but the seedlings do not develop properly. Seed DS 6 m at 70 is dead.

Aethionema (Brassicaceae): *A. grandiflorum* germ. 40(92%, ind. t 7 d, rate 5%/d) and 70(40-45%, ind. t 2 d, rate 10%/d) using seed DS 6 m at 70 or 40. Although germination is faster at 70, the lowered percentage makes it preferable to use the D-40 pattern. Fresh seed gave a long drawn out germination as shown by 70(45%)-40(1%)-70(54%) and 40(23%)-70(15%). Several other species of *Aethionema* are commonly offered. They closely resemble *A. grandiflorum* and presumably have similar patterns.

Agalinis (Scrophulariaceae). *A. setacea* germ. best in outdoor treatment using either fresh or DS seed. Fresh seed sown early in November germ. about 100% in mid-March to mid-April. DS seed started in July germ. about 100% in April. It is difficult to determine the exact percent germination because the seed is small and intermixed with debris. Fresh seed germ. none in 70-40, 40-70D, or 40-70L. Seed DS 6 m at 70 germ. 40(24%)-70(6%) and none at 70.

Agapanthus (Liliaceae). *A. africanus* germ. 70(100% in 2nd w) and 40(60% in 5-12 w)-70(13%).

Agastache (Lamiaceae). Results were complex with the stimulation of germination by light and GA-3 being eliminated by 3 m at 40 in *A. foeniculum* but not in *A. nepetoides* and *A. scrophulariaefolia*. The seedlings from GA-3 treatment had normal cotyledons. Commercial samples of *A. anisata* and *A. fragrans* gave only 3-6% germination in 70D or 70L. Possibly these seeds had been stored a y or more since in the three studied below there was no significant deterioration in 6 m DS.

A. foeniculum germ. 70L(11% in 5-11 d), 70D GA-3(59% in 3-7 d), 70D(none), 40-70D(52% in 4th d), and 40-70L(42% in 4th d) using fresh seed. When part of the sample in 70D was shifted to 70L after 3 w, 58% germ. in 1-3 w. Seeds placed outdoors in October germ. 4% in November and 41% in April. Seeds DS 6 m at 70 germ. 70L(20%), 70 GA-3(50%), and 70D(12%), all in 2nd w, and 40(70% in 3rd w).

A. nepetoides germ. 70L(57% in 5-15 d), 70D GA-3(95% in 5-13 d), 70D(none), 40-70L(92% in 4-8 d), and 40-70D(none) using fresh seed. Outdoor treatment germ. 4% in April. Seeds DS 6 m at 70 germ. 70L(22% in 2nd w), 70 GA-3(98% in 2nd w), 70D(none), and 40(none).

A. scrophulariaefolia germ. 70L(41% in 3-15 d), 70D GA-3(67% in 5-17 d), 70D(none), 40(2%)-70L(54% on 4th d), and 40(2%)-70D(none) using fresh seed. When part of the sample in 70D was shifted to 70L after 3 w, 49% germ. in the 2nd w. A second sample gave similar results. Seeds placed outdoors in October germ. 6% in November and 45% in April. Seeds DS 6 m at 70 germ. 70L(85%), 70 GA-3(85%), and 70D(13%), all in 4-6 d, and 40(50% in 3rd w).

A. urticifolium germ. 70D or 70L(13% in 5-8 d). Seed sown at 40 rotted.

Agave (Liliaceae). *A. (Manfreda) virginica* germ. 40-70D(4/8 in 5th w), 70D(1/4 in 6th w), and 70D GA-3(2/6 in 3rd w). The seedlings from the GA-3 treatment soon rotted.

Aichryson (Crassulaceae). *A. divaricatum* germ. 70D GA-3(64% in 1-4 w), 70L(3%), and 70D(9% in 2nd w).

Allanthurus (Simaroubaceae). *A. altissima* seeds have an absolute photorequirement for germination of fresh seed, but this is gradually eliminated either by DS at 70 or by 3 m moist at 40. The effects of the two are additive. It is possible that longer DS and/or longer exposure to 40 would have completely eliminated the requirement of light, but the experiments were not carried that far. Fresh seed germ. 70L(50%, ind. t 8 d, rate 6%/d) and 70D(none). The 50% ungerminated are probably still alive, although this was not tested. Seed DS 6 m at 70 germ. 70D(20%). That the other 80% were still alive was shown by carrying the seed through three more 3 m cycles after which shifting to 70 and light gave complete (80%) germination of the remaining seed. The effect of chilling at 40 and the cumulative effect of chilling plus DS were shown by 40-70(12%) for fresh seed compared to 40-70(50%) for seed DS 6 m at 70. DS at 70 was more effective than DS at 40 in eliminating the requirement of light.

Ajania (Asteraceae). *A. tibetica* germ. in 2nd m at 70.

Ajuga (Lamiaceae). *A. chamaepitys* gave a complex behavior. When treated with GA-3, it germ. 83% in the 2nd w, and the seedlings were normal and healthy. Without GA-3 germination was basically a 70-40-70 pattern. The data were 70(3%)-40-70(50% in 2nd w). Light did not have much effect.

Albizzia (Fabaceae). *A. julibrissin* has an impervious seed coat and exhibits dramatic effects on puncturing the seed as described in Chapter 9. See also Chapter 10 for its behavior under outdoor treatment. Seeds collected in Nepal behaved identically to seeds collected in New Jersey.

Alchemilla (Rosaceae).

A. mollis germ. 70L(37%, ind. t 7 d, half life 5 d) and 70D(none). When the sample in 70D was shifted to 70L after 6 w, germination began and proceeded with exactly the same rate characteristics as if the 6 w in 70D had not occurred. Subjecting the seeds to 3 m at 40 partially removed the photorequirement as shown by 40-70L(31% in 3-11 d) and 40-70D(9% in 3-7 d). The removal of the photorequirement was also shown in outdoor treatment where 16% germ. in April and May. The seeds used in these experiments had been DS for 2 y and 40% of the seeds quickly rotted.

A. saxatilis germ. 40-70L(38% in 4-15 d, largely in 4-6 d) and none in 40-70D, 70L, or 70D. There was some evidence that cold periods were starting to remove the light requirement as seeds set outdoors in November germ. 22% the following April.

Aletris (Liliaceae). *A. farinosa* has a photorequirement as shown by 70L(90%, ind. t 31 d, 8%/d), 40-70L(87%, ind. t 12 d. 8%/d), and none in 70D or 40-70D. A prior ten weeks in 70D reduced germination in 70L to 40% showing that 70D is deleterious.

Alisma (Alismaceae). *A. plantago-aquatica*, *Typha latifolia*, and *Zizana aquatica* were reported to germinate only under water and only if the daily T oscillated in ranges varying from 50-68 to 68-86 (ref. 31, Ch. 7). This is discussed in Chapter 12. Since *Typha latifolia* germ. in either 70L or 40-70L, it is possible that all the results in

ref. 44 were related to failure to control light as a variable, and that *Alisma* would have germ. with light as the only requirement.

Allium (Liliaceae). This genus showed much diversity. Germination patterns ranged from simple D-70 in *A. azureum*, *carolinianum*, and *tanguticum* to 70-40 in *A. giganteum* to extended patterns in *A. karataviense* and *pulchellum*. The type of germination ranged from epigeal in most species to an epigeal-hypogeal combination in *A. cernuum* to hypogeal in *A. tricoccum*. Photoeffects were not studied, and GA-3 did not initiate germination in the several species in which it was tried.

A. albopilosum germ. at 40 as shown by 40(87% in 5-13 w) and 70(2%)-40(87% in 3-7 w). The seed slowly dies in DS as shown by 70-40(50% in 4-8 w) and 40(62%)-70-40(12%) for seeds DS 6 m at 70. The death rate was slower in DS at 40. Fresh seeds placed outdoors in July germ. 70% in November, probably just due to the lower temperatures. Seeds treated with GA-3 rotted in 3 m. A sample labelled *A. christophii* is presumed to be this species. It gave identical results.

A. azureum germ. in 2nd w at 70.

A. carolinianum germ. 70(100%, ind. t 4 d, 13%/d). A prior 3 m at 40 had no effect.

A. cernuum germ. best in 70(50-65%, ind. t 3 d, 0.7%/d) for both fresh seed and seed DS 6 m at 70 or 40. Further cycles added only 10% more germination. There is no reason to sow at 40 as it is less convenient, but fresh seed and DS seed gave contrasting behavior which is interesting. Fresh seed germ. 40(0-10%)-70(50-55%)-40(20-25%)-70(20-25%) whereas seed DS 6 m at 70 or 40 germ. 40(37%)-70(50%). The data for DS seed is an average of several experiments.

A. christophii, see *A. albopilosum*.

A. falcifolium germ. 70-40-70(1/3 in 2nd w) and none in 40-70.

A. giganteum germ. primarily in a 70-40 pattern. However, germination was extended over many cycles with germination being less extended with fresh seed and more extended with DS seed. Fresh seed germ. 70-40(52%)-70(17%)-40-70 and 40(4%)-70-40(70%). Seed DS 6 m at 70 germ. 70-40(1/10)-70-40-70(9/10) and 40(4/8)-70(1/8)-40-70. Seed DS 6 m at 40 germ. had an intermediate behavior. The more extended germination in DS seed could be due to the seed coat becoming impervious on drying.

A. goodingii germ. 70D(60% in 2nd w) and 40(30% in 4-11 w).

A. karataviense gave some of the most extended germination observed. Germination occurred at both 70 and 40 and with both fresh and DS seed in comparable percentages. No pattern could be discerned other than that significant germination never began until the 4th cycle and sometimes the major burst of germination occurred as late as the 7th cycle. The data is given in full. Fresh seed germ. 70-40-70(6%)-40(27%)-70(10%)-40(15%)-70(15%) and 40-70-40(2%)-70(14%)-40(2%)-70(28%)-40(2%)-70(6%)-40(18%)-70(6%)-40(18%). Seed DS 6 m at 70 germ. 70-40-70(7%)-40(13%)-70(9%)-40(3%)-70(55%) and 40-70-40-70-40-70(1%)-40(69%)-70(12%). Seed DS 6 m at 40 germ. 70(5%)-40(4%)-70(4%)-40(11%)-70(16%)-40-70(23%) and 40-70-40-70-40(1%)-70(1%)-40(83%)-70(6%). Some of these must look like typographical errors but in fact they are all correct. Seeds treated with GA-3 largely rotted.

A. moly germ. 40(90% in 9-11 w) for seed DS 6 m at 40. Germination extended over 3-5 cycles in all other treatments as shown by the following data. Fresh seed germ. 70-40-70(3/9)-40-70 and 40(1/7)-70-40(3/7)-70. Seed DS 6 m at 70 germ. 40-70-40(3/9)-70(1/9)-40-70 and none over four cycles when sown at 70. Treatment with GA-3 led to total rotting of the seeds.

A. pulchellum like *A. karataviense* gave some of the most extended germination observed. Germination occurred at both 70 and 40 and in comparable overall percentages for fresh seed or DS seed. Some of the experiments were closed prematurely. The seed was still firm and, in retrospect, would probably have given further germination. The data is given in full. Fresh seed germ. 70-40-70-40-70 none and 40-70(5%)-40(15%)-70(5%). Seed DS 6 m at 70 germ. 70-40-70-40(6%)-70-40-70(6%) and 40-70-40-70-40(15%)-70(15%). Seed DS 6 m at 40 germ. 70-40-70-40(4%)-70(4%)-40(4%)-70(20%) and 40-70(5%)-40-70-40(20%)-70(25%).

A. tricoccum germination was complex and is not completely understood. Seed collected in October 1989 germ. best in 40-70(95% in 10-16 w) and much less in 70-40-70-40(2%)-70(7%). Note that in the 40-70 treatment the seed was kept an additional 4 w at 70 in the last cycle because germination was continuing. This same seed germ. 86% in August and October of 1990 from sowing outdoors in October 1989. Note that this is not the usual germination in spring from sowing in fall. These results taken together indicate that a prolonged period at 70 is necessary, and it is intended to conduct an experiment in which fresh seed is kept for a year at 70. A small sample of seed collected a year earlier (September 1988) gave considerably different results. This seed germ. 70(3/5 in 9-10 w) and 40-70-40(4/4 in 3 d) for the fresh seed, 40-70(1/3) and 70-40-70(none) for seed DS 6 m at 70, and 40-70(2/3) and 70(4/4 in 8th w) for seed DS 6 m at 40. The germination is intermediate between epigeal and hypogeal in that the cotyledons partially develop and do some photosynthesis but never completely emerge from the seed coats. The seedlings must in general be kept at least 3 m at 40 before the true leaf will develop on shifting to 70.

A. tanguticum germ. in 3rd w at 70.

Alonsoa (Scrophulariaceae).

A. linearis germ. 70(90-100% in 12-15 d) and 40(4%)-70(1%). Light or GA-3 had no effect.

A. warszewiczii germ. 5% in 4th w in 70D. Light or GA-3 did not have much effect, but the seed had such poor viability that the results are not conclusive.

Alophia (Iridaceae). *A. drummondii* germ. 70-40-70(1/6 in 3rd w).

Alstroemeria (Amaryllidaceae). Four samples of wild collected seeds were obtained from the Archibalds. All four samples were collected in altitudes of 5000-8000 feet so that they may be hardy here and provide the basis for further efforts to breed hardy *Alstroemerias*. Already Don Hackenberry has two fine clones that have survived several winters in Central Pennsylvania. Germination is generally best at 40 with a prior 4 w at 70 sometimes improving the germination.

A. aurantiaca showed two unusual features in its germination. Although both fresh seed and DS seed gave good germination, germination occurred in contrasting patterns. Fresh seed germ. 70-40(3/4 in 3rd w) whereas seed DS 6 m at 70 germ. 70(4/4 in 5-10 w). The long induction period for seed germinating directly at 70 is unusual, and inhibitors must be present. Germination is hypogeal.

A. aurea germ. 50% in 4th w at 40 if the seed had been subjected to a 4 w period at 70 first. Without this prior 4 w at 70, none germ. at 40 in 2 m. The first 4 w at 70 can be in either 70D or 70L with the same results. The remaining seeds germ. over the next year, but only in cycles at 40. The final percent germination was 100%.

A. haemantha germinated in the 2nd w at 70 similar to *A. aurantiaca*.

A. hybrids seeds (fresh or DS 6 m at 70) germ. 70(80-100% in 2-8 w) and 40(40-60% in 7th w). Later experiments indicated some deterioration on DS for 6 m at 70.

A. pallida germ. 80% in 4th w at 40 if the seeds had been subjected to a 4 w period at 70 first. Without this prior 4 w at 70 the seeds germ. 40(25% in 2-4 w). This was confirmed with a second sample.

A. sp. (Archibald's 12470, intermediate between *A. pallida* and *A. umbellata*) germ. 6/6 in 2-4 w at 40 if the seeds had been subjected to a 4 w period at 70 first. Without this prior 4 w at 70 the seeds germ. 40(3/6 in 4-7 w). This last sample was shifted to 70 after 7 w at 40 whereupon 2/6 germ. in 1-3 d.

A. umbellata germ. 40(7/9 in 2-4 w). A prior 4 w at 70 lowered the germination to 4/9 with the rest rotting.

Alyssoides (Brassicaceae). *A. utriculata* germ. 70D(60% in the 2nd w) and 40(46% in 4-8 w). Light or GA-3 had no effect.

Alyssum (Brassicaceae). *A. saxatile* is a D-70 germinator.

Amelanchier (Rosaceae). *A. alnifolia* (ref. 43, Ch. 10) and *A. canadensis* (ref. 44, Ch. 6) were reported to require a cold treatment to induce germination.

Amsonia (Apocyanaceae).

A. montana germ. in 2nd w at 70.

A. tabernaemontana germ. 40-70(4/14 in 3-7 d)-40-70. When sown at 70, there was no germination over three cycles.

Anacyclus (Asteraceae). *A. depressus* germ. in 6-20 d at 70.

Anaphalis (Asteraceae). *A. virgata* germ. at either 70 or 40 with the same ind. t of 7 d and the same rate of 6%/d. *A. triplinervis* germ. 100% in the 3rd w when sown at 70.

Anchusa (Boraginaceae). *A. azurea* germ. 70D(50% in 2nd w), 70L(77% on 5th d), 70D GA-3(91% on 5th d), and 40(70% in 6-8 w).

Androcymbium (Liliaceae). *A. rechingeri* germ. 70-40(2/6 in 4th w) and 40(none).

Andropogon (Poaceae). See Chapter 22

Androsace (Primulaceae). The book "Androsaces" by G.F. Smith and D. Lowe is devoted entirely to the genus. The only specific information on seed germination is that a low T cycle is not necessary which is not entirely in accord with the present work. The genus is divided into four sections: *Pseudoprimula* (P) which resemble *Primula*, *Chamaejasme* (C) which are mats of rosettes spreading by runners, *Aretia* (Ar) which are high alpine cushions, and *Andraspis* (An) which are winter annuals of lower elevation. The section is indicated for each species. Most of the data was obtained before the standardization of experiments.

A. alpina (Ar) germ. in the 3rd m at 70, a long ind t for germination at 70.

A. armeniaca (An ?) germ. 100% on the 7th d at 70.

A. barbulata (An ?) germ. on the 14th d at 70.

A. chamaejasme ssp. *carinata* (C) germ. 70(60% in 2-40 d)-40(10%), 40(10%)-70(50% in 4-16 d), and 75% in early April in outdoor treatment. The outdoor behavior was verified with a second sample.

A. charpentieri (Ar) germ. outdoors in late April and 70(none).

A. cylindrica (Ar) germ. outdoors in April after being outdoors one year.

A. elongata (An) germ. abundantly at 70 in the 5th w.

A. geraniifolia(P) germ. 30% in 1-3 w in either 70D or 70L. A prior 3 m at 40 was injurious and germination dropped to 2%.

A. hedreantha (Ar) germ. outdoors in April and 70(none).

A. kochii ssp *tauricola* (C) germ. 70(4/6 in 2-8 w) and 40-70(4/5 in 3rd m).

A. lactea (Ar) germ. 40-70-40(1/10)-70(2/10) using fresh seed and 40-70-40(1/18)-70 and 70(none) using seed DS 6 m at 70..

A. lanuginosa (C) germ. 70(17% on 5th d) and 40-70(20% in 6-10 d). A second sample germ. abundantly at 70 in 2-4 w.

A. mucronifolia (C) germ. 40-70(2/5 on 12th d) and 70(none).

A. multiscapa (?) germ. 70L(3/7 in 3rd w)-40-70L(1/7), 70D GA-3(4/7 in 2nd w), and 70D(1/12).

A. muscoides (C) germ. 70(1/5 on the 7th d) and 40-70(none).

A. obtusifolia (Ar) germ. 40(3/15 in 6th w) and none in 70D and 70D GA-3.

A. rotundifolia (An) germ. in 6-10 w at 70.

A. sempervivoides germ. one seed in 70L from several samples.

A. septentrionalis (An) germ. 70(90% in 2-6 d) and 40(60% in 3rd w) using fresh seed or seed DS 6 m at 70 or 40.

A. sericea germ. 40(1/8)-70(5/8 on 2nd d) and 70(none).

A. spinulifera (C) germ. 70(100% in 4-8 w).

A. studiosorum (C) germ. 70(4/5 in 5-20 d) and 40-70(10/14 in 6-12 d).

A. vandellii (Ar) germ. like *A. spinulifera* and was possibly that species.

A. villosa (C) germ. a few in the 10th w at 70.

A. villosa var. *congesta* (C) germ. 70(1/5 on 14th d) and 40-70(3/4 in 2-4 w).

Androstephium (Liliaceae). *A. breviflorum* germ. 40(9/9 in 3rd w), 70(3/5 in 2-5 w)-40(2/5 in 3rd w), and 5/9 in February and March in outdoor treatment. The seeds that germ. at 40 grew normally after an immediate shift to 70.

Andryala (Asteraceae). *A. agardhii* germ. in a few days at 70.

Anemonastrum (Ranunculaceae).

A. fasciculatum var. *roseum* germ. 40-70-40(1/3).

A. protractum sown outdoors in May germ. the following April. Only the two cotyledons develop the first year. A second sample of 8 seeds was divided. The loose brown seed coats were removed from 4 and these germ. 70(2/4 in 5-7 w) whereas the controls germ. 70D-40-70D(1/3 in 2nd w) and 40-70(1/10 in 5th w). The data is too meagre to draw the conclusion that the seed coat contains an inhibitor.

A. speciosum seed all rotted.

Anemone (Ranunculaceae). This genus divides into two groups. The first group are early spring bloomers with hairless seed coats, multicycle germination patterns, and intolerance of DS. The second group are taller and bloom in summer and fall, the seed is embedded in cotton in a spherical cluster, and germination is largely D-70 with curious differences between DS seed and fresh seed.

A. altaica germ. in 2nd m at 70.

A. baicalensis germ. 70(77% in 2-5 w) and 40(46% in 4-12 w)-70.

A. baldensis germ. 70(95-100%, ind. t 18 d, 5.1%/d) and 40(95-100%, ind. t 44 d, rate 4.0%/d) using fresh seed. Seed DS 6 m at 70 or 40 gave the same results when sown at 70, but germination was more extended when sown at 40. The data were 40(64%)-70(36%) for seed DS at 70 and 40(42%)-70(58%) for seed DS at 40.

A. biamiensis germ. 70(100%, ind. t 13 d, 11%/d) using either fresh seed or seed DS 6 m at 70 or 40. Curiously fresh and DS seed showed divergent behavior when started at 40. The fresh seed germ. largely at 40 with ind. t 15 d and 1%/d rate whereas the DS seed did not germinate at 40, but waited until the shift to 70. In all patterns germination was ultimately 80-100%.

A. biflora, four samples of DS seed failed to germinate. This is mentioned because it belongs to the first group that cannot tolerate DS.

A. blanda germ. 70-40(75%, ind. t 63 d, 3%/d) and 40-70-40(95%, ind. t 43 d, 2%/d) with fresh seed. Germination of DS seed was reduced to the 0-15% range showing that DS is not tolerated. More important, germination of DS seed gave weak seedlings that largely died.

A. caucasica seeds all rotted. This is mentioned only since it indicates that this species belongs in the *A. blanda* group which are highly intolerant of DS.

A. crinita germ. best in 70(95-100% germ. in 11-15 d) using seed DS 6 m at 70 or 40. Fresh seed germ. with slightly longer ind. t and slightly slower rate as shown by 70(95-100%, ind. t 18 d, 5%/d) and 40(95-100%, ind. t 44 d, 4%/d). The identification of this species is in doubt. As grown here it has a single large cream-colored flower on a six inch stem over a rosette of much divided foliage resembling a *Pulsatilla* but with a cotton ball type seed head. It is an attractive plant worthy of more cultivation. It was received under other names.

A. cylindrica seed must be DS 6 m at either 70 or 40 after which germination is 100% over 3 m when sown at 70. If fresh seed is sown at 70, germination is zero. Curiously the difference between DS and fresh seed is not so great when the seed is sown at 40. The patterns were 40(78% over 3 m)-70(20% over one m) for DS seed and 40-70(76% over 3 m) for fresh seed.

A. demissa germ. 2/5 in 3-5 w at 70.

A. drummondi germ. in 6th w at 70.

A. fasciculata germ 70(87% in 2-11 w), 40-70(95% in 4th w if cleaned), and 40-70(84% in 3-9 w if not cleaned). The term cleaned as used here means that the dark brown wafer like covering was removed leaving the seeds in their light brown seed coat. Treatment with GA-3 on shifting from 40 to 70 did accelerate germination so that 90% germ. in 16-18 d, but the seedlings were weak and died, and in any event is of no practical importance. This species may well be the seed listed as *A. fasciculatum* in the first edition. Germination is hypogeal which is unusual for a *Ranunculaceae*.

A. fasciculatum var. *roseum* is sometimes placed in *Anemonastrum*. Seeds germ. 40-70-40(3/6) and 70-40-70(none).

A. kurilensis germ. 70(65% in 3rd w) and 40-70(31% in 3rd w). The wool encasing the seeds was largely removed before planting.

A. lesseri germ. 70D(84% in 3rd w), 70D GA-3(45% in 3rd w) and 40-70(72% in 4-8 d).

A. loesseri rubra germ. 70(95-100% in 10-30 d) for both fresh seed and seed DS 6 m at either 70 or 40. However, when started at 40, there was a sharp contrast between fresh and DS seed. Fresh seed germ. 40(99%)-70(1%) whereas seed DS 6 m at either 70 or 40 germ. 40-70(100% in 1-18 d).

A. narcissiflora germ. outdoors in April. The variety *zephyra* germ. 1/20 after 5 m at 70, probably a non-optimum treatment.

A. nemorosa seed always rotted. This is mentioned because it belongs to the group intolerant of DS.

A. obtusiloba is in the first group and several samples received as DS seed all rotted showing that DS had been fatal as is typical for this group.

A. occidentalis germ. a few in the 9th w at 70.

A. palmata was probably *A. biamiensis* and the data is given there.

A. pavoniana germ. a few in the 6th w at 70 in one sample, 2/28 in 4th w in another, and the third sample all rotted at 70. The Archibalds have pointed out that this species comes from areas with desiccating summers so that the problem of low percent germination would not be intolerance to DS.

A. polyanthes is in the first group and several samples received as DS seed all rotted showing that DS had been fatal as is typical for this group.

A. rivularis germ. 40-70L(3/4 in 5-10 d), 40-70D(1/5), 70D-40-70D(4/9 in 4-9 d), and none in 70L-40-70D. Taking the results overall and in view of the small sample, it does not appear that light had much effect on germination and that the species is basically a 40-70 germinator.

A. rupicola germ. a few in the 6th w at 70 in the two samples studied.

A. sylvestris germ. a few in the 10th w at 70. Six other samples failed to germinate.

A. tetonensis seed all rotted and this is in the group intolerant of DS.

A. tetrasepala seed collected in the wild germ. 70(10%)-40(40%)-70(40%) and 40-70(90% in 1-3 m) indicating that a 40-70 pattern is best.

A. vitifolia germ. 100% in 3rd w in 70L or 70D. A prior 3 m at 40 had little effect.

Anemonella (Ranunculaceae). *A. thalictroides* germination has been very low despite the fact that this species is native on the property. The only germinations so far were from two samples of fresh seed in 70D-40-70L(3% in 3rd w) and 40-70D-40-70D(3% in 3rd w). The cotyledons develop within a week of germination, and the seedlings developed normally. DS seed immediately rots on contacting moisture and is dead. Outdoor treatment and GA-3 need to be tried.

Anemonopsis (Ranunculaceae). *A. macrophylla* germ. 70-40-70-40(20% in 12th w)-70(60% in 1-11 d) and 40-70-40-70 none. Germination is epigeal, and the cotyledons open in the 2nd w after germination. Light had no effect.

Anethum (Apiaceae). *A. graveolens* germ. 70(84% in 5-16 d), 40(100% in 4th w), and 70% in April in outdoor treatment. The outdoor treatment was started in March, and it is possible that the seed cannot tolerate the temperatures around 10 which were experienced in March. Light had no effect.

Angelica (Apiaceae). Both species germ. best in 70L. *A. gigas* germ. 70L(73% in 3rd w), 70D GA-3(23% in 3rd w), 70D(none), and 40-70(2/9). *A. grayi* germ. 70L(2/8 in 4th w) and 70D-40-70L(2/5 in 4th w). Seeds started at 40 all rotted.

Anisotome (Apiaceae). *A. haastii* germ. 40(2/5 in 8-11 w)-70(1/5), 70D(all rotted), and 70D with GA-3(all rotted). *A. aromatica* germ. 40-70(1/8 in 4th d) and 70D(none).

Anthemis (Asteraceae). *A. montana* and sp. (Turkey) germ. in 2-4 w at 70.

Anthericum (Liliaceae). The very low germinations are a puzzle, particularly because both *A. liliago* and *A. racemosum* self sow here.

A. liliago germ. erratically and in low percentage. Seed collected in August germ. 70-40-70(none), 40(3%)-70(4%), and 5% in April in outdoor treatment. When this seed was DS for 6 m at 70 it germ. 70(3%)-40(3%), 40-70(12% in 1-4 w), and 4% in April in outdoor treatment. Germination is hypogeal, and the seedlings developed normally despite the low percent germination. Two other samples gave the same low and erratic germinations. Treatment with GA-3 had no effect.

A. racemosum germ. 40(5%)-70(14%)-40-70 and 70-40-70(6%) using fresh seed and 40(3%) and 70(none) for seeds DS 6 m at either 70 or 40.

A. torreyi germ. 70D(12% in 2nd w), 70D GA-3(26% in 3rd w), and 40(none).

Anthriscus (Apiaceae). *A. cerefolium* germ. 70D(4% in 2nd w)-40(2%)-70D(6%), 70L(12% in 1-3 w)-40, and 40(10% in 3-8 w)-70.

Anthyllis (Fabaceae). *A. montana* and *A. vulneraria* germ. 100% in the 6th d if a hole was made in the seed coat. Although none germ. in the controls, seeds placed outdoors all winter germ. 2/3 in *A. montana* and 7/12 in *A. vulneraria* in early April. This germination is due to the opening of microfissures by the oscillating temp.

Antirrhinum (Scrophulariaceae). *A. majus* was a classic D-70 germinator. Seed DS at either 70 or 40 germ. 90% on the 3rd d at 70 whereas fresh seed germ. 70(5%)-40-70 and 40-70(5%)-40-70. When started at 40 the rate was slower (ind. t 11 d, 2.6%/d), but germination was still 85-90%.

Aphananthe (Ulmaceae). *A. aspersa* germ. 40(2/5 in 4-6 w) and 70-40-70(1/3). Grinding a hole through the seed coat did not initiate germination.

Aquilegia (Ranunculaceae). Three treatments gave germination, and all other treatments failed. The three were (a) treatment of fresh or DS seed with GA-3 at 70, (b) sowing of DS seed at 70, and (c) outdoor treatment. All three of the treatments were used in only a few of the species so that it is not certain that all three will work with every species. Stewart and Presley (ref. 9) were the first to report that GA-3 was valuable in stimulating the germination of *A. jonesii* x *saximontana*. This has now been demonstrated for a number of species and should always be tried on *Aquilegia*. For *A. canadensis* DS gradually removes the GA-3 requirement, but it takes two years of DS at 70 to finally remove the requirement completely. The seedlings from GA-3 treatment are normal and healthy. The germination of some samples at 70 is attributed to the seeds having been already DS before they were received in midwinter. It is likely that germination in these samples would have been higher if they had been subjected to GA-3 treatment, outdoor conditions, or additional DS. It can be expected that the response to these three treatments will vary with the species. A series of experiments on *A. canadensis* and *A. vulgaris* showed that rubbing the seeds between sandpaper had no favorable effect. Impervious seed coats are not a factor. A few experiments indicated that light had no effect, and it was not used in this genus. Delayed germination in *Aquilegia* has been attributed to immature embryos, but what does that mean?

A. akitensis germ. a few in the 10th w at 70.

A. atraviosa germ. 40-70-40(1/3 in the 11th w) and none in 70-40-70.

A. barnebyi germ. 70 GA-3(90% in 2nd w), 70(none), and 40(20%)-70(80% in 2nd w).

A. canadensis has germination initiated either by DS of the seed, by treating fresh seed with GA-3, or by certain outdoor treatments. The seedlings from the GA-3 treatment are healthy, and GA-3 treatment is the most rapid method for achieving germination. The seeds are held in upright capsules for months so that seeds collected late in the season have already been subjected to DS and will increasingly behave like DS seed. Seeds collected from capsules that had just opened germ. 70 GA-3(81% in 2-5 w, ind. t 9 d, first order rate, half time 4 d) and 70D(0-9% in 3-5 w) in several control experiments. Dry storage of the seeds at 70 increased the germination in 70D to 53% (in the 4th w) after 6 m of DS and 70% (in 1-4 w) after 12 m of DS. These DS seeds continued to germinate around 85% in 1-3 w at 70 if treated with GA-3, the same as fresh seeds. Sowing fresh seeds at 70 caused permanent injury, and such seeds ultimately rotted. Sowing the seed at 40 gave lower germinations.

A. coerulea germ. 70 GA-3(93% in 3rd w), 70(none), and 40-70(40% in 2nd w).

A. elegantula germ. 70 GA-3(100% in 4th w) and none in 70 or 40-70.

A. eximia germ. 70D(20% in 2-5 w) and 40(5%).

A. flabellata nana germ. 70 GA-3(100% in 2nd w) and none in 70 or 40-70.

Seeds DS 6 m at 70 germ. 70(28% in 1-3 w), 40-70(17% in 1-4 w), and 65% in April in outdoor treatment from seed sown March 1 a month earlier. Seed DS 2 y was dead.

A. flavescens germ. 40-50% in April for fresh seeds placed outdoors in September or DS seeds placed outdoors in February. None germ. in a year of alternating cycles starting at either 40 or 70 using either fresh seed or DS seed, but when seeds from 6-12 m of such treatments were placed outdoors on December 1, 40-50% germ. the following April.

A. formosa germ. 40-70(52% in 2-6 w) and none in 70-40-70. The seed was received in January and had been in effect DS 6 m at 70. A sample placed outdoors when received germ. 38% in late April and an additional 50% the following October and November. The seed was given an additional 6 m of DS at 70 and sown outdoors in January. This germ. 57% the following October and November indicating that oscillating temperatures promoted germination.

A. fragrans germ. 70-40-70(2/12) with no germination in four additional cycles.

A. jonesii germ. 70 GA-3(95% in 4th w), 70(20% in 4-7 w), and 40-70(none).

A. jonesii x *saximontana* germ. 70(1%)-40-70(21%)-40-70(57%) and 40-70(43%)-40-70(40%) using fresh seed. Treatment with sandpaper was without effect. This is a beautiful strain of *Aquilegia* with large flowers on 4-6 inch stems. The plants closely resemble *A. jonesii*, but are much more amenable to culture in gardens in Eastern U.S. Plants do not live more than 2-4 years here.

A. jucunda germ. 100% in outdoor treatment with germination occurring in the last 2 w of April. There was no germination when sown at 70. Seed DS 6 m at 70 germ. 4-10% in all treatments, and the germination extended over 2-3 cycles. When DS seed was placed outdoors in January, only 5% germ. the following April, but an additional 43% germ. the second April, 15 m later.

- A. laramiensis germ. 70 GA-3(81% in 3rd w) and none in 70 and 40-70.
- A. micrantha germ. 15% in 6-10 d at 70.
- A. olympica germ. 50% in outdoor treatment in the first 2 w of May. None germ. in a year of alternating cycles starting either at 40 or 70.
- A. pyrenaica germ. a few in the 5th w at 70.
- A. saximontana germ. 70 GA-3(86%, 3rd w), 70(none), and 40-70(15%, 2nd w).
- A. scopulorum germ. 70 GA-3(98%, 2nd w), 70(none), and 40-70(30% 2nd w).
- A. skinneri germ. 30% in the 5th w at 70.
- A. sp. (Darwas) germ. 70(24% in 1-4 w) and 70 GA-3(76% in 1-5 w).
- A. tridentata germ. 70-40(46%) and 40(100%).
- A. vulgaris seeds collected from capsules that had just opened germ. 70 GA-3 (98% in 1-3 w, zero order rate, ind. t 5 d, 14%/d) and 70(none). The GA-3 requirement gradually disappears on DS. The percent germinations at 70 were 0%, 10%, and 44% after 3 w, 6 m, and 9 m of DS at 70. The DS is not only eliminating the need for GA-3, but it is also slowly killing the seeds. This is seen by the slow decline in percent germination in 70 GA-3 on continued DS. The percent germinations after 0, 2 m, and 6 m DS at 70 were 98%, 93%, and 88%.

Arabis (Brassicaceae). All species are probably D-70 germinators.

A. albida germ. under all conditions nearly as fast at 40 as at 70. Germination of fresh seed was 95-100%, but this dropped to around 50% in DS seed showing some intolerance to DS.

- A. alpina germ. in the 4th w at 70.
- A. bellidifolia germ. in 3rd w at 70.
- A. blepharophylla germ. in 1-4 w at 70, but the seeds were likely misnamed as most samples of this species in seed exchanges turn out to be other species.
- A. petraea germ. at 70.
- A. pumila germ. 75% in 2nd w at 70.
- A. purpurea germ. a few in the 2nd w at 70.

Aralia (Araliaceae). A. racemosa germ. 2/4 in May in outdoor treatment and none in 70D, 70L, or 40. A. hispida was reported to be a 40-70 germinator (ref. 31, Ch. 7).

Arbutus (Ericaceae). A. menziesii was reported to be a 40-70 germinator (ref. 44, Ch. 7).

Arctostaphylos (Ericaceae). Wild collected seeds of seven species were studied. The seeds vary greatly in size. Only the larger seeds ever germ., and the undersize seeds were not counted. Puncturing the seed coats had no effect so the long extended germinations do not seem to be a question of impervious seed coats despite a literature claim that A. uva-ursi required a sulfuric acid treatment followed by a 70-40-70 pattern (ref. 5, Ch. 10).

A. columbiana x uva-ursi seeds placed outdoors in December germ. 1/14 in April sixteen months later.

- A. nevadensis germ 70-40-70(3/10)-40(2/10).
- A. pungens germ. 70 GA-3(2/16 in 8th w), 70L(1/60), 70D(none), and 40-70D(1/60). The experiments are only for 14 w and are incomplete.
- A. uva-ursi germ. 70-40-70(1 in 2nd w). None germ. in all other conditions.

Arenaria (Caryophyllaceae). All species are probably D-70 germinators. *A. kingii*, *A. procera*, *A. purpurescens*, and *A. polaris* germ. in 3-14 d at 70.

A. caroliniana germ. a few outdoors in March from January sowing.

A. pseudoacantholimon germ. a few in 1-3 w at 70, but the seedlings developed abnormally without opening cotyledons, and they soon perished.

A. saxosa germ. 70(40%, ind. t 8 d, 6%/d) and 40(40%, ind. t 6 w, 6%/d). It is of interest that the rate of germination was the same at 70 and 40 although the ind. t was much longer at 40.

A. stricta germ. in the 6th w at 70.

A. tmolea showed stimulation of germination by both light and GA-3. The data were 70 GA-3(90% in 2nd w), 70L(53% in 1-6 w), 70D(10% in 1-7 w), 40-70L(58% in 3rd w), and 40-70D(15% in 3rd w).

Argemone (Papaveraceae). *A. pleicantha* germ. 40(8% in 7th w)-70(2%), 70-40(none), and 80% in April in outdoor treatment. This shows that the oscillating temperatures of outdoor treatment are required for germination.

Argyllia (Bignoniaceae). Collected in Chile by the Archibald's.

A. adscendens germ. 70L(8/8 in 1-6 w), 70D(6/13 in 2-6 w, 7/13 rotted in 2nd w), and 40(1/8 in 5th w)-70(1/8 on 3rd d). Any treatment other than 70L leads to deterioration.

A. potentillifolia germ. 70L(1/10 in 2nd w), 70D(0/9), and 40(0/7). The ungerminated seeds all rotted

A. sp. (Archibald's 12390) germ. 70L(10/12 in 1-4 w), 70D(7/16 in 2-8 w)-40-70(4/16 in 2-4 d), and 40-70D(9/11 in 1-3 d). A preliminary 3 m at 40 markedly stimulated germination and is the optimum treatment with 70L being the next best.

Arisaema (Araceae). The Asiatic species were received as dried berries in midwinter and germ. readily at 70 after WC for 7 d. The American species exhibited complex behavior. Germination is hypogeal in all species. The seed forms a corm and root system before sending up the single true leaf. This first true leaf is a single leaflet in *A. consanguineum*, *dracontium*, *flavum*, *tortuosum*, *triphyllum*, and *quinquifolium* (presumably) and trifoliate in the others. However, *A. consanguineum* seedlings had both single and trifoliate first leaves so that this feature may not be a constant character. Although GA-3 increased the rate of germination in *A. dracontium* and *A. triphyllum*, the effect was modest so that GA-3 treatment is not advised.

A. consanguineum germ. 70(6/6 in 2-4 w) and 40(4/7 in 8th w)-70(3/7 in 1-3 w).

A. dracontium germ. best by leaving the cluster of berries outdoors overwinter until March 1 and then WC them for 2 w. These seeds germ. 70(85%, ind. t 13 d, 5%/d), 40(51%)-70(19%), and 75% in May-July in outdoor treatment. The seedlings developed normally, although there was a time gap of 1-2 m between completion of radicle development and emergence of the true leaf. If the WC was only 7 d, germination was reduced to 70(50%) and 30% in May and June in outdoor treatment. Seeds collected in October and immediately WC for 7 d germ. 70(7%)-40-70(56% in 2-5 w) and 40-70(7%). It is possible that WC with detergents would have improved all of the germinations. This certainly needs to be investigated, particularly because the berries are oily and because small differences were found between WC for 7 d relative to 14 d with better germination from the longer washing. Treatment with GA-3 was also tried with the GA-3 being applied after the 7 d WC and using seeds collected in

October. The GA-3 treated seeds germ. 60% in 3-6 w and none in the control. The seedlings from the GA-3 treatment appeared normal and developed a leaf after 1-2 m.

A. flavum germ. 70(6/6 in 2-5 w) and 40-70(3/4 in 3rd w).

A. jacquemonti germ. 70(90% in 3-6 w) and 40(5/7 in 8th w)-70(1/7).

A. nepenthoides germ. best in 40(2/2 in 7th w). The seedlings developed a radicle, root system, and a tuber within 4 w at 40 whereupon a shift to 70 led to development of a leaf (hypogeal) in 4 w. The seeds also germ. in 70D(2/3 in 5th w), but the leaf did not develop readily. Starting at 40 is recommended.

A. quinquifolium gave 100% germination and normal leaf development under the procedure recommended for *A. draconium*.

A. sikokianum germ. 70(100% in 5-10 d) and 40(100% in 5th w) using either seed received in December as dried fruit or seed given an additional 6 m DS at 40 in the dried fruit. Leaf development was best in the seed germ. at 40. The trifoliate leaf begins to develop at 40 in 2nd w after germination, and the seedling can be immediately shifted to 70 and planted to complete the development of the leaf.

A. thunbergii germ. readily, but difficulties were encountered in getting the trifoliate leaf to develop. The majority of seedlings ultimately rotted and never developed a leaf. Seed received in December in dried fruit germ. 70(100% in 2-4 w) and 40(20% in 9-12 w) -70(80% in 1-7 d). Leaf development was erratic. A few seedlings developed the leaf at 70 in 2-4 w after germination, but the majority did not. Shifting the seedlings to 40 for 3 m and back to 70 led to a few seedlings developing a leaf, but again the majority did not. Seed kept an additional 6 m at 40 in the dried fruit germ. 70(81% in 2-4 w)-40(12%) and 40(82% in 5-12 w)-70(6%). These seedlings produced a system of branching roots up to 3 inches long, but the roots were very thin and colorless. On shifting to 70, these fine roots died back to the tuber, and leaves failed to develop over several alternating cycles.

A. tortuosum germ. 70(100% in 2-4 w) and 40-70(100% in 1-3 w).

A. triphyllum germ. best if the seed was left outdoors in the berries until March 1 and then WC (7 d or 14 d gave similar results). This seed germ. 95% in 1-3 w at 70 and 95% in April-May in outdoor treatment. The leaf developed in the 2nd w after germination. Seed collected in October and immediately WC for 7 d germ. 70(23%)-40-70(77% in 1-3 w) and none in either 40-70 or outdoor treatment. Light had no effect. As with *A. draconium*, experiments are needed on WC with detergents. Treatment with GA-3 was also tried with the GA-3 applied after the 7 d WC and using seeds collected in October. The data were 70 GA-3(40% in 2-4 w) and 70(22% in 2-5 w). The GA-3 seedlings were normal

***Aristolochia* (Aristolochiaceae).**

A. baetica showed some photoresponse, but unfortunately the experiments were not ideal. Data for DS seed were 40-70L(50% in 4-8 w), 40-70D-40-70D(50% in 6-7 w), and 70D(20% in 3-7 w).

A. serpentaria had extended germination as shown by 70-40-70(1/6)-40-70(1/6) and 40-70-40-70(4/12)-40-70(4/12). Germination is hypogeal. A true leaf develops in the 5th w after germination. Seed DS 6 m at 70 or 40 all rotted. GA-3 should be tried.

Armenaica (Rosaceae). *A. sibirica* germ. best at 40(100% in 2-7 w), and the seedlings formed a stem and leaves within 2 w after an immediate shift to 70. Seeds started at 70 germ. 2/13 in 7-11 d. After 5 w at 70, the sample was shifted to 40 whereupon 7/13 germ. in 3-9 w. However, these seedlings were reluctant to form stems and leaves on shifting to 70, so that sowing at 70 is to be avoided.

Armeria (Plumbaginaceae).

A. caespitosa germ. under all conditions. The percent germinations were probably comparable, but the copious chaff made seed counts inaccurate. Generally there was a burst of germination in 1-4 w when started at either 70 or 40.

A. corsica germ. in the 4th w at 70.

A. tweedyi germ. 70D(2/2 in 4th w) and 40(2/2 in 9th w).

Arnebia (Boraginaceae). *A. euchroma* germ. 70(2/8 in 6-10 d). *A. echioides* germ. 70 GA-3(3/4 in 9th w) and none in 70D, 70L, or 40.

Arnica (Asteraceae). *A. frigida* and *A. montana* germ. 100% in 1-3 w at 70.

Artemisia (Asteraceae). All species are D-70 germinators. Germination in 70D was *A. caucasica* (100% in 4-6 d), *A. frigida* (84% on 3rd d), and *A. pamirica* (100% on 5-7 d). Germination at 40 was 40-70(100% in 2-5 d) for *A. caucasica* and 40(4%)-70(96% on 2nd d) for *A. pamirica*, but lower and more extended for *A. frigida*.

Arthropodium (Liliaceae). *A. cirrhatum* germ. 70(4/11 in 3-11 w) if treated with GA-3 and none in the control. The GA-3 seedlings were normal.

Arum (Araceae). *A. maculatum* germ. best in 40-70-40-70(80% in 3-21 d) and less in 70-40-70-40(30% in 9-11 w). It is curious that the T at which the seed is sown directs the T at which germination ultimately occurs. Seed DS 6 m at 40 or 70 gave similar results. Germination was hypogeal like all Araceae. The true leaf did not develop properly unless the seedling was kept at 40 for 4 m after germination.

Aruncus (Rosaceae). Abundant chaff prevents accurate seed counts.

A. dioicus required light, GA-3, or outdoor treatment. Seeds germ. 70L(56% in 2-14 w), 70D GA-3(33% in 2nd w), 70D(none), 40-70L(70% in 2nd w), and 40-70D(none). Seed DS 6 m at 70 germ. 70L(25% in 1-5 w) and 70D(none). Seeds placed outdoors in September germ. 49% in April.

Aruncus sylvestris germ best in 70L or 40-70L(100% in 3rd w, first order rate, ind. t 15 d, half life 2 d). Seeds DS 6 m at 70 germ. 70L(86% in 2-6 w) and 70D(none). GA-3 had no effect. Seeds placed outdoors in September germ. 14% in April.

Asarina (Scrophulariaceae). *A. procumbens* germ. 70L(54% in 2-4 w), 40-70L(15%), and none in 70D, 40-70D, or outdoor treatment. Light is required and 3 m at 40 is detrimental.

Asarum (Aristolochiaceae). The two species had large numbers of empty seed coats. The tips of the radicles tended to die in the seedlings which led to death of the seedling. For the moment it is recommended to transfer the germinated seedlings immediately to media and place outdoors. GA-3 needs to be tried.

A. canadensis seed was collected in June and WC for 2 w. The long WC treatment is essential and seeds not WC failed to germinate. After the WC each seed was gently squeezed and 50% found to be empty seed coats. These were discarded. Fresh WC seed put outdoors in June germ. 48% in October suggesting that oscillating temperature were required. Seed sown at 40 germ. 40(2%)-70(53% in 10-13 w), note

the long induction time at 70. Seed sown at 70 germ. 70-40(19% in 3rd w). To add to the confusion, the same seed sown in 70L failed to germinate and all rotted. All DS seed rotted and was dead so at least that point is settled.

A. europaeus seed was WC 7 d. Seed all rotted in 40-70D or 40-70L. The only germination was in 70-40(3% in 5th w).

Asclepias (Asclepiadaceae). The four species studied have wind born seed indicating that DS is tolerated. This was generally true, but some deterioration on DS was noted in *A. incarnata*. Photorequirements are interesting ranging from no photorequirement in the dry land *A. tuberosa* through complex photoresponses in *A. phytolaccoides* and *A. syriacus* to the swamp species *A. incarnata* which germ only in 40-70L.

A. incarnata germ. 40-70L(100% in 1-3 w) and none in 70L. None germ. in up to two years of alternating 3 m cycles in the dark starting at either 40 or 70. When such seed was shifted to 70L, 90-100% germ. in 3-5 d. It is evident that seed of *A. incarnata* could lie buried for years and still retain viability and germination would be immediate on exposure to 70L. There is some dieing of the seeds in 6 m of DS with more dieing at 70 than 40 as shown by 40-70L(65%) for seed DS at 70 and 40-70L(91%) for DS at 40. A second effect of DS and a most peculiar one was that it replaced in part the need for a preliminary 3 m at 40 as shown by 70L(35%) for seed DS at 70 and 70L(53%) for seed DS at 40. An odd result was that 74% germ. outdoors in April from seed sown in October. Since this was the only dark treatment that gave germination, it suggests that the temperature oscillations experienced in outdoor treatment have some special efficacy in destroying inhibitors. However, it is important to note that these seedlings from outdoor treatment were noticeably less vigorous and this treatment is not recommended. GA-3 did not initiate germination.

A. phytolaccoides germination is strongly augmented by light as shown by 70L(99% in 8-18 d), 40-70L(100% in 4-8 d), none in 70D, and 40-70D(7%) This was for seed collected in February which had already undergone considerable DS in the seed capsule. Fresher seed collected in November gave a little more germination in the dark as shown by 70-40-70(6%) and 40-70(21%). Seed DS 12 m at 70 showed the same photorequirements as fresh seed, but the percent germination was reduced to 25% showing that there had been some death of the seed over this extended DS. Treatment with GA-3 in 70D gave about the same percentage and rate of germination as in 70L.

A. quadrifolia germ. 70L-40-70L(3/6 in 1-3 w) and none in 70D-40-70D.

A. syriacus germ. under three conditions. These were 70D if treated with GA-3, 70L if given a preliminary 3 m at 40, and outdoor treatment. Such a combination is unusual. The data were 70D GA-3(97% in 5-18 d) and 40-70L(47% in 1-3 w for fresh seed and 58% in 1-3 w for seed DS 6 m at 70). Outdoor treatment gave 3% in October and 84% in April for fresh seed placed outdoors in September and 70% in April for seed DS 6 m at 70 and placed outdoor March 1. All other treatments failed to give a single germination with fresh seed. However, the DS seed germ. 70L(21% in 3-10 d), 70D(18% in 12th w), and 40-70D(10%). It is as if the DS destroyed some of the inhibiting systems. The seedlings from the GA-3 treatment developed normal cotyledons and radicles.

A. tuberosa germ. best in 40-70(100% in 2-7 d) using either fresh seed or seed DS 6 m at 70 or 40 and less in 70-40-70(75%). Outdoor treatment germ. 100% in March from fall sowing of fresh seed in accord with the 40-70 pattern. Light had no effect, and in particular, it did not induce immediate germination at 70. However, GA-3 treatment did effect immediate germination in 70D with 58% germ. in 4-14 d.

A. viridiflorus germ. 40-70(75% in 2nd d) and 70(none). Light had no effect.

Asimina (Annonaceae). *A. triloba* fruit was collected in November and the seed WC for 2 w. The seed continues to exude material so that periodic WC were done until the seed germ. *A. triloba* is a strict 40-70 germinator as shown by 40-70(76% in 2nd d-5 w). A prior cycle at 70 causes lower germination as shown by 70-40-70(40% in 2-6 w). A thick radicle up to 6 inches in length forms first, and branching roots develop before epicotyl development. A 2-3 m period (at 70) elapses between completion of radicle development and emergence of the stem and leaves (hypogeal). Seed sown outdoors and all DS seed failed to germinate.

Asparagus (Liliaceae). *A. officinalis* seed is embedded in a red berry, and this seed can be collected anytime during fall and winter. After WC for 4 d, the seed germ. 70(96% in 5-6 d) and 40(43%)-70(55%). Seed DS 6 m at 70 germ. 70(90% in 3-5 d) and 40(94% in 3-9 w).

Asperula (Rubiaceae). Larger samples are needed.

A. arvensis germ. 40(3/4 in 3rd w) and 70-40(10/11 in 2-5 w).

A. orientalis germ. 70(5/10 in 2-6 d) and 40(7/8 in 3rd w). A second sample germ. 70 GA-3(12% in 2nd w), 70D(6%), and 40(none).

A. pontica germ. 70(1/10 on 7th w) and 40(1/10 on 11th w).

A. tinctoria germ. 70(2/8 in 8-11 w).

Asphodeline (Liliaceae). *A. lutea* germ. 70(7/7 in 2nd w) A preliminary 4 w at 40 had no effect.

Asphodelus (Liliaceae). *A. fistulosus* germ. 40(1/14 in 11th w) and 70(all rotted).

Astelboides (see *Rodgersia*).

Astelia (Liliaceae). *A. nervosa* germ. 40-70-40-70(1/6 on 8th d).

Aster (Asteraceae). Nearly all species in this genus are D-70 germinators. The following were received as DS seed and germ. in 2-4 w at 70: *A. alpellus*, *brachytrichus*, *farreri*, *himalaicus*, *likiangensis*, *sibirica*, and *tibeticus*. Seven species were studied in more detail.

A. alpinus germ. 70(100% in 2nd w) and 40(6%)-70(94% in 2 d-2w). Seed DS 6 m at 70 germ. 70(70%) and 40(55%)-70(2%). Seed DS 6 m at 40 germ. under 15%.

A. bigelovii germ. 70(100% in 3-6 d) and 40(100% in 2nd w).

A. coloradoensis germ. 70(100% in 2nd w) using seed DS 6 m at 70 or 40 and none after 5 cycles with fresh seed showing that the species is a D-70 germinator.

A. ericoides germ. some at 70 and none in all other treatments using either fresh seed or seed DS 6 m at 40. The abundant chaff makes seed counts inaccurate.

A. nova-anglae germ. 70(95-100% in 3-8 d) for either fresh seed or seed DS 6 m at 70 or 40. Seed sown at 40 germ. slower and germination extended over two cycles for either fresh or DS seed.

A. oblongifolius germ. 70(100% in 2nd w) and 40(100% in 3-5 w) using seed DS 6 m at 70. Fresh seed required two cycles to complete germination.

A. sp. (Central China, CLD 494) germ. 70D(73% in 2nd w) and 40(96% in 3-5 w).

A. sp. Nepal germ. 70(100% in 2nd w) and 40(40% in 4-8 w)-70(60% in 2-4 d).

A. sp. from the Rocky Mountains germ. 40-70(100% in 3-5 d) and none in 70.

This is one of the rare 40-70 germinators in Asteraceae and is cited for that reason despite the lack of positive identification. It is of course possible that it is not an Aster.

Asteromoa (Asteraceae). A. mongolica germ. 70(60% in 4-18 d) and 40(38% in 5-8 w)-70(24% in 2-3 d). Light had no effect.

Astilbe (Saxifragaceae). Although there was some stimulation of germination in 70D with GA-3, the results in 70L were superior so that the GA-3 result is only of academic interest. The seeds are enclosed in chaffy receptacles so that seed counts are uncertain.

A. biternata germ. 70L(100% in 2-9 w), 70D GA-3(100% in 3-6 w), and 70D(none). The seedlings from the GA-3 treatment had normal cotyledons.

A chinensis germ. 70L(100% in 12-21 d) and 70D(none). This photorequirement is removed by the oscillating temperatures of outdoor treatment where germination is 100% in April. The photorequirement is partially removed by a preliminary 3 m at 40 as shown by 40-70L(100% in 2nd w) and 40-70D(50% in 2nd w). These percent germinations are inaccurate because of the fine seed and the abundant chaff. The photorequirement was also slightly removed by DS for 6 m at 70 as shown by 70L(100% in 2nd w) and 70D(8%). An interesting fact was that seeds were collected from three different hybrid strains. One gave the above abundant germination, but the other two produced only empty seed coats. The seed heads were similar in external appearance so that viable seed is not easily distinguished from empty seed coats.

Astragalus (Fabaceae). It is probable that impervious seed coats are generally present and immediate germination is best achieved by making a hole in the seed coat. However, some germination was achieved in early work without any treatment. A. sp. Alps, A. sp. Colorado, A. sp. Utah, and A. sp. Wyoming germ. some in 2-6 w at 70 and A. whitneyi gave good germination without treatment.

A. glycyphyllus has an impervious seed coat and germ. only if a hole was made in the seed coat. However, the behavior was unusual in that the punctured seeds swelled to four times their volume and the seed coats became soft within 3 d at 70D (typical of Fabaceae), but germination was extended over months (untypical), 60% by the 7th w. This behavior was not affected by a prior 3 m at 40.

A. whitneyi germ. 70(83% in 1-6 w) and 40(65% in 3-8 w).

Astrantia (Apiaceae). A. major germ. 40(1/7 in 12th w)-70-40-70(1/7).

Athamanta (Aplaceae). A. turbith germ. 70(1/6 in 11th w).

Atropa (Solanaceae). A. belladonna was reported to be a 40-70 germinator (ref. 28, Ch. 10). It was also reported (J H) that soaking overnight in alcohol or hydrocarbon solvents hastened germination. The following experiments are only six w old. Seeds germ. 70 GA-3(58% in 3-6 w) and none in 70D, 70L, or 40.

Aubrieta (Brassicaceae). A. deltoides germ. well in 2-4 w at 70.

Aucuba (Cornaceae). A. japonica germ. 2/5 in the 5th w at 70. The cotyledons are slow to develop, and it was 2 m before the first unfolded.

Aureolaria (Scrophulariaceae). *A. virginica* germ. 40-70(30% in 5-24 d) and none at 70 using fresh seed. Light had no effect. Outdoor treatment led to 17% germination in March and April, but this is in effect a 40-70 treatment. Germination was much reduced by DS at either 70 or 40. The data were 70(0-5%) and 40-70(4-10%). Percent germination is difficult to determine as the seed is small.

Ballota (Lamiaceae). *B. pseudodictamnus* germ. 70(1/2 in 3rd w).

Balsamorhiza (Asteraceae).

B. hookeri germ. 2/6 in 5-9 d at 70 whereas seed sown at 40 failed to germinate after 4 cycles.

B. sagittata germ. 70(2/9 in 3rd w) if treated with GA-3 and 70(0/7) if untreated. It is possible that the sample treated with GA-3 contained the only two viable seeds. In any event the seedlings were normal and healthy.

Baptisia (Fabaceae).

B. australis germ. 70(90-95% in 1-10 w) using either fresh seed or seed DS 6 m at 70 or 40. Grinding a notch in the seed did not significantly increase the rate of germination and caused severe increases in rotting which lowered the percent germination. Sowing at 40 ultimately gave about the same percent germination, but germination extended over two cycles. Rates are not presented because they are probably governed largely by rates of diffusion of moisture through the seed coat and in fact did not fit zero or first order rate laws.

A. leucophaea germ. in April from sowing of DS seed outdoors in December.

Bauhinia (Fabaceae). *B. monandra* germ. 70D(7/7 in 4-6 d) and *B. purpurea* germ. 70D(100% in 4-6 d). Puncturing the seed coat had no effect.

Begonia (Begoniaceae). All three species studied were D-70. *B. evansiana* germ. 70(95% in 10-12 d) and 40-70(95% in 10-15 d). This is the one hardy member of an otherwise tropical genus. *B. dioica* and *B. picta* germ. 100% in the 3d w in either 70D or 70L and none in 40-70 showing that even 3 m at 40 was completely fatal.

Belamcanda (Iridaceae). *B. chinensis* seed germ. 70(35-50% in 10-15 d)-40-70(2%) and 40(6% in 4-8 w). An interesting set of experiments were conducted in which the seed was started at 40 and portions shifted to 70 at 2 w intervals. After the shift to 70 the germination occurred in 3-6 d and percentages were 76%, 44%, and 18% for 4, 8, and 12 w at 40. The unusual result is that 4 w at 40 is beneficial, but further time at 40 leads to steadily decreasing percent germinations after the shift to 70. Experiments were conducted using seed collected in September, November, and March. There was no marked differences in behavior indicating that DS at 40 is tolerated. Seeds DS for 12 m at 70 germ. nearly as well as fresh seed. Outdoor treatment germ. 75% in February and March. The seed is enclosed in a dryish berry. Seed WC 5 d and seed with no WC gave similar results so that the only value of WC is in giving cleaner seed and less debris.

Bellevalia (Liliaceae). All three species (*B. dubia*, *B. pycnantha*, and *B. romana*) were D-40 and germ. 40(90-100% in 4th w) with or without a prior 3 m at 70.

Bensoniella (Saxifragaceae). *B. oregona* germ. 70L(15% in 6-8 w) and none in either 70D or outdoor treatment. A preliminary 3 m at 40 was fatal.

Berberis (Berberidaceae).

B. julianae germ. best at 40(92% in 8-12 w) or outdoor treatment (88% in late April and early May) and poorer in 70(18% in 3-11 w)-40(57% in 9-12 w)-70(12% in 2-7 d). Seeds DS 6 m at 70 in the WC state also germ. best at 40(94% in 4-7 w) and less in 70(74% in 1-8 w). Although germination at 70 was markedly improved by DS; starting at 40 was still the best. Treatment of the DS seeds with GA-3 had no effect on the rate or percent germination at 70.

B. sphaerocarpa was received as the dried fruit. After WC for 7 d, it germ. 70-40(2/9 in 12th w)-70(4/9 in 2nd d) and less in 40(2/8 in 7-9 w)-70-40(1/8).

B. thunbergii germ. 40-70(98%, ind. t 12 d, rate 2.6%/d) using seed that had been DS 6 m at 70 in either the WC state or in the dried fruit. Germination was less with both seed DS 6 m at 40, 40-70(81-87%), and fresh seed, 40(32% in 6-12 w)-70(3%)-40-70(3%). The DS increases the percent germination and speeds up the germination. The most amazing feature of the germination was that all seed sown at 70 gave only 0-7% germination and is essentially a fatal treatment. The total germination after four cycles starting at 70 were 0-7% for seed DS at 70, 0-4% for seed DS at 40, and none for fresh seed. The ranges reflect results with different samples. The seed is in red berries, and all seed was WC for a week before sowing.

Bergenia (Saxifragaceae). *B. ciliata* germ. 70(54%) and 40-70(54%). The ind. t was 7 d and the rate was 14%/d.

Betula (Betulaceae). *B. lenta*, *lutea*, and *populifolia* have been reported to be 40-70 germinators (ref. 18, Ch. 10; ref. 22, Ch. 7). This is not in accord with my results on *B. populifolia*.

B. delavayi germ. 1-2% at 70 using DS seed.

B. ermanii seeds were received after several years of DS. They germ. 70L(8% in 3rd w), 70D(1%), 40-70D(5% in 2nd w), 40-70L(1%), and 4% in March-May in outdoor treatment.

B. pendula germ. at both 40 and 70 for both fresh and seed DS 6 m at 70 or 40. Germination extended throughout the 3 m of the first cycle whether starting at 70 or 40, and a few limited experiments showed that germination would have continued if the cycle were extended beyond 3 m. Percent germination ranged from 15% to 55%, but it is possible that all the percentages were about the same because of difficulties in assessing the number of seeds.

B. populifolia germ. 70L(11% in 2-6 w), 70D GA-3(8%), 70D(none), 40-70L(11% in 4-10 d), and 40-70D(4% in 4-17 d). Results were similar for seed DS 6 m at 70. Treatment with GA-3 or outdoor conditions gave the same 10-15% germ.

B. tianschanica germ. 40-70L(2/18 in 6th d) and none in the other treatments.

Bixa (Bixaceae). *B. orellana* germ. 10% in 3rd w in 70D, 70L, or 70 GA-3.

Blackstonia (Gentianaceae). *B. perfoliata* germ. in 2nd w at 70.

Bongardia (Berberidaceae). A species collected by J. Halda germ. 40(4/5 in 4-7 w) and 70-40(3/3 in 2-4 w).

Borago (Boraginaceae). *B. officinalis* germ. 70D GA-3(90% in 3-6 d), 70D(18% in 3-12 d), and 70L(20% in 1-3 w) using fresh seeds. Seeds DS 6 m at 70 germ. 70D GA-3(97% on 4th d), 70L(26% on 4th d), and 70D(6%). The seedlings from the GA-3 stimulated germination were normal and healthy.

Bouteloua (Poaceae). See Chapter 22.

Brachycome (Asteraceae). *B. iberidifolium* germ. 70(100% on 3rd d) and 40 (100% in 4th w). Light had no effect.

Brassica (Brassicaceae). *B. olearaceae* germ. 72% in 3-15 d in 70D. Light or GA-3 increased the percent germination to 94% and increased the rate to 2-4 d for light and 2-7 d for GA-3. Both effects are small.

Briggsia (Gesneriaceae). *B. aurantiaca* germ. 70L(80% in 2nd w) and 70D(5%). After 2 w the sample in 70D was shifted to 70L, but no more germ. indicating that even short exposures to 70D are fatal.

Brimeura (Liliaceae). *B. amethystina* germ. best in 40-70(3%)-40(92% in 5-7 w) and less in 70(3%)-40-70-40. Starting at 40 is much superior to starting at 70.

Briza (Poaceae). See Chapter 22

Brodiaea (Liliaceae).

B. congesta germ. 40(4/5 in 8-12 w) and 70-40(4/6 in 10-12 w) using fresh seed. Seed DS 6 m at 70 germ. 40(3/4 in 6th w).

B. douglasii germ. at both 70 and 40. The patterns were erratic as shown by 70-40(5%)-70(42% in 3-22 d) and 40(24% in 10-12 w)-70(26%).

B. pulchella germ. 40(97% in 2nd w) and 70(5%)-40(95% in 3-8 w) using fresh seeds. Seeds DS 6 m at 70 germ. 70(53% in 1-4 w) and 40(98% in 3-6 w), a remarkable change in the germination pattern on DS.

Bromus (Poaceae). See Chapter 22

Bruckenthalia (Ericaceae). *B. spiculifolia* germ. 70(95% in 2-12 w)-40-70(1%) and 40-70(50%).

Buddleia (Loganiaceae).

B. davidi germ. 70L(100% in 4-6 d), 70D with GA-3(100% in 4-6 d), and 40-70L(100% in 6th d). None germ. in any dark treatment. Results were the same for either fresh seed or seed DS 6 m at 70. The seeds are very sensitive to light so that germination is zero in 70D only if the towels with seeds are kept in total darkness.

Bulbinella (Liliaceae). *B. hookeri* germ. 40-70-40(2/4 in 8th w) and none in 70 GA-3 or 70-40-70.

Bulbocodium (Liliaceae). *B. vernum* germ. best with fresh seed in 70-40-70-40(5/6 in 7-10 w). Germination is hypogeal. It is best to keep the seedlings at 40 until the true leaf is well started before shifting to 70. Fresh seed sown at 40 germ. 40-70-40-70-40(1/6). DS is not tolerated well as shown by 40-70(1/3) and 70(none) for seed DS 6 m at 70 and 70-40(1/4) and 40(none in 2 y of alternating cycles) for seed DS 6 m at 40.

Bupleurum (Apiaceae).

B. aureum germ. best in 40(99% in 3rd w) or outdoor treatment (96% in March) and poorer in 70(25% in 1-11 w)-40(18% in 2-5 w)-70. This last sample was treated with GA-3 after 5 w at 70 whereupon the remaining 57% germ. in 1-3 w. It is likely that GA-3 treatment would have led to 100% germination immediately at 70. Light had no effect. Seeds placed outdoors March 1 germ. 96% in April, a result of the low T.

B. spinosum germ. 70D(14% in 8-11 w)-40(28% in 3d w) and 40-70-40(1/7).

Butomus (Butomaceae). *B. umbellatus* requires light for germination, but the light is more effective after 3 m moist at 40. The data were 40-70L(31% in 5-16 d), 70L(8%), and none in 70D and 40-70D. In the mildly anaerobic atmosphere as described in Chapter 12, 2% germ.. Treatment with GA-3 did not initiate germination.

Cajophora (Loasaceae).

C. coronata germ. 70L(30% in 2nd w). All rotted in 70D or when started at 40.

C. laterita germ. 70D(50% on 12th d) and 40-70D(none). Light and GA-3 had no effect.

Calamagrostis (Poaceae). See Chapter 22.

Calandrinia (Portulacaceae)

C. caespitosa germ. 40(33% in 7-9 w)-70(29% in 6-10 d) and 70-40(1/18 in 4th w). Sowing at 70 is deleterious.

C. grandiflora germ. 70(100%, ind. t 2 d, 21%/d) and 40(50% in 3rd m).

C. umbellata germ. 70(95% in 4-14 d) and 40(84% in 7-10 w).

Calceolaria (Scrophulariaceae). *C. falklandica* germ. 70(50%, ind. t 2 d, 8.5%/d) and 40(63%, ind. t 40 d, 2%/d)-70(7%).

Callianthemum (Ranunculaceae). Four samples of DS seed failed to germinate, and this is probably one of the Ranunculaceae that cannot tolerate DS.

Callicarpa (Verbenaceae). It is puzzling that *C. dichotoma* germ. in 70D whereas *C. callicarpa* had a photorequirement for germination.

C. dichotoma germ. 70(40% in 2-5 w).

C. japonica requires light for germination. Fresh WC seed or seed DS 6 m at 70 either in the WC state or in the dried berries (followed by WC before starting) all germ. 90-95% in 70L with identical rate behavior of ind. t 11 d, first order rate, and half life of 2 d. Extending the DS to 12 m at 70 germ. almost the same, but the rate slowed to a 7 d half life. All dark treatments gave either zero or very low germination, and all prior exposure to dark treatments lowered either the rate or percent germination. For example a preliminary 3 m at 40 caused germination (in 70L) to be more extended and occur over 1-7 w, and a prior 5 w in 70D lowered germination (in 70L) to 20-25%.

Callistemon (Myrtaceae). Seeds are small and difficult to count.

C. sp. New Zealand germ. 70D(37% in 1-4 w), 70L(78% in 4-15 d), and 70D with GA-3(72% in 8-17 d). These apparent differences in percent germination may not be significant. It also germ. 70% in October from seed placed outdoors in late Sept.

C. speciosus germ. 70D(50% in 1-4 w), 70L(78% in 4-15 d), 70D GA-3(37% in 8-12 d), 40(100% in 3rd w), and 100% in October from seeds placed outdoors in Sept.

Calluna (Ericaceae). *C. vulgaris* germ. 70D GA-3(52%), 70L(14%), 70D(4%), and 40(none) in 3rd w. Data for only first 6 w.

Calochortus (Liliaceae). These germ. at 40 like many cold desert plants. Sowing at 70 is harmful. Even a brief 4 w at 70 could lower germination and produce seedlings that did not grow well.

C. aureus germ. 40(100% in 3-5 w) and 87% in early March in outdoor treatment. None germ. at 70, even 4 w at 70 reduced the germ. at 40 to 79% in 2-11 w.

C. gunnisonii germ. 40(72% in 4th w) and 76% in early March in outdoor treatment. None germ. at 70, even 4 w at 70 reduced the germ. at 40 to 83% in 3-9 w. These results are for a sample collected at 7000 feet. A sample collected at 9000 feet germ. in lower percentage and in a more delayed manner.

C. sp. Oregon germ. 40(91% in 6-10 w), 70-40(17%)-70(33%), and 12% in outdoor treatment. However, this is not the whole story as only those germ. in the initial cycle at 40 went on to grow well. The others tended to die off.

C. sp. Oregon (Siskiyou Mtns.) germ. 40(3/3 in 7-10 w) and 70-40(1/3 in 9th w). As with the previous species, the seeds germ. in the initial cycle at 40 developed better. Seed DS 6 m at 70 germ. 40(5/5 in 5-12 w).

Caloscordum (Liliaceae). *C. neriniflorum* germ. 70(3/6 in 2nd w, epigeal).

Calothamnus (Myrtaceae). *M. quadrifidus* germ. 70L(30% in 1-5 w), 70D GA-3(30% in 4-15 d), 70D(8%), 40(22% in 5th w), and 30% in October and November with seeds placed outdoors in September. The differences in percent germinations may not be significant because of difficulties in counting the seeds.

Caltha (Ranunculaceae).

C. palustris sown outdoors in April germ. in the following April.

C. leptosepala germ. best (4/8) in outdoor treatment, less in 70(1/8)-40-70(2/8), and none in 40-70 treatment.

C. biflora germ. 40-70(1/8 in 7th w) and none in 70-40.

Calycanthus (Calycanthaceae). *C. floridus* collected in January germ. 70(84-87% in 2nd w) and 40-70(81-93% in 3rd d) using either fresh seed or seed DS 6 m at 70 or 40.

Calylophus (Onagraceae). *C. lavandulifolius* germ. 95% in 3-5 d in either 70L or 70D, 40-70(100% in 3rd d), and 70% in April in outdoor treatment. Seeds treated with GA-3 germ. 92% in 5-7 d at 70, which is slower than untreated seeds.

Calyptridium (Portulacaceae). *C. umbellatum* germ. best in 70L(60% in 1-3 w) and none in 70D. Germination also occurs at 40(35% in 3rd w) in the dark. Interestingly, when this latter sample was shifted to 70 after the 3 m at 40, the half placed in light germ. an additional 46% whereas there was no further germination in the half kept in 70D. This curious situation needs further study.

Camassia (Liliaceae). *C. leichtlinii* and its var. *suksdorfii* gave the same results. Both germ. best in 40(100% in 5-14 w) using either fresh seed or seed DS 6 m at 70 or 40. A preliminary 3 m at 70 lowered the percent germination to as low as 40% in one sample. Germination is hypogeal. The leaf does not develop properly unless the seedling is kept at least 2 m at 40 after germination.

Campanula (Campanulaceae). Most species are D-70 germinators. There are some that are 40-70 germinators and photorequirers and *C. americana* required both 3 m at 40 followed by light at 70. There were other complexities. Two species (*C. alliarifolia* and *altaica*) showed some deterioration of the seed on DS. In the following species DS seed germ. in 2-4 w at 70: *C. allioni*, *alpina*, *aucheri*, *barbata*, *bellidifolia*, *cochlearifolia*, *collina*, *finitima*, *formanekiana*, *gracilis*, *garganica*, *glomerata*, *hawkinsiana*, *jenkinsae*, *linifolia*, *longistyla*, *moesica*, *napuligera*, *pilosa*, *pulla*, *raddeana*, *sarmatica*, *saxifraga*, *scheuzeri*, *steveni*, and *tridentata*.

C. alliarifolia is primarily a 40-70 germinator as shown by 40-70(70% in 3-17 d) for seed DS 6 m at 70 and 40-70(40% in 5-15 d) for fresh seed. A curious divergence appeared in the 70-40-70 treatment. Fresh seed germ. 70(2%)-40-70(98% in 3-5 d) whereas the DS seed germ. none

C. altaica is a 40-70 germinator with fresh seed as shown by 40(6%)-70(68%, ind. t 2 d, 14%/d). A prior 3 m at 70 had an inhibiting effect as shown by 70-40-70(4%)-40-70(40%). This is one of the rare examples where a germination inhibitor may be formed after the seed is dispersed. DS for 6 m at 40 destroyed inhibitors much like 3 m moist at 40 as shown by 70(30%, ind. t 2 d, 25%/d) and 40(8%)-70(40%, ind. t 2 d,

25%/d). All seed was dead after DS 6 m at 70. This is one of the rare examples of a big difference between DS at 40 relative to DS at 70.

C. americana requires DS 12 m at 70 or 40, an initial 3 m at 40, and light at 70 to get the optimum germination of 100%(in 5-8 d). The DS factor is least important and germination is still 60% if the DS is omitted. Omission of the 3 m at 40 or the light leads to total failure in germination.

C. betulaefolia germ. in 3-8 w at 70.

C. caespitosa germ. in 1-3 w at 70.

C. carpathica germ. 70(70-85% largely on 7th d) and 40(25%)-70(3%) using seed DS 6 m at 70 or 40 whereas fresh seed germ. under 8% over several cycles whether sown at 70 or 40. This species is a D-70 germinator.

C. cashmeriana germ. in 5-7 d when sown at 70. Neither light nor a prior 3 m at 40 had any effect on the germination at 70.

C. cenisia germ. in 4-12 w at 70.

C. chamissonii germ. 70(10% in 3rd w) and none in 40-70. Light had no effect.

C. coriacea germ. 68% in 6-12 d in either 70D or 70L and 40-70(3/16 in 2nd w).

C. glomerata acaulis germ. 70L(90% in 6-8 d), 70D(97% in 1-8 w), and 40-70D(none). The slower germination in 70D could have been a temperature effect due to light absorption. The complete failure to germinate when started at 40 is striking, and this is a fatal treatment.

C. latiloba germ. 40(3% in 10th w)-70(1%) and 70-40(none). The seeds had been DS for several years and were largely dead.

C. linearifolia germination showed some stimulation by both light and GA-3. Seeds germ. 70L(100% in 8-10 d), 70D GA-3(100% in 10-16 d), 70D(28% in 8-18 d), 40-70L(24% in 2nd w), and 40-70D(none).

C. lyrata germ. 70(85% in 1-5 w) and 40(64% in 6-9 w).

C. medium germ. immediately at 70.

C. ossetica has an absolute photorequirement for germination. The seeds germ. 70L(50% in 1-3 w), 70D(none), 40-70L(90% on 6th d), and 40-70D(none).

C. pallida germ. 70(10%)-40-70(30%) and 40(30%)-70(20%).

C. persicifolia is a D-70 germinator and germ. 70(71% in 9-13 d) for seed DS 6 m at 70 compared to 70-40(2%)-70(31%) for fresh seed. Germination was more extended for seed sown at 40 as shown by 40(11%)-70(4%) for DS seed and 40(1%)-70-40(51%)-70(9%) for fresh seed. Seed DS 6 m at 40 was intermediate in behavior.

C. punctata germ. best in 70L(80% in 6-12 d) and less in 70D(35% in 6-12 d). This photoeffect diminishes on DS, and seed DS 6 m at 70 germ. 80-90% in either 70L or 70D. Starting seed at 40 gave less than 10% germination with fresh seed, but the DS seed germ. 40(50% in 3-8 w).

C. pyramidalis germ. 70(100% in 2-6 d) and 40(5%). Light had no effect.

C. ramosissima germ. 70L(95%, ind. t 5 d, half-time 1.0 d in a first order rate), 70D(15% and six times slower), and 40(15% in 8th w) using seed DS 6 m at 70. Fresh seed did not germinate at 40, 70L, or 70D showing that DS was essential.

C. rapunculoides is like *C. americana* in that DS 6 m at 70 or 40, an initial 3 m at 40, and light at 70 all promote germination. Omission of either the DS or the 3 m at 40 causes total failure. Germination of 90% can be achieved in the following three ways: fresh seed in 40-70L(90% in 2-4 d), fresh seed in outdoor treatment with germination in February through April, and DS seed in 70L(90% in 3-7 d). Other treatments including certain dark treatments give satisfactory (but not optimum) germination. For example 40-70D(40%) for fresh seed and 70D(60-80%) for DS seed.

C. rotundifolia germ. 70(65% in 1-8 w) for seed DS 6 m at 70 or 40 in contrast to 70(4%)-40(32%)-70(45%) for fresh seed. Seed sown at 40 failed to germinate.

C. sarmakadensis germ. 70L(100% in 2nd w), 70D GA-3(100% in 2nd w), 70D(6% in 2nd w), and 40(50% in 2nd w).

C. scabrella germination was strongly promoted either by light or by GA-3. The data are 70L(40% in 2-8 w), 70D GA-3(56% in 2nd w), and 70D(7% in 2-8 w). The seedlings from GA-3 promoted germination were normal, however the GA-3 treatment is unnecessary in view of the good germination in 70L. The above data is for seeds DS one y at 40. Seeds collected from the same source and DS 3 y at 70 germ. 70L(11%) and 70D(none) showing that there had been significant deterioration of the seeds in the longer DS. A preliminary 3 m at 40 had no effect.

C. sibirica germ. 70(70-85% in 6-25 d) and 40(10%)-70(75%) using seed DS 6 m at 70 or 40. Fresh seed germ. less than 10% in several cycles.

C. spicata germ. 66% in 2nd w in either 70L or 70D and 40(61% in 3-7 w).

C. takesimana is closely related to *C. punctata* and exhibited a similar disappearance of the photorequirement on DS. Fresh seed germ. 70L(78% in 6-10 d) and none in 70D, 40-70D, or 40-70L. This failure to germinate in 40-70L shows that an initial 3 m at 40 is fatal. Seed DS 6 m at 70 germ. 100% in 6-8 d in either 70L or 70D and 40(11% in 3-5 w).

C. taurica germ. 40% in 1-6 w in either 70D or 70L.

C. trautvetteri germ. 70(85-90% in 2nd w) and 40(1%)-70 showing that starting at 40 is a fatal treatment. Light had no effect.

Campsis (Bignoniaceae). *C. radicans* requires light to germinate. The seed is in the shape of two connected circular disks covered with a thin tan membrane, a structure suited for photoresponses. After being moist for a day, the membrane can be readily removed. Such seeds are termed stripped to distinguish them from unstripped seeds. At the end of 2 m after sowing at 70, germination in the dark was zero whereas germination in the light was 80% for both stripped and unstripped seed with the ind. t for stripped seed being 3 w and the ind. t for unstripped seed being 6 w showing that the membrane was significantly shielding the embryo from the light. The rate of germination for both stripped and unstripped seed was 3%/d. Seeds sown in dark ultimately gave a little germination. When sown at 40, there was 10% germination over four cycles, a total of one year. Germination was erratic and occurred at both 40 and 70 indicating that the germination was perhaps due to the brief exposures to light which occurred on taking observations. No germination occurred when the seed was sown in dark at 70. The seed was collected November after it had already been subjected to drying outdoors. A further 6 m DS at 70 or 40 had no effect on germination patterns or rates, but seeds DS 2 y at 70 were all dead.

Canna (Cannaceae). *C. indica* has an impervious seed coat (J H).

Capparis (Capparidaceae). *C. spinosa* germ. 70 GA-3(2/31 in 3rd w) and none in the first month in 70D, 70L, or 40. Data for only first 6 w.

Capsicum (Solanaceae). *C. frutescens* was studied using the commercial sweet green, red, and yellow peppers. Seeds germ. 70D(100% in 9-11 d) after removal from the fruit and a brief WC of as short as 2 hours. Light or GA-3 had no effect. The seeds contact the flesh of the fruit through a narrow attachment. Presumably inhibitors are transmitted through this attachment.

Cardiocrinum (Liliaceae). *C. giganteum* requires several cycles before germination starts, and only fresh seeds have germ. Germination is epigeal and so far light and GA-3 have not stimulated germination. A sample sent from a self sowing colony in British Columbia germ. 40-70-40-70(2% in 1-7 d)-40(97% in 5-11 w) and 70-40-70(5%)-40(5%)-70(7%). A sample from New York State germ. 70L-40-70D(25% on 7th d)-40(30% 9-12 w) and 70D-40-70D-40(25% in 8th w)-70D(50% in 2nd w). The stems had been cut before frost, the seeds ripened indoors, and the seeds sent to me immediately. Twenty five other samples have been received over the years without a single germination. However, the extended germination pattern had not been appreciated, and it is possible that DS is not tolerated.

Cardiospermum (Sapindaceae). *C. halicacabum* germ. 70D GA-3(4/5 in 3rd w), 70L(5/5 in 3rd w), 70D(1/6 in 4th w), 40-70D(1/3), and 40-70L(0/3). Germination is stimulated by light or GA-3, and 3 m at 40 is harmful.

Carica (Caricaceae). *C. papaya* required WC (7 d) and either light or GA-3. Seeds germ. 70L(43% in 2nd w), 70D GA-3(95% in 3rd w), and 70D(none). The photorequirement was surprising in view of the jet black color of the seeds. Part of the samples in 70D and 70L were treated with GA-3 after 4 w whereupon the remaining seeds germ. 90-100% in the 2nd w after the GA-3 treatment. A prior 3 m at 40 was nearly fatal as shown by 40-70L(10%), 40-70 GA-3(none), and 40-70D(none).

Carlina (Asteraceae). *C. acaulis* has an absolute photorequirement and germ. best in 70L(3/9 in 1-3 w) and 40-70L(2/4 on 6th d) and none in 70D or 40-70D.

Carthamus (Asteraceae). *C. tinctorious* germ. 43% in 3-10 d in either 70L or 70D and 40(67% in 4th w).

Caryopteris (Verbenaceae). *C. incana* showed some deterioration on DS. Fresh seed germ. 70(73%, ind. t 3 d, 53%/d) and 40(6%)-70(94%). Note the unusually fast germination rate at 70. Seed DS 6 m at 70 or 40 germ. 70(30%) and 40(10%)-70(35%).

Cassiope (Ericaceae). *C. fastigiata* germ. only in light as shown by 70L(44% in 4th w) and none in 70D. After 4 w in 70D, the sample was shifted to 70L whereupon 8% germ. showing that the seed is rapidly dying in 70D. A prior 3 m at 40 was fatal.

Castilleja (Scrophulariaceae). There have been suggestions that *Castilleja* seed is difficult to germinate and that chemical exudate from the roots of host species (*Castilleja* are parasitic) are needed to induce germination. None of this is in accord with the results herein, and patterns were found that gave excellent germination without the addition of any exogenous chemical. Most of the species germinate largely at 40. The seedlings grow vigorously until the stem has elongated to the point of producing 5-10 true leaves. Then the seedlings lose vigor and die off showing the need for a host plant. These conclusions were based on studies on

seventeen samples. No photoeffects were found in five experiments. Although the germination of the seed occurs without any exudate from a host, it is still possible and perhaps probable that an exudate from a host is required for the development of the haustoria. DS is tolerated for a y, but seeds DS for 4 y were all dead.

C. integra germ. 100% at both 70 (ind. t 2 d, 26%/d) and 40 (ind. t 10 d, 4%/d). Light had no effect nor did DS for an additional year.

C. miniata germ. best in 70(3%)-40(88% in 3-11 w) and less in 40(22%)-70(4%). This latter pattern might have given more germination if extended for another cycle. Germination was unaffected by light.

C. parviflora germ. 70D(15% in 1-5 w) and 40-70(4%).

C. rhexifolia germ. 70-40(3%) and none in 40-70-40-70.

C. sp. Colorado germ. 40(90% in 8-12 w) and 70(none) in each of two samples.

C. sp. (Kelaidis 2740) germ. 40(80% in 8-11 w) and 70-40(80% in 8-11w).

Seed stored an additional year at 70 gave lower and more extended germination as shown by 40(16%)-70(5%) and 70(1%)-40(20%)-70(3%).

C. sp. (Kelaidis 2750) germ. only at 40 as shown by 40(80% in 8-10 w) and 70-40(80% in 8-10 w). Seed stored an additional year at 70 gave lower and more extended germination as shown by 40(2%)-70(11%) and 70-40(66%)-70(14%).

C. sp. dwarf germ. 70-40(8%) and 40-70(4%).

Catalpa (Bignoniaceae). *C. bignonioides* required light, GA-3, or DS for germination. The data for seed collected in October were 70L(100% in 1-3 w), 70D GA-3(100% on 6th d), and 70D(none). The light requirement gradually disappears on DS. For example seeds collected in March (already extensive DS) germ. 70(44%)-40(2%)-70(47%) and 40-70(32%) and the same seeds given a further 6 m DS at 70 germ. 70(76%) and 40-70(94%). Where germination was incomplete, the remaining seeds would germinate immediately on shifting to 70L even after three dark cycles.

Caulophyllum (Berberidaceae). *C. thalictroides* was reported to germinate 10% or less after extended time (ref. 28, Ch. 10). Shoot development was reported to be a further problem, and the shoot must develop to a certain stage at 70 before 3 m at 40 and a return to 70 will result in further development. The seed is in a blue berry and was WC 7 d. The only germination in my work resulted from a year of alternating cycles after which the seed was placed outdoors in October whereupon 2/7 germ. the following April. Neither seedling developed normally. Neither light or GA-3 initiated germination.

Ceanothus (Rhamnaceae). *C. americana* seed was removed from the stiff husk. Germination is best (41%) in outdoor treatment with half of the germination occurring in September through November and the other half in March. A 40-70 treatment was almost as good as shown by 40(1%)-70(28% in 1-21 d), but 70(1%) was nearly fatal. Germination of seed DS 6 m at 40 or 70 was similar to fresh seed as shown by 70(5%)-40-70(8%) and 40(1%)-70(14% in 2-10 d)-40-70(3%). The results show that germination is promoted by oscillating temperatures.

Cedrus (Pinaceae). *C. atlantica* germ. 40(4/6 in 6th w) and 70(1/6 in 12th w). Sowing at 70 was deleterious.

Celastrus (Celastraceae). *C. scandens* germ. 100% in all six standard patterns after the seed was WC. Germination at 70 was in 10-20 d and germination at 40 was in 5-8 w. The berries can be collected anytime during the winter. Seeds DS for 2 y in the dried fruit germ. only 4% and was almost all dead.

Celmisia (Asteraceae). These are reputed to be poor germinators, but in fact they are immediate germinators at 70 of the D-70 type. Past problems have been the result of a preponderance of empty seed coats. Samples of wild collected seeds of *C. armstrongii*, *C. monroi*, *C. semicordata*, *C. spectabilis*, and *C. traversii* were started at 70 with and without GA-3 treatment. The germinations were respectively 2/8 and 1/9, 1/4 and 3/5, 0/9 and 1/8, 3/15 and 2/17, and 1/20 and 0/16. All germinations occurred in the 2nd w. A small sample of *C. dallii* germ. one seed in the 5th w at 70. The GA-3 does not seem to have any significant effect.

Celtis (Ulmaceae). *C. tenuifolia* germ. best with seed DS 6 m at 40 and sown outdoors in May. This germ. 65% the following April and May. It is not just the outdoor treatment as fresh seed sown outdoors in November germ. only 2% the following May. The standard treatments gave germination that were not only low, but germination extended over at least nine alternating cycles with most of the germination occurring in bursts near the end of these extended alternating cycles. The data are 70-40-70(2%)-40-70(6%)-40-70-40-70(14%) and 40-70(1%)-40(1%)-70(8%)-40(1%)-70(1%)-40-70(29%)-40-70(2%) for fresh seed, 70(3%)-40-70-40-70-40-70(13%) and 40-70-40-70(14%)-40-70(12%) for seed DS 6 m at 70, and 70(3%)-40-70-40-70-40-70(5%) and 40-70-40-70(12%)-40-70 for seed DS 6 m at 40. Producing a hole in the seed coat had no effect on germination. All seed was WC for 7 d before sowing or before DS. The cotyledon develop in a week or two after germination. A remarkable verification of the efficacy of oscillating temperatures and outdoor treatment was that the sample started at 70 had a total of 22% germ. and 8% rotted after 2 years. At that time the sample was shifted to outdoors in late November whereupon the remaining 70% germ. the next March.

Centaurea (Asteraceae). *C. maculosa* seed was collected in October. Seed DS 6 m at 70 germ. best as shown by 70(73% in 2-8 d) and 40(34% in 3-8 w). Fresh seed germ. 70(20% in 2-24 d) and 40(7%)-70(20%). Light had no effect. The seeds had already been exposed to a month or two of DS in the seed capsule when collected. The data show that an additional 6 m of DS at 70 is desirable.

Centaureum (Gentianaceae).

C. erythraea germ. 70(55-70%, ind. t 18 d, 3%/d) and 40-70(80-85% in 2-3 d) for seed DS 6 m at 70 or 40 and 70(1%)-40-70(38%) and 40-70(18%) for fresh seed.

C. meyeri germ. in the 2nd w at 70.

C. pulchellum requires both DS and light for germination. Seeds DS 2 y at 70 germ. 70L(100% in 9-12 d), 70D GA-3(100% in 2nd w), and 70D(none). Shortening the time of DS lowered the percent germination. Seed DS 6 or 12 m at 70 germ. 70L(80% in 2-4 w). Outdoor treatment germ. 42% in April. Not a single seed germ. in 70D, 40-70D, or 40-70L with the DS seed or in 70D or 70L-40-70L with fresh seed showing that DS as well as light (or GA-3) are required for germination.

C. scilloides germ. 70L(92% in 2-4 w) and 70D(15% in 2-4 w) for fresh seed and 70L(70%) and 70D(2%) for seed DS 6 m at 70. This promotion of germination by light was largely eliminated by an initial 3 m at 40 as shown by 40-70L(100% in 5-6 d)

and 40-70D(87% in 3rd w) for fresh seed and 40-70L(92%) and 40-70D(20%) for DS seed. However, the germination rate was greater in the light showing that even in the 40-70 pattern there was still some residual photoresponse.

Centranthus (Valerianaceae). *C. ruber* germ. 70(100% on the 3rd d) and 40(100% in 4-6 w). Light had no effect.

Cephalanthus (Rubiaceae). *C. occidentalis* has an absolute light requirement for germination, and none germ. in the dark as shown by 70L(80-90% in 1-3 w), 40-70L(80-90% in 1-3 w), and none in 70D or 40-70D. Results were the same for fresh seed or seed DS 6 m at 70 or 40.

Cephalaria (Dipsaceae). *C. leucantha* germ. 70L(70% in 1-7 w), 70D(56% in 1-5 w), 40(57% in 2-6 w), and 50% in April in outdoor treatment. It is interesting that the rate of germination at 40 and at 70 are equal.

Cerastium (Caryophyllaceae). The five species (*C. alpinum*, *candidissimum*, *maximum*, *montanum*, and *uniflorum*) were D-70 germinators and germ. in 2-6 w at 70.

Cercidiphyllum (Cercidiphyllaceae). *C. japonicum* germ. best with fresh seed in 40-70(50%, ind. t 3 d, 10%/d) and 70(1%)-40-70(71%). DS both lowers and extends germination as shown by 70(9%)-40-70(13%) for seed DS 6 m at 40 and 70(1%)-40-70(21%)-40-70(33%) for seed DS 6 m at 70.

Cercis (Fabaceae).

C. canadensis alba germ. fastest when a hole was made in the seed coat. Germination was 35% in 5-12 d at 70. The abrasion seemed to injure some of the seeds as the remaining 65% soon rotted. Untreated seeds gave higher overall germination as shown by 40-70(35%)-40-70(46%) and 70-40-70(71%) for both fresh seed and seed DS 6 m at 70 or 40. Presumably the technique of producing the hole in the seed coat could be refined to give higher germination.

C. chinensis germ. best in a 40-70 pattern. The actual percentages varied with fresh seed and seed DS 6 m at 70 or 40, but the differences may be of little significance since the temperature cycles may be acting to open microfissures in the seed coat. Thus ranges will be given. These were 70-40-70(15-45%) and 40(3-30%)-70(20-40%)-40-70(10-50%). Abrading a hole in the seed coat led to complete rotting of the seed. Attempts to refine this technique should be made as it seems that the seed has an impervious seed coat.

Cercocarpus (Rosaceae). *C. betuloides* germ. 70D(85% in 2nd w) and 40(75% in 2-4 w). Light or GA-3 had no effect.

Chaenactis (Asteraceae). *C. douglasii* germ. 100% in 4-10 w when sown at 40. When sown at 70, germination was 100% but extended over three cycles.

Chaenomeles (Rosaceae). *C. japonica* germ. best in 40(86%, ind. t 52 d, 5%/d)-70(14%) for fresh WC seed. DS causes deterioration, faster at 70 naturally, as shown by 40(80%) for seed DS 6 m at 40 and 40(50%) for seed DS 6 m at 70. The most striking result with this species was that an initial 3 m at 70 was totally fatal either for fresh or DS seed.

Chaenorrhinum (Scrophulariaceae). *C. oreganifolium* germ. 70L(41% in 1-5 w), 70D(11% in 5-8 d), and 40(2%)-70(2%). The data suggests that light promotes germination and that the germination in 70D may have been due to exposure of the dry seed to light.

Chamaechaenactis (Asteraceae). *C. scaposa* germ. 70(100% in 7-9 d) and 40(100% in 6-8 w).

Chamaecytisus (Fabaceae). *C. austriacus* germ. 100% in 2-3 d at 70 providing a hole was made in the seed coat. Without this treatment only 22% germ. over 6 w at 70 and 42% germ. over 3 m at 70. The seeds are typical of many legumes in having an impervious seed coat, but in this species the seed coat breaks down faster than most in moist conditions.

Cheiranthus (Brassicaceae). *C. cheiri* germ. 70(60-85% in 2-18 d) and 40(60-85% in 3rd w) for either fresh seed or seed DS 6 m at 70 or 40.

Chelidonium (Papaveraceae). *C. majus* germ. 70(48% in 2-7 w)-40(3%)-70(3%). Fresh seed sown at 40 or DS seed sown at either 70 or 40 all rotted and these are fatal treatments.

Chelone (Scrophulariaceae). *C. glabra* requires light. DS seed germ. 70L(50% in 3-8 w)-40-70L(24%), 70D(none), 40-70L(17%), and 40-70D(none).

Chenopodium (Chenopodiaceae). *C. ambrosioides* germ. 70L(10% in 2-6 w), 70D(0.75%), and 40(4% in 5-12 w)-70D(2%). Light promotes germination.

Chiastophyllum (Crassulaceae). *C. oppositifolia* germ. only in 70D GA-3 (60% in 3-12 w). None germ. in 70D or 70L. A prior 3 m at 40 had no effect.

Chilopsis (Bignoniaceae). *C. linearis* germ. 70D(100% on the 3rd d) with fresh seed. Germination declined to 50% in seed DS 6 m at 40 and to 15% for seed DS 6 m at 70. The deterioration of the seed in DS is faster at 70 than at 40.

Chionanthus (Oleaceae). *C. virginica* is both a 70-40-70 and a two step germinator. Seed germ. best in 70-40-70(52% in 5-10 w)-40(4%)-70(28% in 5-7 w) for fresh seed and 70-40-70(45% in 5-10 w)-40(9%)-70(46% in 6-10 w) for seed DS 6 m at 70. A preliminary 3 m at 70 had little effect as shown by 40-70(4%)-40-70(58% in 4-8 w) for fresh seed and 40-70-40-70(15% in 4-6 w) for seed DS 6 m at 70. Outdoor treatment of fresh seed germ. only 4% in October thirteen months later from seed planted outdoors in September. It is expected that more will germinate in the next year paralleling the 70-40-70 pattern. All seeds were WC for 7 d before planting. A stout radicle forms and lengthens to four inches with branching rootlets. Growth then stops. The optimum treatment after that has not been completely determined. After two months at 70 some of the seedlings send up a stem with leaves, but the stem and leaf development are more certain if the seedlings are given 3 m at 40 and shifted to 70. Seeds are enclosed in a berry and require WC. The above results were confirmed with seeds collected the following year. Puncturing the seed coat has no effect, and so far GA-3 has not promoted germination.

Chionodoxa (Liliaceae). *C. luciliae* self sows abundantly here and seed was plentiful. Seed was collected in three successive years. The three consistent results were (a) all DS seed rotted (DS is fatal), (b) seed WC for a week to remove the aril germ. much better than unwashed seed, and (c) the cycles at 40 should be extended to 4-5 m instead of the usual 3 m. Seed collected in May 1989 and WC germ. 70-40(50% in 12-16 w)-70-40-70(15%). The first 40 cycle was extended to 16 w as evident from the data, and the last 15% that germ. at 70 would probably have germ. in the preceding 40 cycle if it had been extended beyond 4 m. Unwashed seed germ. 70-40-70(7%)-40(10%), but the cycles at 40 should have been extended beyond 3 m, and the experiments need repeating. The 1989 and 1988 collections should have

been given outdoor treatment because the 1990 seed germ. 22% in March in outdoor treatment. Cotyledons developed normally only if the seedlings were left for 1-2 m at 40 after germination before the shift to 70.

Chloranthus (Chloranthaceae). Five samples of seeds including four species all rotted. Are they intolerant of DS?

Chlorogalum (Liliaceae). *C. pomeridianum* germ. 40(74% in 2-4 w) and none in 70D, 70L, 70 GA-3, or 40. The data is for the first 6 w only.

Chrysanthemum (Asteraceae). The following species are D-70 and germ. in 1-4 w at 70: *C. djilgense*, *koreanum*, and *pyrethroides*.

C. leucanthemum germ. 70(100% in 4-10 d) and 40(10%)-70(40%) for both fresh seeds and seeds DS for 6 m at 70 or 40.

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C. leucanthemum germ. 70(100% in 4-10 d) and 40(10%)-70(40%) for both fresh seed and seed DS 6 m at 70 or 40.

Chrysopsis (Asteraceae). *C. villosa* germ. in 3-20 d at 70.

Cichorum (Asteraceae). *C. intybus* germ. better in 70L(6/13 in 8-14 d) than in 70D(1/10), 40-70D(none), or outdoor treatment (1/12). The photopromotion was largely removed by DS for 6 m at 70 as shown by 70L(53% in 2-12 d) and 70D(40% in 1-9 d).

Cimicifuga (Ranunculaceae). *C. racemosa* germ. best with DS seed in 70-40(100% in 5th w) for seed DS 6 m at 70, 70-40(90% in 5-8 w) for seed DS 6 m at 40, and 70-40(15%)-70-40(85% in 4th w) for fresh seed. An initial 3 m at 40 had little effect as shown by 40-70-40(100% in 5-7 w) for fresh or DS seed. Radicle development is complete at 40, but the two cotyledons do not develop until the temperature shift to 70. Curiously all seed rotted in outdoor treatment, and most rotted in GA-3 treatment.

Circaea (Onagraceae). *C. lutetiana* germ. 70L(5%), 70 (GA-3)-40-70(2%), 70D(none), none in 40-70D or 40-70L, and 10% in early April in outdoor treatment. The seeds were collected from a large colony.

Cistus (Cistaceae). *C. laurifolius* germ. 70(60% in 5-16 w) and 40-70(80% in 1-12 d).

Citrullus (Cucurbitaceae). *C. vulgaris* is the watermelon. Fresh seeds require light or GA-3, but these requirements disappear on DS. Two strains of commercial seed were obtained in April and had been DS for about 6 m. These germ. 70-90% in either 70L or 70D. In contrast, fresh seeds WC for 10 minutes germ. 70L(90% in 5-16 d), 70D GA-3(50% in 5-22 d), and 70D(none). Part of the sample in 70D was shifted to 70L after 2 w whereupon 90% germ. in the 3rd d confirming the effect of light. Fresh seeds WC for 7 d gave about half as much germination. The efficacy of just 10 minutes WC suggests that there are no inhibitors in the fruit. DS for 2 m at 70 does not affect the 100% germ. in 70L, but the germ. in 70D increases to 13% in 2nd w confirming the disappearance of the light requirement on DS.

Citrus (Rutaceae). *C. nobilis*, the tangerine, germ. 70L(85% in 4-13 w), 70 GA-3(86% in 4-6 w), and 70D(80% in 8-13 w).

Cladastris (Fabaceae). *C. lutea* germ. 95-100% at either 70 or 40 using fresh seed shelled from the pods while the pods were still slightly green. Germination at 70 was in 3-7 d, and germination at 40 was in 3-8 w. Seed DS 6 w at 70 germ. 70(12% in 1-4 w)-40-70(28%). Seed DS 6 m at 70 germ. 70(6%), but if a hole was made in the seed coat, it germ. 70(80% in 3-5 d). Clearly DS hardens the seed coat making it impervious.

Clarkia (Onagraceae). *C. amoena* germ. 100% in 4-10 d in 70D, 70L, or 40. Note the very fast germination at 40.

Claytonia (Portulacaceae).

C. megarhiza germ. in spring after sowing outdoors in October. Seed that had been DS for several years at 70 germ. immediately at 70, but only 2%.

C. virginica germ. 70-40(79%) and 40-70-40(78%)-70 using fresh seed. All DS seed rotted and DS is a fatal treatment.

Clematis (Ranunculaceae). Light and/or GA-3 are required for the germination of some species. Although a number of species germ. significantly in the dark, light and GA-3 needs to be tried on all species. Multicycle patterns were common and some species germ. largely at 40. The seeds of all species are designed to be dispersed by wind so that it was presumed that DS would be tolerated. This was supported by the data for seeds DS 6 m, however seeds of *C. virginiana* that had been DS at 70 for 2 years were all dead.

C. addisonii germ. 70D GA-3(65% in 7-11 w). None germ. in 70D, 70L, 40-70L, or 40-70D. Even 8 w in 70D or 3 m at 40 and a shift to 70 GA-3 led to total rotting. Seeds DS 6 m at 70 germ. 70 GA-3(60%) and none in 70D or 70L.

C. albicoma var. *coactilis* germ. 70(25% in 8-10 w) and 40-70(20% in 9th w)-40(10%). Germination is epigeal, and the cotyledons develop in 1-2 w after germination. No further leaf development occurs in the first year. DS for 6 m at 70 was injurious, and such seed germ. 70(7%) and 40-70(none). Light did not seem to have an effect, but the sample was small and this needs to be checked.

C. alpina germ. 70-40(80% in 5-11 w) whereas seed sown at 40 all rotted.

C. columbiana required light for germination and germ. 70L(50% in 2-10 w) and none in 70D, 40-70L, or 40-70D using either fresh seed or seed DS 6 m at 70. An initial 4 w in 70D had no effect on the germination in 70L. Seeds treated with GA-3 rotted in a month. A sample from a year earlier germ. 40-70(8% in 6th w)-40(46% in 6-10 w)-70(8% in 2 d) and 4% after three cycles when started at 70.

C. connata germ. 40(6% in 12th w)-70(12% in 3-20 d) and 70(14% in 2-6 w)-40-70(1% in 3rd w). After 10 w in this last cycle the seed was shifted to light whereupon 9% germ. in 4th w suggesting that germination might have been greater if the seed had been given 70L directly. It is likely that DS is not tolerated well because not only was germination low in the above sample, but another sample totally rotted in all treatments.

C. crispa germ. 1/2 at 40 in the 5th cycle starting at 40. Six seeds sown at 70 all rotted.

C. forsteri germ. 70 (GA-3)-40(6/8 in 12th w), 70D(1/7)-40-70D, and 40-70D-40(none). Light should be tried.

C. grata required either light or GA-3 for germination. Seeds germ. 70L(63% in 3-8 w), 70 GA-3(50% in 2nd w), and 40-70L(68% in 1-5 w). None germ. in 70D, 40-70D, or outdoor treatment.

C. hirsutissima is a 40-70 germinator and is unaffected by light. The meagre data were 40-70(2/3 in 8-11 w), 70-40(1/5 in 4th w), and 70L(1/7 in 10th w)-40-70L(1/7).

C. integrifolia germ. 30% in the 6th w in either 70D or 70L. Removal of the seed coat had no effect. A preliminary 3 m at 40 germ. faster (3rd w at 70), but the percentage was still 30%.

C. ladakhiana germ. 70D(87% in 2nd w) and 40(25% in 10-12 w)-70(60% in 2 d). Germination was so rapid in 70D that it is doubtful that light or GA-3 would have any effect.

C. lanuginosa hybrid seed was collected in October. The plumes are abundant on all seed heads whether or not there is any good seed. The good seed is evident as the seed coat is relatively large being disk shaped and about 8-10 mm. across. Seed germ. in the dark albeit after several cycles. The seedlings show the same behavior as described for *Abeliophyllum distichum*. The radicle develops to a length of 3-4 inches. Growth ceases for 2-3 m after which stem and leaves form in a hypogeal germ. Chilling or any other treatment does not accelerate this process, and the best treatment is to allow the seedlings to stay in the moist towel at 70 in a vertical position until stem growth starts and then plant. Seed sown when collected germ. 70-40-70-40-70(88% in 10-14 w) and 40-70-40(4%)-70(85% in 10-14 w). Seed DS 6 m at 70 germ. 70-40(10%)-70(80%) and 40-70-40(3%)-70(76%). Seed DS 6 m at 40 germ. 70-40-70(95%) and 40-70(30%)-40-70-40(8%). Light and GA-3 need to be tried.

C. maculata germ. 70-40(100% in 4-8 w). Light had no effect.

C. occidentalis germ. 70(24% in 1-4 w)-40(30% in 2-6 w), 40(33% in 8-10 w)-70(44% in 5-7 w), and 60% in April in outdoor treatment. Light had no effect.

C. pitcheri germ. 70(3/13 in 4-7 w)-40(5/13 in 4th w) and 40-70(1/7 in 2nd w)-40(4/7 in 3-6 w).

C. recta germ. 70(47% in 9th w)-40(20% in 5th w)-70-40(7%) and 40-70(26% in 4-7 w). Note the 8 w ind. t in the germination at 70. A second sample was studied to determine the effect of GA-3 and of light. This second sample germ. 70D(43% in 9th w), 70D GA-3(15% in 8th w), 70L(44% in 10th w), and 40-70D(20%). This seed DS 6 m at 70 germ. 70D(12%). Light has little effect. A prior 3 m at 40, GA-3, or DS are deleterious.

C. rehderiana germ. 70-40(1/35).

C. sp. Kashmir germ. 70(40% in 4th w). Light had no effect.

C. sp. China germ. 70(50% in 3rd w) and none in 40-70L or 40-70D showing that sowing at 40 is a fatal treatment. Light had no effect.

C. vernayi germ. 70D(1/5 in 2nd w) and 40(2/7 in 4th w) in one sample and 70(20% in 5-9 d) and 40-70(none) in another sample. None germ. in 70L, but larger samples need to be studied.

C. verticillata germ. 70L(3/5 in 4-6 w), 70D(none), and 40-70D(none).

C. viorna germ. 70D(7/10 in 9th w), 70L (9/23 in 8-12 w), and 40-70-40-70(67% in 8-12 w). The small sample makes the small effect of light questionable. Sowing at 40 gives delayed germination.

C. virginiana requires light or GA-3. Either fresh seeds or seeds DS 6 m at 70 germ. 70L(98% in 2nd w), 70D GA-3(91% in 2nd w), and 70D-40-70D(none). A prior 3 m at 40 lowered the percent germination. Seeds DS at 70 for 2 y were dead.

Cleome (Capparaceae). *C. serrulata* germination is promoted either by light or oscillating temperatures. Seed DS 6 m at 70 germ. 70L(92% in 2-3 d), 70D(none), 40-70L(90%), and 40-70D(none). Fresh seed germ. less as shown by 70L(21% in 5-9 d), 70D(4%), 40-70L(87%), and 40-70D(none) in one sample and 70L(44% in 3-21 d) and 70D(none) in a second sample collected a month later. However, it is the behavior of these two samples under outdoor conditions and conditions of oscillating temperatures that is so remarkable. The results are described in detail in Chapter 10. Although seed DS 6 m at 70 germ. far better than fresh seed, seed DS 3 y was dead, and some samples of commercial seed were dead.

Clethra (Clethraceae). Both species required light for germination.

C. alnifolia germ: 40-70L(60% in 3rd w), 40-70D(none), 70L(10% in 5th w), and 70D(none). Seed DS 6 m at 70 gave the same results, but seed DS 12 m was dead.

C. fargesii germ. 70L(15% in 2-11 w), 40-70L(49% in 2-11 w), and none in 70D, 70 GA-3, 40-70D, or outdoor treatment. A preliminary 6 w in 70D had no effect.

Clanthus (Fabaceae). Although *C. puniceus alba* has an impervious seed, 30-35% of the seed coats have a fissure already present. Furthermore, the seed coats break down readily so that further germination occurs over the following weeks. The seeds germ. 100% on the 3rd d if the seed coat was punctured. If the seed coat was not punctured, the seeds germ. 35% in 3-5 d at 70 and 31% in the 3rd w at 40. After 3 m the total germination at 70 was 55% and the total at 40 was 81%.

Clintonia (Liliaceae). Germinations were extended in all three species.

C. andrewsiana germ. 40-70(5/9 in 2-7 w)-40(1/9), 70 (GA-3)-40-70(4/7 in 2nd w), and 70D-40-70D(none). The cotyledon develops within a month.

C. borealis germ. 2/4 in March and April from seed started outdoors 14 m earlier.

C. umbellata germ. 70-40-70-40-70(1/6) and 40-70-40-70(2/5 in 3rd w). Germination is epigeal.

Cochlearia (Brassicaceae). *C. alpina* germ. in the 3rd w at 70.

Codonopsis (Campanulaceae).

C. clematidea germ. 70(50-60% in 3rd w) using two samples of commercial seed. However, wild collected seed germ. 70(3%)-40-70 and 40(48%)-70(6%). It is probable that the commercial seed and the wild collected seed were different species.

C. ovata germ. 20% in the 2nd w at 70.

C. viridis germ. 16% in 3rd w in 70D or 70L. A prior 3 m at 40 was fatal.

Colchicum (Liliaceae). Germination was hypogeal in the two species studied. Germination occurred at 40 and the seedlings must be kept at 40 for a month after radicle development is complete and until the true leaf begins to emerge before the shift to 70.

C. autumnale germ. 70-40(2/6 in 6th w)-70 and none when sown at 40 after four cycles. A second sample was received in August and had presumably been DS for 9 m. This germ. 3/9 on December 1. Outdoor treatment needs to be further studied.

C. luteum germ. 70-40(5/6 in 1-3 m) and 40-70-40(2/8). Seed placed outdoors in March germ. 5/7 the following October. Germination occurs only at low T.

Collinsonia (Lamiaceae). *C. canadensis* germ. best (45%) in outdoor treatment with germination occurring in April and May. Seeds also germ. 40-70(6%) and 70-40(none). Seed DS 6 m at 70 germ. 70-40-70(6%)-40-70(41% in 1-3 w). The results are incomplete but suggest that oscillating temperatures are required and that DS is tolerated.

Collomia (Polemoniaceae). This genus has been reported as difficult to germinate. It is now found that GA-3 initiates germination in both *C. debilis* and *C. sp.* Andes, and it is probable that it is a natural requirement for both species.

C. debilis germ. 70D GA-3(2/4 in 2nd and 7th w), 70D(none), 40 GA-3(1/5 in 3rd w), and 40(none).

C. grandiflora germ. best in 40(100% in 2-6 w) and less in 70(2/6 in 6-8 d)-40(2/6). Light had no effect.

C. sp. (Andes, small orange flowers) germ. 70D GA-3(95% in 4th w) and none in 70D or 40-70D. The seedlings were etiolated, but they survived. Presumably conditions for producing normal seedlings could be found.

Colutea (Fabaceae). *C. arborescens* germ. 100% in 3-5 d at 70 providing a hole is made through the seed coat. If this same seed (with the hole in the seed coat) is sown at 40, germination falls to 10% because 90% of the seed rots. Without the hole in the seed coat, germination is long delayed.

Commelina (Commelinaceae). *C. dianthifolia* germ. immediately at 70.

Conanthera (Tecophiliaceae). *C. bifolia* germ. 40(2/2 in 5th w) and 70-40(none). Germination is hypogeal, and the true leaf develops in a week.

Convallaria (Liliaceae). *C. majalis* has germination blocked by light. Germination was best using seed DS 6 m at 70 or 40 in 70D(90-95% in 4-8 w). Germination was more extended with fresh seed as shown by 70D(57%)-40-70D(30%). A prior 3 m at 40 served only to reduce the ind. t at 70 as shown by 40-70D(90-100% in 0-4 w) for both DS and fresh seed. The germination in 70D is unaffected by 5 w in 70L with or without a prior 3 m at 40 as shown by germination of 90-100% in 1-5 w after a shift to 70D. Outdoor treatment gave 96% germination in May. The seed is enclosed in an orange berry, 1-8 seeds per berry, and it must be WC. Germination is hypogeal, and only the radicle develops in the first cycle at 70. After radicle development is complete, the seedlings are shifted to 40. After 3 m at 40 and a shift to 70, a shoot with leaves develops. However, with some sets of seedlings leaf development did not occur until after 6 w at 70. It is likely that more time should be given in both the radicle forming cycle at 70 and the following cycle at 40 in order to get more rapid and more vigorous leaf development.

Convolvus (Convolvulaceae).

C. compactus germ. 70(1/2 in 4th w)-40-70 and 40-70(1/2 in 2nd w).

C. lineatus ssp. *angustifolius* germ. 40(1/2 in 3rd w)-70(1/2 in 2nd w) and 70(none).

C. sp. (Bulgaria) germ. 70(1/8 in 3rd d)-40-70(1/8 in 4th w) and 40(3/10 in 3-9 w).

Coreopsis (Asteraceae). *C. lanceolata* seed DS 6 m at 70 germ. 70(100% in 1-7d). All other treatments gave much lower percent germination.

Coriandrum (Apiaceae). *C. sativi* germ. 90% in 5-9 d in either 70D or 70L, 40(83% in 3-5 w), and 73% in early April in outdoor treatment.

Coriaria (Coriariaceae). *C. terminalis* germ. 70L(90% in 2-5 w) and 70D(21% in 2-5 w) indicating promotion by light. This photopromotion disappeared after 3 m at 40 as shown by 40-70D(9/15 in 1-3 w).

Cornus (Cornaceae). Seeds are always in berries so that WC was performed on all seeds before planting. Grinding a hole in the seed coat had no effect in *C. alternifolia*, *florida*, *kousa*, and *stolonifera*. This was expected as discussed in Chapter 8. Outdoor treatment was best with *C. alternifolia*, *C. nuttallii*, *C. siberica*, and *C. suecica*. It is suspected that outdoor treatment would have been optimum for the other species, and experiments are in progress to test this. Treatment with GA-3 did not initiate germination in *C. alternifolia*, *C. amomum*, or *C. kousa*.

C. alternifolia germ. best in outdoor treatment. Seed was collected in August and WC for 2 w. This seed germ. 65% in March in outdoor treatment. The next best was 40-70-40(4%)-70(14%)-40-70(26% in 2 d-4 w)-40-70(6%). All other treatments germ. 0-10%, but many of these were carried through only three cycles, and it is apparent that germination could have been continuing out to the the seventh cycle and beyond. DS is injurious. After a year in various treatments including outdoors, seeds DS 6 m at 70 or 40 in the WC state germ. only 0-2% and seeds DS in the dried berries germ. only 0-10%.

C. amomum also germ. best in outdoor treatment using either fresh seed or seed DS 6 m at 70. The seeds germ. in March and April from planting the previous September. One-third of the seeds had densities less than one (they float in water) and two-thirds have densities greater than one (they sink in water). This was true even after WC for two weeks. Both groups of seeds germ. the same in outdoor treatment, 32% for the less dense seeds and 29% for the more dense. Thus the time honored practice of separating "good" seed from "bad" seed by floatation certainly is not applicable to this species. Germination in the other treatments was 0-5% after a year of alternating cycles.

C. florida seed was collected in October and in February. Seed collected in October germ. 40-70(41% in 2-21 d) and 40% in April in outdoor treatment from seed sown in October. When sown at 70 germination was much lower as shown by 70-40-70(5%)-40-70(5%). When this October seed was DS 6 m at 70 or 40, germination dropped to 0-10%. The seed collected in February germ. somewhat differently as shown by 40(28%)-70(20%) and 70-40-70(43% in 2-6 d). This February collected seed tolerated DS better as shown by 40(46% in 9-10 w)-70(8%) and 70-40-70(47% in 4-10 d) for seed DS 6 m at 40 and 40-70(29%) and 70(none over 5 cycles) for seed DS 6 m at 70.

C. kousa germ. best in 40(26% in 5-9 w) for fresh seed, 40(25% in 4-5 w) for another sample of fresh seed, 40(22% in 3-4 w)-70(11%) for seed DS 6 m at 70, and 40(38% in 4-7 w)-70(8%)-40-70(8%) for seed DS 6 m at 40. This shows that DS seed germ. as well as fresh seed. Seed started at 70 germ. in an extended manner, for example 70(3%)-40(7%)-70(11%)-40-70(21%) for fresh seed, so that it is inconvenient although the final percent germinations are comparable to sowing at 40. Outdoor treatment is yet to be tried.

C. nuttallii germ. under all treatments. Most convenient is 40-70(50% in 8-10 d) for either fresh seed or seed DS 6 m at 70. Less convenient was outdoor treatment (2/7) and 70-40-70(3/4 in 4-12 d).

C. racemosa gave low percent germination, but unfortunately outdoor treatment has not yet been tried and probably would have been better in view of the results with other species of *Cornus*. Fresh seed and DS seed gave comparable results. A 70-40-70 pattern predominated as shown by 70-40-70(3%)-40-70(9%) for fresh seed and 70-40-70(4%) for seed DS 6 m at 70. A preliminary 3 m at 40 had little effect as shown by 40-70-40-70(3%) for fresh seed and 40-70-40(3%)-70(5%)-40-70(5%) for seed DS 6 m at 70.

C. sibirica germ. 40-70(22% in 2-14 d)-40(5%)-70(5%)-40(2%)-70(24%), 70-40-70(44% in 1-12 d)-40(2%)-70(2%), and 30% in March and April in outdoor treatment. Seeds WC 7 d and seeds WC 5 d followed by WC 2 d with detergent gave identical results.

C. stolonifera has two sets of seeds each year. One is ripe in July from May bloom and the other is ripe in October from August bloom. Both gave similar results as shown by 70-40(1%)-70(51% in 2-6 d) for July seed and 70-40(8%)-70(64% in 1-14 d) for October seed. Germination had ind. t 2 d and rate 20%/d (based on just the seeds that germ.). Germination extended over six and more cycles for fresh seed started at 40, and this was true for either July or October seed. Germination also extended over six and more cycles for seed DS 6 m at 70 or 40 when started at either 70 or 40 and for both July and October seed. Ultimately germination reached 20-50% in these extended germinations, but such extended germination is inconvenient. Outdoor treatment must be tried in view of results on other *Cornus*. An indication that such outdoor treatment may be best is that seed DS 6 m at 40 had germ. only 10% after 2 years of alternating cycles. The seeds were then shifted to outdoors in January whereupon an additional 35% germ. the following April.

C. suecica germ. only in outdoor treatment, but unfortunately the seed was not placed in the outdoor treatment until after a year of alternating 3 m cycles. Fresh seed and seed DS 6 m in the dried berries behaved identically. Germination occurred in both fall and spring and ultimately as much as 55% germ. in one of the samples after 2 y of the outdoor treatment. One seed germ. five y later. The seedlings develop the two cotyledons within a month of germination.

Coronilla (Fabaceae). *C. varia* germ. 70(80-85%, ind. t 3 d, 14%/d) and 40(80% in 4-25 d) using seed in which the enclosing capsule had been removed. If the seed is left inside the capsule, the ind. t. is increased somewhat. The seed coats harden and become impervious on DS so that seeds DS 6 m at 70 germ. 70(35-50%) and 40(0-25%). In the commercial production of seed in Central Pennsylvania, DS seed is put into a centrifugal chamber which hurls the seed against an abrasive wall. This serves to clean the seed and variously nick the seed coat. This treatment raises the germination from the 20-30% range to the 70-80% range.

Cortusa (Primulaceae). DS seed of both *C. matthioli* and *turkestanica* germ. in 4th w at 70.

Corydalis (Fumaraceae). Seeds of the monocarpic species (*C. cheilanthifolia* and *C. lutea*) and the many perennial species all die quickly in DS. Seeds of many species have been received over the years. All have rotted on contacting moisture indicating that they were dead. The following data are on fresh seeds obtained from my own colonies.

C. cheilanthifolia germ. 70(2%)-40(58% in 3-24 d) and 40-70(17% in 10-15 d)-40-70. Note the strange patterns. All DS seed rotted and this is a fatal treatment.

C. lutea germ. 70-40(5/7)-70 and 40-70-40(4/6) using fresh seed. All DS seed rotted and this is a fatal treatment.

C. nobile germ. 35% in outdoor treatment with germination occurring in February and early March from seed collected in May. The oscillating temperatures of outdoor treatment are needed not only in spring but in the preceding fall. During the fall 35% of the seeds expand and split the seed coat, and it is only these seeds that germinate the following spring. Of the remaining 65% of the seeds, 20% rotted and 45% remained firm and possibly will germinate the next spring. Seeds subjected to alternating cycles give germination extending from the 4th to 8th cycles with overall germination under 20%. Seed DS 6 m at 70 is all dead. Treatment with GA-3 led to total rotting of the seeds.

Corylopsis (Hamamelidaceae).

C. pauciflora germ. 10% in April after DS 6 m at 70 and placing outdoors in May. Fresh seeds germ. 40-70-40-70(1/5 in 2nd w) and none after four cycles starting at 70.

C. spicata germ. best after DS for 6 m, removing the husks, and placing outdoors. These germ. 15% in June when placed outdoors in mid-May. These seeds also germ. 40(5%)-70, 70D GA-3(18% in 2nd w), and 70D(none). It is not known whether removal of the husks is a factor because it was extremely difficult to remove these husks in fresh seed. The GA-3 seedlings were badly etiolated.

Corylus (Betulaceae).

C. avellana seeds were given three separate treatments in view of the claims of Bradbeer (ref. 11) that the seed coats and testa contained germination inhibitors. The three treatments were (a) shell removed, (b) shell and testa removed, and (c) control. Seeds given treatment (a) germ. 40-70(35% in 3-7 d) and 70-40(10%). Seeds given treatment (b) germ. 40-70(25% in 3-5 d) and 70(all rotted). The control, treatment (c), germ. none. There was no difference in treatment (b) between removing just the shell or removing the shell plus testa. Soaking the seeds for seven days after removing shell or shell plus testa led to more rotting. The results are interpreted to mean that there is a simple impervious seed coat, and that the conclusions of Bradbeer are incorrect.

C. cornuta germ. best in 70-40-70(86% in 1-3 w). Germination is hypogeal. Stem and leaves develop in 1-2 w after germination. Germination was more extended when the seed was sown at 40 as shown by 40-70(14%)-40-70(57% in 1-6 w)-40-70(14%). Germination in outdoor treatment was unsatisfactory as only 1/14 germ. in April and 1/14 in September from sowing in December. In view of the results with *C. avellana*, studies are needed on removing the seed coats.

Cotoneaster (Rosaceae). *C. acutifolia*, *apiculata*, and *divaricata* were reported to require treatment with sulfuric acid followed by cold treatment before germination would occur at 70 (ref. 7, Ch. 8). This would suggest that impervious seed coats were present, but the present work does not support such a view. The general picture is that germination is extended in either alternating cycles or outdoor treatments.

C. dammeri germ. over a number of cycles using either fresh seed or DS seed. No dominant pattern emerged. Fresh seed germ. 40(20%)-70(3%)-40-70(20%) and none over five cycles starting at 70. Seed DS 6 m at 70 germ. 70(10%)-40-70(20%) and 40(40%)-70(5%)-40-70. Seed DS 6 m at 40 germ. 70-40-70(43%)-40-70(4%) and 40(4%)-70-40(17%)-70-40-70(8%).

C. depressa seed was stored for 6 m at 40 in the dried fruit. This seed germ. 70-40-70(50% in 4-15 d)-40(11%) and 40(55% in 4-11 w)-70(9%).

C. divaricata germ. 40-70-40-70-40-70(14% in 3-8 d) and 70-40-70-40-70(4%) using fresh WC seed and 40-70-40-70(12% in 3-21 d) using WC seed that had been DS 6 m at 70. Seeds placed outdoors in October did not start germinating until the April 18 m later (10-20%). Grinding a hole in the seed coat had no effect. It is likely that germination would have continued in further cycles.

C. horizontalis germ. 70-40-70(50% in 2nd d) and 40(20%)-70-40-70(40%)-40(5%)-70-40-70. Seed DS 6 m at 70 germ. 70(9%)-40(9%)-70(55%) and 40(55%). Seed DS 6 m at 40 germ. 70-40-70-40(55%) and 40-70(55%). Seed DS for one year at 40 germ. less and more extended.

C. microphyllus v. *cochleatus* germ. 70D GA-3(40% in 4-10 w), 70D(2%), and 40(none).

Coryphantha (Cactaceae). *C. vivipara* germ. 22% in 1-4 w at 70. A few more germ. in the following year outdoors.

Craspedia (Asteraceae). *C. incana* germ. 70D(100% in the 11th w) in one sample and 70D(2/3 in 2nd and 4th w) and 70 GA-3(2/4 in 3rd w) in another.

Crataegus (Rosaceae). *C. coccinea*, *cordata*, and *mollis* were reported to be 40-70 germinators (ref. 22, Ch. 7), and *C. crus-galli*, *flava*, *oxycantha* were reported to be 70-40-70 germinators (ref. 7, p. 33). *C. punctata* and *rotundifolia* were also reported to be 70-40-70 germinators (ref. 18, Ch. 10).

C. monogyna germ. 70-40-70(31% in 5-17d)-40-70(4%), 40-70(4%)-40-70-40-70(55% in 1st w), and 15% in March and April in outdoor treatment from seed placed outdoors the previous October. Seeds DS 6 m at 70 gave similar multicycle germinations as shown by 70-40-70(17% in 2nd w) and 40-70-40-70(70% in 1st w).

C. phaenopyrum was collected in January and WC before sowing. Seeds germ. 70(6%)-40-70(50% in 4-8 d) and 40(51% in 4-10 w)-70-40-70 using fresh seed or seed DS 6 m at 70 or 40 or after DS 6 m at 70 in the dried fruit. GA-3 had no effect. An inhibitor system is being destroyed at 40, but a prior 3 m at 70 appears to inhibit this process.

Cremanthodium (Asteraceae).

C. arnicoides germ. 57% in 2nd w in either 70D or 70L.

C. ellisii is one of those species that germinate in either 70L or 40D as shown by 70L(70% in 4-6 w), 40(70% in 6th w), and none in 70D.

Crocoshmia (Iridaceae). *C. aurea* germ. 70L(93% in 2-4 w), 70D(56% in 2-4 w)-40-70D(10%), 70D GA-3(25% in 3rd w), 40(20%)-70(43% in 1-9 w), and 12% in October from seed placed outdoors in early September. The GA-3 treatment led to much immediate rotting. Germination is hypogeal and the leaf develops rapidly. The increased germination in 70L relative to 70D may be just a temperature effect as explained in Chapter 11. Seeds DS 3 m at 70 germ. the same as fresh seed. Seeds placed outdoors in November all died in our winter temperatures of zero to -10 although the parent plant was hardy.

Crocus (Iridaceae).

C. speciosus is a 70-40 germinator. Germination occurs 1-2 m after the shift to 40 in either a 70-40 or a 40-70-40 pattern. Like species in the genus *Tulipa*, the seedlings cannot be shifted to 70 too quickly or the cotyledons fail to develop properly.

C. tomasianus seed was WC for 4 d to remove most of the aril. Germination was 70-40(93% in 3-7 w) and more extended in 40(60% in 8-10 w)-70-40(40% in 2-4 w). Germination is hypogeal. The seedlings must be kept at 40 for 3 m and until leaf growth is evident before shifting to 70.

Crowea (Rutaceae). *C. angustifolia* was reported to germinate if soaked for 30 minutes in aqueous detergent (J H).

Cruckshanksia (Rubiaceae). Germination has been very low.

C. glacialis germ. 40(2/19 in 12th w)-70 and 70-40(1/3 in 12th w). Treatment with GA-3 led to rapid rotting of the seeds.

C. hymenodon was given 4 w at 70 and then shifted to 40 whereupon 1/15 germ. in the 3rd w. The seedling was vigorous and developed a 2 inch radicle in a few days although three more weeks elapsed before the epicotyl had lengthened to one inch and the cotyledons expanded. A seed that germ. in the 4th w at 40 was weak and soon died. Seeds placed outdoors in October germ. 1/28 in April 18 m later.

Cryptantha (Boraginaceae). *C. thompsonii* germ. 70D(1/4 in 9th w) and 70L-40(1/6 in 4th w).

Cucumis (Cucurbitaceae). *C. melo* is the common melon. Both the cassaba or honeydew and the netted or canteloupe types were studied.

C. melo (cassaba) germ. 100% in 4-6 d after washing the seeds for only 10 minutes. When the WC was continued for 7 d, the seeds also germ. 100%, but not until 4-6 d after removal from the washing water. This shows that immersion in water inhibits germination, possibly because the germinating seeds require abundant oxygen. The seeds are connected to the interior of the fruit by a thin filament. It is suspected that inhibitors are transmitted through this filament as in *Capsicum*. When the filament is broken, germination begins. Light, GA-3, or DS at 70 for 2 m had no effect.

C. melo (netted) seeds were WC for 10 minutes. These fresh seeds had germination stimulated by light and GA-3. They germ. 70L(61% in 1-3 w), 70D GA-3(48% in 1-3 w), and 70D(8%). Germination was much lower in seeds WC for 7 d. The light requirement diminishes on DS. Seeds DS for 2 m at 70 germ. 70L(87%) and 70D(35%). Two commercial strains were received after months of DS and germ. 90% in 2-5 d in either 70D or 70L showing the elimination of the light requirement on DS.

Cucurbita (Cucurbitaceae). The seeds are connected to the interior of the fruits through a filament. It is suspected that the inhibitors are transmitted through this filament. This would explain why short periods of WC of only ten minutes are effective in conditioning the seeds for germination.

C. maxima (Butterbush squash) that had been DS for months germ. 70D(95% on 4th d), 40 (GA-3)-70(64% in 4-6 d), and 40-70(10%). This effect of GA-3 in protecting viability at 40 is interesting.

C. maxima (Acorn squash) removed from the fruit and WC 10 minutes germ. 70L(100% in 10-27 d), 70D GA-3(62% in 9-19 d), and 70D(26% in 2-4 w). Seeds WC for 7 d germ. 70D GA-3(33%) and 70D(43%). The effect of light disappears on DS and seeds DS 2 m at 70 germ. 70D(80% in 4-6 d).

C. maxima (Spaghetti squash) removed from the fruit and WC 10 minutes germ. 70L(100% in 10-21 d), 70D GA-3(100% in 4-6 d), and 70D(none). Seeds DS for 2 m at 70 germ. 70L(90% on 2nd d) and 70D(10%). Perhaps further DS would have eliminated the light requirement.

C. pepo (pumpkin) was received as DS seed and germ. 100% in 2-5 d in either 70D or 70L. Fresh seeds should be studied for photoeffects.

C. sativus (horned melon) seeds WC 3 d germ. 100% on the 6th d starting from the beginning of WC. Light, GA-3, or 6 m DS at 70 had no effect.

C. sativus (cucumber) was received as DS seed and germ. 100% in 2-5 d in either 70D or 70L. Fresh seed should be studied for photoeffects.

Cunninghamia (Pinaceae). *C. lanceolata* was grown from cuttings from a tree in Indiana, Pennsylvania, that had grown to a height of 40 feet and had survived temperatures of minus 30. This clone must be much hardier than is usual for this species. After 15 y two trees bloomed and set seed. As might be expected from a single clone 95% of the seed coats were empty, and these were not counted. Fresh seeds germ. 70D(100% in 2nd w) and 40(60%)-70(40%). Seeds DS 6 m at 70 germ. 70D(100% in 2nd w) and 40-70(100% in 1-3 d).

Cuphea (Lythraceae). *C. petiolata* germ. 65% in April in outdoor treatment using seed DS 6 m at 70 and placed outdoors March 1. All other treatments failed, but outdoor treatment was not tried on fresh seed. No attempt was made to remove the sticky covering on the seed coats.

Cupressus (Pinaceae). *C. macrocarpa* was reported to be 40-70 (ref. 31, Ch. 7).

Cyananthus (Campanulaceae).

C. lobatus germ. 50% in 2nd w in 70D or 70L. A prior 3 m at 40 was fatal.

C. sp. yellow (CLD 1492) germ. 70D(28% in 3rd w), 70L(66% in 3rd w), and 40-70D(10% in 2nd d).

Cyclamen (Primulaceae). Germination is hypogeal with first formation of a corm and multiple branching root system followed after an interval of 1-2 m by emergence of a true leaf.

C. neapolitanum had markedly different germination patterns for fresh seed and DS seed. Fresh seed germ. 70-40(25% in 3rd w)-70-40(50% in 5th w) and 40-70-40-70-40(90% in 4th w). Seed DS at 70 or 40 germ. 70(75% in 11th w)-40(20% in 3rd w) and 40-70(15% in 12th w)-40(60% in 12th w)-70.

C. persicum germ. 70(78% in 9-16 w), 70L(none), and 40(25% in 9th w). The seedlings that germ. at 70 were kept at 70, and a true leaf developed (hypogeal germination) in 1-2 m. The seedlings that germ. at 40 all rotted and no further germination took place on shifting to 70. None germ. in 70L-40-70D. The sample in 70L should have been shifted to 70D after 3 m at 70L to determine whether the 70L had permanently injured the seed. This is one of the few examples found in the present work where light blocks germination. Seed deteriorates on DS.

Cymopterus (Apiaceae). Both species germ. strictly at 40.

C. sp. (Washington) germ. 40(40% in 6-11 w), 70-40(31% in 5th w)-70-40(56% in 6-9 w), and 20% in March in outdoor treatment.

C. terebinthinus germ. 40(53% in 6-13 w)-70(6%)-40(3%)-70(3%), 70(1%)-40(41% in 3-12 w)-70-40(20%)-70-40(17%), and 40% in March and October in outdoor treatment. Light in the cycles at 70 had no effect on the germination at 40.

Cynoglossum (Boraginaceae). *C. amabile* germ. either in 70L or 40D as shown by 70L(100% in 2-3 d), 40(70% in 4th w), and none in 70D. When the sample at 40 was shifted to 70, there was no further germination for one m. The seeds were then shifted to 70L whereupon the remaining 30% germ. in 2-3 d. The seeds in 70D were also shifted to 70L after one m whereupon they too germ. 100%.

Cytisus (Fabaceae). *C. scoparius* seed germ. 100% in 4-7 d if a hole is ground through the seed coat. Untreated seed does not germinate.

Dalea (Fabaceae). One unidentified species germ. 1/10 on the 5th d at 70 and none when sown at 40 over three cycles. Experiments should have been conducted on making a hole in the seed coat.

Daphne (Thymelaceae). Germination is stepwise with a time gap between splitting of the seed coat and development of the radicle although both may occur in the same cycle. Germination is further complicated by extended germination over several cycles and by rapid rotting of part of the seed on contact with moisture suggesting internal infection. Two of the most popular species (*D. caucasica* and *cneorum*) set little seed. It is probable that *Daphne* are self-sterile. Good seed set was obtained on *D. genkwa* and *D. giraldi* only by hand pollinization between different clones. Experiments on *D. genkwa* showed that DS is not tolerated, and this may further account for the poor germination in seed received from outside sources.

D. causicum germ. 40(5% in 10th w)-70(17% in 6th w)-40(11%)-70(17%). None germ. after a year starting at 70, and all rotted on treatment with GA-3.

D. genkwa, fresh seed germ. 70(4%)-40-70(3%)-40(2%) and 40(23%). No further germination occurred over five further cycles. Fresh seed from a year earlier germ. 40(5%)-70(17%)-40-70(5%). These results are not consistent, and in fact germination was generally erratic. Germination failed with seed DS 6 m at 40 or 70.

D. giraldi germ. 40-70(2/27), 70 GA-3(2/11 in 6th w), and 70-40-70(1/36). Another sample germ. erratically over two years, mainly in cycles at 40.

D. oleoides was received in midwinter as wild collected seed. It failed to germinate confirming the intolerance of *Daphne* to DS.

Datura (Solanaceae). *D. stramonium* germ. 100% in 70L if the seed had been DS 6 m at 70 whereas fresh seed germ. only 70L(27% in 8-10 d). There is some germination in the dark as shown by 70D(25% in 3-7 d) for seed DS 6 m at 70 and 70D(15% in 5-8 d) for seed collected in November. Germination failed in outdoor treatment. Germination was only 5% over two cycles when sown at 40.

Daucus (Apiaceae).

D. carota exhibited complex germinations. Fresh seed germ. 23% in March and April in outdoor treatment and seed DS 6 m at 70 germ. 70L(40% in 3-8 d). All other treatments germ. less than 3% including 40-70L.

D. carota v. *sativus* is the edible carrot. Seeds germ. 70D(92% in 4-9 d) and 40(63% in 3-7 w)-70(24% in 4-8 d). An attempt to increase the rate of germination at 40 with GA-3 led to total rotting of the seeds at 40.

Decaisnea (Lardizabalaceae). *D. fargesii* germ. 70-40(1/5)-70. At this point the sample was shifted to outdoors (in August) and 2/5 germ. the following April. None germ. in 40-70-40.

Degenia (Brassicaceae). *D. velebitica* germ. 30% in 1-4 w in either 70L or 70D, 40(10% in 5-11 w)-70(6% in 4-6 d), and only 6% in outdoor treatment. It is possible that the seed cannot tolerate the winter temperatures of 10 which were experienced in March.

Deinante (Hydrangaceae). *D. bifida* required light and germ. 70L(25% in 13-15 d) and 70D(none). The sample in 70D was shifted to 70L after 4 w whereupon it germ. at the same rate and percentage as seed sown initially in 70L showing that there was no deterioration or any other change in 4 w in 70D. A preliminary 3 m at 40 also had no effect on the germination at 70.

Delosperma (Mesembryanthemaceae). *D. cooperi* germ. in 4 w at 70.

Delphinium (Ranunculaceae). This genus is composed of a group of medium height monocarpic species typified by *D. grandiflorum*, a group of tall perennials typified by *D. exaltatum*, and a group of low spring bloomers typified by *D. tricorne*. The germination behavior was similar within each group but varied between groups.

D. belladonna germ. 70(50% in 10-12 d) and 40(63% in 5th w). Treatment with GA-3 had no effect on the rate or percent at 70.

D. bicolor germ. best with seed DS 6 m at 40 in 40(75% in 8-12 w)-70(3% in one d). Seed DS 6 m at 70 germ. nearly as well as shown by 40(31% in 8-12 w)-70(37% in one d). Both of these DS seeds gave zero germination when sown at 70, a fatal treatment. With fresh seed germination dropped to 27% when sown at either 40 or 70 and extended over four cycles occurring mainly in the 4th cycle.

D. cashmerianum germ. 70(90%, ind. t 6 d, 25%/d) and 40-70(90%, ind. t 6 d, 25%/d).

D. exaltatum germ. only under the oscillating temperatures of outdoor conditions. Seed collected in September germ. 12% in March and failed to germinate under other conditions including 70L.

D. elatum germ. in the 8th w at 70.

D. geraniifolium germ. 70D(100% on 11th d) and 40-70D(100% in 6-8 d).

D. geyeri germ. 57% at the end of March from outdoor sowing in late fall. Germination dropped to 5% when sown at 70 or 40 as shown by 70-40(5%)-70 and 40-70-40(5%).

D. glaucum germ. 70-40(25% in 4-6 w) and none in 40-70-40.

D. grandiflorum germ. 100% in 5-7 d at 70 and 72% in 10-14 d at 40 using fresh seed.

D. lipskyi germ. in April from sowing outdoors in January.

D. oreophilum germ. 70(12% in 3rd w) and 40(10% in 6-11 w).

D. oxysepalum germ. 70-40(1/12)-70(2/12)-40(1/12).

D. tatsiense germ. in 2nd m at 70.

D. tenuisectum germ. 70(90% in 2-5 w) and 40(10%)-70(77%, ind. t one d, 25%/d).

D. tricornis germination extends over two years using the alternating 3 m cycles between 40 and 70. Although the exact patterns varied in seeds collected in different years, the one consistent result was that germination was not significant until the fourth cycle with germination concentrating anywhere from the fourth to the seventh cycle. Data ranged from 70-40-70-40-70(1%)-40(5%)-70(10% in 2nd w) to 40-70-40-70(28%). Rubbing the fresh seeds between sandpaper gave some increase in percent germination with 70-40-70-40(33%)-70(10%) being a typical result. However, the results were erratic. Germination was stimulated by GA-3 as shown by 70 (GA-3)-40(24% in 7-12 w)-70(4%), but the seedlings were not healthy. Outdoor treatment gave the same extended germinations. Seeds DS for 6 m at 70 or 40 gave lower percent germination, but again the results were erratic. Once germination took place, the cotyledons developed in 1-2 w. Some preliminary results indicated that increasing the length of the 3 m cycles might produce seedlings faster.

D. virescens sown in fall germ. the following spring.

D. xantholeucum germ. 40(1/23 in 11th w) and none in 70 or outdoors.

Dentaria (Brassicaceae). *D. laciniata* germ. best when the seeds were treated with GA-3 and started at either 70 or 40. The data were 40-70(27% in 10-12 w) and 70-40(20% in 6-12 w). The seedlings from the GA-3 treatment appeared normal but more time is needed to be sure that healthy plants will develop. Germination of *D. laciniata* is most unusual for Brassicaceae. Not only is DS not tolerated, but germination is hypogeal with the radicle growing to a length of a cm. in one day and producing branching roots before the true leaf forms a few weeks later. The European *D. pentaphylla* and *D. hexaphylla* were received in midwinter as DS seed and both promptly rotted on contacting moisture further confirming that DS is not tolerated in *Dentaria*. Before the GA-3 experiments, germinations were below 10% and occurred only after 2-3 y. It is possible that these small amount of germinations were due to fungal infections that finally invaded the the seed coats.

Desfontainea (Loganiaceae). *D. spinosa* failed to germinate in 70D, 70L, or 40-70. Unfortunately GA-3 was not tried.

Deutzia (Saxifragaceae). *D. staminea* germ. 100% in 4-7 d in 70D or 70L. A prior 3 m at 40 had no effect.

Dianthus (Caryophyllaceae). Fresh or DS seed of all species studied germ. in 1-4 w at 70 and 2-5 w at 40 except for *D. armeria* which is discussed below. In a few species germination at 70 started as quickly as 2 d but 7 d was more typical. Germination was always in the 70-100% range. The species in which both fresh and DS seed were studied were *D. barbatus*, *deltoides*, *nardiformis*, *plumarius*, and *stenocalyx*. The species in which only DS seed was studied were *D. alpinus*, *broteri*, *crinitus*, *darwasica*, *erinaceus*, *fragrans*, *frigidus*, *glacialis*, *haematocalyx*, *leptopetalus*, *myrtinervis*, *neglectus*, *pancici*, *repens*, and *seguieri*.

D. armeria germ. 70L(100% in 2-3 d) and 70D(1%). The same results were found for fresh seed and seed DS 6 m at 70 or 40. Initial dark cycles of 40, 70-40, and 40-70-40 had no effect on the germination in 70L, and germination proceeded as if the prior treatments had never occurred.

Dicentra (Fumariaceae). DS is either fatal or severely deleterious. J. Forrest reported that *D. citrina* and *D. scandens* required 3 m at 40 after which they germ. in a few days on shifting to 70.

D. cucullaria germ. best with fresh seed in 70-40(21%)-70-40(7%) and 40-70(38%)-40-70. A branching root system is formed. The seedlings then require several months at 40 before the cotyledons will develop at 70. During this time many of the germ. seedlings will rot if the the seedlings in the towel are not aerated with sufficient frequency. The exact requirements for inducing cotyledon development need more study.

D. eximia germ. best with fresh seed in 40-70(25%)-40(2%)-70(6%). Seed DS 6 m at 40 germ. 40(23%), a curious divergence in behavior between fresh and DS seed. Germination completely failed with both kinds of seed when sown at 70 even after several cycles. Seed DS 6 m at 70 was dead and all rotted. The seeds germinate by first splitting. Radicle and cotyledon development does not take place until 2-4 w later.

D. spectabilis germ. best with fresh seed in 70-40(1%)-70(28% in 3-9d, mainly on 3rd d) and 40(19%)-70(5%)-40(11%)-70. DS 6 m at 70 or 40 is completely fatal. As with the two other species the seed splits first and radicle and cotyledon development follow a few weeks later. Germination was dramatically stimulated by GA-3 at 70, however the seedlings were weak and died.

Dictamnus (Rutaceae). *D. alba* germ. basically in a 40-70 pattern with additional increments after each additional 40-70 cycles. However, the germination is a bit difficult to define. What happens is that near the end of the 3 m at 40, many of the seeds increase in volume about 50%. This causes splitting of the seed coat. The radicle may also emerge 1-2 mm. at this time, but does not develop further. On shifting to 70 the radicle rapidly elongates in a day or two, and a shoot with leaves (hypogeal) develops within a week. A few more germinations are triggered over the next two weeks, and then the pattern is repeated in the following 40-70 treatment. The germinations were counted as taking place when the radicle started to elongate at 70, but many could have been counted as occurring at the end of the preceding cycle at 40. Both fresh seed and seed DS 6 m at 70 or 40 germ. 70-40-70(53-58% largely on the 2nd d)-40-70(35%). Results were more varied when sown at 40 as shown by 40-70(6%)-40-70(28%)-40(10%)-70(18%) for fresh seed, 40-70(11%)-40-70(77%) for seed DS 6 m at 70, and 40-70-40(2%)-70(41%) for seed DS 6 m at 40. A set of

experiments were conducted on seed DS 12 m at 70 to see how much time was required at 40 before the shift to 70. The times at 40 were 4, 8, 12, 16, and 20 w with the percent germinations 0, 0, 42%, 64%, and 73% (in 2-6 d) respectively. Thus at least three months at 40 is required and five months is better. A sample of seed DS 2 y at 70 germ. much like fresh seed.

Dictyolimon (Plumbaginaceae). *D. macrorrhados* germ. 70L(4/4 in 5-7 d).

Dierama (Iridaceae). *D. pulcherrima* germ. 70D(90% in 5th w) and 40-70(100% in 4-6 d). Light or GA-3 had no effect on the rate or the percent germination.

Digitalis (Schrophulariaceae). *D. purpurea* germ. 90-100% at both 70 and 40. Germination at 70 followed a first order rate law, ind. t 3 d and half-life 6 d. Germination occurred in the 3rd m when sown at 40.

Dimorphotheca (Asteraceae). *D. aurantiaca* germ. in the 2nd w at 70.

Dionea (Droseraceae). *D. muscipula* germ. 70L(64% in 3-9 w), 70D GA-3 (17% in 5-8 w), 70D-40-70D(14% in 2nd w), 40-70L(71% in 3-6 w), and 40-70D(none). The seedlings from GA-3 treatment appeared normal, but 70L is best.

Dionysia (Primulaceae). Two wild collected samples of *D. involucrata* germ. 40(6/6 in 6-8 w) and 70-40(7/15 in the 12th w) for one sample and 40(14/31 in 6-8 w)-70-40(2/31) for the other. Light had no effect. An earlier sample had germ. 70-40-70(4/8), but it is believed that the seeds had actually germ. in the 12th w at 40 and this did not become evident until the shift to 70.

Dioscorea (Dioscoriaceae).

D. quaternata germ. 70-40-70(2/5 in 2nd w) and 40-70(1/5 in 2nd w)-40(1/5 in 8th w) using fresh seed

D. villosa germination (at 70) was benefitted by both DS and by a preliminary 3 m at 40. Germination was best using seed DS 6 m at 70 in 40-70(77% in 1-8 d). It also germ. 70(11% in 1-3 w) for DS seed and 70(20% in 3-8 w)-40-70(37%), 40-70(44% in 2nd w), and 52% in spring in outdoor treatment using fresh seed. Light had no effect. Seed DS 12 m at 70 germ. 70(6%)-40-70(5%) showing that DS for this long was detrimental. The seeds are thin wafers like *Lilium* and empty seed coats can be detected readily making seed counts accurate.

Diospyros (Ebenaceae). *D. virginiana* germ. best in 40-70(50-60% in 1-4 w) and 70-40-70(50-60% in 1-4 w) showing that it is a 40-70 germinator. Outdoor treatment led to complete rotting, and this fatal treatment was a surprise considering that the plant is hardy. Germination is epigeal, but the stout six inch tap root with branching rootlets forms before the cotyledons laboriously extricate themselves from the seed coat. The cotyledons do not get expanded until 2-3 m after the initial germination. True leaves form simultaneously with the cotyledons. The seeds are embedded in the pulpy fruit. They were WC 7 d, but even after that they had to be periodically washed to remove exudate. Some limited data indicated that WC for one month was fatal.

Dipsacus (Dipsaceae). *D. sylvestris* germination was promoted by light, DS, a prior 3 m at 40, and outdoor treatment. Fresh seed germ. 70L(17% in 5-7 d), 70D(none), 40-70L(54% in 5-17 d), 40-70D(none), and 55% in March and April in outdoor treatment. Seed DS 6 m at 70 germ. 70L(86% in 2-12 d), 70D(33% in 2-12 d), 40-70L(16% in 6-10 d), and 40-70D(none).

Diplacus (Schrophulariaceae). This genus could be included in *Mimulus*. *D. bifidus* germ. largely in light at 70 as shown by 70L(100% in 11-21 d) and 70D(5%). After 2 m in 70D the seed was shifted to light whereupon the remaining 95% germ. in 7-26 d showing that the 2 m in 70D had no effect. There was some germination in the dark at 40 as shown by 40(12%)-70L(20%) and 40(12%)-70D(none). Note that the 3 m at 40 lowered the overall percent germination showing that this treatment led to significant deterioration of the seed.

Disporum (Liliaceae). Seeds are enclosed in red berries and must be WC. *D. hookerianum* var. *trachyandrum* germ. only at 40 as shown by 40(100% in 4-8 w) and 70-40(100% in 3-5 w). Seed sown outdoors germ. a few in January, but these died as did the rest of the seed, and the seed and seedlings are not winter hardy here. Seed deteriorates on DS with the deterioration faster at 70 than 40. Seed DS 6 m at 70 was all dead whereas seed DS 6 m at 40 germ. as well at 40 as fresh seed, but the seed all rotted in a 70-40 pattern unlike fresh seed. This suggests that some changes had taken place in the seed even on DS at 40. Germination is hypogeal. A stem starts to emerge near the end of the cycle at 40 at which germination occurred. The stem and leaves develop over 1-4 w at 70.

D. lanuginosum germ. best at 40(91% in 6th w). Seed sown at 70 with or without GA-3 completely rotted within 2 m. Germination is hypogeal, and the true leaf starts to emerge while still at 40.

Dodecatheon (Primulaceae). *D. amethystinum*, *media*, and *pulchellum* develop only the two cotyledons in the first year of growth so that it is important to keep these photosynthesizing as long as possible. *D. jeffreyi* starts forming true leaves in 1-2 w after the cotyledons open.

D. alpinum germ. 70D GA-3(80% in 1-3 w), 70L(90% in 2nd w), 70D(7%), and 40-70D(78% in 4-8 d). This is an interesting combination of germ. patterns.

D. amethystinum germ. 70D GA-3(1%)-40-70(33% in 5-12 d) and 70D-40-70D(none). This is puzzling because an earlier sample germ. 70-40-70(34% on 4th d) and 40-70(6%). Germination failed with all DS seed.

D. jeffreyi germ. much better in a 40-70 pattern than when sown at 70 as shown by 40(4%)-70(90% in 1-5 d) and 70(21%)-40-70(2%). Seed sown on November 1 in outdoor treatment germ. 78% in February and March. This outdoor treatment was in effect similar to direct sowing at 40. Germination was nearly as good with seed DS 6 m at 70 or 40 as shown by 40(12%)-70(65% in 1-7 d) and 70(12%). As with fresh seed germination was lower and more extended when the DS seed was sown at 70.

D. media has inhibitors that are destroyed at 40 followed by germination at 40. It takes 8-12 w for the inhibitors to be destroyed in fresh seed and 6 w in seeds DS 6 m at 70. Fresh seeds germ. 40(98% in 8-16 w), 70-40-70(15%), and 97% in April for seeds placed outdoors in September. Seeds DS 6 m at 70 germ. 40(100% in 5-7 w). Light or GA-3 did not initiate germination.

D. pulchellum germ. 70(50%, ind. t 6 d, 11%/d) and 40-70(40%, ind. t one d, 15%/d).

Doronicum (Asteraceae). *D. caucasicum*, *D. columnae*, and *D. orientale* germ. 100% in 2-6 w at 70.

Dorycnium (Fabaceae). *D. rectum* germ. 4/8 on the 3rd d at 70.

Douglasia (Primulaceae).

D. laeviagata did not germ. until the April fourteen months after sowing DS seed in February. Two qualitative experiments germ. a few after four cycles. Outdoor treatment is best until there is better data.

D. nivalis germ. 4/10 in December-February in outdoor treatment. This is one of the very few species that germ. in mid-winter.

Draba (Brassicaceae). Most *Draba* are D-70 germinators. A comparison of the high germination of DS to low germination of fresh seed was given in Table 5-1. Sowing of fresh seed at 70 not only gives low germination, but is often fatal.

D. acaulis germ. best in 40-70(100% in 2-10d). None germ. when sown at 70 in one collection and 30% in another indicating that it is best to start the seed at 40.

D. aizoon showed the favorable effects of DS at 70 with germination being 93% for seed DS 12 m, 54% for seed DS 6 m, and zero for fresh seed. The ind. t and rate were 6 d and 10%/d. Seed DS at 40 gave results similar to seed DS 6 m at 70. Seed germ. in about the same overall percentage if sown at 40, but it is inconvenient because there are comparable amounts of germination in both the 40 and 70 cycle.

D. argyrea was received in October. There was no germination in 2 w at 70, so the seed was placed outdoors for 2 m and returned to 70 on January 1. The seed germ. in 10-30 d. The species is probably a 40-70 germinator with germination benefitted by DS.

D. brunifolia germ. 70(2/3 on 8th d) and 40-70(2/3 in 2-14 d).

D. compacta germ. best with seed DS 6 m at 70 in either 70(96% in 5-9 d) or 40(100% in less than 3 w). Fresh seed was curious in that germination was extended at 70 but not at 40 as shown by 40(80% in 3-7 w) and 70(1%)-40(54% in 1-3 w)-70(1%).

D. cretica germ. 70D(90% in 2nd w). Treatment with GA-3 had little effect.

D. dedeana germ. best when sown at 40 as shown by 40(79% in 2-12 w) for fresh seed and 40(70%, ind. t 3 d, 3%/d) for seed DS 6 m at 70 or 40. When sown at 70, germination was 70(40%) for DS seed and 70(none) for fresh seed. It is probable that further cycles would have given more germination for the DS seed because fresh seed did give considerable germination in further cycles as shown by 70-40(34%)-70(15%).

D. densifolia germ. 70(99% in 5-11 d) and 40(100% in less than 3 w) with seed DS 6 m at 70. Germination in fresh seed is lower as shown by 40(53%)-70-40(2%) and 70-40(3%)-70.

D. hoppeana germ. 70(86% in 5-9 d) and 40(84% in 7th w).

D. incerta germ. best at 40 as shown by 40(61% in 3-7 w)-70(4%) and 70(18% in 2-9 w)-40-70(25%). The seed was received in the DS state.

D. lasiocarpa germ. best with seed DS 6 m at 70 in 70(94%, ind. t one d, 8%/d) and 40(100% in less than 3 w). Germination was very poor with fresh seed as shown by 70(2%)-40(4%)-70 and 40(8%) with no further germination over 3 more cycles.

D. lemmonii was received with *D. argyrea* and was given the same treatment with the same results.

D. parnassica germ. best after DS 6 m at 70 as shown by 70(100% in 5-8 d) and 40(100% in less than 3 w). Fresh seed germ. poorer as shown by 70-40(23%)-70 and 40(27%)-70-40(1%)-70(1%).

D. polytricha was received in January and failed to germinate in fifty days at 70. It was placed outdoors on March 1 whereupon germination began in late March. It is probably a 40 or 70-40 germinator.

D. sartori germ. best after DS 6 m at 70 as shown by 70(100% in 5-10 d) and 40(100% in less than 3 w). Fresh seed germ. poorer as shown by 70-40(17%)-70 and 40(30%)-70-40-70(10%).

Dracocephalum (Lamiaceae). *D. renati* germ. 70L(84% in 5-9 d), 70D(63% in 6-14 d), 40(21% in 7th w)-70(28% in 1-3 w), and 62% in April in outdoor treatment.

Dryandra (Proteaceae).

D. formosa germ. 70D(40% in 4-8 w), 70D with GA-3(31% in 3rd w), and 40(80% in 8th w). Starting at 40 is best. The GA-3 seedlings were normal.

D. serra germ. 40-70D(2/9 in 3rd w). Seeds started at 70 with or without GA-3 all rotted, but the samples consisted of only 9 seeds.

Dryas (Rosaceae).

D. octapetala germ. 70(3/3 in 8-12 d), one in the fourth w, and one in the sixth w in three separate samples.

D. sundermannii germ. 1/2 on 7th d at 70.

Dudleya (Crassulaceae). *D. cymosa* germ. 70(66%, ind. t 7 d, 9%/d) and 40(21% in 6-12 w).

Echinocereus (Cactaceae). The discovery that GA-3 was required for the germination of seeds of *E. pectinatus* hybrids (*E. baileyi*, *pectinatus*, and *reichenbachii*) led to the recognition that fungal products of the gibberelin type are natural requirements for germination and that this has important survival value (Chapter 12). Prior treatments seem to have little effect, and germination was about the same for fresh seeds (51% in 1-14 w), seeds that had been DS up to 3 y (44% in 1-14 w), and seeds that had been exposed to outdoor treatment for up to 3 y (45% in 1-14 w). A second sample germ. 80% with fresh seed, and the detailed rate data are presented in Chapter 19. The seedlings from the GA-3 treatment were normal in every respect and grew on to mature plants. Prior to the use of GA-3 a number of treatments were tried varying times at 40 and 70 and varying the DS. None of these treatments gave more than 5% germination and germination extended over 1-2 y of alternating cycles. The GA-3 is virtually a must for germinating *E. pectinatus* hybrids, and should be tried more generally on Cactaceae. There are two problems in obtaining seed of *Echinocereus*. The flowers last only 2-3 d, are self sterile, and require hand pollination. The anthers ripen on the first day or two and the stigma on the following day so that there is usually just one day when one or the other is ripe. Even in a sizable colony it is rare to find a flower with ripe anthers and another flower with receptive stigma on the same day. The second problem is that the seed capsule splits while still green. The seeds are enclosed in a sweet sticky pulp, and the seeds are carried away and dispersed by insects much like seeds with an aril. Thus a close watch must be kept, and when the capsule first splits, the capsule is collected and the seeds washed free of the sweet pulp. It has been claimed that scarification effects immediate germination, but all abrasion experiments in the present work failed to enhance germination.

E. triglochidiatus germ. in the 6th w at 70.

E. viridiflorus self sows here. Seed has failed to germinate, but GA-3 has not been tried.

Echinocystis (Cucurbitaceae). *E. lobata* germ. only in outdoor treatment and all other treatments failed completely. Seed collected in October and given outdoor treatment germ. 90% in March and April. Seed that had been DS 6 m at 70 and placed outdoors in mid-March germ. 2/6 germ. on April 1 and 2/6 the following April over 12 m later. The results indicate that DS is tolerated but is inconvenient.

Echioides (Boraginaceae). *E. longiflorum* germ. 50% in 2nd w at 70.

Edraianthus (Campanulaceae).

E. dalmaticus germ. 70D GA-3(42% in 10-18 d), 70L(29% in 3-6 w), 70D(5%), 40(20% in 8-10 w)-70D(10%), and 40(20%)-70L(20% in 4th d).

E. graminifolius germ. well in 15-25 d at 70.

E. pumilio germ. 70L(10% in 6th w), 70D GA-3(all rotted), 40-70(12% in 3rd d), and 70D(none).

E. tenuifolius germ. 70(70-85% in 2nd w) and 40(16-33%)-70(0-4%) using either fresh seed or seed DS 6 m at 40.

Eleaganus (Eleaganaceae).

E. angustifolia was reported to be a 40-70 germinator (ref. 18, Ch. 10).

E. umbellata seed is contained in red berries, and the pulp clings tightly to the seed so that two weeks of WC are required. Fresh seed germ. 70-40(24%)-70(25%)-40(6%)-70(18%) and 40(7%)-70(30%)-40(32%)-70(7%). Seed DS 6 m at 70 or 40 was carried through only three cycles. At the end of the three cycles the germination of seed DS at 40 was comparable to fresh seed and the germination of seed DS at 70 was half that of fresh seed. The seed tolerates DS fairly well, but some deterioration was evident particularly at 70.

Eleusine (Poaceae). See Chapter 22

Elmera (Saxifragaceae). *E. racemosa* germ. only in light as shown by 70L(93% in 4-8 w) and none in 70D. A preliminary cold period is fatal and none germ. in 40-70L, 40-70D, or outdoor treatment. The above data are for seeds received in midwinter which had been DS about 6 m at 70. Experiments were conducted on this same seed that had been DS for an additional 18 m making a total of 2 y. This seed germ. 70L(3% in 3-5 w), 70D(none), and 70D(100% in 3rd w) if treated with GA-3. The seedlings from the GA-3 treatment appeared to be healthy. It is remarkable that the GA-3 gave 100% germination on the seeds DS 2 y when this long DS period drastically reduced the germination in 70L. To be certain that the seeds subjected to 70L were viable, the sample was treated with GA-3 after 6 w whereupon 70% germ. in 4-12 d.

Eminium (Araceae). *E. regellii* germ. 70-40(2/3 in 8th w). Only a corm and root formed. The true leaf (hypogean) did not emerge until 3 m at 70, 3 m at 40, and a return to 70. This behavior was unique.

Enceliopsis (Asteraceae). *E. nudicaule* germ. at comparable rates at 70 or 40 as shown by 70(3/4 in 2-4 w)-40(1/4) and 40(4/4 in 3-6 w).

Enkianthus (Ericaceae). *E. campanulatus* germ. 31% in April in outdoor treatment. All other treatments failed. Over half of the seed coats were empties. These can be distinguished and were not counted in calculating the percent germination.

Ephedra (Ephedraceae). Germination is immediate at 70.

E. fedtschenkoi germ. 4/5 in 6-7 d at 70 and none in 40-70 treatment.

E. intermedia germ. 100% at either 70 or 40 and at the same ind. t of 3 d and rate of 16%/d.

E. minuta germ. 70(7/9 in 8-11 d), 40(7/9 in 4th w), and 1/10 in outdoor treatment. Germination was hypogean.

Epigea (Ericaceae). *E. repens* germ. best in 70L(88%, ind. t 8 w, 5%/d) and none in 70D using fresh seed. The results were identical for two separate collections of seed in two different years. Note the long induction time indicating that the rate of destruction of inhibitors was slow. The results were unaffected by a prior 40 or 40-70-40 treatment. Not a single seed germ. in any dark treatment even in samples of hundreds of seeds. There was some deterioration and changes in seed DS for 6 m at 70. The percent germination dropped to 25% and the induction time was reduced a bit to 5-6 w, but the rate was still 5%/d providing only germ. seed was included in the rate calculation.

Epilobium (Onagraceae). *E. tasmanicum* germ. 100% in 2-4 d in either 70D or 70L and 40-70(2%). Exposure to moisture at 40 or GA-3 at 70 is fatal.

Epimedium (Berberidaceae). *E. colchicum* germ. 40(1/10 in 12th w) and none in 70-40-70 and *E. pinnatum* germ. 40-70(1/10 in 4th w). Three other samples of *Epimedium* seed completely rotted indicating either that DS is not tolerated or that seed is not viable despite being full size.

Eranthis (Ranunculaceae). *E. hyemalis* germ. best in 70-40(90% in 55-59 d). A detailed study of the rates of inhibitor destruction at 70 and the clock reaction at 40 are described in Chapter 7. Treatment with GA-3 is not of practical importance, but is interesting from a chemical viewpoint. Seeds treated with GA-3 germ. 89% in 76-87 d if placed directly at 40 and 100% in 47-56 d at 40 if given 4 w at 70 first. Both results show that the GA-3 nullifies the effect of the inhibitor system that was destroyed at 70, but has only a minor effect on the inhibitor system destroyed at 40.

Eremostachys (Lamiaceae). *E. speciosa* germ. 70-40-70(1/2 on 2nd d) and 40-70-40(none).

Eremurus (Liliaceae). Germination occurred at 40 as is typical of cold desert plants.

E. altaica germ. 40(1/15 in 10th w)-70(1/15 in 8th w) and 70-40(6/11 in 5-9 w)

E. robustus germ. 70-40-70-40(2/2 in 4th w).

E. stenocalyx germ. 40-70-40(1/2).

Erigenia (Apiaceae). *E. bulbosa* germ. 70-40-70(1/10) using fresh seed.

Erigeron (Asteraceae). These are mainly D-70 germinators. Germination failed in 60% of the samples received, and this is believed to be due to the absence of viable seed among the copious chaff. The following species germ. in 4-10 d at 70: *E. borealis*, *compositus*, *elegantulus*, *linearis*, *ochroleucus*, *politus*, *radicatus*, and *simplex*. The following DS seed germ. in 1-4 w at 70: *E. alpinus*, *aurantiacus*, *eatonii*, *flagellaris*, *fremonti*, *glabellus*, *nanus*, *pinnatisectus*, *speciosus*, *subtrinervis*, *trifidus*, *uniflorus*, and *villarsii*.

E. compositus germ. 70(100%) and 40(32%)-70(68%) using fresh seed. Seed DS 6 m at 70 or 40 germ. 70(100%) and 40(18%)-70(82%).

E. elegantulus germ. 70(78%) and 40(36%)-70(64%). Seed DS 6 m at 70 or 40 germ. under 10% indicating that in this species DS is not tolerated well.

E. flettii germ. 70D(100% in 5-7 d) and 40(100% in 7th w).

E. leimoerus germ. 70(1%)-40(2%)-70(17%). This was the only species showing extended germination for DS seed.

E. sp. Nepal germ. 70(100% in 6-9 d) and 40(50%)-70(50% in 1-4 d).

Eriogonum (Polygonaceae). Germination often occurred at comparable rates at 40 and 70, it often occurred throughout each 3 m cycle, and it often extended over two cycles. The data is summarized in the following Table except for *E. allenii* and *E. umbellatum*. Germination occurred throughout each cycle unless otherwise specified. The GA-3 treatment was tried on *E. allenii* where it caused total rotting, on *E. ericifolium* where it killed most of the seeds, and on a four year old sample of *E. caespitosum* where germination was 30% in the 2nd w in 70D with or without GA-3. GA-3 is deleterious in this genus. Light had no effect. A four year old sample of *E. caespitosum* still germ. 35%, but four year old samples of *E. ovalifolium* and *E. sphaerocephalum* had germination reduced to 10%, and *E. strictum* was dead.

E. allenii germ. 72% in late March from seed placed outdoors in November. It also germ. 70D(12%) and 40-70D(30% on 2nd d). Light and GA-3 were deleterious.

E. umbellatum germ. 70(3 on 9th d)-40(5 in 3-7 w). Seed DS 6 m at 70 failed to germinate. Seed DS 6 m at 40 germ. 70(1 in 3rd m)-40(2 in 3rd m). Equal amounts of material were used in each experiment so relative numbers are meaningful, but numbers of seeds could not be determined.

Eriogonum Species	Germination	
<i>E. brevicaule</i> ssp <i>oredense</i>	70(1/15 in 3rd w)	40(3/15)-70(8/15)
<i>E. brevicaule</i> ssp <i>oredense</i> (red)	70(3/5 in 1-3 w)	40(3/10)-70(6/10 in 2-4 d)
<i>E. caespitosum</i>	70(1/10)-40(3/10)-70(3/10 in 3-5 d)	
<i>E. caespitosum</i> (red)	70(4/10)-40(2/10)-70(1/10)	40(8/8)
<i>E. compositum</i>	70(50% in 3-13 d)	40(30% in 6-11 w)
<i>E. douglasii</i>	70(43% in 2-12 w)	40(25%)-70(8%)
<i>E. ericifolium</i> v. <i>pulchrum</i>	70(25% in 3-12 d)	40(80% in 3-6 w)
<i>E. flavum</i>	70(50% in 4-8 d)	
<i>E. flavum</i> var. <i>xanthum</i>	70(62% in 1-6 w)	40(72% in 3-10 w)
<i>E. morifolium</i>	70(11/15)-40(3/15)	40(18/21)-70(3/21 2nd d)
<i>E. niveum</i>	70(3/18 in 6-12 w)-40(6/18)	40(25/28)-70(3/28)
<i>E. ovalifolium</i> var. <i>depressum</i>	70(3/10)-40(1/10)	40(3/10)-70(3/10 2nd d)
<i>E. shockleyi</i>	70(100% on 3rd d)	40-70(100% on 3rd d)
<i>E. sphaerocephalum</i>	70(11/22)-40(1/22)	40(9/24)-70(13/24 3rd d)
<i>E. strictum</i> ssp <i>proliferum</i>	70-40(1/7)	40(5/17)-70(2/17 on 3rd d)
<i>E. thymoides</i>	germ. outdoors in April	
<i>E. tumulosum</i>	70(100% in 3 d - 2 m)	40-70(100% in 1-10 w)

Eriophyllum (Asteraceae). *E. lanatum* germ. 40(100% in 3-6 w).

Germination at 70 was reduced to 25% but the rate was about the same.

Eritrichum (Boraginaceae). *E. howardi* germ. in 4-6 w at 70.

Eryngium (Fabaceae). The two species gave different behaviors.

E. alpinum germ. 75% in 3rd w in either 70D or 70L and 100% in 6-8 w at 40.

E. yuccifolium germ. 40(84% in 8-11 w), 70-40(none), and 2/10 in April in outdoor treatment.

Erysimum (Brassicaceae).

E. kotschyianum germ. 70(100% in 3rd w) and 40-70(100% in 1-4 d).

E. nivale germ. 70(10/12 in 5-8 d) and 40(6/13 in 3-6 w)-70(2/13). Light had no effect.

E. perofskianum germ. 85% at both 70 and 40, but the rates differed with ind. t 2 d, 6%/d, at 70 and ind. t 14 d, 21%/d, at 40.

Erythronium (Liliaceae).

E. americanum germ. in an extended pattern as shown by 70-40(7/12 in 10-12 w)-70-40-70-40(5/12 in 2nd w) and 40-70-40(3/19 in 9th w)-70(8/19 in one d to 5 w) using fresh seed. The cotyledons develop in 10 d on shifting to 70.

E. citrinum germ. 40(65% in 10-12 w)-70(35% in 2nd d) and 70-40(80% in 12th w)-70(20% on 2nd d) using fresh seed. The hybrid with *E. hendersonii* was similar.

E. grandiflorum germ. 70L-40-70L(1/2 in 3rd w). Although none germ. in the dark, the data is obviously too meagre to conclude that light is required.

E. hendersoni germ. 40(93% in 8-12 w)-70(7% on 2nd d) and 70-40(80% in 11th w)-70(20% on 2nd d) using fresh seed.

E. mesochorum germ. 70-40(2%)-70(73%) and 40-70(24%)-40-70(48%) using fresh seed. A second sample of fresh seed germ. 40-70-40(80%). This is not as divergent as might first appear because in the first of the two starts at 40, the germination in the 4th cycle at 70 occurred in 1-4 d suggesting that germination may have already started in the previous cycle at 40. The cotyledons develop shortly after radicle emergence and while still at 40. Seed DS 6 m at 40 was nearly as good as fresh seed and germ. 70-40(38%)-70(24%) and 40-70(9%)-40(76%). Seed DS 6 m at 70 was severely damaged and germ. 40(3%)-70(3%) and 70(none).

E. revolutum germ. 70-40(33% in 12th w)-70(40% in 0-7 w) and none in 40(all rotted). Seed that germ. at 40 formed the cotyledon (epigeal) within a week at 40 and grew better than the seed that germ. at 70. Most of the seed would probably have germ. at 40 if the time were extended beyond 3 m.

E. sibiricum germ. 70-40(60% in 8th w) and 40-70-40(60% in 6-8 w)-70(10% on 4th d). The radicles develop slowly at 40, and the cotyledon did not expand until the shift to 70 after 3 m at 40.

Eucalyptus (Myrtaceae). *E. doratoxlyn* and *E. leucoxlyn* germ. 100% on the 4th d in either 70L or 70D. Treatment with GA-3 did not affect the rate of germination.

Eunomia (Brassicaceae). *E. oppositifolia* germ. 100% in all six standard conditions. Germination occurred in the 3rd d at 70 and the 9th d at 40.

Euonymus (Celastraceae). Germination was low and extended in *E. alatus* and *europaeus* until it was discovered that good germination can be obtained only under outdoor treatment after 15 months and only if the seed is WC for 4 w with intermittent washes with detergent. The berries are oily, and the inhibitor in the fruit must be oil soluble. The detergent washes were conducted for only a few minutes, but longer times are probably tolerated since the berry is in the gut of birds where there is strong emulsifying action. It is possible that much shorter washing times would be effective if the washings were conducted entirely in detergent. Several other species germ. more readily, but even with these it would be of interest to compare washing in water with washing in detergent solutions.

E. alatus seed was WC for 4 w with intermittent detergent washes as described above. This seed was placed outdoors in December 1989. There was no germination the following spring but 54% germ. a year later in March and April of 1991. All other treatments failed to germinate a significant amount. In these other treatments the seed would split and expand after several cycles but fail to exert any radicle. If such seeds were placed outdoors in December after a year of alternating cycles, they germ. 70% in March and April the same as if it had been outdoors the whole time. The remaining seed in these outdoor treatments remained firm and turgid and further germination is expected. Light or GA-3 failed to promote germination. Seed WC only in water without detergent failed to germinate a single seed under conditions that gave good germination with the detergent washed seed, a dramatic difference. The effect of DS has not been studied properly as yet, but the indications are that DS of WC seed is not tolerated because seed DS 6 m at 70 rotted instead of remaining firm.

E. atropurpurea germ. in long extended patterns and in low percentages. Experiments on extensive washing with detergents coupled with outdoor treatment are in progress, and such treatments are expected to give much better germination based on the results with the similar *E. alatus*. Seed collected in November and WC 7 d germ. 70-40-70(10% in 2nd w)-40-70(15% in 1-5 w)-40-70(5%) and 40-70(2%)-40(9%)-70(2%)-40-70(2%). Seed DS 6 m at 40 or 70 in the WC state all rotted, but seed DS in the dried fruit germ. about the same as fresh seed.

E. bungeana seed was WC for 7 d in water. This seed either fresh or after DS 6 m at 70 germ. 40(90-100% largely in 5th w). When either fresh or DS seed was sown at 70, germination extended over 2-3 cycles with comparable amounts of germination in each cycle.

E. europaeus has the same requirements of outdoor treatment and 4 w WC with detergents that were found for *E. alatus*. Seed collected in November, WC for 4 w with weekly short detergent washes, and given outdoor treatment germ. 45% in March and April in the first spring and 15% the second spring. Seed WC for just 7 d without detergent failed to germinate. Other treatments gave either no germination or germination in the 10-20% range in the 3rd-6th cycles of alternating cycles. Light or GA-3 had no effect. Like *E. alatus*, seed of *E. europaeus* will remain firm, unrotted, and ungerminated for years if not given the detergent washes and outdoor treatment.

E. radicans germ. best if the seed was WC for 7 d, DS 6 m at 70 or 40, and sown at 70. This gave 80-90% germination with ind. t 15 d and rate 6%/d. Fresh seed under the same treatment germ. over three cycles as shown by 70(53%)-40(27%)-70(17%) so that germination is more convenient with DS seed. The DS seed also germ. at 40 (70-85%), but the rate of germination was slower (ind. t 55 d, 2.6%/d), and the germination extended into the following cycle at 70.

Eupatorium (Asteraceae). Seed counts were difficult so the percent germinations are calculated on the basis that total germination was 100%. The 40-70 germination pattern found in *E. purpureum* is unusual in Asteraceae.

E. coelestinum germ. in 4-12 d in either 70D or 70L. A prior 3 m at 40 gave much lower percent germination.

E. purpureum germ. 40(2%)-70(98% in 2-4 d) using fresh seed or seed DS 6 m at 70 or 40.

E. urticaefolium germ. best in 70(100% in 5-12 d) and 40(54%)-70(46%) using seed DS 6 m at 70 and 70(20%)-40-70(80%) and 40(5%)-70(95%) using fresh seed.

Euphorbia (Euphorbiaceae).

E. aristata germ. 91% in April in outdoor treatment. It also germ. 70D(50% in 4-8 d)-40-70(4%)-40-70(12%) and 40(4%)-70(20% on 4th d).

E. francheti germ. 40(4% on 5th d)-70 and 70D(none). The rest rotted.

E. polychroma seeds are enclosed in a hard case which is not readily removed until the seeds have been moist for a few days. Germination was 70(40% in 2-4 w) with seed DS 6 m at 40, 70(20% in 1-4 w) with seed DS 6 m at 70, and 70-40-70(none) with fresh seed. The DS promotes germination. All seed started at 40 failed to germinate through four cycles, and outdoor treatment germ. only 5% in March and April. Light had no effect.

Eustoma (Gentianaceae). See *Lisianthus*.

Evodia (Rutaceae). *E. daniellii* germ. best when treated with GA-3, and the seedlings were normal and healthy. All other procedures gave long extended germinations in less than 1%. The GA-3 treatment was applied to seeds that had been 3 m at 40 (85% germ. in 1-6 w at 70), seeds that had been outdoor until April (85% germ. in 9-12 d), and seeds that had been DS for 6 m at 70 (55% germ. in 1-3 w). Even much lower dosages than those described in Chapter 3 were effective. The seeds were collected in November. The seed coats are in pairs with a larger viable seed and a smaller non-viable seed that soon rots.

Exochorda (Rosaceae). *E. grandiflora* germ. best at 40(97% in 7-12 w) and poorer in 70(41% in 1-12 w)-40(36% in 5th w). Light blocks the germination at 70, but has no permanent effect since germination occurs at the same percentage and rate when shifted to 70D. Seeds DS 6 m at 70 germ. faster as shown by 40(92% in 3-6 w) and 70(79% in 1-4 w).

Ferocactus (Cactaceae). GA-3 was required. Expts. are only 6 w old.

F. acanthoides germ. 70 GA-3(12% in 1-4 w) and none in 70D.

F. wislizenii germ. 70 GA-3(8% in 4th w) and none in 70D.

Ferula (Apiaceae). All species are 40-70 germinators (ref. 6, p. 61).

Festuca (Poaceae). See Chapter 22

Fibigia (Brassicaceae). *F. clypeata* germ. 70(40-50% in the 2nd w) and 40(50% in 3-9 w). Light or GA-3 had no effect on the rate or percentage germination.

Filipendula (Rosaceae). *F. ulmaria* germ. 70L(7% in 2nd w), 70 GA-3(3%), and none in 70 or 40. Experiments are only 6 w old.

Forsythia (Oleaceae). *F. suspensa* germ. 70(10%)-40-70(20%) and 40-70(10%).

Franklinia (Theaceae). *F. alatahama* seed coats were 95% empty, and this was true in eight separate samples. The empties could be distinguished by being thinner. The 5% of thicker seed coats germ. in 1-3 w at 70 in percentages varying from 2-40%. The seedlings grew satisfactorily. It is likely that viability is poor because of the practice of growing single specimens and the circumstance that all stock may be descended from a single plant.

Frasera (Gentianaceae). Germination extended over several cycles. Treatment with GA-3 was tried only on samples that had been subjected to a year of alternating 3 m cycles. There was no effect.

F. albicaulis germ. 40(50% in 4-8 w)-70-40(10%) and 70-40(40% in 3-8 w)-70-40(30%). Seeds placed outdoors in December germ. 33% in March and 6% more the following March.

F. fastigiata germ. 70-40-70-40-70(20% in 1-3 w). Seeds placed outdoors in December germ. 4% the following April and another 3% a year later.

F. speciosa placed outdoors in December germ. 5% in April and an additional 20% a year later. Seeds also germ. 40(1%)-70-40(0.5%)-70(2%) and 70-40-70-40(1%).

Fraxinus (Oleaceae). *F. pennsylvanica* was reported to be a 40-70 germinator (ref. 28, Ch. 10) and *F. excelsior* was reported to need extensive after-ripening. (ref. 31, Ch. 5). *F. mandschurica* and *nigra* were reported to require a long warm period in moisture followed by a long cold cycle (ref. 7, p. 47). *F. americana*,

lanceolata, oxycarpa, pennsylvanica, and syriaca were reported to have germination improved by a cold cycle (ref. 7, p.47), although the same reference said that "many species" germinate in 15-30 d in warmth which appears to be contradictory.

Although *F. americana* self sows here (see Chapter 12), an examination of large amounts of seed coats showed that all seemed to be empty. A species of *Fraxinus* on the Penn State Campus has abundant seed which appeared to contain plenty of endosperm. Germination failed until a sample that had been DS 6 m at 70 was placed outdoors in June. The following April 3/8 germ. The seedlings developed the cotyledons within 2 w of germination. Unfortunately this was the only sample subjected to outdoor treatment. This result suggests that outdoor treatment may be needed. It also suggests that the confusing results reported in the literature have been due to failure to recognize that outdoor treatment and oscillating temperatures are required and that the germination that was observed was due to treatments that ultimately effected some degree of oscillating temperature. A possible promotion of germination by rotting wood was described in Chapter 12.

Freesia (Iridaceae), *F. hybrids* germ. 70(90% in the 4th w) and 40(50% in 7-9 w). Light or GA-3 had no effect.

Fritillaria (Liliaceae). This genus germ. primarily at 40. Sometimes this had to be preceded by a cycle at 70 making the species a 70-40 germinator. The seedlings did not always develop, and it is probable that this was the result of shifting them to 70 too suddenly. More study is needed on this problem. Some species showed intolerance to DS, particularly *F. acmopetala* and *F. meleagris*. The following germ. outdoors at the end of March after being outdoors for over a year: *F. armena*, *aurea*, *forbsii*, *graeca*, *kurdica*, *lanceolata*, *michaelowskii*, *pallidiflora*, *pluriflora*, *pudica*, *pyrenaica*, and *raddeana*.

F. acmopetala germ. best with fresh seed in 40(45% in 9-12 w)-70(23% in 2-6 d). A prior 3 m at 70 had no effect. DS for 6 m at 70 is fatal.

F. carica germ. 40(100% in 6-10 w) and 70-40(45% in 11th w).

F. gantneri germ. 40(4/8 in 8-10 w) and 70-40(2/5 in 9-11 w).

F. glauca germ. 40(100% in 6-8 w), 70-40(60% in 6-8 w), and 24% in February and March from seed placed outdoors in November.

F. graeca v. thessalica germ. 40-70D(1/11 on 4th d).

F. imperialis germ. 40-70-40-70(2/3 in 1-3 w) and none when started at 70.

F. lanceolata germ. 40(100% in 6-8 w), 70-40(90% in 6-8 w), and 25% in March in outdoor treatment.

F. meleagris germ. best with fresh seed in 70-40-70(70% largely in 1-5 d). The cotyledon develops within a week of germination. Germination was less when sown at 40 as shown by 40-70-40(3%)-70(8%)-40-70(5%). Seed DS 6 m at 70 was dead and seed DS 6 m at 40 was largely dead.

F. pallida germ. 40-70-40-70(20%)-40(60%) using fresh seed. Seed DS 6 m at 70 germ. 70-40-70(4%)-40(37%)-70(15%)-40(22%)-70(15%) and 40(2%)-70(7%)-40(7%)-70(30%)-40(47%)-70(5%). These patterns are essentially of the 70-40-70-40 type. It is possible that these would have been reduced to a 70-40 pattern if longer cycle times had been used.

F. persica germ. best with fresh seed in 40(97%, ind. t 54 d, 8%/d). A prior 3 m at 70 or DS 6 m at 70 had no effect, but DS for 2 y was fatal.

F. pontica germ. best in 40(60% in 10-12 w)-70(10% on 3rd d). A prior 3 m at 70 had no effect.

F. pudica germ. best in outdoor treatment (36% in April) and less in 40-70-40(20% in 2-9 w). Germination failed when sown at 70.

F. recurva germ. 40(38% in 8-11 w)-70(11%) and 70-40(80% in 2-8 w) using fresh seed and 40(64% in 7-10 w) with seed DS 6 m at 70.

F. sp. Oregon germ. 40(60% in 6-8 w)-70(40% in 2-10 d), 70-40(15%), and 60% in February and March in seed placed outdoors in November. The seed in outdoor treatment was shifted to 40 on June 15 whereupon 22% germ. in the 3rd w.

F. thunbergii germ. 40-70-40(100% in 4th w) and 70-40(50% in 5-7 w)-70(30%).

F. tubiformis germ. 40(12% in 10-12 w)-70(25% in 2 d-8 w) and 70-40(none).

F. ussuriensis germ. one in the 40-70-40(1) pattern and none when sown at 70.

Fumana (Cistaceae). *F. viridis* germ. 70D(30% in 1-8 w)-40-70(15% in 7-10 w) and 40(16% in 8-11 w)-70(5%)-40-70(5%).

Fuschia (Onagraceae). *F. hybrids* germ. 70D GA-3(90% in 3rd w), 70L(50% in 2nd w), 70D(30% in 2nd w), and 40-70D(10%).

Gagea (Liliaceae). *G. sp.* sown outdoors in February germ. in April.

Gaillardia (Asteraceae). *G. aristata* germ. 70(100% in 3-6 d) and 40(60% in 2-8 w)-70(40% in 1-3 d) using either fresh seed or seed DS 6 m at 70 or 40.

Galanthus (Amaryllidaceae). Germination was hypogeal and largely at 40. When the 3 m cycle at 40 was over and the seedlings shifted to 70, the true leaf developed in a week or two. DS is deleterious but not completely fatal.

G. elwesii germ. 70-40(45% in 5th w)-70-40(3%)-70-40 and 40-70(25% in 3-5 w)-70-40(4%) using fresh seed. Seed DS 6 m at 70 germ. 40-70-40(3/7) and none in 2 y starting at 70 indicating deterioration on DS.

G. nivalis germ. 70-40(45% in 2-5 w) and 40-70-40(80% in 4th w) in a sample WC for 7 d. Germination was less without the WC. Seed DS 6 m at 70 was dead, and seed DS 6 m at 40 was largely dead.

Galtonia (Liliaceae). *G. candicans* germ. 70(1/6 in 3rd w).

Gaultheria (Ericaceae). Seed is enclosed in a berry and was WC.

G. depressa germ. only in light, 70L(12% in 5-8 w) and 70D(none).

G. procumbens germ. 50-60% in 2-6 w at 70. A prior 3 m at 40 reduced germ. to 30%. Light had no effect. The results were confirmed with a sample a year later.

G. trichophylla germ. 70L(55% in 3-7 w) and 70D(none). When the sample in 70D was shifted to 70L after 4 w, 25% germ. in 2 d-4 w.

Gaura (Onagraceae).

G. biennis germ. 70D GA-3(26% in 3rd w), 70L(10%), 70D(none), and 25% in April for seed placed outdoors in October. Seeds DS 6 m at 70 germ. similarly.

G. coccinea germ. 40-70(2%) and 70-40(1%).

G. lindheimeri germ. 70D(100% in 8-12 d), 40-70(100%) and 100% in April in outdoor treatment. Light had no effect. There were 80% empty seed coats.

Genista (Fabaceae). *G. subcapitata* sown outdoors in January germ. in spring. This probably has an impervious seed coat like other legumes, and germination would be immediate if a hole is produced in the seed coat.

Gentiana (Gentianaceae). A number of species show initiation of germination when treated with GA-3. Conditions of treatment are critical for *Gentiana verna* (ref. 9) and would be true presumably for other species. Photorequirements were found in some species (*G. affinis*, *autumnalis*, *saponaria*, and *scabra*) and an oscillating temperature requirement in *G. lutea*. It is unfortunate that light experiments, GA-3 experiments, and outdoor conditions were not conducted on all species. In early qualitative experiments the following species germ. in April from seed sown outdoors in January: *G. algida*, *asclepediae*, *autumnalis*, *bisetata*, *brachyphylla*, *frigida*, *grossheimii*, *makinoi*, *pneumonanthe*, *przewalskii*, *punctata*, *rubricaulis*, *triflora*, and *wutaensis*. Some of these gave a small amount of germination when sown directly at 70. The following germ. in April after being over a year outdoors: *G. aspera*, *austriaca*, *barbata*, *dahurica*, *depressa*, *gracilipes*, *linearis*, *nesophila*, *olivieri*, *platypetala*, *procera*, *quinquifolia*, *turkestanicum*, and *walujewii*.

G. acaulis germ. 70-40-70(7%)-40(31% mainly in 3rd m)-70(2%) and 40-70-40(23%). Seed sown outdoors in February germ. some in April and more a year later, again demonstrating the extended germination behavior.

G. affinis germ. best (98% in the first 2 w of April) when sown outdoors in February. Seeds also germ. 70L(67% in 11-15 d), 70D(25% in 5-15 d), 40-70L(70% in 2-16 d), and 40-70D(none). Another sample germ. 70(28%)-40(15%)-70(11%) and 40(13%)-70(72%). It is possible that the photoresponse disappears on DS, and that the latter seed had experienced longer DS.

G. asclepediae gave low (5-10%) germination at 70 with or without a prior 3 m at 40. Unfortunately photoeffects were not studied, and it is possible that this species requires light, particularly because three other samples failed to give any germination in the dark.

G. autumnalis had germination promoted by light, by 3 m moist at 40, and by DS for 6 m at 70. Fresh seeds germ. 40-70L(100% in 4-20 d), 40-70D(64%)-40-70L(36%), 40-70D(64%)-40-70D(none), 70L(11%)-40-70L(31%), 70D-40-70L(44%), and 70D-40-70D(8%). Seeds DS 6 m at 70 germ. 40-70L(100% in 8-18 d), 40-70D(34%), 70L(68% in 3-5 w), and 70D(none). The 40-70L pattern is best.

G. bellidifolia germ. 70 GA-3(38% in 2-7 w) and none in 70-40-70 with or without light.

G. boisseri germ. best in 40(14%)-70(79%) and less in 70(3%)-40(9%)-70.

G. cachmerica germ. abundantly in the 3rd m at 70.

G. calycosa germ. 70L(51% in 2nd w), 70D GA-3(97% in 2nd w), 70D(4%), and 40(65% in 7-12 w).

G. clusii germ. 70-40-70(a few).

G. corymbifera germ. 70 GA-3(2% in 5th w) and none in 70L or 70D.

G. crinita germ. 70D GA-3(96% in 2nd w), 40-70(5% in 2nd w), and none in 70L or 70D. Another sample sown in October germ. in April.

G. decumbens germ. 70(50% in 4th w) and 40-70(75% in 3-20 d). Light and GA-3 were not studied. Many names in seed exchange lists turn out to be this species.

G. dinarica germ. 70D GA-3(85% in 2nd w), none in 70D or 70L, and 40(61% in 8-12 w).

G. farreri germ. 70(25%)-40-70(62%).

G. fischeri germ. 70(15% in 8-17 d) and 40(none).

G. flavida germ. in the 4th w at 70.

G. gelida germ. 70(2%)-40(15%)-70-40(6%).

G. lagodechiana germ. in 3rd w at 70.

G. loderi germ. one in 2nd w at 70.

G. lutea seeds placed outdoors in January germ. 39% in April and May and an additional 27% in April a year later. No other treatment gave a single germination except seeds treated with GA-3 germ. 5% in the 4th w at 70.

G. macrophylla germ. 73% in 3rd w in either 70D or 70L. Treatment with GA-3 had no effect on this rate.

G. occidentalis germ. 40-70-40-70(4/9 on 6th d), 70D GA-3(5/9 in 4th w), and none in 70L or 70D. The seedlings from GA-3 treatment did not survive, but this perhaps could be corrected by optimization of the GA-3 treatment.

G. paradoxa germ. 40(40% in 6-10 w)-70(7%), 70D GA-3(100% in 5th w), 70L(10%)-40(5%)-70L(10%), and 70D-40-70D(40% on 8th d). The GA-3 seedlings did not survive.

G. parryi germ. 70(100%, ind. t 3 d, 13%/d). Light had no effect. Sowing seed at 40 gave much lower germination even after the shift to 70.

G. pseudoaquatica germ. 40-70(60% in 4 d-2 w) and 70(25% in 1-3 w).

G. pterocalyx germ. in 4th w at 70.

G. puberulenta germ. 40(45%)-70(24%) and 70(3%)-40-70(12%). Seed sown outdoors in January germ. in spring.

G. saponaria germ. best in 70D-40-70L(80% in 2-4 w), less in 40-70L(9%), and none in 70L-40-70D, 70D-40-70D, and 40-70D-40-70L. DS 6 m at 70 was fatal.

G. scabra germination was strongly promoted by light and by GA-3. Fresh seeds germ. 70L(93%), 70D GA-3(72%), 70D(none), 40-70L(100%), and 40-70D(94%). Seeds DS 6 m at 70 germ. 70L(25%), 70D(none), 40-70L(75%), and 40-70D(15%). All germinations took place in 1-4 w. Note that the photorequirement was eliminated by a prior 3 m at 40 with fresh seed. The low germinations in dark experiments may have been due to short exposures to light made in the course of the observations. Seeds had partly died after 6 m DS at 70, but only slightly after 6 m DS at 40. Seeds also die in 70D so that even a 4 w exposure kills 70% of the seeds.

G. septemfida germ. in 3-7 w at 70.

G. sino-ornata germ. 70(20%)-40-70(5%) and 40(5%)-70(2%).

G. siphonantha germ in 2-4 w at 70.

G. tianschanica germ. in the 4th w at 70.

G. tibetica germ. 70(90% in 2-4 w) and 40-70(none). Light had no effect.

G. trichotoma germ. 70(50% in 2-4 w) and 40-70(none). Light had no effect.

G. verna germination is dramatically promoted by GA-3, and it is likely that gibberelins are natural requirements for germination. A GA-3 experiment was set up in which part of the seeds were removed each day for 10 d. On removal the seeds were placed on a fresh moist towel and planted immediately in soil when they germ. Germination started about the 10th d for all exposures and was about 50% in each sample (other GA-3 experiments gave as high as 85% germination). Somewhat surprisingly the healthiest seedlings resulted from the 10 d exposure. However, exposures longer than 10 d led to weak and etiolated seedlings. The sample of seed used in the GA-3 experiments completely failed to germinate in 6 m under all other

treatments. However, earlier samples had given some germination when started at 40. The data for three of these earlier samples are 40(36%)-70(10%), 40(25%), and 40(25%)-70(9%). None germ. when started at 70 for all three samples, however a fourth sample germ. in the 2nd w at 70. All samples of seeds were received in winter, and there had been varying amounts of DS which may account for varying results. Also *G. verna* has many variants. *G. verna* is often a crevice plant as in the Burrens in Ireland, and it is reasonable that survival is enhanced if the seeds are programmed to delay germination until falling into a pocket of leaf mold.

Gentianella (Gentianaceae). The splitting out of this genus and *Gentianopsis* from *Gentiana* has not been helpful as species have been shuttled around between the three genera. Light and GA-3 need to be tried.

G. barbellata germ. 70(45%)-40-70(42%).

G. moorcroftiana germ. nearly 100% at 70 with ind. t 5 d and 25%/d.

G. paludosa germ. a few in 3rd w at 70.

G. sp. Nepal germ. 55% in 3-5 w in either 70D or 70L and 40(19%)-70(5%).

G. turkestanorum sown outdoors in January germ. well in April. A second sample germ. 70 GA-3(25% in 4-6 w) and none in 70D or 70L.

Gentianopsis (Gentianaceae). Light and GA-3 need to be tried.

G. crinita, see *Gentiana crinita*.

G. stricta sown outdoors in March germ. in April thirteen months later.

G. thermalis germ. 40-70(15% in 4-6 d) and none over three cycles when sown at 70. Photoexperiments and outdoor treatment need to be tried.

Geranium (Geraniaceae).

G. maculatum germ. best (77%) in February through April from fresh seed sown the previous July and given outdoor treatment. Fresh seed also germ. 70-40(2%)-70(39% in 2-9 d) and none in 40-70-40. Seed DS 6 m at 40 or 70 is largely dead.

G. sanguineum germ. best in 70D(77% in 6-12 w), poorer in 70L(15% in 2-7 w) and 40-70(14%), and none in outdoor treatment.

G. transbaicalicum germ. 70(4/4 in 16-26 d) and 40-70(6/7 in 1-3 d).

G. traversii germ. 94% in 70D in 2-4 w.

G. wallichianum germ. 70(90-95% in 3 d-3 m) and 40-70(85-100% in 2 d-3 w) using either fresh seed or seed DS 6 m at 70 or 40..

Gerardia (Scrophulariaceae). *G. grandiflora* sown outdoors in January germ. in April.

Geum (Rosaceae). Three species (*G. borisii*, *montanum*, and *reptans*) germ. in April when sown outdoors in January.

G. coccineum germ. 70L(3/4 in 3rd w) and none in 70D, 40-70L or 40-70D.

G. montanum germ. either in 70L or in 40-70D as shown by 70L(3/5 in 5th w), 70D(none), and 40-70D(2/7 in 2-4 w).

G. radicans germ. in 2nd w at 70.

Gillia (Polemoniaceae). *G. androsacea* germ. in 7 d at 70 and *G. tricolor* germ. 100% in 4-10 d in 70D, 70L, or 40. Note the fast germination at 40.

Gillenia (Rosaceae). *G. trifoliata* germ. best in 40-70 GA-3(55% in 1-5 w), less in 70 GA-3(15%), and none in 70D, 70L, 40-70D, or 40-70L. Seeds placed outdoors in September germ. 55% in April. Seeds DS 6 m at 70 germ. 40(50% in 8-10 w), 70 GA-3(4%), and 70D(none), but these expts. are only 3 m old.

Ginkgo (Ginkgoaceae). *G. biloba* was WC 7 d after which it germ. 70(80% in 5-10 w). If the seed is WC for 3 w, germination is reduced to 40% in 5-10 w. If the seed is WC 5 d in water and then 2 d in aqueous detergent, germination is reduced to 10% in 5-10 w. The WC treatment is necessary as without it there is no germination. A prior 3 m at 40 had no effect. The seed all rotted in outdoor treatment.

Gladiolus (Iridaceae). This genus germ. largely at 40.

G. anatolicus germ. 40(91% in 7-9 w) and 70-40(100% in 4-7 w).

G. caucasicus sown outdoors in March germ. in April thirteen months later.

G. imbricata behaved like *G. caucasicus*.

G. kotschyanus germ. 40(80-100% in 6-12 w) and 70-40(6%)-70(4%).

Glaucidium (Ranunculaceae). *G. palmatum* germ. 70D(4/5 in 4-7 w), 70 GA-3(5/5 in 2nd w), and none in 40. Another sample germ. a few in April fifteen months later and a few more a year after that. *G. palmatum album* germ. 70 GA-3(100% in 2nd w) and 70D(50% in 5-7 w).

Glaucium (Papaveraceae). *G. elegans* germ 70D(7/41 in 13-15 d) and *G. squamigera* germ 55% in 1-3 w at 70.

Gleditsia (Fabaceae). *G. triacanthos* germ. 100% in 3-5 d at 70 if a hole is made through the seed coat. Without the hole only an occasional seed germ. over several years.

Gomphrena (Amaranthaceae). *G. haageana* germ best (91% in 2-4 d) in a regime of 90 daytime and 70 nighttime temperatures. This supports a report from Ralph Cramer (a commercial grower of *Gomphrena*) that the seed germ. best if given 4 d at 100 and then shifted to 70. Germination was poorer at a constant temperature of 95(70% in 4-15 d) and even less at 70. The seed is enclosed in a papery husk which can be readily removed and experiments were conducted on both seed in the husk and seed with the husk removed. There was no essential difference although in a 70L experiment the seeds in the husk germ. faster which is attributed to a greenhouse effect with the husk trapping light and raising the effective T. A preliminary 3 m moist at 40 led to complete rotting of the seeds. Germination was not stimulated with GA-3 and such treatment was detrimental.

Goniolimon (Plumbaginaceae). *G. tataricum* germ. 70(100% in 2-8 d), 40(50% in 12th w)-70(50% in 2-4 d), and 100% in April in outdoor treatment. The sample started at 40 would presumably have all germ. at 40 if sufficient time had been given.

Grumolo (?). *G. verde scuro* (name ?) germ. 20% in 4-10 d in either 70D or 70L and 40(4%)-70(4%).

Gunnera (Haloragidaceae). *G. manicata* was reported to germinate either after washing the seeds for 6-24 hours in cold running water or after pouring boiling water over the seeds and allowing the seeds to remain in the water for 24 hours as it cooled (J H). Seeds of *G. flavida*, *G. prorepens*, and *G. sp.* were received in January and rotted quickly after moistening indicating that DS is not tolerated.

Gutierrizia (Asteraceae). *G. sarothrae* germ. in 6 d at 70.

Gymnocladus (Fabaceae). *G. dioica* germ. 100% within a w if a hole is made through the seed coat. Without the hole only an occasional seed germ. over several years. Extensive studies on hot water treatments are described in Chapter 9.

Gymnospermium (Berberidaceae). *G. altaicum* germ. 70-40(50% in 12th w)-70(40% in 2nd d) and 40(70% 7-10 w)-70.

Gypsophila (Caryophyllaceae). The four species studied (*G. bungeana*, *capitoliflora*, *cerastoides*, and *pacifica*) were D-70 and germ. in 7 d at 70. *G. pacifica* was studied in more detail and germ. 70(66% in 3-5 d) and 40(87% in 3rd w).

Haberlea (Gesneriaceae). *H. rhodopensis* can be germ. simply and efficiently by the Bagging procedure described in Chapter 14. The seeds germ. in 4-6 w at 70. Germination was better under the lights than in dark. Seedlings have been left enclosed in the polyethylene bag under fluorescent lights for a year with excellent development. The bags need not be examined more often than once every two months to be sure that there is no excessive drying due to a tear in the bag.

Habranthus (Amaryllidaceae). *H. andersonii* germ. 70(90% in 4-5 d) and 40(75% in 6th w).

Halesia (Styracaceae). *H. caroliniana* was extensively studied by Barton (ref. 31, Ch. 8). The best germination was obtained by treatment with sulfuric acid, keeping moist for 3 m at 70, and overwintering outdoors. No germination occurred if the 3 m at 70 was omitted. *H. caroliniana* self sows here abundantly, much seed was available, and extensive experiments were conducted. Germination occurs after 2-4 y of alternating 40 and 70 cycles with germination almost always occurring within a week of shifting to 70. Seeds from a several trees ran consistently 80% empty seed coats. After correcting for these germination was ultimately 50-100% after 4 y. Outdoor treatment is also effective, but again germination occurs only in 2-4 y. It was convenient in these studies to soak the seeds in water and scrape away the corky outer layer. Efforts to produce holes in the seed coats along the side or at either end resulted in rapid rotting of the seed. Seed DS 6 m at 70 or 40 or seed collected anytime from fall to spring all behave identically to fresh seed.

Hamamelis (Hamamelidaceae). *H. virginiana* has a pattern of the seeds splitting during a cycle at 40 followed by a burst of germination in 14 d on shifting to 70. This pattern extends through many alternating cycles for both fresh and DS seed. Fresh seed germ. 70-40(14%)-70(23%)-40-70(22%), 40(1%)-70(16%)-40(7%)-70(15%)-40-70(16%), and 14% in April in outdoor treatment. Seed DS 6 m at 70 germ. 70-40-70(37% in 0-8 w)-40-70(11%) and 40-70(18%)-40-70(63%).

Haplopappus (Asteraceae). *H. lyallii* and *H. spinulosus* germ. in 1-4 w at 70.

Hardenburgia (Fabaceae). *H. comptoniana* has an impervious seed coat. Germination was 7/8 in 4-11 d if a hole was made in the seed coat and none otherwise. Interestingly treatment with GA-3 initiated a growth of mold and led to 3/8 germinating in 3rd w.

Hastingsia (Liliaceae). *H. alba* produced healthy seedlings only if the seed received in midwinter was DS until midsummer, sown in moist towels, and kept outdoors. Germination continued from July to December. A total of 78% germ. with most (40%) germinating in November. Radicles were well formed by January 1 so the seedlings were shifted to 70 where they developed a true leaf (hypogeal) in a week and became healthy seedlings. Although seed germ. under the other sets of conditions, not only was the germination in lower percentage, but the seedlings

developed rot of the radicles and/or the radicles failed to develop so that the final result was that the seedlings died.

Hebe (Scrophulariaceae).

H. chatamica germ. 40-70(91% largely in 6-8 d)-40-70(4%) and 70(37% in 10 d-3 m)-40(1%).

H. guthreana germ. 40 (96%, ind. t 48 d, 4%/d)-70(4%) and 70(5%). The seed sown at 70 might have given better germination if the experiment had been continued.

Hedyotis (Rubiaceae). Species shuttle between this genus and *Houstonia*.

H. pygmaea germ. 70L(80% in 2nd w) and 70D(none). A prior 3 m at 40 caused all the seeds to rot. About a third of the seed coats were empty.

H. rubra germ. 70L(38% in 2nd w) and 70D(10%). A prior 3 m at 40 caused all the seeds to rot.

Hedysarum (Fabiaceae). *H. cephalotes* germ. on the 7th d at 70.

Helianthemum (Cistaceae).

H. ledifolium germ. 70(30% in 3-7 d)-40-70 and 40(16% in 4-11 w)-70(5%).

H. nummularium germ. 70(1/15 on 16th d)-40-70 and 40(3/15 in 2nd w).

H. oelandicum germ. 70(4/17 in 3-24 d)-40(1/17)-70 and 40-70(1/23)-40(2/23).

H. salicifolium germ. 70(80% in 5-7 d) and 40(71%)-70(12%).

Helianthus (Asteraceae). *H. sp.* seed collected in November or seed DS 6 m at 70 or 40 germ. at 70 in 1-3 d. When sown at 40 a few germ. at 40, but the main germination is in 1-2 d after the shift to 70. The seed head are so full of chaff and debris that numbers of seeds could not be counted.

Helichrysum (Asteraceae). *H. sp.* Basutoland (possibly *H. milfordiae*) germ. immediately at 70 or 40 at about the same rate. This is one of the few plants of Central Africa that is entirely hardy here. The gray-green leaves remain evergreen with no trace of browning all winter and the species self sows.

Helleborus (Ranunculaceae). *H. argutifolius*, *H. niger*, and *H. orientalis* were strictly 70-40 germinators, and DS was fatal. A sample of DS seed of *H. corsicus* was dead.

H. argutifolius germ. 70-40(57% in 7-11 w). Treatment with GA-3 at 70 not only failed to stimulate germination but led to rapid rotting of the seeds. A prior 3 m at 40 also led to complete rotting of the seeds.

H. niger germ. 70-40(93% in 9th w) and 40-70-40(19%)-70(25% in 2 d)-40(44%). The 25% germination at 70 may have begun at 40.

H. orientalis germ. 70-40(100% in 5-10 w) and 40-70-40(100% in 6-11 w).

Helonias (Liliaceae). *H. bullata* germination is augmented by light. Fresh seed in dark germ. 70(11% in 4th w)-40-70. In this last shift to 70 half was put in light and half left in dark. The sample in light germ. 56% of the remaining seeds in 2-5 w whereas the sample in dark germ. 6% in the same time period. The results were similar for seed started at 40 which germ. 40-70(5%). After 2 m at 70 the sample was shifted to light and 100% of the remaining seeds germ. in 6-10 d. Seed DS 6 m at 70 germ. 70(5% in dark and none in light) showing that DS is not tolerated. It was unfortunate that fresh seed was not immediately subjected to 70L, but the data does indicate that germination takes place on shifting to 70L and is insensitive to prior treatments. This is on the list of federally endangered species. It could be so easily propagated from seed.

Hemerocallis (Liliaceae). Seed of *H.* hybrids germ. under all conditions. Fresh seed germ. 70(91% in 2-9 w) and 40(15%)-70(77%). Seed DS 6 m at 70 or 40 germ. 70(50% in 3rd w) and 40(88% in 6-12 w). A different hybrid germ. 70(55% in 1-4 w)-40(40%) and 40(90% in 6-9 w)-70(10% on 4th d) for fresh seed and 70(56%)-40(13%) and 40(60%)-70(6%) for seed DS 6 m at 70.

Hepatica (Ranunculaceae). The three species germ. strictly at 40 and best if preceded by a 3 m cycle at 70. DS was fatal. Only the radicle develops at 40, and a major problem was getting the cotyledons to develop on shifting to 70. It is likely that gradually increasing the T from 40 to 70 would have given much better results. *H. acutiloba* opened the cotyledons if the seedlings were kept at 40 for 3 m after radicle development was complete. This was only partly effective with *H. americana* and failed with *H. nobilis*.

H. acutiloba germ. 70-40(36% in 7-10 w). Germination was somewhat better if the seed were washed with dilute Clorox (dilute aqueous NaOCl) and such seed germ. 70-40(88% in 4-6 w). Curiously those sown outdoors or at 40 all rotted.

H. americana (triloba) germ. 70-40(31% in 8th w).

H. nobilis seeds were received from Sweden in a moist paper towel so that they had already been subjected to at least a month moist at 70. Seeds kept an additional 3 m at 70 all rotted. Seeds placed in 40 when received germ. 40(29% in 8th w).

Heracleum (Apiaceae). *H. nepalense* germination benefits greatly from DS. Seed DS at 70 gave higher germination than seed DS at 40 showing that the necessary chemical reactions were not complete in 6 m at 40. Seed DS 6 m at 70 germ. 70(93% in 10-27 d) and 40(59%)-70. Seed DS 6 m at 40 germ. 70(68%)-40-70-40-70(4%). Fresh seed germ. 70(3%)-40-70-40-70 and 40(22%)-70-40-70.

Hermodactylus (Iridaceae). *H. tuberosus* germ. 70D(1/4 in 6th w)-40(1/4 in 3rd w) and 40-70(none).

Hesperis (Brassicaceae). *H. matronalis* is largely a D-70 germinator. Seed DS 6 m at 70 or 40 germ. 70(20% in 2-6 d)-40-70 and 40(5%)-70 whereas fresh seed germ. 70-40-70(17%)-40-70 and 40-70(2%)-40-70.

Heterotheca (Asteraceae). *H. fulcrata* germ. 70(100% in 3-5 d) and 40(100% in 2-4 w).

Heuchera (Saxifragaceae). The small seeds cannot be readily separated from the capsules and chaff so that seed counts are inaccurate.

H. cylindrica germ. 70D(5% in 3rd w), 70L(13% in 3rd w), 40(4%)-70, and 40% in April in outdoor treatment. These behaviors contrast sharply with the behaviors of seeds that had been DS for 2 y. These germ. 70L(43% in 3rd w), 70D GA-3(31% in 2-4 w), and 70D(none). The GA-3 seedlings were normal.

H. cylindrica v. *alpina* germ. 70(30-40% in 2-4 w) and 40-70(none). Light had no effect. In view of the results with *H. cylindrica*, outdoor treatment might have given even higher germination. Note that in both species, a prior 3 m at 40 was deleterious. Seeds DS for 2 y was dead.

H. hallii required light in a 3 cycle treatment as shown by 70L-40-70L(12% in 2nd w) and none in 70D-40-70D.

H. hispida germ. 70L(a few in 2-4 w) and 70D(none).

H. richardsonii germ. 70(92% in 8-20 d), 40(32% in 8-12 w)-70(10%), and 34% in outdoor treatment. Light had no effect.

H. villosa germination was improved by DS for 6 m at 70. The DS seeds germ. 70L(30% in 2nd w), 70 GA-3(18%), and 70D(none). Fresh seeds germ. 70L(12% in 3rd w), 70D GA-3(30% in 2nd w), 70D(none), 40-70(10% on 6th d), and 40-70D(none).

Hibiscus (Malvaceae).

H. moscheutos germ. best with fresh seed in 70(45% in 2-4 w) and less in 40-70(17% in 4-6 d). Seed DS 6 m at 40 germ. the same as fresh seed, but seed DS 6 m at 70 germ. much less.

H. syriacus showed similar behavior for fresh seed and seed DS 6 m at 70 when sown at 70 but a sharp difference when sown at 40. Both germ. immediately at 70 as shown by 70(90% in 4-6 d) for DS seed and 70(70% in 10-17 d) for fresh seed. However, when sown at 40, DS seed germ. 40(100% in 7-12 w) whereas fresh seed germ. 40-70(98% in 3-5 d).

Hippolytica (Asteraceae). *H. darwasica* germ. 90% in 3-5 d in 70D or 70L and 40(10%)-70(70% in 4-14 d).

Hippophae (Eleagnaceae). *H. salicifolia* germ. 100% in 3rd w in 70D or 70L and 40(40% in 8th w)-70(60% in 6th d).

Holodiscus (Rosaceae). *H. discolor* germ. 40(10% in 12th w)-70(33% in 4-8 d), 70-40 (none), and 1/17 in May in outdoor treatment.

Horminum (Lamiaceae). *H. pyrenaicum* germ. 70(40% in 4-14 d), 40(1%)-70(none), and 3% in outdoor treatment from sowing March 1. The data show that initial low temperatures have a deleterious effect on the seed. Light had no effect.

Hosta (Liliaceae). Germination was hypogeal. The seed slowly deteriorated on DS at 70.

H. nakiana germ. 70(90% in 2nd w) and 40(30%)-70(60%) using fresh seed. Seed subjected to extended DS for a year gave very little germination.

H. sieboldi germ. 70(73% in 1-3 w) and 40(75% in 8th w) using seed that had been DS outdoors until February. This seed was given an additional 6 m DS at 70 after which it germ. 40(55% in 6-10 w) and 70(none).

Houstonia (Rubiaceae). *H. coerulea* germ. 70(85% in 6-9 d) and 40(9%)-70(21%).

Hudsonia (Cistaceae). *H. ericoides* germ. 70L(61% in 1-6 w), 70D(43% in 1-5 w), and 40(12%)-70(43% in 0-20 d). Seed DS 6 m at 70 germ. 70L(9%) and 70D(none) showing that DS is injurious to the seed.

Hutchinsia (Brassicaceae). *H. alpinus* germ. in 4th w at 70.

Hyacinthus (Liliaceae). *H. orientalis* germ. 70-40(100% in 6-8 w) and 40(2%)-70(20%). This latter would probably have given more germination if the experiment had been continued for another cycle. Seed DS 6 m at 70 is all dead, and seed DS 6 m at 40 is largely dead.

Hydrangea (Saxifragaceae). *H. quercifolia* had an absolute photorequirement for germination as shown by 70L(95%, ind. t 10 d, 12%/d) and 70D(none). Neither a prior 3 m at 40 nor DS for 6 m at 70 had any effect.

Hydrastis (Ranunculaceae). *H. canadensis* germ. 40-70(1%)-40-70(1%)-40-70(6% in 8-12 d) and none in six cycles starting at 70. Seed DS 6 m at 70 or 40 all rotted. The seedlings from the last germination opened their cotyledons, but did not appear to be vigorous. After the 2 y of alternating cycles the samples were placed outdoors on January 1, and 3-10% germ. the following April. Outdoor experiments need to be conducted on fresh seed.

Hymenocallis (Amaryllidaceae). *H. occidentalis* seed was collected just before heavy frost in October. The seeds germ. best by placing the seed capsules on moist towels, enclosing the whole in a polyethylene bag closed with a twister, and placing the bags under fluorescent lights. After 3 m the radicles start emerging at a zero order rate of 0.4%/d. Immediately after each seed germinates it is placed in moist media. Germination was ultimately 97%. After the radicle emerges it takes another 1-2 m before a leaf emerges. The seedling develop better if the pots are kept in polyethylene bags (100% relative humidity) for some months rather than placing them in the open air which suggests that the growth of the seedlings is aided by high humidity such as would occur in their native swamps. Any other procedure fails, and it is evident that the seed capsules photosynthesize and produce products necessary for the germination of the seeds.

Hymenocrater (Lamiaceae). *H. bituminosus* germ. 68% in 4-8 d in either 70D or 70L and 40(65% in 2-8 w).

Hymenoxys (Asteraceae).

H. acaulis ssp *caespitosa* germ. 70(100% in 3-5 d) and 40(100% in 3-9 w).

H. grandiflora germ. 70(100% in 3-8 d) and 40(100% in 3-9 w).

H. lapidicola germ. 70(2/3 in 7-9 d) and 40(1/1 on 12th d).

H. sp. (?) germ. 40-70(1/2 in 2nd w), 3/4 in October through February in outdoor treatment, and none at 70. This is a high alpine composite and is mentioned despite the unsatisfactory identification because it is one of the few Asteraceae that germ. at low T or required 3 m at 40 to germinate at 70.

H. subintegra germ 100% in 2-4 d at 70 and 40(100% in 3-9 w).

Hypericum (Hypericaceae).

H. choisianum required light and germ. 70L(50% in 3rd w) and 70D(none).

H. densiflorum germ. 70(25-50% in 4-10 d) and 40(none) using fresh seed or seed DS 6 m at 70 or 40. In view of the photoresponse with *H. perforatum*, it is possible that germination would have been higher in light.

H. perforatum germ. 70L(90-100% in 1-4 w), 70D GA-3(100% in 1-4 w), 70D(20-40% in 1-4 w), and 40-70L(10-35%) using seed DS 6 m at 70. Fresh seed germ. 70D-40-70L(100%) and 70D-40-70D(none). The photorequirement dies away with DS.

H. pulchellum germ. 70(100% on 5th d) and 40(100% in 6-8 w).

H. spathulatum germ. 70L(44% in 1-7 w), 70D GA-3(76% in 1-3 w), 70D(2%), 40-70L(52% in 2nd w), and 40-70D(none). Seeds placed outdoors in November germ. 27% in April. This is an unusual combination of germination patterns.

Hypoxis (Amaryllidaceae). *H. hirsuta* seed was received four times, but the seed seemed to be largely empty seed coats. The single germination was 70(1/33 in 4th w). Germination was hypogeal and the seedling developed normally.

Hysopus (Lamiaceae). *H. seravshanicus* germ. 70(73% in 4th d) and 40(54% in 4-7 w).

Iberis (Brassicaceae). *I. sempervirens* germ. 70(80%, ind. t 8 d, first order rate with half time 3 d) and 40(93% at same ind. t and rate as at 70). It is interesting that the ind. t and germ. rates are identical at 70 and 40. Seed DS 6 m at 70 or 40 germ. 40(45-60%) and 70(0-7%) with the germination extending over two cycles. It is evident that there is deterioration of the seed in DS.

Ikonnikovia (Plumbaginaceae). *I. kaufmanniana* germ. 70(12% in 6th d). Light had no effect.

Ilex (Aquifoliaceae). This genus is notorious for poor and extended germination. All *Ilex* seed is enclosed in a berry and all were WC for 7 d.

I. glabra germ. best in outdoor conditions with 18% germinating in June and July from starting WC seed outdoors in January. Germination was strongly promoted by GA-3 (54% in 1-4 w), but the seedlings were badly etiolated and died. Seed started in 40-70 or 70-40 cycles had not germ. after a year.

I. japonica seed collected in January germ. best in 40-70(87% in 6-18 d). A prior 3 m at 70, DS 6 m at 70 or 40, or producing a hole in the seed coat had no effect.

I. monticola seeds germ. best in outdoor treatments. Seeds WC 14 d and placed outdoors in March germ. 27% in April 2 y later. Germination was only 6% if the seeds had been WC 7 d. Seeds WC 7 d and placed outdoors in November germ. 21% in April 30 m later. Other treatments gave under 10% germination in 2 y of alternating cycles including treatment with GA-3, but germination in the 3rd y increased to 10-20%.

I. opaca seed is difficult to germinate. This is the consensus in the literature and is in accord with my own experience. Nikolaeva (ref. 7, p. 34) recommends soaking the seeds in concentrated sulfuric acid for 30-75 minutes, placing the seeds in moist media for 3-4 m at 77-86, and giving the seeds a cold treatment. J H recommends 2 m at 85 followed by 2 m cold after which sowing in fall will give germination in spring whereas in nature germination takes 16 m to 3 y. Clearly more work is needed to define what is really the critical factors and pattern.

I. serrata seed collected in December germ. 70(1%)-40(95% in 1-3 w) and 40-70(97% in 3-5 d). These results are discordant and need to be restudied.

I. verticillata germ. best in outdoor treatment and when the seed was WC for 14 d rather than the usual 7 d. It is possible that even longer WC time would have been better. Seed DS 6 m at 70 in the dried fruit and started outdoors in January germ. 52% in April when the seed were WC 14 d and only 24% when WC 7 d. The superiority of the 14 d WC was also evident in other treatments: 70-40-70(34% in 1-5 w)-40-70(16% in 2-14 d) for seeds WC 14 d and 70-40-70(4%, 13%, and 24% in three samples) for seed WC 7 d. Seed sown when collected in December had a similar pattern, but germination was more extended as shown by 70-40-70(4%)-40-70(21%). Fresh seed or seed DS 6 m at 70 or 40 failed to germinate when sown at 40. Germination was not initiated by puncturing the seed coat, light, or GA-3.

Illiamna (Malvaceae). Both *I. longisepala* and *I. rivularis* had impervious seed coats. The seeds are small, but it is possible to make a hole in the seed coat by rubbing against sandpaper. Both species germ. 100% in 1-2 w if the seed coats were punctured and gave only an occasional germination otherwise.

Impatiens (Balsamaceae). The temperate zone species, *I. biflora* and *parviflora*, have curious behaviors that would require considerable study to elucidate.

I. biflora requires a chilling period followed by the oscillating temperatures of outdoor treatment. Seed collected in September and given outdoor treatment germ. 90% in mid-March through the first week of April with no further germination through May. The seed also germ. 40-70-40-70(19% in 6th d). After 3 m in this last cycle at 70, the seeds were shifted to outdoors in January whereupon 46% germ. in March and early April. All other treatments including sowing at 70, 70L, or abrasion experiments led to complete rotting of the seed. Seed DS 6 m at 70 all rotted immediately on contacting moisture. The rotting is interesting in that the entire inner contents turn a uniform peacock blue. There are reports in the literature claiming that extensive chilling is required and that even a day or two at 70 causes the seed to return to the original condition and again require long chilling. All of this is in error due to poorly constructed experiments and the failure to recognize the role of oscillating temperatures.

I. parviflora was reported to require 6 m at 32-44. Seed begins to germinate in the fourth m at 40 (ref. 7, p. 60). It was also claimed that a small rise in T during the cycle at 40 cancels out the previous time at 40 and the cycle at 40 must start all over again to achieve germination. The seed will sit at 70 for at least 2 y without germinating or rotting. I am dubious of these reports and suspect that germination is simply promoted by oscillating temperatures.

I. scabrifolia germ. 70(2/5 in 19-21 d) and 40(2/4 in 5th w).

Incarvillea (Bignoniaceae). All appear to be D-70 germinators.

I. arguta germ. 100% in 6-9 d in either 70D or 70L and 40-70(92% in 2-6 d).

I. mairei germ. 70(9/10 in 3-5 d) and 40-70(6/11 in 2-6 d).

I. olgae germ. 70(4/5 in 3-10 d). The seed all rotted when sown at 40.

Indigofera (Fabiaceae). *I. heteranthera* germ. 100% on the 2nd d at 70 and 100% in 5-8 w at 40 providing a hole is ground through the seed coat. Without this hole germination is 9/15 in 4th w. when sown at 70.

Inula (Asteraceae). All appear to be D-70 germinators.

I. ensifolia germ. 70(100% in 5-15 d) and 40-70(100% in 2 d-2 w) using fresh seed or seed DS 6 m at 70 or 40.

I. obtusifolia germ. 70(2) and 40-70(1), absolute numbers given.

I. rhizocephala germ. 70(100% in 5-6 d) using fresh seed or seed DS 6 m at 70.

Ipomoea (Convolvulaceae). *I. leptophylla* germ. 70(42%, 3-13 d) and 40(19%, 6-11 w).

Ipomopsis (Polemoniaceae).

I. aggregata germ. 70(50% in 5-10 d) and 40(10%)-70(70% in 1 d). Light had no effect.

I. spicata germ. 70(29% in 5-10 d)-40(36% in 3rd w) and 40(22% in 12th w)-70(22% in 8th d). Light had no effect.

Iris (Iridaceae). This genus gave not only great diversity in germination behavior but also some of the most extended multicycle germination observed. Germination is always hypogeal, and true leaves develop in a week or two once the radicle emerges even when germination was delayed for years. Empty seed coats and deformed seeds are relatively easy to recognize so that seed counts and percent germination are accurate. A major problem is how to stimulate the germination of *Oncocyclos* and *Regelia* Iris since they have such extended natural germinations.

Panayoti Kelaidis of the Denver Botanical Garden has informed me that Fritz Kummert in Austria, Frank Norris in Tennessee (USA), and David Shahak in Israel are growing *Oncocyclus Iris* from seed in large numbers. Panayoti said that there are reports that germination was much improved by rinsing the seed in dilute Chlorox (aqueous NaOCl) and rubbing off the seed coats after which the seeds germ. readily at 40. There are also reports that gibberelic acid and other chemicals stimulate germination. Data is needed using scientific procedures.

A recent book, "The Iris" by B. Mathew, is devoted to this genus. Mathew divides the genus into six subgenera with further division into sections and series. His arrangement is used only in part. The species are arranged in alphabetical order for convenience with subgenus or section indicated in parentheses using the abbreviations B (bearded), Bx (beardless), E (Evansia), N (Nepalensis), O (*Oncocyclus*), P (*Pardanthopsis*), R (*Regelia*), Rt (*Reticulata*), and X (*Xiphium*). *I. dichotoma* is retained in *Iris*, but the Juno group appear under the genus Juno.

G. I. Rodionenko has published a book entitled "The Genus *Iris*" which has been translated into English and which describes the physiology of *Iris* in detail. The chapter on seed germination briefly reviews the field and describes some original experiments. These are of limited value because the author was unaware of the complex photoeffects and because the seeds were sown in soils so that variables were not well controlled. Even his claim for an impervious seed coat in *I. aphylla* is strongly doubted because the seed coats of *Iris* are thin fragile membranes and not suited to serve as impervious barriers.

I. acutiloba (R) germ. 70-40-70(1/10)-40-70-40-70(7/10).

I. barnumae (O) sets seed if hand pollinated and an occasional self sown seedling appears.

I. bracteata (Bx) germ. 40(6/7 in 8th w) and 70-40(6/6 in 6th w) using fresh seed. A sample received two years later gave somewhat lower germination but in the same patterns.

I. brandzae (Bx) germ. 70-40(3/6 in 3rd w)-70(1/6 in 6th w). This is a form of *I. sintenesii* and the results can serve for that species.

I. chrysophylla (Bx) germ. 40(2/2 in 6-10 w) and none at 70. A sample that had been DS 6 m at 70 germ. 40(3/3 in 4th w) and 70-40(4/4 in 4th w). Germination occurs only at 40.

I. decora (N) germ. 70(100% in 7-9 d) and 40-70(90% in 6-12 d).

I. dichotoma (P) germ. in 16-25 d at 70.

I. douglasiana (Bx) germ. better if the DS seed were WC 4 w instead of 7 d as shown by 40(100% in 4th w) and 70(80% in 0-2 w) for seed WC for 4 w and 40(40%) and 70(30%)-40(70%) for seed WC for 7 d. Seed sown outdoors in November all rotted, but this is possibly a hardiness problem.

I. elegantissima (O) was received as wild collected seed from Armenia and from Sevan National Park of USSR. The Armenia seed failed to germinate either after five cycles starting at either 40 or 70 or in outdoor treatment. The Sevan seed germ. 70-40(1/8 in 10th w) and 2/8 in March from placing outdoors in October. The seed started at 70 was shifted to outdoors in October one year later and one germ. the next June. None of those sown at 40 have germ. as yet after 20 m.

I. ensata (Bx) sown in March germ. in November.

I. foetidissima (Bx) germ 40-70-40(2/4) and none when sown at 70.

I. forrestii (Bx) germ. best (100% in March and April) if the DS seed was WC 7d or 4 w and sown outdoors in November. Other treatments germ. less or in a more extended manner as shown by 40-70(2/4)-40-70(2/4) and none when sown at 70.

I. germanica (B) germ. best when fresh seed or seed DS 6 m at 70 or 40 was sown at 40. Typical data are 40(31% in 7-12 w)-70(31% in 1-6 d)-40(2%)-70(2%). It is possible that many of the seeds that germ. in the 2nd cycle at 70 would have germ. in the first cycle at 40 if this cycle had been extended beyond 3 m. Germination was usually reduced in fresh or DS seed if the seed was sown at 70. Typical data were 70-40(0-25%), although light seemed to have some effect as shown by 70L(10%)-40(60%). Outdoor treatment germ. 78% in April. It is probable that the samples were hybrids and that germination behavior will vary, particularly the response to light.

I. goniocarpa (R) sown in outdoor treatment In November 1989 germ. 1/6 in October 1991 and 1/8 in February 1992. The seed had been DS over the summer of 1991 which may be a factor.

I. histroides (Rt) germ. in outdoor conditions, but unfortunately the seeds were shifted to these outdoor conditions only after 2-3 y of alternating 40-70 cycles. The following two examples are typical. Seed placed outdoors on August 1 after 3 y of alternating cycles germ. 6/10 in October; and seed DS 6 m at 70, given 2 y of alternating cycles, and placed outdoors on August 1 germ. 2/3 in October.

I. hoogiana (R) germ. 40-70-40(1/4) and none in four more cycles and none in 3 years of cycles starting at 70 using fresh seed. Seed DS 6 m at 70 germ. 1/3 in the 11th cycle (at 40).

I. hookeri (Bx) germ. 70-40-70(5/5 in 6-10 d) and 70-40-70L(1/5)-40-70(1/5) suggesting that light may inhibit germination somewhat. Outdoor treatment gave much slower germination.

I. illlyrica (B) germ. 40-70(7/10 in 1-5 d) and 70-40(10/13 in 7-12 w). This is interpreted to mean that about 12 w at 40 are required to destroy the germination inhibitors. It is probable that the seed started at 40 would have germ. at 40 if kept for a longer time at 40.

I. innominata (Bx) germ. 70-40(5/8 in 5-8 w) and 40(2/12)-70-40(4/12)-70-40(1/12)-70-40(1/12). Germination is entirely at 40 like so many cold desert plants.

I. junoniana (B) germ. one seed after 10 w at 70. This species is a variant of *I. germanica*. It is likely that sowing at 40 would have given better germination in view of the results with *I. germanica*.

I. kemaensis (R) germ. 70(1)-40(2)-70(1)-40-70(1) in a sample of six seeds.

I. lactea (Bx) germ. best in outdoor treatment. Unfortunately this was tried only on seed that had been DS for 2 y at 70 and had been soaked for 7 d and 4 w. Both samples germ. 90% in March and April from sowing in November. It can only be presumed that fresh seed would have given similar behavior and that the soaking and WC treatment is probably not necessary. Germination is much extended in other treatments as shown by 70(6%)-40-70(19%)-40-70-40-70(21%)-40-70(8%) and 40-70(9%)-40-70(3%)-40-70(6%).

I. latifolia (X) germ. 70-40(90% in 3-6 w) and 40(50% in 3rd w)-70-40(40%) using seed WC for 4 w. Seed WC for 7 d germ. 40-70-40(80%) and 70(10%)-40(80%)-70. Seeds germ. over 2 y in outdoor treatment and always in midwinter.

I. lutescens (B) germ. a few in the 10th w at 70. It is likely that sowing at 40 would have given better germination in view of the results with *I. germanica*.

I. mandschurica (R) germ. 70L(2/2 in 3rd and 6th w) and 70D(none).

I. milesii (Bx) germ. 40-70L(4/4 in 10-12 d), 70D-40-70L(4/5), 70D-40-70D-40-70L(3/3), and none in 40-70D or 70D-40-70D. In the latter two treatments a shift to 70L after 4 w in the last 70D cycle gave 4/4 germ. in both treatments. If the dark cycles are continued for two years, deterioration results and now placing the seeds in 70L germ. only 1/4. All of this was on DS seed and unfortunately the seed was not subjected to 70L directly. However, the results indicate that light is an absolute requirement for germination.

I. missouriensis (Bx) germ. 70L(2/9 in 7-10 w), 70D(none), 40-70L(1/3), and 40-70D(none) suggesting a light requirement. Another sample germ. 2/21 after over 2 y of alternating cycles and 1/23 after 2 y of outdoor treatment. Both samples had been subjected to at least 6 m DS. Treatment with GA-3 has not initiated germination as yet.

I. nepalensis (N) germ. immediately at 70.

I. oncocyclus hybrids (O) germ. 70-40-70-40(1/7)-70(1/7)-40(2/7).

I. orientalis (Bx) germ. only at 40 as shown by 70-40(100% in 3rd w). Light had no effect.

I. paradoxa (O) was received as wild collected seed from Armenia and from Sevan National Park in USSR. The Armenia seed germ. 40-70(1/7 in 2nd w)-40-70-40-70 and none when sown at 70 or in outdoor treatment. The Sevan seed germ. 70(2/7 in 3-5 w)-40-70-40-70-40 and none when sown at 40. A single seed germ. in the 4th y and was normal and healthy.

I. pseudoacorus (Bx) germ. 70L(55% in 2-12 w)-40-70L(9%), 40-70L(3/4), and none in 70D or 40-70D using seeds which had been DS 6 m at 70 followed by WC for 4 w. Germination was lower without the WC as shown by 70L(1/6), 70D-40-70L(5/7), 40-70L(6/11), and none in dark treatments. Fresh seed germ. 40-70L(50%) and 70-40-70L(50%). Unfortunately fresh seed has not yet been subjected to 70L, but presumably it would act much like DS seed. The requirement of light was also observed in seed of *I. pseudoacorus alba* from Finland.

I. pumila (B) germ. 70(5/6 in 3rd w), 40(2/10)-70(1/10 in 12th w), and 7/9 in outdoor treatment with 2/9 in November and 5/9 in February and March from October sowing.

I. reticulata (Rt) germ. 70-40-70-40(4/12 in 5th w)-70-40(1/12) and two more in the 3rd y. None germ. in all other treatments including 70L and outdoors.

I. ruthenica (E) germ. 70D(4/7 in 9-12 w with a fifth germinating in the 11th w) and 40-70(4/6 in 3rd w). This is one of the rare examples of a temperate zone Iris that germ. immediately.

I. setosa (Bx) seeds that had been DS 2 y at 70 germ. 90-100% in March and April from seed sown in November. A WC treatment for 7 d or 4 w had no effect. Other treatments germ. less as shown by 70(10%)-40 and 40(4%)-70(71% in 2-6 d) for seed WC for 7 d and 70(12%)-40 and 40-70(2%) for seed WC for 4 w. The efficacy of outdoor treatment was further demonstrated by taking seeds that had been subjected

to 70-40-70-40-70 with only a total of 10-12% germ. and shifting them to outdoors in January. In the following late March and early April 90% germ. The seed floats in water even after 4 w of soaking so that good seed cannot be separated by the sink-float technique.

I. sibirica (Bx) had germination stimulated by light, and this effect increased with DS. Fresh seed germ. 70L(83% in 2-7 w) and 70D(55% in 3-12 w). When this seed was DS for 6 m at 70, it germ. 70L(82% in 2-5 w) and 70D(6%). Three dark cycles had little effect. Treatment with GA-3 did not initiate germination in 70D.

I. sintenesii, see *I. brandzae*.

I. sogdiana (Bx) germ. 1/6 at 40 after 3 years of alternating cycles. Since this is only a form of *I. spuria*, it would probably have germ. immediately in 70L. The experiment is reported only to show how long these seeds remain viable in 70 moist.

I. spuria (Bx) germ. best in 70L(92% in 7-10 w), 70D(none), 40-70L(96% in 3-16 w), and 40-70D(none). Seed DS 6 m at 70 gave similar results. All dark treatments gave less than 15% germination.

I. spuria var. *halophila* (Bx) was received as seed DS 15 m at 70. It germ. well in the dark as shown by 70(67% in 4-9 w). It is not clear whether the difference in photoresponse between this species and the previous species was due to species difference or to longer DS times.

I. subbiflora (B) germ. 70(2/12 in 3rd w)-40-70-40-70 and three more in 3rd y, 40(2/8 in 12th w)-70(1/8)-40-70-40(1/8), and 3/8 in April in outdoor treatment.

I. taochia (B) germ. 70L(1/6 in 4th w), 70D(0/5), and 40(1/5 in 9th w)-70D(1/5 in 2nd d).

I. tectorum (E) germ. better in light as shown by 70L(50% in 5th w) and 70D(14% in 6th w) using seed DS 6 m at 70. There was no further germination over one year. Germination was much lower with fresh seed or with DS seed sown at 40.

I. tectorum alba (E) germ. 70L(100% in 4-9 w), 40-70L(100% in 5th w), and none in 70D or 40-70D using fresh seed. If the sample in 70D is shifted to 70L after 2 m, germination is 100% in 5th w showing that 2 m in 70D had no effect. Germination is much extended in the dark, and some samples germ. significant amounts in dark treatments. An example is 70(24%)-40-70(36%)-40-70(8%)-40-70(20%). There was some deterioration in seed DS for 6 m at 70.

I. tenax (Bx) germ. at 40 as shown by 40(90% in 3-12 w) and 70(10%)-40(60%)-70-40(10%) using DS seed that had been WC for 4 w. If the seed is WC 7 d instead of 4 w, germination is in the same patterns but drops to 50%. Seed WC 7 d germ. 1/5 in outdoor treatment, but the single germination did not occur until March 16 months later. Seed WC 4 w all rotted in outdoor treatment.

I. trojana (B) germ. 1/5 one w after shifting to 70D after a previous 7 w in 70L.

I. unguicularis (Bx) germ. 70-40(5/5 in 3-8 w).

I. versicolor (Bx) germ. 70L(50% in 3-11 w), 70D(none), 40-70L(40%), and 40-70D(none). The sample in 70D was shifted to 70L after 8 w whereupon 55% germ. in the 2nd w. The photorequirement is typical of swamp Iris. Germination is much extended if the seed is kept in the dark as shown by 70-40-70(2/10)-40-70(1/10) and 40-70-40-70(5/20).

I. wilsoni germ. 70L(100% in 2-5w) and 70D(none). When the sample in 70D was shifted to 70L after 5 w, 5/6 germ. in 3rd w.

Isopyrum (Ranunculaceae). *I. biternatum* germ. 70-40(25% in 8-11 w) and none in 40-70-40 using fresh seed. The seedlings must be kept an additional 2 m at 40 after radicle development is complete in order for the cotyledons to develop properly on shifting to 70. Seed DS 6 m at 70 or 40 rotted showing that DS is not tolerated.

Itea (Saxifragaceae). *I. virginica* germ. best in 40-70L(50-65% in 1-3 w) and less in 40-70D(11% in 3-6 w) and 70D-40-70D(3%). Seed DS 6 m at 70 gave similar results to the fresh seed. Seed would presumably given good germination in 70L, but this was not tried.

Ivesia(Rosaceae). *I. gordonii* germ. 70(45% in 5-20 d) and 40(80% in 3-7 w).

Ixolirion (Amaryllidaceae).

I. kerateginium germ. a few in April after a year outdoors.

I. tataricum germ. 40(65% in 5-8 w), 70-40(2/6), and 33% in March in outdoor treatment. A second sample gave similar behavior.

Jacaranda (Bignoniaceae). *J. mimosifolia* germ. in 2nd w (J H).

Jankae (Gesneriaceae). *J. heldrichii* germ. abundantly in the 4th w at 70.

Jasione (Campanulaceae). *J. crispa* germ. 70(65% in 2nd w). Light or a prior 3 m at 40 had no effect.

Jasminum (Oleaceae). *J. humile* germ. 70L(4/5 in 2nd w), 70D(1/7), and 40-70D(2/2 in 4th d). The promotion by light is suspect because of the small sample.

Jeffersonia (Berberidaceae). For the two species studied, DS is fatal with only a few percent surviving DS 6 m 40 and none surviving DS 6 m 70. Some of the fresh seeds rot quickly after contacting moisture and these are internally infected.

J. diphylla seeds collected in June 1987 germ. 70-40(4%)-70(8%)-40(34%)-70(12%)-40-70(4%)-40-70(2%) and 40-70-40(2%)-70(34%)-40(24%)-70(8%). Seeds collected in June 1988 germ. 70(none over six cycles) and 40-70-40-70(5%)-40-70(63% in 2-12w). Seeds collected in 1990 were all internally infected and soon rotted. In view of the results with *J. dubia*, it is likely that outdoor treatment would have been effective. Germination is hypogeal and begins with development of a four inch radicle. The single true leaf may emerge as soon as the 3rd w after radicle emergence or it may take another cycle or two. About half of the seedlings ultimately have the radicle rot and the seedling die before any leaf development.

J. dubia germ. 48% in March in outdoor treatment from seed collected the previous June. Seed also germ. 70-40(4%)-70-40(2%)-70(4%)-40(14%)-70(24%)-40(6%)-70-40-70(2%) and 40-70-40(8%)-70. There is a prominent aril. Removal of this aril has no effect. As with *J. diphylla* germination is hypogeal, and the single true leaf usually emerges a week or two after the radicle has finished lengthening to four inches. Also like *J. diphylla*, about half of the seedlings had the radicle ultimately rot and the seedling die before leaf emergence.

Juglans (Juglandaceae). *J. cinerea* and *nigra* were reported to germinate best in outdoor treatment. *J. nigra* abundantly self sows here, but experiments have not been conducted as yet. Experiments were conducted on a sample of 16 seeds of a hybrid known as heartnut, 8 were sown at 70 and 8 at 40. Those sown at 40 germ. 2/8 in the 4th cycle at 70 whereas those sown at 70 germ. 2/8 in the 2nd cycle at 40. The remaining seeds ultimately rotted.

Juniperus (Pinaceae). *J. virginiana* germ. 40(1%)-70(38% in 1-3 w)-40(6%)-70(29%), 70(2%)-40(22%)-70(4%), and 24% in April in outdoor treatment. These results are not in accord with reports that impervious seed coats are present. Juniper seeds are reported to be viable after 20 y of DS (J H). A sample of *J. horizontalis* has so far germ. only 1/200 in a 4th cycle at 40.

Jurinella (Dipsaceae). *J. moschus* germ. 70(1/3 on 3rd d).

Juno (Iridaceae). This genus has been separated from *Iris*, and this separation is adopted here. Germination can extend over periods as long as 4 y and probably more. Treatment with GA-3 has not as yet initiated germination.

J. aitchisonii germ. 70(3/6 in 4th w).

J. albomarginata germ. 70-40(3/6 in 7-12 w)-70 and none when sown at 40.

J. aucheri germ. 70-40(1/12)-70-40(3/12)-70-40-70(1/12) and 40-70(2/12)-40-70-40-70-40(1/12). After eight more cycles the seed remained firm and alive. One seed germ. after 4 y and another after 6 y. Both were healthy. Seed DS 6 m at 70 germ. 70-40(1/9)-70-40(1/9)-70(1/9) and 40-70-40(1/9)-70-40(1/9). Seed DS 6 m at

40 germ. 70-40-70-40-70(2/15)-40-70(8/15)-40-70-40-70(4/15). There seems to be no pattern or T preference to these extended germinations.

J. baldshuanica germ. 40-70-40-70-40(2/3).

J. bucharica germination was much extended in the alternating cycle treatment. The best was with seed DS 6 m at 70 which germ. 1/19 in the 6th cycle and 8/19 in the 8th cycle starting with a cycle at 70. Fresh seed germ. 1/14 in the 3rd and 7th cycles and 2/14 in the 8th cycle starting with a cycle at 40 and 1/14 in the 4th and 14th cycles starting with a cycle at 70. Seed sown outdoors in open sowing germ. well, but accurate records were not kept so that it can only be estimated that germination occurred 2-4 y after planting. Unfortunately outdoor treatment has not been tried yet in controlled experiments. Treatment with GA-3 has not initiated germination as yet.

J. coerulea germ. 40-70-40-70-40-70(2/14 in 3rd w).

J. cycloglossa germ. 70-40(5/6 in 6-8 w) and 40(1/3)-70(1/3)-40-70-40(1/3).

J. graeberiana germ. best with fresh seed in 40-70-40(10/11 in 6-11 w) and nearly as well in 70-40(5/12)-70-40(2/12). Germination was more extended with DS seed. Seed DS 6 m at 70 germ. 40(3/20)-70(1/20)-40-70-40(2/20)-70-40-70(2/20) and 70-40-70-40-70-40(1/20). Seed DS 6 m at 40 germ. 40-70(2/14)-40(3/14)-70-40(2/14)-70(1/14)-40-70 and 70-40(4/14)-70(1/14)-40(2/14)-70-40-70-40(2/14)-70-40-70-40(2/14). Several seeds germ. after 4 y of alternating cycles and appeared to be normal and healthy.

J. kuschakewiczii germ. 40-70-40(2/5).

J. magnifica germ. 40(30-100% in 10-12 w in six samples). The true leaf starts to form at 40, and development accelerates on shifting to 70. In samples where germination was below 100%, germination occurred in further cycles.

J. orchoides germ. 70(1/18 in 3rd w).

J. sp. were obtained as six samples collected by J. Halda in Tazekhistan. All were started at 40 and 70. Four of the samples have given some germination. JH 265 germ. 70-40-70-40(1/5 in 9th w)-70(1/5 on 2nd d) and 40-70-40-70(1/5 in 4th w). JH 267 germ. 40-70-40(1/5 in 2nd w)-70-40(2/5 in 8th and 10th w). JH 268 germ. 70-40-70-40-70-40-70-40-70(1/5 in 3rd w) and 40-70-40(1/5 in 8th w)-70-40(1/5 in 12th w). JH 270 germ. 70-40-70-40(6/7 in 7th w).

J. stenophylla v. allisonii germ. 40-70(1/3 in 8th w).

J. subdecolorata germ. 70-40(1/5 in 5th w).

J. vicaria germ. 40-70-40-70-40(1/3).

J. wilmottiana sown outdoors in March germ. 1/3 in April over a year later.

J. zaprajagejewii germ. 40-70-40-70(1/2).

Kalanchoe (Crassulaceae). *K. hybrids* germ. 70L(34% in 3rd w), 70D with GA-3(42% in 3rd w), 70D(13% in 3rd w), 40-70D(6%), and 40-70L(none).

Kalmia (Ericaceae). *Kalmia* requires light as found by R. Jaynes for *K. angustifolia*, *K. cuneata*, *K. hirsuta*, *K. latifolia*, *K. microphylla*, and *K. polifolia* (ref. 41) and confirmed by myself for *K. angustifolia* and *K. latifolia*. In my studies it was found for *K. angustifolia*, and *K. latifolia* that a prior 3 m at 40 had no effect on percent germination, the induction time, the rate law, and the rate constant. Jaynes claimed that an eight week period at 40 was necessary for germination of *K. latifolia* (and *K. cuneata*). Jaynes also found that the cold requirement disappeared after a year of DS.

My samples were collected in midwinter so that it is possible that they were equivalent to the DS seed of Jaynes, which would resolve the discrepancy. The seed hangs on the bushes all winter so that DS should have little effect, and this was found to be true. The seed is contained in hard spherical capsules. These must be crushed to allow light to reach the seed. The seed is small and hard to separate from the hard capsules so that seed counts and percent germination are inaccurate.

K. angustifolia germ. 70L (50-60% in 2-4 w) and 40-70L(35-60% in 2nd w) using either fresh seed or seed DS 6 m at 70 or 40. Overwintering outdoors or a prior 3 m at 40 had no effect. All dark treatments failed.

K. hirsuta was reported by Jaynes to have germination improved by treatment with very hot water ranging from two minute treatment with water at 90 deg. C to twenty hours treatment with water at 60 deg. C. Light is then required for germination.

K. latifolia germ. 70L(95% in 4-6 w) and 70D(none). This was true for both fresh seed and seed DS 6 m at 70 or 40. A prior 3 m at 40 had no effect on the germination in 70L and promoted a small germination in 70D as shown by 40-70D(4%).

Kirengoshima (Saxifragaceae). *K. palmata* seed collected in November was still green with an immature appearance, yet it germ. abundantly at 40 in 4th m. The cotyledons develop in a week after radicle emergence.

Koeleria (Poaceae). See Chapter 22

Koelreuteria (Sapindaceae). *K. paniculata* is primarily a 70-40-70 germinator. However, near the end of the cycle at 40 (in the 12th w) splitting of the seeds starts and the radicle may emerge and grow a few millimeters. When such seeds are shifted to 70, the radicle grows rapidly. For simplicity the seeds were counted as germ. after the shift to 70. Germination was best with DS seed as shown by 70(10%)-40-70(85% in 1-2 d) for seed DS 6 m at 70, 70-40-70(90% in 1-2 d) for seed DS 6 m at 40, and only 70(2%)-40-70(49%) for fresh seed. Seeds can be DS for 12 and 18 m with only a small decline in percent germination as shown by 70-40-70(68%) for seed DS 12 m at 70 and 70-40-70(69%) for seed DS 18 m at 70. A preliminary 3 m at 40 had no effect. Seeds in which a hole had been produced in the seed coat germ. 70(29%) and 40(40%) suggesting that the seed coat is impervious and delays water transport which delays germination, but the effect is not as dramatic as in many of the species discussed in Chapter 9. The effect of the hole in the seed coat also indicates that the favorable effect of DS may be to open microfissures.

Kolkowitzia (Caprifoliaceae). *K. amabilis* germ. best with either fresh seed or seed DS 6 m at 70 or 40 in 70(25%, ind. t 3 d, 15%/d). Starting the seed at 40 is fatal. The seed is held in a dry state on the shrub all winter and is not shed until the warmth of May when growth starts. Seeds blown off in winter encounters low T and moisture and die.

Korolkowia (Liliaceae). *K. sewerzowii* germ. in April after over a year outdoors.

Kunzea (Myrtaceae). Starting at 70 was better than starting at 40. The result that *K. vestita* required GA-3 or light while *K. Baxteri* did not requires checking.

K. baxteri germ. 70L(60% in 4-6 d), 70D(46% in 6-8 d), 70D GA-3(60% in 6-10 d), 40(18% in 7-12 w)-70(1%), and 50% in October from seed placed outdoors in late September.

K. vestita germ. 70L(66% in 1-3 w), 70D GA-3(72% in 1-3 w), 70D(none), 40(10% in 7--12 w), and 12% in October from seed placed outdoors in late Sept.

Laburnum (Fabaceae). *L. vossi* germ. 100% in 5-7 d at 70 providing a hole is ground through the seed coat. Germination is negligible without this pretreatment.

Lagarus (Poaceae). See Chapter 22

Lagotis (Scrophulariaceae). *L. ikonnikovii* germ. in 1-3 m at 70. *L. uralensis* germ. 70(1/13)-40 and 40-70-40-70(1/8).

Lallemantia (Lamiaceae). *L. canescens* germ. 60% in 3-8 d in either 70D or 70L, 40(26% in 5th w), and 80% in March and early April in outdoor treatment.

Lamium (Lamiaceae). *L. maculatum* seems to require light based on a small sample as shown by 70L(2/11 in 4th w) and no 70D(none). These results are for seed DS 6 m at 70. This species self sows here, but seed ripens over a long period and is hard to collect.

Lapeirousia (Iridaceae). *L. laxa* germ. 70L(90% in 4-6 w), 70D(40% in 2-7 w), 70D GA-3(20% in 4th w), and 40(45% in 11th w). *L. laxa alba* germ. 70D(2/7 in 6th w) and 40-70(5/8 in 4-6 d).

Larix (Pinaceae). *L. kaempferi* germ. 70(14% in 2-10 w) and 40(20% in 6-8 w) for either fresh seed or seed DS 6 m at 70 or 40. Germination would have been much higher if the empty seed coats were not counted.

Larrea (Zygophyllaceae). *L. tridentata* germ. 70D(1/6 in 3rd w).

Lathyrus (Fabaceae).

L. latifolius germ. 70(100%, ind. t 14 d, 12%/d) for fresh seed and 70(91%, ind. t 12 d, 5%/d) for seeds DS 6 m at 70. Note the reduction in rate. Germination was lower and more extended for seed sown at 40 or seed DS 6 m at 40.

L. vernus germ. 40(100% in 4-6 w) and much lower in 70(10%). The seed used was fresh and shelled from pods that were still slightly green. Seed DS 6 m at 70 germ. 70(none) and 40(2/6 in 8-10 w). The DS hardens the seed coat creating an impervious seed coat.

Lavandula (Lamiaceae). *L. spica* germ. 70L(10% in 1-7 w), 70D(5% in 1-7 w), 40(20% in 5-7 w), and 14% in April in outdoor treatment. Remaining seeds rotted.

Ledum (Ericaceae). *L. groenlandicum* germ. 70D GA-3(63% in 2-4 w), 70D-40-70D(23% in 4th w), and 40-70-40(none). Light had no effect.

Leiophyllum (Ericaceae). *L. buxifolium* germ. only in 70L. The seed deteriorates on DS at 70 with germination being 33% in 4-10 w for fresh seed, 15% for seed DS 6 m, and 4% for seed DS 12 m. The seed also deteriorates rapidly in 70D. After 9 w in 70D, only 5% germ. on shifting to 70L.

Leontice (Berberidaceae). *L. incerta* germ. in the 4th w at 70.

Leontopodium (Asteraceae). DS seed of *L. alpinum*, *calocephalum*, *nivale*, and *souleii* germ. in 4-8 w at 70. DS seed of *L. ochroleucum* germ. in 2-4 w at 70. *L. himalaicum* germ. 70(100%, ind. t 6 d, 17%/d) and 40(100%, ind. t 10 d, 17%/d).

Lepidium (Brassicaceae). *L. sativum* germ. 70(95% in 2-8 d) and 40(95% in 11-15 d). Light had no effect.

Leptarrhena (Saxifragaceae). *L. pyrolifolia* germ. 70L(84% in exact first order, ind. t 6 d, half time 1.5 d), none in 70D or outdoor treatment, 40-70L(80% in 7-10 d), and 40-70D(none). Seeds DS 2 y at 70 were all dead.

Leptodactylon (Polemoniaceae). *L. pungens* germ. 100% in 3-5 d in either 70D or 70L, in 3rd w at 40, or in winter and early spring in outdoor treatment. The seedlings died after developing their cotyledons.

Leptosiphon (Polemoniaceae). *L. hybrids* germ. 90-100% in 2nd w at 70. Light or GA-3 had no effect.

Lespedeza (Fabaceae). *L. bicolor* germ. 70(50%)-40(25%)-70(10%) for fresh seed or seed DS 6 m at 70 or 40. Puncturing the seed coat should be tried.

Lesquerella (Brassicaceae). Six species (*L. condensata*, *fendleri*, *ovalifolia*, *pinetorum*, *rubicunde*, and *purshii*) germ. at 70 in 4-20 d.

L. fendleri germ. 70(70% in 2-6 d) and 40(41%)-70(14%)-40(5%) for seed DS 6 m at 70 or 40 and 70(83% in 10 d-3 m) and 40(40%)-70(13%) for fresh seed.

Leucojum (Amaryllidaceae). Germination is hypogeal.

L. aestivum germination was erratic and no consistent pattern emerged. Fresh seed germ. 70(20%)-40-70(12%)-40-70(40%) and 40-70-40-70(75% in 4-8 w)-40(15%). Seed DS 6 m at 70 germ. 70(30% in 4-10 w)-40(8%) and 40(none).

L. vernum germ. 70(95% in 3rd m) and 40-70(98% in 3rd m) using my own seed. A sample from J. Gyer in New Jersey gave a much different germination pattern as shown by 70-40(43% in 12th w)-70(3%)-40(6%) and 40-70-40(37% in 12th w)-70(1%). It is a mystery why one sample germ. predominately at 70 and the other predominately at 40. In either germination, the leaf (hypogeal) does not start to develop until after 3 m at 40. DS for 6 m at 70 or 40 is fatal.

Leucothoe (Ericaceae). *L. racemosa* germ. 70L(15-25% in 2-7 w) and 70D(none) using seed DS 6 m at 70. A 10-15% germination in 70L also occurred with fresh seed, but only after a prior 40 or 70-40 cycle.

Levisticium (Apiaceae). *L. officinale* germ. 70L(2%) and 70D(none).

Lewisia (Portulacaceae). Germination of *L. tweedyi* and *L. pygmaea* are dramatically stimulated with GA-3. Both GA-3 and outdoor treatment should be tried on all species.

L. brachycalyx germ. 70-40(2/3 in 10th w) and 40(6/6 in 10th w).

L. cotyledon germ. largely at 40 in a number of qualitative experiments.

L. nevadensis sown outdoors in February germ. in April and none in 70D.

L. pygmaea sown outdoors in February germ. in April and none in 70D.

Another sample was given 15 m of alternating cycles after which 100% germ. in 2-4 w at 70 after treating with GA-3. The 75% empty seed coats were not counted. Treatment with GA-3 needs to be tried on fresh seeds.

L. rediviva germ. best when sown at low T as shown by 40(65% in 2-7 w) and 70% in February in outdoor treatment. A prior 3 m at 70 or DS is detrimental as shown by 40(15%) for seed DS 6 m at 70 and 70-40(8%) for fresh seed. The cotyledons develop completely at 40.

L. tweedyi gave low germination despite the fact that the seed was collected from our own self sowing colony. The best germinations were 5% for seed DS 6 m at 70 and sown at 40. Seed set is poor despite hand pollination indicating potential interfertility problems. Treatment with GA-3 has been reported to initiate germination.

Liatris (Asteraceae). *L. spicata* germ. 70(100%, ind. t 7 d, 5%/d) and 40(100% in 3rd m) using seeds DS 6 m at 70 and 70(100% ind. t 7 d, 2.5%/d) and 40(60%)-70(40%) using fresh seed. Light had no effect.

Libanotis (Scrophulariaceae). *L. montana* germ. in November from seed sown in June suggesting that this species is either a low T germinator or requires oscillating temperatures.

Libocedrus (Pinaceae). *L. decurrens* germ. 70D(14% in 2nd w) and 40-70D(12% in 2nd). Light or GA-3 had no effect. These results are not in accord with a report in the literature that *L. decurrens* was a 40-70 germinator (ref. 48, Ch. 7).

Ligularia (Asteraceae).

L. amplexicaulis germ. 70D(50% in 5-12 d) and 40(50% in 3rd w).

L. dentata germ. 70(21% in 6-8 d)-40-70(21%) and 40(36%)-70(50%).

Ligustrum (Oleaceae).

L. obtusifolium has naturalized extensively in central Pennsylvania. The seed was collected in December and WC as with all berries. Germination rates were increased by DS. Fresh seed germ. 70(2%)-40-70(82% in 12-15 w) and 40(5%)-70(84% in 13th w)-40(5%). Seed DS 6 m 70 germ. 70(100% in 13th w) and 40(4%)-70(4%)-40-70. Seed DS 6 m at 40 germ. 70(100% in 11-13 w) and 40(4%)-70(58%)-40(15%)-70(19%). Seed DS 6 m at 70 in the dried fruit germ. about the same percentage (but lower rate) as seed DS in the WC state. Note the long induction time of 12 w in the germination in a cycle at 70.

L. japonicum germ. 97% when sown at either 70 or 40. More remarkable, the ind. t of 6 d and the rate of 16%/d were identical at both 70 and 40.

Lilium (Liliaceae). This genus gave diverse behaviors with both epigeal and hypogeal germinators, single step and two step germinators, and 70 and 40 germinators. It is important to know the exact pattern if success is to be achieved. Of the 86 species in the genus, 40 were studied. Germination is epigeal unless otherwise noted. No photoeffects were found in *L. auratum* and *L. centifolium*, and they are presumed to be absent throughout the genus, particularly in view of the generally successful germinations in dark. The species with hypogeal germination are usually two step germinators with a time gap between radicle formation and development of leaves, and they usually produce a single leaf the first season and continue to produce one leaf each season until enough strength is built up to form a stem. It is likely that all species tolerate DS at 70 for at least 6 m. This conclusion is based on direct tests for some species and the fact that many samples of DS seed gave good germination.

L. albanicum germ. 70-40(57% in 2-7 w). It is unusual for an epigeal germinator to be a strictly 40 germinator.

L. alexandrae germ. one in the 3rd m at 70.

L. amabile germ. abundantly in 6th w at 70.

L. amabile luteum germ. 70(92% in 1-8 w) and 40(8%)-70(89% in 1-5 d).

L. auratum germ. 90% at 70(90% in 11-18 w, largely in 11-16 w). Germination is slightly faster if the seeds are DS 6 m at 70 or if there is a prior 3 m at 40. Seed DS 12 m at 70 is 50% dead. A bulb with root develops at 70. The single true leaf does not emerge until after the seedling is shifted to 40 for 3 m and returned to 70.

L. canadense editorum has been extensively studied with some surprising results. Fresh seeds germ. 70(96% in 7-9 w) and 40-70(94% in 11-16 w). Germination consists of forming a small bulb, often barely emerging from the seed coat, with or without a small root. At the end of 16 w at 70 the seedlings were shifted to

40 for 3 m and back to 70 whereupon the root elongated and a true leaf (hypogeal) formed in a w or two. The seedlings develop slowly. Each year a single leaf is produced until the seedling builds up enough strength to form a whorl of leaves. This signals that a stem and flowers (usually one) will be produced the following year. If the seedlings get plenty of light, the first flowering will occur about five years after sowing. However, seedlings often persist in deep woods for years forming a single leaf each year. When a tree falls or is cut and light gets in, flowering follows in a couple of years. Seeds DS 6 m at 70 germ. 70(83% in 1-4 m), 40-70(23% in 4th m), and 23% in August in outdoor treatment from sowing March 15. However, the somewhat lower germination is only part of the story. The seedlings from these latter treatments formed weak radicles and most ultimately rotted and died. This deleterious effect of DS may seem surprising in view of the fact that the seeds are dispersed by wind. However, they are dispersed late in the fall and drop onto moist ground. Also surprising was the observations that fresh seed placed outdoors in September failed to germinate a single seed by the end of the following July. Fresh seeds were treated with GA-3 in 70D. There was no difference in the rate of germination in the first step (formation of bulb), but the percent germination was reduced from 86% to 70%. The surprising result was that nearly all that germ. in the 4th and 5th weeks (30%) sent up a true leaf by the 6th week whereas those that germ. in the 6th to 11th week (40%) did not. This result indicates that there is some potential for eliminating the second step in this two step germinator using GA-3, but more work is needed to refine any such procedure.

L. canadense flavum germ. 70(97% in 5-10 w) and 40-70(96% in 9-13 w). The treatment, growth, and development of the seedlings are identical to that of *L. canadense editorum*. Like *L. canadense editorum* seed placed outdoors in September failed to germinate a single seed by the end of the following July. Seed DS for 6 m at 70 germ. 70(92% in 4-15 w). Although the ultimate percent germination was nearly as high as for fresh seed, the rate of germination was a little slower, and the seedlings from the DS seed showed the same tendency to rot as found with *L. canadense editorum*.

L. candidum germ. 70(9/11 in 3rd w) and 40(3/8 in 4-10 w).

L. caucasicum germ. 70(3/8 in 9-11 w)-40(1/8) and 40-70(3/8 in 7-9 w).

Germination is hypogeal and the development of the seedlings are identical to those of *L. szovitsianum*.

L. centifolium hybrids are hybrids of *L. centifolium* x *henryi* in which the *L. centifolium* character predominated in the stem and leaves but the flower color was more often yellow than white. The germination behavior varies. Some of the seed germ. 80-100% at 70 providing the time at 70 was extended to 5 m with germination occurring at an approximate constant rate from 2 w to 3 m. Other seed had a more extended germ. as shown by 70(45%)-40(16%)-70(24%)-40(2%)-70(1%) and 40(60%)-70(22%)-40(1%)-70(1%). The germination at comparable rates at both 40 and 70 is unusual for an epigeal germinator. Fresh seed and seed DS 6 m at 70 or 40 gave similar behavior, but seeds DS 12 m at 70 were 50% dead.

L. cernuum germ. abundantly in 6-9 w at 70.

L. chalcedonicum germ. 70-40-70(100% in 5-7 w) and 80% germ. in April from seed sown outdoors in January.

L. ciliatum germ. 70(4/6 in 3-6 w). Germination is hypogeal and two step. A 3 m period at 40 is required before the seedlings will form the single true leaf at 70.

L. concolor germ. abundantly in 3rd m at 70.

L. concolor var. *partheneion* behaved so differently from *L. concolor* in regard to germination that it is a new species. Seeds germ. 70(84% in 3-8 w) and 40-70(81% in 6-12 w). The seedlings develop a long slender 1-2 cm radicle with a tiny bulb at the end. This appearance suggests that this species is adapted to dry climates. The leaf did not appear until after a cold cycle.

L. davidi germ. in 3rd m at 70. Hybrids of this species with *leichtlinii* and *cernuum* tend to have more extended germination patterns resembling the germination of *L. centifolium* hybrids.

L. debile germ. 70(6/8 in 3-11 w) and 40-70(7/9 in 7-11 w). Germination is hypogeal with a bulb and radicle forming at 70, and the leaf forming after 3 m at 40.

L. formosanum germ. in 4th w at 70.

L. grayi merges into *L. canadense editorum* and probably has the same germination behavior.

L. kelleyanum germ. 70-40(94% in 4-6 w) and 40(1%)-70(8%)-40(85%) for either fresh seed or seed DS 6 m at 70 or 40. The germination at 40 consists of forming a tiny bulb barely outside of the seed coat and a radicle of only 1-2 mm. This is typical of American species of *Lilium* (except *L. catesbaei* and *L. philadelphicum*). Germination is hypogeal. When the seedlings were shifted to 70 after the 3 m at 40, only about 25% of the seedlings lengthened the radicle and developed the single true leaf. Probably longer times at 40 and/or cooler temperatures are needed for proper development of the seedling as discussed in Chapter 15.

L. martagon germ. 70(73% in 1-12 w)-40(23%) and 40(2%)-70(87%) using seed DS 6 m at 70. Fresh seed germ. 70(68%)-40-70(2%)-40(23%) and 40(6%)-70(22%)-40(18%)-70(40%). Only the bulb and root develop at 70, and a 3 m at 40 and a return to 70 is required for development of the single true leaf. Germination is hypogeal. Treatment with GA-3 had no favorable effect.

L. martagon album germ. 70(74% in 11-25 d) and 40-70(69%). Seedling development is the same as with *L. martagon*.

L. maximowiczii germ. in 3rd m at 70.

L. michauxii germ. 70-40(2/11 in 8th w).

L. michiganense germ. 70(95%) and 40-70-40(24%) using fresh seed. Seed DS 6 m at 70 germ. 70(83%) and 40-70(100%). Seed DS 6 m at 40 germ. 70(50%)-40(17%) and 40-70(100%). *L. michiganense* is closely related to *L. canadense* and *L. superbum* and has similar germination behavior and seedling development.

L. monadelphum is close to *L. ciliatum* and *L. szovitsianum*. DS seed germ. 70-40(3/6 in 3-15 d)-40(2/6 in 5th w) and 40-70(5/6, 4 on 1st d). See *L. ciliatum* for the handling of seedlings in the two step germination.

L. nanum gave a single germination in the 4th w at 70.

L. nepalense germ. 70(100% in 3rd w) and 40(50% in 7th w)-70(50% in 2nd w).

L. nobilissimum has a germination pattern unique in the genus. The germination is 100% at 40 in 2nd m and seed sown at 70 does not germinate until shifted to 40. The germination is hypogeal but not stepwise. The true leaf develops at 40 within 2 w of radicle emergence and continues to develop on shifting to 70. Leaves

continue to develop in the first growing season which is also unlike most hypogeal germinators in *Lilium*.

L. pardalinum is part of a group of lilies from the west coast of U.S. that have their own unique hypogeal pattern. The group includes *L. kelleyanum*, *pardalinum*, *parvum*, *shastense*, *washingtonianum*, and probably the other western U.S. species. Seed was sown in September and left outdoors until a year later. It was then placed at 40 whereupon 80-90% germ. in 2nd w. On shifting to 70 3 m later, the single true leaf develops. The bulb formation is similar to the *L. michiganense* group in that the bulb forms inside or barely outside the seed coat.

L. parvum germ. identically to *L. pardalinum*.

L. pomponium germ. 70(15%)-40(65% in 3rd m). Germination is epigeal at 40 and in this respect it resembles *L. albanicum*, another southern European lily.

L. ponticum germ. 70(38% in 4th w)-40-70(62% in 5-10 w). The development of the seedlings are like that of *L. ciliatum*.

L. pulchellum germ. 70(100% in 7-8 d), unusually rapid for *Lilium*.

L. pumilum germ. 70(50-100% in 4-10 d) and 40(50-100% in 1-3 m) using fresh seed or seed DS 6 m at 70 or 40.

L. pyrenaicum germ. outdoors in April from January sowing.

L. regale germ. abundantly at 70.

L. sachalinense germ. 5/11 in 4-10 w at 70.

L. shastense was identical in behavior to *L. pardalinum*.

L. superbum was identical in behavior to *L. michiganense*.

L. szovitsianum seeds from an old plant were twice the diameter of seeds from seedlings blooming for the first time. Both types of seed gave the same germination behavior. Germination is hypogeal and in two steps. Seedlings are treated in the same way as those of *L. auratum*. Fresh seed and seed DS 6 m at 70 or 40 germ. 70(80-95% in 2-12 w) and 40-70(57%)-40(19%)-70(7%).

L. tenuifolium has been long confused with *L. pumilum*, and both Hortus and Index Kewensis treat them as synonyms. The differences and the history relating to the confusion has been treated in detail in a recent paper (ref. 42). Fresh seed germ. 70(78% in 2-17 d) and seed DS 6 m at 70 or 40 germ. 70(98% in 2d-10 w). Wild collected seed germ. similarly.

L. tsingtauense germ. 70(4/4 on 4th w) and 40-70(4/4 in the 3rd w) using fresh seed. The radicle and bulb form in the 70 cycle. The seedling must be shifted to 40 for 3 m after the 3 m at 70 is completed. On shifting back to 70 the true leaf soon forms.

L. washingtonianum germ. 70-40(61% in 3-12 w), less in 40(10%)-70(2%)-70-40, and very little in outdoor treatment using either fresh seed or seed DS 6 m at 70. Only the radicle forms at 40, and leaf development does not occur until the shift to 70.

Limnanthus (Limnanthaceae). *L. douglasii* germ. 70(3/3 on 2nd d) and 40(3/3 on 11th d). The rapid germination is unusual for such large seeds.

Limonium (Plumbaginaceae).

L. latifolium germ. 70(100% in 2nd w) and 40(81% in 7-9 w). Light had no effect, but GA-3 lowered the percent germination to 82% due to rotting.

L. minutum germ. 70(2/2 in 2nd w) There are 80% empty seed coats and these were not counted. A prior one m at 40 had no effect.

Linanthus (Polemoniaceae). *L. grandiflora* germ. in a week at 70.

Linanthrastum (Polemoniaceae). *L. nuttallii* germ. 70 GA-3(82% largely in 3-5 d), 40(100% in 2-8 w), and none in 70D or 70L.

Linaria (Scrophulariaceae).

L. kurdica germ. in 2 w at 70.

L. purpurea germ. 70L(33% in 2nd w), 70D GA-3(55% in 2nd w), 70D(8%), 40(6%)-70L(22% in 2nd w), and 40(6%)-70D(17% in 2nd w).

L. pyramidata germ. in 2 w at 70.

L. trystis 70(83%, ind. t one d, 23%/d) and less in 40(6%)-70(15%) using seed DS 6 m at 70. Fresh seed germ. 70(10%)-40-70(5%) and 40(1%)-70-40-70(2%). Seed DS 6 m at 40 is intermediate in behavior. Seeds should be DS 6 m at 70.

Lindelofia (Boraginaceae). *L. longiflora* germ. 70(100% in 3-5 d) and 40(3/9 in the 8th w). Light had no effect.

Lindera (Lauraceae). *L. benzoin* seed is enclosed in a red berry and requires WC. Germination is best in 70(7%)-40-70(21% in 1-6 w). DS 6 m at either 70 or 40 or outdoor treatment are all fatal. The low germination is mainly due to the high percentage of seeds that are internally infected and rot in 1-3 w in moisture.

Linum (Linaceae). The yellow flowered Linums centering around *L. capitatum* require fungal products of the gibberelin type for germination as discussed in Chapter 12. Outdoor treatment gave superior results in some species.

L. boreale germ. 70D(41% in 3-7 d) and 40(2/7 in 5th w). Seeds treated with GA-3 all rotted.

L. bulgaricum germ. 93% in 9-20 d if treated with GA-3. As with *L. capitatum* which was studied more extensively, careful control of the GA-3 treatment is needed to achieve healthy seedlings. The use of GA-3 is not necessary with *L. bulgaricum* because good germination was achieved in 70L(72% in 4-14 d), 70D(28% in 4-22 d), 89% in April in outdoor treatment, and 40(25% in 6-11 w)-70-40-70. In this last experiment the remaining seeds were not dead even after the four cycles, because when treated with GA-3 at 70, 87% of the remaining seeds germ. in 5-7 d.

L. capitatum has germination dramatically stimulated by GA-3, and this was extensively studied in order to find optimum conditions for achieving healthy seedlings. This is described in detail in Chapter 12.

L. catharticum germ. 70D GA-3(48% in 6-18 d) and 70D(9% in 2nd w).

L. dolomiticum germ. 91% in April for seed placed outdoors March 1. It also germ. 70L(24% in 6-13 d) and 70D(11% in 6-10 d).

L. extraaxillare is a minor variant of *L. perenne*. Germination extended over a number of cycles in all treatments. Fresh seed germ. 70-40(11%)-70(52%)-40(12%)-70(2%)-40(1%)-70(7%) and 40(33%)-70(12%)-40(36%)-70(11%). Seed DS 6 m at 70 germ. 70(22%)-40(15%)-70(15%) and 40(77%)-70(1%).

L. kingii germ. 70(1/4 in 11th w) and 40(1/1 in 5th w).

L. perenne germ. 70L(77% in 6-20 d), 70D(88% in 3-16 d), 40(100% in 4th w), and 100% in March in outdoor treatment.

L. veitatisi germ 100% in the 2nd d at 70 and 100% in the 10th d at 40.

Liquidambar (Hamamelidaceae). *L. styraciflua* seed is contained in spheres in which the pointed tips of the capsules gives the sphere a spiny appearance. By the time the capsules fall to the ground the seed has been shed. Drying causes the tips of the capsules to open. Many flakes of resin fall out, and these could be mistaken for seed. The true seeds are relatively larger and fewer. Germination was best with seed DS 6 m at 70 which germ. 75% when sown at 70 and none when sown at 40. Germination with seed DS 6 m at 40 was similar as shown by 70(62%) and 40(6%)-70(6%). Germination was more extended with fresh seed as shown by 70(14%)-40-70(48%) and 40-70(82%)-40-70(18%).

Liriodendron (Magnoliaceae). *L. tulipifera* was reported to be a 40-70 germinator (ref. 4, Ch. 27). Anecdotal data is given in Chapter 12.

Liriope (Liliaceae). *L. spicata* germ. 70L(80% in 3-5 w), 70D(93% in 3-5 w), and 40-70(93% in 1-3 w). Light has little effect.

Lisianthus (Gentianaceae). *L. russelianum* germ. 70L(60% in 7-15 d) and 70D(25% in 10-12 d). A prior 3 m at 40 lowered the percent germination markedly, but did not alter the photoresponse.

Lithospermum (Boraginaceae).

L. incisum germ. 70L(2/6 in 2nd w), 70D(0/6), and 40-70D(0/5).

L. multiflorum germ. 70L(9/11 in 1-3 w), 70D(4/10 in 1-3 w), and 40(6/10 in 2nd w). Curiously, in the sample started in 70D one more germ. a year later at 70.

Lloydia (Liliaceae).

L. serotina germ. 70(50% in 11-19 d) and 40(56% in 4-11 w).

L. triflora germ. 70(none) and 40(1/9).

Loasa (Loasaceae).

L. nana germ. 70D(4/22 in 6-9 d), 70L(1/28 in 2nd w), and 40(1/23 in 4th w).

L. sigmoidea all rotted in two samples suggesting that DS may not be tolerated.

L. vulcanica germ. 70L(91% in 1-4 w), 70D GA-3(83% in 2nd w), 70D(18% in 5th w), 40(20% in 5th w)-70D(none), and 40(20%)-70L(none). Seeds placed outdoors in October germ. 51% in October and November and 38% more in April. Seeds DS 6 m at 70 germ. 70D(80% in 4-12 d), 70L(93% in 4-6 d), and 70 GA-3(91% in 6-10 d) showing that DS eliminates the need for light or GA-3 to stimulate germination.

Lobelia (Lobeliaceae). Both *L. cardinalis* and *L. syphilitica* required light or GA-3 for germination with germination faster with GA-3 in the conditions used.

L. cardinalis germ. 70L(85-90%, ind. t 4-7 d, 3.0-6.5%/d), 70D GA-3(90% in 2nd w), and 40-70L(90%, ind. t one d, 15%/d) using either fresh seed or seed DS 6 m at 70. Prior moist cycles of up to a year had little effect. No germination occurred in any dark treatment including outdoor treatment. Seed DS for 10 y germ. only 0.5% in 70L. Germination in 70L was unaffected by placing the seeds on different colored papers including black paper, see Chapter 11.

L. inflata germ. 70D GA-3(100% in 10-12 d), 70L(74% in 5th w), 70D(none), 40-70L(97% in 2nd w), and 40-70D(none) using fresh seed or seed DS 6 m at 70.

L. sessilifolia germ. 70L(24% in 2nd w)-40-70L(16%), 70D GA-3(58% in 3-5 w), 70D-40-70D(44% in 4th w), 70D-40-70L(63% in 2-6 d), and 40-70-40(none). The results show some initial stimulation of germination at 70 by light, but this effect largely disappears after 70D-40 treatment.

L. syphilitica germ. 70L(75-85%, ind. t 30 d, 2.3%/d), 70D GA-3(100% in 2nd w), 40-70L(80%, ind. t 2-4 d, 30%/d) and none in any dark treatment using seeds DS 6 m at 70. Fresh seed germ. in the same patterns but slower.

L. tupa germ. 70(80% in 2nd w) and 40(80% in 2nd m). Light had no effect.

Lomatium (Apiaceae). As typical of cold desert plants these germ. only at 40. In two of the six species studied, a preliminary 3 m. at 70 was fatal, and in one of the six it was deleterious. In the other three it had little effect on the subsequent germination at 40. Clearly the best procedure is to start the seeds directly at 40. The effect of light was studied on the 1st and 4th-6th species listed below. It had no effect.

L. columbianum germ. 40(100% in 7th w), 70-40(20% in 8th w)-70-40(20%), and 40% in March for seeds placed outdoors in December.

L. grayi germ. 40(70% in 4th w)-70(10% on 5th d). 70(7%)-40(71% in 2-4 w), and 20% in March in outdoor treatment.

L. laevigatum germ. 40(90% in 3-6 w), 70(13% in 3-8 w)-40(57% in 10-14 d), and 47% in March in outdoor treatment.

L. macrocarpum germ. 40(80% in 6-11 w), 70-40-70-40(4%), and 62% in February for seeds placed outdoors in December.

L. martindalei germ 40(67% in 7-12 w), 70-40(45% in 5-12 w)-70-40(26%), and 24% in April and 4% more the following March for seeds placed outdoors in December.

L. nudicaule germ. 40(23% in 6-12 w), 70-40(3%)-70-40(12%), and 16% in March for seeds placed outdoors in December.

Lomatogonum (Gentianaceae). Several samples of a species of *Lomatogonum* were received. The pale tan seed suggested that light might be required, and the only germination was 40-70L(1/20).

Lonicera (Caprifoliaceae). All seeds are in berries and were WC for 7 d. Treatment with GA-3 was tried on *L. maacki* and *L. tatarica*. There was no major effect.

L. hallii germ. 40(71% in 4-9 w)-70(24%) and 70-40(85% in 10-13 w)-70(3%). Seed DS 6 m at 70 or 40 failed to germinate over four cycles.

L. maacki germ. 40(90-95% in 2-9 w) using either fresh seed or seed DS 6 m at 70 or 40. Germination was more extended when sown at 70 as shown by 70(65%)-40(35%) for DS seed and 70(3%)-40(31%) for fresh seed.

L. obovata germ. 1/5 in the 9th w when sown at 70 and 0/3 when sown at 40.

L. pyrenaica germ. 70-40-70-40-70(2/13 in 2-8 d). Despite this long delayed germination, the two seedlings developed cotyledons immediately and grew strongly. Seed sown at 40 never germ.

L. sempervirens germ. best in 40(100%, ind. t 40-60 d, 3%/d) and less conveniently in 70-40(100%, ind. t 25-50 d, 5%/d) for either fresh seed or for seed DS 6 m at 70 or 40.

L. tatarica germ. best with fresh seed in 70(100% in 2nd m) and less conveniently in 40(14%)-70(85% in 3rd m). DS 6 m at 70 reduced germination to 70(68%) and 40-70(81%) with similar values for seed DS 6 m at 40. Seed left on the bushes until January had much lower and more extended germination.

Lotus (Fabaceae). *L. corniculatus* germ. 5-10% either in 2-5 d at 70 or 2-4 w at 40 using either fresh seed or seed DS 6 m at 40. Germination was even lower for seed DS 6 m at 70. The low germination was associated with rapid rotting of the

ungerminated seed showing that the low germinations were not due to impervious seed coat problems.

Lunaria (Brassicaceae). *L. annua* germ. 70(91%, ind. t 5 d, 30%/d) and 40(94%, ind. t 10 d, 10%/d) for seed DS 6 m at 70 and 70(1%)-40(95%, ind. t 24 d, 5%/d), 70D GA-3(75% in 4-6 w), and 40(67%, ind. t 24 d, 2.5%/d) for fresh seed. The DS causes the seed to germinate at 70 as well as 40. Seed DS 6 m at 40 gave an intermediate behavior showing that the chemical changes were only partially completed. It is important to collect the seed when it is fully ripe and turning brown as seed collected in a partially green state gave lower germination. Seed DS at 70 for 2 y was 20% dead. The stimulation by GA-3 in fresh seed is noted.

Lupinus (Fabaceae). Impervious seed coats are generally present. *L. lepidus* v. *lobbii* and *L. lyalii* v. *lobbii* germ. 100% on 5th d if a hole was ground through the seed coat, and none otherwise.

Lychnis (Caryophyllaceae).

L. alba germ. 70L(100% in 4-9 d), 70D GA-3(100% in 3-7 d), and 70D(1-10%) using fresh seed or seed DS 6 m at 70.

L. alpina germ. 70(55% in 2-8 d) and 40-70(55% in 2-8 d) using fresh seed or seed DS 6 m at 70 or 40.

L. chalcedonica germ. 70(100% in 3-8 d) and 40(10%)-70(90%) for fresh seed and 70(70%) and 40(25%)-70(75%) for seed DS 6 m at 70 or 40.

L. sieboldi germ. 70(94% in 4-8 d) and 40(90% in 2-5 w). Light had no effect.

L. wilfordii germ. 70L(100% on 5th d), 70D(48% in 5-12 d), and 40(50%).

Lycopersicon (Solanaceae). *L. esculentum* is the common tomato. An inhibitor in the juice of the fruit is the only inhibitor because germination was 100% in 3-5 d after WC. This was true for seeds removed from the WC after 2 d or for seeds left in the water. Tomatoes stored for some time will start germination while the seeds are still in the fruit because the inhibitor runs out. A collection of twelve strains were received from the Burpee Seed Company in December. They had been DS in effect for 2-3 m. They germ. 90-100% in 3-5 d except for one called Celebrity which germ. in 6-12 d. However, three strains (Delicious, Early Girl, and Supersteak) were purchased in November from a store where the seeds had been left outdoors since spring. These germ. 70D(80-100% in 1-3 w), 40-70D(85-100% in 1-3 w), and 40 GA-3(80-90% in 5-11 w). Note that GA-3 was able to initiate germination at 40 which could have some practical value. Light had no significant effect.

Lycoris (Amaryllidaceae). *L. pumila* was received in moist towels in late February and had already started to germinate. The seedlings were kept at 70 for 3 m during which the small bulb and radicle formed. On shifting to 40 the true leaf forms after 4 w and grows vigorously so that the seedlings must be kept in light at 40.

Lygodesmia (Asteraceae). *L. texana* germ. 40-70(one in 1 m).

Lyonia (Ericaceae). *L. mariana* germ. 70L(40% in 3rd w), 70D(none), 40-70L(38% in 7-11 d), and 40-70D(28% in 2nd w) using fresh seed. Seed DS for 6 m at 70 germ. 70L(67% in 1-3 w), 70D(none), 40-70L(67% in 1-3 w), and 40-70D(none). It is peculiar that the 3 m at 40 seemed to remove the photorequirement with fresh seed but not with DS seed. When the sample in 70D was shifted to 70L after 6 w, 30% germ. in the 3rd w showing that the period in 70D had no effect.

Lysichiton (Araceae).

L. americanum seed from commercial sources and from seed exchanges seed failed to germinate, and it is believed that DS is fatal. Wild seed is not easy to collect as deer are fond of the fleshy seed capsules and are the agents of dispersal. Wild seed was obtained from B. Mineo and good germination was achieved by 3 m at 40, shifting to 70, and nicking each seed with a knife after 4 w. Germination was 70% in 10-20 d after nicking. Unfortunately no comparative experiments were run.

L. camschatense germ. one in a 70-40-70 pattern. Light had no effect.

Lysimachia (Primulaceae). *L. ciliata* germ. 70(1/6 in 12th w).

Lythrum (Lythraceae). *L. salicaria* germ. 70L(100% in 1-2 d), 70D(39%), 40-70L(4%), 40-70D(none), and 73% in February through April in outdoor treatment using fresh seed. Seed DS 6 m at 70 germ. 70L(100% in 1-2 d), 70D(12%), 40(29%)-70L(71% in 1-2 d), and 40(29%)-70D(none). Seeds DS 12 m at 70 germ. 70L(90% in 1-5 d), 70D(none), and 40-70D(90% in 3-4 d). Note the remarkably rapid germination, the germination in dark outdoors, and that the continuing DS ultimately eliminates the light requirement in the 40-70 treatment but intensifies the light requirement at 70. All of the above detail is of little horticultural interest for a plant that is often regarded as an invasive weed, but it does show some remarkable effects of DS.

Machaeranthera (Asteraceae). *M. tanacetifolia* germ. 70(20-30% in 3-10 d) with either fresh seed or seed DS 6 m at 70 or 40. Seed sown at 40 gave lower germination.

Macleaya (Papaveraceae). *M. cordata* requires light for germination. Unfortunately the experiments were not ideal. Fresh seed was subjected to 70-40-70. After a month in the 3rd cycle, half of the seeds were shifted to light and half kept in dark. Germination was 32% in 2-4 w in light and none in the dark. The sample in the dark was then shifted to light and 32% germ. in 2-4 w as expected.

Maclura (Moraceae). *M. pomifera* was reported to be a 40-70 germinator (ref. 28, Ch. 10). This report is in error and results from failure to WC the seeds. The seeds are enclosed in a large fruit. This fruit contains not only germination inhibitors but a large amount of latex which polymerizes to a sticky gum when exposed to air. It is recommended that the seeds be removed from the pulp under water in a large pail. Even then some sticky polymer will form on one's hands and can only be removed with an organic solvent like turpentine followed by soap and water. Experiments were conducted varying the time of WC with water from 1-14 d followed by WC with detergent, and the detergent wash was varied from 2-10 d. All treatments gave over 80% immediate germination. The WC with detergent served only to remove some red-brown tar and make the operation cleaner. The recommended procedure is WC with water 1-5 d followed by WC with detergent for 2-5 d. Seeds so treated give 90-100% germination in 2-5 w. A prior 3 m at 40 and DS for 6 m at 70 had no effect.

Magnolia (Magnoliaceae). Seeds are enclosed in an oily red berry, and were WC with daily brief detergent washes. Germinations might have been improved if there had been extended detergent washes. Empty seed coats make seed counts inaccurate. Germination is epigeal and the cotyledons develop in 1-3 w after germination. Outdoor treatment killed the seeds and seeds of *M. sieboldi* and *M. wilsoni* that had been stored for 2 y were dead.

M. denudata germ. 70-40(1/5 in 10th w) and 40(1/5 in 3rd m)-70(1/5 on 11th d).
M. glauca germ. 40-70(15% in 2nd w) and 70-40-70(none). A second sample germ. 70 GA-3(40% in 3-7 w) and 70-40-70(65% in 4-9 w). There was no further germination as the remaining seeds rotted. Seeds DS 6 m at 70 or 40 all rotted as did seeds given outdoor treatment. The seedlings from GA-3 treatment died.

M. kobus var. *stellata* germ. 40-70(40% in 1-3 w)-40-70(20%), 70-40-70(3%), and none in outdoor treatment. Seed DS 6 m at 70 germ. 70-40(2/13)-70(1/13)-40-70(2/13) and 40-70(6/18)-40-70.

M. tripetala germ. 40-70-40-70(70% in 1-3 w) and less in 70-40-70(8%)-40-70(36% in 3rd w). Seeds given outdoor treatment or DS 6 m at 70 rotted.

Mahonia (Berberidaceae). *M. aquifolium* germ. over many cycles. Seeds WC for 7 d and DS 6 m at 70 germ. 40(1%)-70(4%)-40(4%)-70(3%)-40(39% in 3-12 w)-70(10%). This extended germination was also found in seed DS 6 m at 40 which germ. 40(4%)-70(10%)-40(3%)-70(1%)-40(25%)-70(4%). Fresh seed also gave extended germination, but the overall germination fell to 5-10%. When the cycles were started at 70, germination was equally extended, but the overall was reduced to 20-30% for DS seed and 5% for fresh seed. All of the above is for seed collected in July. The fruit continues to hang on the branches into the winter. Seed collected in November gave only 0-4% germination under all condition, a most important observation since it might be imagined that November seed was more ripened. Outdoor treatment needs to be tried.

Maianthemum (Liliaceae). *M. canadense* germ. 70(39% in 3rd m)-40-70(26% in 4th w) and 40-70(65% in 3-11 w). DS seed was not studied. Germination is hypogeal and the true leaf forms one m after germination.

Majorana (Lamiaceae). *M. hortensis* germ. 100% in 2-4 d in 70L or 70D, 100% in 4th w at 40, and 100% in late March and early April in outdoor treatment.

Malesherbia (Malesherbiaceae). *M. linearifolia* germ. 40(4/10 in 3-9 w) and less in 70D(1/21 in 2nd w) and 70L(none).

Malus (Rosaceae). One species, one commercial apple, and four hybrid crabapples were studied. Most of the germination occurred in the first cycle if sown at 40 and in a 70-40-70 pattern if sown at 70. The fruits were collected in winter and the seeds WC for a week. The data is presented in a Table. Storing the seed for 6 m in the dried fruit gave the same results as seed stored WC. Seeds of *Malus* "Red Splendor" germ. slower and in lower percentage when treated with GA-3.

	Fresh Seed	Seed DS 6 m at 70 or 40
<i>M. baccata</i>	70(2%)-40-70(44%) 40(88% in 2-11 w)	70-40-70(60-90% in 1-4 d) 40(50% in 2-11 w)-70(30%)
<i>M. "Bob White"</i>	40(86% in 2-8 w)	40(86% in 3-8 w)
<i>M. "Donald Wyman"</i>	40(86% in 2-9 w)	40(70%)-70(9%)
<i>M. "Red Splendor"</i>	70(15%)-40(3%)-70(70%) 40(100% in 2-10 w)	70(3%)-40-70(85%) 40(75% in 2-5 w)
<i>M. "Yellow Delicious"</i>	40(100% in 5-9 w)	
<i>M. (yellow fruit)</i>	70(11%) 40(12%)-70(75% in 2nd w)	70(15%)-40(25%)-70(25%) 40(65% in 10-12 w)-70(20%)

The commercial hybrid Joneliscious germ. 40-70(100% on 3rd d) and 70D(all rotted by the 11th w). Treatment with GA-3 led to extensive rotting at 40 or 70.

Malva (Malvaceae). *M. moschata* germ. 70(100% in 2-4 d) and 40(100% in 2nd w).

Marshallia (Asteraceae). *M. obovata* germ. in the 6th w at 70.

Matelea (Asclepiaceae). *M. obliquus* required GA-3 and germ. 70D GA-3(26% in 2nd w), 40-70D GA-3(30%), and none in 70L, 70D, 40-70L, 40-70D, or outdoor treatment. Germination is hypogeal. The seedlings from the GA-3 treatment were healthy.

Mathiola (Brassicaceae). *M. incana* germ. 70L(84% in 2nd w), 70D(60% in 2nd w), and 40(61% in 3-7 w).

Meconopsis (Papaveraceae).

M. aculeata germ. 70L(64% in 3-5 w) and none in 70D, 40-70L, or 40-70D. A 7 w period in 70D was fatal.

M. betonicifolia and the *alba* form germ. 70D(70% in 3rd w). Light, GA-3, or a prior 3 m at 40 had little effect

M. betonicifolia pratensis germ. 70D(24% in 17-21 d). Light had no effect and GA-3 was deleterious.

M. cambrica seed collected in June germ. differently from seed collected in October. June seed germ. 70-40-70(24% in 3-20 d) and October seed germ. 70(24%)-40-70(4%). Germination failed on all seed sown at 40 and all DS seed.

M. paniculata germ. 48% in 1-3 w in either 70L or 70D. A 3 m at 40 was fatal.

Melaleuca (Myrtaceae).

M. diosmafolia germ. 70D(40% in 4-8 d), 70D GA-3(100% in 2nd w), 40(50% in 5-7 w), and 32% in Oct. for seeds placed outdoors in September. Light had no effect.

M. huegeri germ. 3/3 in 4th w in 70D.

Melampodium (Asteraceae). *M. cinereum* germ. in 2-4 w at 70.

Melampyrum (Scrophulariaceae). *M. lineare* germ. 70-40(55% in 4-8 w) and 40-70(10%)-40(20%)-70. In outdoor treatment seeds started germinating in February, but they were killed by low temperatures. All DS seed was dead. Light did not initiate germination.

Melandrium (Caryophyllaceae). *M. sachilinense* germ. in 9-14 d at 70.

Melasphaerula (Iridaceae). *M. graminea* germ. 70(90% in 10-18 d)-40(10% in 8th w).

Melica (Poaceae). See Chapter 22.

Melilotus (Fabaceae). *M. alba* germ. has an impervious seed coat. If a hole is made in the seed coats, 100% germ. on the 2nd d. If not, 10% germ. in 1-2 w. The 10% germination is attributed to imperfections in the seed coats since there was no further germination over the next 2 m. This behavior was shown by both fresh seed and seed DS 6 m at 70. Although this is clearly an example of an impervious seed coat, the seed coats break down with moderate ease so that 10-20% germ. in the next 3 m in 70D, 70L, or 40 and 100% germ. in late March from seeds placed outdoors in October.

Menodora (Oleaceae). *M. scabra* germ. 70(100% on 3rd d) and 40-70(100% in 4-12 d). Light had no effect. Seed sown outdoors germ. 100% in mid-March.

Mentha (Lamiaceae). *M. spicata* germ. 70L(85% in 1-4 w), 70D(34% in 1-3 w), 40(2%)-70L(42% in 1-4 w), and 40-70D(none). Experiments on *M. microphylla* have just started. Seeds germ. in 70L and 70 GA-3, but not 70D.

Mentzelia (Loasaceae). Light reduced the percent germination.

M. chrysantha germ. 70D(70% in 3-8 d), 70L(27%), and 40(15%)-70.

M. decapetala germ. 40(90% in 3rd w) and less in 70D(6%) and 70L(none).

M. nuda germ. 40(70% in 3-12 w) and less in 70D(20%) and 70L(5%).

Merendera (Liliaceae). Although samples were small, germination appears to occur only at 40 and a preliminary 3 m at 70 is beneficial.

M. pyrenaica germ. 70-40(4/8 in 4th w) and 40-70(none).

M. sobolifera germ. 40(3/3 in 8-12 w) and 70-40(5/5 in 4-10 w).

M. trigyna germ. 70-40(1/1 in 4th w) and 40-70(none).

Mertensia (Boraginaceae). In view of the results with *M. cana* and other Boraginaceae, photoexperiments should have been conducted on all species. Treatment with GA-3 also needs to be tried.

M. alpina germ. 70L(1/5 in 5th w) and 70D(0/5).

M. bakeri germ. 40-70(2/6 in the 10th w) and none at 70.

M. cana germ. 70L(3/3 in 3rd w), 70D(1/4)-40-70, and 40-70(none).

M. lanceolata germ. 70(70% in 4 d-4 w) and 40-70(30% on 2nd d).

M. virginica seed germ. 70-40(1/63)-70(1/63) and rotted if DS or sown at 40.

Meum (Apiaceae). *M. athamanticum* germ. 40(2/7 in 7th w) and 70-40(2/8 in 5th w).

Michauxia (Campanulaceae). *M. tchiharchewii* germ. 70D GA-3(93% in 6-8 d), 40(58% in 5-11 w)-70-40-70(6%), 51% in late April and early May in outdoor treatment, and 0-1% in 70L or 70D.

Mimosa (Fabaceae). *M. pudica* seed germinates in 2nd w if the seed is placed in water at a temperature of 140 for twenty minutes (T & M). Probably it would also germinate if a hole were made in the seed coats.

Mimulus (Scrophulariaceae). Light was required for some species.

M. "Andean Nymph" germ. 70(1%)-40-70 and 40(34% in 5th w).

M. "Calypso hybrids" germ. some in the 10th w at 70.

M. cardinalis germ. some in the 3rd w at 70 using fresh seed.

M. guttatus germ. only 3% in 5-11 d at 70 and none at 40.

M. lewisii germ. 70(100% in 8-10 d) and 40-70(100% in 4-12 d). Light had no effect.

M. luteus germ. 70(100% in 2-16 d) and 40(88% in 2-6 w). Germination was lower in DS seed with 1-20% germ. at 70 and zero at 40.

M. primuloides germ. 70L(86% in 1-3 w) and less and slower in 70D(22% in 1-7 w). This 70D sample was shifted to 70L in the 7th w whereupon 53% more germ. in 1-3 w. *M. primuloides* also germ. 40-70L(90% in 6-8 d) and none in 40-70D. Seed DS 6 m at 70 germ. 70L(44% in 8-10 d), 70D(14% in 9-20 d), 40-70L(90% in 5-6 d), and 40-70D(4%). The data indicates that there is some deterioration on DS.

M. puniceus germ. immediately at 70.

M. ringens required either light or GA-3 for germination. Fresh seed germ. 70D GA-3(100% in 2nd w), 70L(15% in 1-5 w), and 70D(none). A prior 3 m at 40 had no effect. If either fresh seed or seed DS 6 m at 70 were subjected to three to four cycles

starting at 40 and 70 and then shifted to 70L, 90-100% germ. in the 2nd w. Shifting seed in 70L to 70D GA-3 caused the rest to germinate in the 2nd w.

Minuartia (Caryophyllaceae).

M. biflora germ. 70(1/60 in 4 w) and 40(1/60 in 2nd w).

M. laricifolia germ. 70(90% in 1-5 w) and 40(50% in 4-10 w)-70D(26% in 2-8 d).

Light had no effect.

M. recurva germ. in 10-20 d at 70.

Miscanthus (Poaceae). See Chapter 22

Mitchella (Rubiaceae). *M. repens* germ. best in 40-70(5%)-40-70(36% in 1-11 w)-40-70(6%)-40-70(25%) and 70(5%)-40-70(14%)-40-70(23%)-40-70(33%)-40-70(2%). Note the extended multicycle germination. Seed DS 6 m at 70 germ. 70-40-70(4%) and 40-70-40-70(5%) showing that DS is not tolerated. Light had no effect. The cotyledons developed in 1-2 w after germination.

Mitella (Saxifragaceae). *M. diphylla* germ. 70(24% in 4-6 w)-40 and 40(17% in 4-10 w)-70. Seed DS 6 m at 70 or 40 rotted on contacting moisture showing that DS is not tolerated. Photoexperiments need to be tried.

Monarda (Lamiaceae).

M. citriodora germ. 35% in 10-15 d in either 70L or 70D and 40(2%)-70.

M. didyma germ. 70L(3/14 on 5th d), 70D(none), 40-70L(2/4), and 40-70D(0/4).

It is likely that light promotes germination as in *M. fistulosa*. Seed DS 6 m at 70 germ. 70L(3/14) and 70D(none) confirming the photorequirement.

M. fistulosa germ. 70L(70% in 5-7 d), 70D(20% in 7-20 d), 40-70L(40%), and 40-70D(none). Seeds DS 6 m at 70 germ. 70L(86% in 4-6 d), 70D(38% in 5-12 d), and 40(61% in 8-12 w)-70(25% in 4-6 d). A later sample germ. 70 GA-3(60% in 2-8 d), 70L(50% in 1-4 w), 70D(none), 40-70D(99 in 4- d), and 40-70L(43 in 4- d). The results are not entirely consistent, but they do indicate that germination is promoted by light, GA-3, DS, and a 3 m period at 40. Germination was 7% in outdoor treatment.

Monardella (Lamiaceae). *M. odoratissima* germ. 70L(1/20), none in 70D, and 40(1/22)-70(1/22).

Moraea (Iridaceae). *M. huttonii* germ. 70(60% in 1-3 w), 40-70(90% in 1-3 w), and 80% in late April in outdoor treatment. Light had no effect.

Morocarpus (Chaenopodiaceae). *M. foliosus* germ. 70(8/12 in 1-4 w) and 40(4/12)-70(5/12).

Morus (Moraceae). *M. alba* started germination in the 4th d of WC.

Germination was 100% in the next 3 d. This can only happen if the inhibitors are being destroyed by the embryo at a very fast rate of the order of a 1-2 d half life. If the seed at the end of the 4th day of WC is shifted to 40, the seed is irreparably damaged and germination is 40-70(7%). If the seed at the end of the 4th day of WC is shifted to DS at 70 for 6 m; the seed is badly damaged, only 8% germ., and the seedlings are weak. Presumably the seed can be stored in the dried fruit for considerable periods.

Muscari (Liliaceae). *M. botryoides* germ. 95-100% overall in several patterns. The most convenient is to use seed DS 6 m at either 70 or 40 in 70-40(100% in 3rd m). Less convenient is fresh seed in 70-40(74%)-70-40(26%) and 40(5%)-70(7%)-40(87%) or DS seed in 40(85%)-70(15%). The cotyledons develop within a week on shifting to 70. Seed sown outdoors in June starts germinating in October again showing the 70-40 germination pattern.

Mussaenda (Rubiaceae). *M. roxburghii* germ. only in light as shown by 70L(55% in 1-3 w) and 70D(none). When the sample in 70D for 4 w was shifted to 70L, 74% germ. in 10-15 d. A prior 3 m at 40 had no effect.

Mutisia (Asteraceae).

M. spinosa seed was given 4 w at 70 and then shifted to 40 whereupon 10/14 germ. in 7-14 w. Seed placed directly at 40 failed to germinate after 2 m so it was placed at 70 for 4 w and shifted back to 40 whereupon 1/6 germ. The 4 w at 70 followed by a shift to 40 is clearly the best treatment.

M. subulata germ. 40(4/8 in 3rd w) and 70(4/7 in 1-6 w). The seedling that germ. at 40 were shifted to 70 a week after germination. They grew on strongly, stronger than those that germ. at 70.

Myosotis (Boraginaceae).

M. asiatica germ 70(84% largely in 4-6 d) and 40(35% in 1-9 w).

M. sylvatica germ. 70(90% in 3-5 d) and 40(10-20%)-70(90-80%) using seed DS 6 m at 70. Fresh seed germ. 70(70% in 2 d-4 w) and 40(92% in 2 d-4 w)

Myrica (Myricaceae).

M. caroliniensis is a 40-70 germinator (ref. 44, Ch. 7).

M. pennsylvanica seed has a wax coating (bayberry wax). Removing this wax promotes germination. Fresh seeds with wax off germ. 70-40(85%) and 70-40-70(29%). Fresh seeds with wax on germ. 40-70(29%) and 70-40(5%)-70(50%). Seeds DS 6 m at 70 with wax on germ. 40-70(62%) and 70-40-70(50%). Grinding a hole in the seed coat did not promote germination.

Myrrhis (Apiaceae). *M. odorata* germ. 100% in outdoor treatment with germination occurring in April. None germ. in all other treatments. Light or GA-3 did not initiate germination. Seed that had been DS 6 m at 70 and placed outdoors in February did not germinate until 13 m later in March, but germination was 90%. This indicates that oscillating temperatures are required in fall as well as spring.

Nandina (Berberidaceae). *N. domestica* should perhaps be omitted from discussion because all seed rotted. The seed was collected in March in Central Pennsylvania. It is suspected that winter cold may have killed the seeds as they rotted in days after being cleaned and subjected to moisture.

Narcissus (Amaryllidaceae). Seed from garden hybrids germ. largely at 40. Fresh seed germ. 70-40(75% in 2-5 w) and 40(60% in 6-10 w)-70-40-70-40(20%). A second sample of fresh seed gave the same behavior when sown at 70 but a somewhat different behavior when sown at 40 as shown by 40-70-40(5%)-70-40(90% in 2-4 w). There was evidence that the seed deteriorated in DS and that the deterioration was slower at 40 than at 70. Typical data is 40(11%)-70-40(89%) and 70-40(20%) for seed DS 6 m at 40 and 40(14%)-70-40(65%) and 70-40(0-20%) for seed DS 6 m at 70. The seedlings must be kept at 40 until the 3 m cycle at 40 is complete in order for the hypogeal leaf development to be vigorous on shifting to 70.

Nasturtium (Brassicaceae). *N. officinale* germ. best with seed DS 6 m at 70 or 40 in 70(100% in 4-10 d). Germination is less with fresh seed as shown by 70(20% in 2-27 d) and 40(81% in 3-8 w). Light had no effect. It is remarkable that a species so aquatic as this germinates best with DS seed.

Nelumbo (Nymphaeaceae). *N. lutea* has an impervious seed coat. Seeds germ. 70D(100% in 2nd w) if a hole is filed through the seed coat, and the seed is submerged in water. If the punctured seeds are placed in moist towels, they rotted.

Nemastylis (Iridaceae). Germination in *N. acuta* and *N. tenuis* was hypogeal whereas germination in *N. pringlei* was epigeal.

N. acuta germination is discussed in Chapter 6.

N. pringlei germ. 70(1/10 in 4th w) and 40-70-40-70(2/10 in 5th w).

N. tenuis germ. 70(1/6 in 3rd w).

Nemophila (Hydrophyllaceae). *N. maculata* and *N. menziesii* germ. immediately at 70.

Neobessya (Cactaceae). *N. missouriensis* hides the berry in its folds until early spring when the cactus expands revealing the red berries. The berries are collected in April and the seed WC. Germination was 65-80% in 3-6 w for a sample collected April 1 and 80% in 8-10 d for a sample collected April 27. Similar results were obtained for seed collected the following year.

Nepeta (Lamiaceae).

N. cataria required light for germination, and germination was low in all dark treatments including outdoor treatment. Germination was 70L(32-46% in 1-4 w), 40-70L(40-65% in 1-4 w), and 40-70D(12%) for either fresh seed or seed DS 6 m at 70.

N. floccosa germ. 70(3/6) and 40-70(5/6).

N. glutinosa germ. 70(44%) and 40(76%).

Nerium (Apocyanaceae). *N. oleander* germ. 70(15% in 1-3 w) and 40-70(none). Light had no effect.

Nomocharis (Liliaceae). Years ago several species were sown in soils and gave immediate germination at 70. However, Thompson and Morgan report difficulties.

Notothlaspi (Brassicaceae). *N. rosulatum* germ. 70D(2/7 on 15th d) using fresh seed. Earlier samples had been DS to various degrees and all rotted.

Nymphaea (Nymphaeaceae). *N. tetragona* germ. 40-70(50% in 2nd w) with or without a mildly anaerobic atmosphere, 70D(10% in 7-9 w) in a mildly anaerobic atmosphere, and 70D(none). The procedure for the mildly anaerobic atmosphere is described in Chapter 12. This atmosphere stimulates germination at 70 slightly, but does not stimulate germination in the 40-70 pattern.

Nyssa (Nyssaceae). *N. sylvatica* was reported to be a 40-70 germinator (ref. 44, Ch. 7). Collections from the wild have as yet failed to germinate. *Nyssa sinensis* germ. 40-70(1/6) and 2/6 in May from sowing outdoors in January.

Ocimum (Lamiaceae). *O. basilicum* (basil) germ. 60% in 3-7 d in either 70L or 70D. When started at 40 or started outdoors in March, all the seeds rotted indicating that temperatures as low as only 40 cannot be tolerated.

Oenothera (Onagraceae). While many species germ. well in dark treatments, *O. biennis* has an absolute light requirement so that photorequirements have to be considered in this genus.

O. albicaulis germ. immediately at 70.

O. argillicola germ. 70D(60% in 4d-3 w), 70L(86% in 4-16 d), 70D GA-3(83% in 2-18 d), and 40(26%)-70(51% in 2-4 d). Seeds placed outdoors in November germ. 85% in April.

O. biennis requires light or GA-3 for germination. The data for fresh seeds were 70L(55% in 2nd w), 70D GA-3(50% in 1-5 w), and 40-70L(85% in 2-3 d). The data for seeds DS 6 m at 40 or 70 were 70L(60-75%) and 40-70L(90-95%). Germination in all other treatments never exceeded 2%.

O. brachycarpa germ. 70(39% largely in 2-3 d) and 40(33% in 1-10 w)-70(49% in 1-5 d) for fresh seed and 70(11%) and 40(77%) for seed DS 6 m at 70.

O. caespitosa germ. 70L(4/8 in 2-9 w) and 70D(none). Seed sown outdoors in March germ. some in May. Seeds received under this name have given plants that are stoloniferous and others that are not. Germinations may vary.

O. cheiranthifolia germ. immediately at 70.

O. cupressus germ. in 4th m at 70.

O. fendleri germ. some immediately at 70.

O. glauca germ. some in 2nd w at 70.

O. pallida germ. well in 3rd w at 70.

O. serrulata germ. abundantly in 5th w at 70.

O. speciosa germ. in 1-3 w at 70. This species has proven to be hardy and floriferous in central Pennsylvania despite its more southern origin.

O. triloba germ. a few in the 3rd w at 70.

O. xylocarpa germ. 70D(2/54 in 3rd w). The rest of the seed soon rotted.

Onosma (Boraginaceae). Germinations were predominantly at 40.

O. armenum germ. 4/13 at 40 and none at 70.

O. nanum germ. 3/20 in 2nd w at 70.

O. stellulata germ. 40(8/8 in 8-10 w) and 70(1/7 in 6th d)-40(5/7 in 8th w).

O. taurica germ. 40(3/7 in 10th w)-70(2/7 on 4th d) and 70-40(3/7 in 8th w).

Ophiopogon (Liliaceae). *O. japonicus* had germination blocked by the diurnal light pattern of 12 h light and 12 h dark when sown at 70. A prior 3 m at 40 eliminated this photoeffect. Germination was 70D(100% in 3-6 w) and none in 70L. The sample in 70L was shifted to dark after 6 w whereupon 100% germ. in 3-6 w. The rate of germ. and the ind. t were the same as if the period in light had never occurred. The light must be continuously producing a short lived germination inhibitor. Shifting to dark causes the seed to revert to its initial state within a day or two. The photoeffect was eliminated by 3 m at 40 as shown by 40-70D(100% in 1-4 w) and 40-70L(100% in 1-4 w). Fresh seed and seed DS 6 m at 70 (in the WC state) gave the same complex behavior. The seed is enclosed in a berry and must be WC. In contrast to the above behavior, a sample from Nanking, China, germ. 70L(4/4 in 6th w) and 70D(7/8 in 3-6 w). The most likely explanation for the divergent behavior is that the second sample had effectively been subjected to a chilling period equivalent to 3 m at 40 which was shown to eliminate the photoeffect. This emphasizes the care that must be taken to control each variable.

Opuntia (Cactaceae). Seeds are in a fruit and were WC for 7 d. *O. tuna* germ 70D GA-3(5/40 in 8th w) and 70D(none), but the seedlings quickly rotted. Extensive experiments on *O. phaeacantha* have failed to give a single germination although this species self sows here. It is significant that seedlings appear years after the plants have been removed. Some germination was obtained immediately at 70 for *O. aurea*, *humifusa*, *imbricata*, *leptocaulis*, *phaeacantha*, *polycantha*, *rhodanthe*, and *rutila*, but these were qualitative experiments performed twenty years ago. It has been

reported that cactus have impervious seed coats. Extensive experiments on *O. phaecantha* showed that at least for this species impervious seed coats are not the problem.

Opithandra (Gesneriaceae). A species was collected on Mount Omei in China by Don Jacobs. Like all gesneriads, fresh seed germ. in 4th w at 70. Seed sown at 40 or seed DS 6 m at 70 germ. none. Seed DS 6 m at 40 gave low germination showing that the deterioration is slower at 40 than at 70.

Origanum (Lamiaceae). *O. vulgare* germ. 100% on the 3rd d in either 70L or 70D and 100% in April in outdoor treatment. Germination was much slower at 40 with only 10% germinating after 4 w.

Ornithogalum (Liliaceae). James Forrest reported that *O. dubium* and *O. maculatum* germ. 100% immediately from his own fresh seed whereas 100 packets of DS seed from other sources gave only a single seedling suggesting that DS is not tolerated. Germination was hypogeal in *O. umbellatum* and epigeal in the others.

O. caudatum germ. 70(5/8 in 4-16 d) and 40(1/8 in 9th w) using fresh seed. This species is not hardy here.

O. nutans germ. 40(92% in 5-10 w), 70L(none), and 70D-40(35% in 7-10 w) showing that even 3 m at 70 is deleterious. In outdoor treatment germination occurred in late fall and early spring.

O. pyrenaicum germ. 40(89% in 5-11 w), 70-40(90% in 5-11 w), and 15% in April from seed placed outdoors March 1. Treatment with GA-3 increased rotting.

O. umbellatum germ. 40(4/6 in 8th w) and 70(1/4 in 8th w)-40(1/4).

Orontium (Araceae). *O. aquaticum* seeds ripen in June and germinate 100% in 4-15 d in either 70D or 70L. Germination is unusual in that a fleshy covering rots off and exposes three true leaves that had already formed. These elongate and roots form within a week. Seeds also germinate at 40, but slower (100% in 2-4 w).

Osbeckia (Melastomaceae). *O. stellata* had germination promoted by light as shown by 70L(70% in 1-3 w) and 70D(15% in 2nd w). A prior 3 m at 40 was injurious as shown by 40-70L(none) and 40-70D(4%).

Ostrowskia (Campanulaceae). *O. magnifica*, it is unfortunate that this magnificent plant has not survived past the cotyledon stage here despite excellent germination, and this observation has been repeated four times. DS seed gave good germination in either a 40 or 70-40 pattern with germination occurring largely in 2-4 w at 40 showing that it is a strictly 40 germinator. The cotyledons develop vigorously, but the seedlings deteriorate after a true leaf forms.

Ostrya (Betulaceae). *O. virginiana* germ. 70D GA-3(2%)-40(2%) and none as yet in other treatments after 6 m.

Ourisia (Scrophulariaceae). *O. macrophylla* germ. 70L(75% in 3rd w), 70D(none), 40-70L(23% in 4th w), and 40-70D(none). Light is required and 3 m at 40 is deleterious. Seeds DS 2 y at 70 were dead.

Oxalis (Oxalidaceae).

O. magellanica germ. 70(3/12 in 2nd w)-40-70(1/12) and 40(3/3 in 3rd w).

O. sp. (CMW 4199) germ. 86% in 5-8 d in either 70D or 70L and 40(9/14 in 4th w).

Oxydendrum (Ericaceae). *O. arborescens* germ. 70L(100% in 3-9 w) and 70D(3% in 3-6 w) showing that light strongly promotes germination. Seed DS 6 m at 70 gave similar results. This photostimulation was eliminated in fresh seed by a prior 3 m at 40 as shown by 40-70L(62% in 1-3 w) and 40-70D(58% in 1-3 w), but not in DS seed which germ. 40-70L(58% in 3rd w) and 40-70D(none). This needs to be checked.

Oxytropis (Fabiaceae). *Oxytropis* is typical of many Fabaceae. Some germination can be achieved without pretreatment, but such germination is generally slow and often extends over several cycles. If the seed is pretreated by grinding a hole through the seed coat, germination is 100% in 1-3 d. The seeds are small so that the grinding is tedious and must be done carefully to avoid mechanical damage, but when done, it is dramatically effective. This was shown with *O. chiliophylla*, *multiceps*, *sericea*, *splendens*, and *viscida*. It would presumably be true for all *Oxytropis*. The data given below is for untreated seeds unless otherwise noted.

- O. besseyi* germ. some in 2-4 w at 70.
- O. cachmerica* germ. 70(100% in 2-4 d) and 40-70(100% in 1-2 d).
- O. chankaensis* germ. in April from seed sown outdoors in November.
- O. chiliophylla* germ. 90% in 3rd w at 70 if the seed coats were punctured and 20% in 2nd w at 70 if untreated.
- O. halleri* germ. in April from seed sown outdoors in January.
- O. humifusa* germ. 70(3/5 in 4-28 d) and 40-70(5/5 in 2-18 d).
- O. lamberti* germ. 70(54% in 3 d-2 m)-40(3%) and 40(41% in 3 w-3 m).
- O. megalantha* germ. in late March from seed sown outdoors in November.
- O. multiceps* germ. 70(25% in 3 d-11 w)-40(17% in 3-6 w) and 40(8%)-70(16%).
- O. sericea* germ. 70(10% in 1-8 w) and 40-70-40(5%).
- O. shokanbetschensis* germ. in late March from seed sown outdoors in Nov.
- O. viscida* germ. 1/15 in 10th w at 40.
- O. williamsii* germ. 70(4/9 in 3-9 d). All rotted in 40-70.

Pachystegia (Asteraceae). *P. insignis* minor germ. 70D(74% in 5-17 d) and 40(92% in 4th w).

Paeonia (Ranunculaceae). Nicking the seeds of *P. officinalis* and *P. suffruticosa* was reported to give some promotion to germination in the first edition, but this has not been confirmed in later and more extensive experiments. *P. anomala*, *emodi*, *lutea*, *mlkosewetschii*, *obovata*, and *vernalis* germ. at 70 similar to *P. officinalis*. Germination consists of forming a radicle and a branching root system. This requires about 2 m after which the seedlings are given 3 m at 40. On shifting back to 70 the true leaf forms (hypogean). Germination was hypogean in all but *P. brownii*,[†] and all germ. at 70 except *P. broteri* and *P. brownii*. These germ. at 40. Treatment with GA-3 gave a small increase in rate of germination in *P. officinalis* and *P. suffruticosa*.

P. broteri germ. 70-40(100% in 3rd w). A prior 3 m at 40 had no effect. This and *P. brownii* are the only two *Paonea* that germ. at 40.

P. brownii germ. 40(6/6 in 5th w) and 70-40(2/6 in 3rd w). A radicle develops at 40, but the two large cotyledons do not develop until shifting to 70. This was the only *Paonea* that germ. in an epigeal manner.

P. cambessedii germ. 70-40(2/4 in 5-7 w). Three seeds germ. 2-3 y later at 40.

P. officinalis germ. at 70 with an approximate first order rate with ind. t. of 40 d and a half life of 10 d. Thus germination at 70 extends much beyond 3 m. Some specific data are 70(67% in 4th m)-40(12%)-70(6%) and 40-70(12%)-40(20%)-70(18%)-40(2%) using fresh seed. Seed DS 6 m at 70 germ. 70(63% in 6-12 w)-40(9%) and 40-70(94% in 3-5 m). Seed DS 6 m at 40 germ. 70(100% in 3-8 m) and 40-70(85% in 2-4 m).

P. suffruticosa germ. at 70 in an approximate first order rate with an ind. t of 40 d and a half life of 11 d. These numbers are very close to those for *P. officinalis*. Some specific data are 70(25% in 4th m)-40(5%)-70(30% on 3rd d) and 40-70(14%)-40(16%)-70(35%)-40(11%) using fresh seed.

P. vernalis germ. 70-40-70(1/3)-40(1/3) and none in 40-70-40 using DS seed.

Panax (Araliaceae). This genus is notorious for difficult germination, and this was born out by the present studies. There is mystery and secrecy surrounding the germination of *P. quinquifolia* because of the market for the roots in China and the controversy over the medical value of such roots. The facts that the price of the roots depends on their shape and whether they are cultivated or wild collected is evidence enough that they have no medical value, and this is well documented.

P. quinquifolium requires oscillating temperatures and outdoor treatment. Unfortunately the seeds were not given outdoor treatment until after a year of alternating 40-70 cycles. Placing such seeds outdoors in December led to 15-25% germination the following March through June.

P. trifolium failed to germinate and outdoor conditions need to be tried.

Panicum (Poaceae). See Chapter 22

Papaver (Papaveraceae). The DS seed of the following species germ. immediately at 70: *P. alboroseum*, *miyabeianum*, *nudicaule*, *orientale*, and *tatrae*. Attention is called to the unusual behavior of *P. somniferum*.

P. atlanticum had germination much reduced in DS seed or seed sown at 40. Fresh seed germ. 70(90%, first order rate with ind. t 12 d, half time 16 d) and none at 40. Seed DS 6 m 70 or 40 germ. 30% at 70 and none at 40.

P. lapponicum germ. 70(3%) and 40-70(22%).

P. ruprifagum required DS for germination. Seed DS 6 m at 70 or 40 germ. 50-75% in 2nd w when sown at either 70 or 40 whereas fresh seed germ. 70-40-70(none) and 40(9% in 3-8 w).

P. somniferum is a dramatic D-70 germinator. Seeds DS 6 m at 70 germ. 70L(60%), 70D GA-3(60%), and 70D(30%) all on the 4th d. Fresh seeds germ. 70D GA-3-40(62% in 2-10 w) and none in any other treatment.

P. tatricum germ. in April from seed sown in winter.

Paradisea (Liliaceae). *P. liliastrum* seeds placed outdoors in February germ. 1/12 in April and none in 70D, 70L, or 40.

Paraquilegia (Ranunculaceae). *P. grandiflora* germ. in April a year later from seed sown outdoors in April. Samples of *P. caespitosa* and *P. microphylla* both rotted quickly at 70 indicating that the seed was dead. It is believed that the seed had been DS for over a year suggesting that seed does not tolerate DS well.

Paris (Liliaceae). *P. quadrifolia* germ. 70(6%)-40-70(69% in 7-12 w) and 40-70-40-70(77% in 9th w). Only the radicle develops at 70. Difficulties were experienced in getting a true leaf to develop and effective conditions have not been found. Some of the seedlings formed the true leaf by shifting to 40 for 3 m and returning to 70. If kept too long at 70 after germination, the seedlings rot. It is likely that as in other early spring species, the shift from 40 to 70 needs to be gradual in order to allow most of the growth to take place at intermediate temperatures. All DS seed rotted.

Parnassia (Parnassiaceae).

P. fimbriata germ. best in 40-70L(20% in 4th w)-40-70L. Germination was lower in 70L(3%)-40-70L(7%), and none in 70D-40-70D or 40-70D.

P. glauca germ. best in 40-70L(100% in 4th w). Germination was lower in 70L(25%), 70D-40-70L(80%), 70D-40-70D(none), and 40-70D(22%).

P. laxmannii germ. in 3rd m at 70. Photoexperiments should be performed in light of the results with the other two species.

P. palustris germ. 70L(48% in 1-3 w), 70D GA-3(88% in 5th w), 70D(17% in 3rd w), and 40-70D(25% in 2nd w).

Paronychia (Caryophyllaceae).

P. chionaea germ. 70(90% in 2nd d) and 40(85% in 1-3 m).

P. sp. (Central Turkey) germ. 70(17% in 9-15 d) and 40-70(1/8 on 6th d). Light had no effect. All seeds rotted when treated with GA-3.

Parrotia (Hamamelidaceae). *P. persica* germ. best in 40(90% in 12th w) and less in 70-40(50% in 9-11 w)

Parrotiopsis (Hamamelidaceae). *P. jacquemontiana* germ. 70-40-70-40-70(2/5 in 2nd w) and an additional seed germ. after 3 y. None germ. after five cycles starting at 40. The seedlings developed cotyledons within a w of germination and appeared to be normal and healthy.

Parrya (Brassicaceae).

P. menziesii germ. 70(10% in 4th w)-40-70(35% in 1-4 w).

P. schugnana germ. 70-40-70(20% in 1-4 w).

Parthenocissus (Vitaceae).

P. quinquefolia seed was collected in October. After WC the 25% empty seed coats float and were discarded. Fresh seed germ. 70-40-70(3/23 in 2nd w) and 40-70(2/28 in 1-4 w)-40-70. The berries hang on all winter showing that DS is tolerated.

P. tricuspidata germ. best in 70(98% in 2-6 d) and 40(98% in 7-14 w) using seed that had been DS 6 m at 40 or 70 in the dried berry and WC 7 d before sowing. Fresh seed germ. less as shown by 70(41%) and 40(92%). Fresh seed is more difficult to wash than dried seed, and this may be a factor.

Passiflora (Passifloraceae).

P. edulis germ. best in 70-40-70(81% in 5th w). None germ. when sown at 40 after six cycles, and outdoor treatment germ. only 5%. Seed DS 6 m at 70 was dead.

P. incarnata germ. 40-70(1/40) and 70D(none).

Paulownia (Scrophulariaceae). *P. tomentosum* requires light for germination. If the fresh seed is kept moist in the dark for a month or two, it is dead. Experiments were conducted with fresh seed on limiting the number of days of exposure to light with the following results. The number of days in light are given followed by percent germination in parentheses: 2(50%), 4(66%), 6(93%), 8(87%), 10(93%), and 20(95%). Germination takes place largely in 7-12 d and is complete by the 15th d. The percent germination in 70L declines on DS at 70 with germination after 12, 18, and 24 m being 91%, 85%, and 58% respectively. The seeds are held in hard capsules. Some of these capsules blow down in winter storms, and this is the most convenient way to collect seed. Each capsule contain hundreds of seeds and all are viable. Incidentally it had been reported (ref. 7, p. 124) that Paulownia required long exposure to light for germination, which is not in accord with the above results.

Pedicularis (Scrophulariaceae). *P. rainierensis* germ. 70D GA-3(72% in 1-4 w) and none in 70D, 70L, or 40.

Pediocactus (Cactaceae). *P. simpsoni* germ. 70(1/10 in 8th w) and 40(2/3 on 17th d).

Pelkovia (Lamiaceae). *P. sp.* from Greece germ. 70D(87% in 5-11 d), 70L(28% in 7-19 d), 40(50% in 8-10 w)-70(none), and 94% in late April and early May in outdoor treatment. Treatment with GA-3 killed all the seeds.

Peltoboykinia (Saxifragaceae). *P. tellimoides* germ. best in 40-70L(30% in 5-15 d) and none in 40-70D. Unfortunately the seed was not given 70L directly, but 70D-40-70L(2%)-40-70L(18%) suggests that a preliminary 3 m at 40 moist is necessary before the seed will germinate in 70L. There was no germination in 40-70D or outdoor treatment. Seed DS 6 m at 40 or 70 was dead.

Pennisetum (Poaceae). See Chapter 22

Penstemon (Scrophulariaceae). Four types of germination were observed. Most Rocky Mountain species of a perennial nature germ. largely at 40 and often sowing at 70 was fatal or near fatal. A second group are short lived species that can flower the first year from seed typified by *P. ambiguus* and *hyacinthus*. These germ. rapidly at 70 with a prior 3 m at 40 having little effect. A third group requires DS for germination and is typified by *P. grandiflora*. The fourth group typified by *P. digitalis* require light for germination. I am much indebted to Panayoti and Gwen Kelaidis and Jim and Jenny Archibald for extensive collections in the Rockies, to Sally Walker for

Southwestern species, and Claude Barr for Great Plains species. Treatment with GA-3 stimulated germination in the seven species in which it was tried. The development of the seedlings was not followed.

- P. acaulis* germ. 70(1/10) and none at 40.
- P. acuminatus* germ. 40(54% in 4-12 w)-70(5%) and 70-40-70(10%).
- P. alpinus* germ. 70(3%)-40(21%)-70(9%) and 40(12% in 3-8 w)-70(27% in 3-4 d). A later sample germ. 70D GA-3(68% in 1-3 w), 70D(6%), and 40-70D(1/16 in 3-d).
- P. ambiguus* germ. 70(94% , ind. t 3 d, 14%/d) and 40(47% in 3-12 w)-70(45% in 2-4 d).
- P. angustifolius* germ. 70(3%)-40-70(20%).
- P. arenicola* germ. 70-40(1/6)-70 and 40(14% in 8-12 w)-70(20% in 2-3 d).
- P. barbatus* germ. 70D or 70L(100% in 3-5 d) and 40(90% in 3rd w).
- P. brevicaulis* germ. 70-40(2/15)-70(1/15).
- P. caespitosus desertipictus* germ. 70D GA-3(30% in 6th w) and 70D-40(none).
- P. cleburnei* germ. 40(4/10 in 4-12 w)-70(1/10 in 2-3 d) and none at 70. A second sample germ. 70-40(3/11)-70(3/11) and 40-70(1/11). Were the two samples the same species ?
- P. cobaea* germ. in 2-6 w at 70.
- P. coerulea*, germ. immediately at 70.
- P. crandalli* germ. 70-40(45% in 4-12 w) and 40(3%)-70(30% in 3-25 d).
- P. davidsonii* germ. immediately at 70.
- P. digitalis* requires light to germinate. Germination was best with seed DS 6 m at 70 or 40 in 70L(90%, ind. t 4 d, first order rates with half life of 1.0%/d) or 40-70L(95-100% largely in 2-3 d) and less with fresh seed in 70L(26% in 7-24 d), 70D GA-3(42% in 2-4 w), or 70D-40-70L(7%). None germ. in any dark treatment other than GA-3.
- P. dolius* germ. 70(1/11)-40(2/11)-70(1/11) and 40(6/11 in 6-12 w).
- P. duchesnis* germ. 40(3/4 in 7-11 w) and 70(none).
- P. eatoni* germ. 70(16%)-40(84% in 2-10 w) and 40(100% in 2-8 w).
- P. eriantherus* germ. 70-40-70(2/24) and 40(30% in 4-12 w)-70(30% in 2-3 d).
- P. flowersii* germ. 70(4%) and 40(100% in 6-12 w).
- P. francisci-pennellii* germ. 70-40(60%, ind. t 5 d, 2%/d) and 40(50%, ind. t 17 d, 3%/d).
- P. frutescens* from Eastern Siberia is the one *Penstemon* that is not native to America. It requires light for germination. Seed germ. 70L(70% in 11-13 d) and none in 70D. A prior 3 m at 40 or 3 m in 70D had no effect.
- P. gairdneri* ssp. *gairdneri* germ. 40(100% in 3rd m) and 70D(10%)-40-70. A second sample germ. 70D GA-3(40% in 5-11 d), 40(64% in 6-11 w), and 70D(2%).
- P. gairdneri* ssp. *oreganus* germ. 40(100% in 3rd m) and 70D(3%)-40-70.
- P. glaber* germ. in 4-6 w at 70.
- P. glabrescens* germ. 40(86% in 5-9 w) and 70(8%)-40(58% in 3-12 w)-70(4%) using seed DS 6 m at 70 and 40(84% in 5-12 w)-70(5%) and 70(2%)-40(2%) using fresh seed.
- P. globosus* germ. 70L(5% in 4-12 d) and 70D(none).
- P. goodrichii* germ. 70-40(13% in 7th w) and 40(35% in 6-9 w).
- P. gormanii* germ. well in 8-10 w at 70.

P. gracilis seed sown outdoors in January germ. 62% in April. Seed sown at 70 or 40 failed to germinate.

P. grandiflora required DS, and it germ. better starting at 40. Seed DS 6 m 70 or 40 germ. 40(100%, ind. t 43 d, 6%/d) and 70(20%)-40(5%)-70(25%). Fresh seed germ. 70(none) and 40-70(3%)-40(3%)-70(3%).

P. hallii germ. 70(100% in 1-3 w, largely in 3-4 d) and 40-70(100% in 3-8 d).

P. hirsutus requires light for germination, and germination is promoted by a preliminary 3 m at 40. Seeds germ. 40-70L(71% in 4-8 d), 70L(6% in 1-6 w), 70D(none), and 40-70D(none) using fresh seed or seed DS 6 m at 70.

P. hirsutus pygmaea requires light. Fresh seed or seed DS 6 m at 70 germ. 70L(65% in 1-11 w), 40-70L(56% in 4-8 d), and none in 70D or 40-70D(none).

P. humilis germ. best in 40(30% in 8-12 w)-70(56% in 2-3 d). Sowing seed at 70 is fatal. This was confirmed with two other samples.

P. hyacinthus germ. abundantly in 4th w at 70.

P. jamesii germ. 70(100% in 5-18 d) and 40-70(100% in 5-18 d).

P. janishae germ. 40(3/6 in 8th w) and 70-40(1/6)-70(4/6 in 2-6 d).

P. johnsoniae germ. 80-100% under all six standard conditions with germination occurring in 4-10 d at 70 and in 3-8 w at 40. This hybrid strain has been bred for quick germination.

P. kunthii germ. at 40.

P. laricifolius germ. 70(1/10)-40(4/10)-70 and 40(4/9 in 10-12 w)-70(5/9 in 2-5 d). A second sample gave even more predominant germination at 40.

P. leiophylla sown outdoors in April germ. in the following April a year later.

P. lemhiensis germ. 40(3/18 in 7-9 w) and 70-40(3/18 in 2-7 w).

P. lentus germ. 40(100%, ind. t 14 d, 1.5%/d) and 70(4/8 in 2-5 w).

P. linearoides germ. 3/7 in 1-11 w at 40.

P. moffatii germ. 40(9/9 in 5-10 w) and 70-40(7/8 in 6-10 w)-70(1/10).

P. montanus germ. 40-70(5/40 in 2-4 d) and none at 70.

P. mucronatus germ. 40(12/12 in 3-12 w) and 70(1/12 in 3rd w).

P. nitidus germ. best with seed DS 6 m at 40 in 40(95% in 3-8 w) and less with fresh seed in 40(74% in 5-12 w)-70(3% in 2-3 d). Seeds sown at 70 and seeds DS for 6 m at 70 were dead.

P. ophianthus germ. 70(91%, ind. t 10 d, first order rate, half life 3 d), 40(75% in 5-12 w), and 59% in March and April in outdoor treatment. Light or GA-3 had no effect.

P. osterhouti germ. immediately at 70.

P. ovatus germ. immediately at 70.

P. pachyphyllus germ. 70D GA-3(75% in 1-5 w), 70D(none), and 40(56% in 5-10 w).

P. palmeri germ. in April from seed sown outdoors in February.

P. peckii germ. in April from seed sown outdoors in February.

P. paysoniorum germ. 70(2/23) and 40(4/15 in 8-12 w)-70(1/15 on 2nd d).

P. pinifolius germ. in April from seed sown outdoors in February.

P. rupicola germ. a few in 3-8 w at 70.

P. "Scarlet Queen" germ. 90% in 3-6 d in either 70D or 70L and 90% in 3-8 w at 40. Germination at 40 was zero order with ind. t 10 d and rate 1%/d.

P. scouleri germ. in 5th w at 70.

P. secundiflorus germ. 70 GA-3(40% in 1-6 w), 70D(4%), and 40(4%). An earlier sample germ. 40(55% in 3-5 w) and 70(5%)-40.

P. serrulatus germ. in April from seed sown in March one m earlier.

P. smallii requires light like the closely related *P. digitalis* and *P. hirsutus*. Like *P. hirsutus* a preliminary 3 m at 40 also promoted germination as shown by 40-70L(15% in 8-30 d) compared to 70L(6% in 1-6 w). None germ. in dark treatments and no more germ. in the light treatments in two additional cycles. Despite the low percentage germinations, the data is significant because the samples consisted of hundreds of normal size seed coats. There is apparently a high proportion of empty seed coats despite the fact that the seeds were collected from a vigorous self sowing colony. Seed DS 6 m at 70 gave similar results.

P. sp. Rocky Mountains is included despite the lack of identification because it was the only Rocky Mountain species that required light. It had another unusual feature in that germination was better (24% in 1-3 w) in 70L if preceded by 2 m moist in 70D. Otherwise fresh seed germ. 70L(8% in 4-8 w)-40-70L(1%), 70D(none), 40-70L(10%), and 40-70D(3%).

P. sp. San Bernardino Mountains germ. 40(57% in 2-4 w), 70-40(5%), and 33% in October and November from seeds placed outdoors in August.

P. speciosus ssp *kennedyi* germ. 70D GA-3(70% in 2-5 w) and none in 40 or 70D.

P. teucრიoides germ. 70(20% in 4-30 d) and 40-70(20% in 4-6 d).

P. tolmei germ. in 3rd w at 70.

P. uintahensis germ. 40-70D(1/7) and none in 70D or 70L.

P. utahensis germ. 40(63% in 3-8 w) and 70-40(7%).

P. virens germ. best with seed DS 6 m at 70 in 40(30% in 4-12 w)-70(5% in 1-3 d). The DS is essential as seed DS 6 m at 40 germ. less as shown by 40(8% in 7-12 w)-70(1%) and fresh seed germ. none in 40-70 treatment. Germination failed with both DS seed and fresh seed when sown at 70. The above data were for seed collected in July. If the seed is allowed to remain on the dry stems all winter and collected in March, the effect is like DS and the seed germ. 40(11%)-70(17%).

P. whippleanus germ. 70(20% in 4-30 d) and 40-70(20% in 4-6 d).

P. wilcoxii did not germinate until shifted from 70 to 40.

P. wicklizenii did not germinate until shifted from 70 to 40.

Periploca (Asclepiadaceae). *P. graeca* germ. 70-40-70(100% in 2-4 d). Light had no effect.

Pernettya (Ericaceae). *P. macrostigma* germ. 70L(48% in 4-8 w), 70D GA-3(30% in 4-7 w), and 70D(none).

Persea (Lauraceae). *P. americana* is the commercial avocado, and it is common for gardeners to germinate the large seed in each fruit. This is done by WC and placing the base in water. Germination occurs in a few weeks.

Petrocoptis (Caryophyllaceae). Seed of *P. glaucifolia*, *hispanica*, and *pyrenaica* germ. in 1-5 w at 70.

Petrophytum (Rosaceae). *P. caespitosum* germ. 70(46% in 2nd w) and 40(6%).

Petroselinum (Lamiaceae). *P. hortense* germ. 72% in 3rd w in either 70D or 70L and 74% in 4th w at 40. Seeds treated with GA-3 failed to germinate.

Phacelia (Hydrophyllaceae).

P. campanularia germ. 70(50% in 1-8 d) and 40(79% in 1-4 w). Seed DS 3 y was dead.

P. dubia self sows abundantly here, but the seed has been difficult to germinate in controlled experiments. Seed given 70-40 and then shifted outdoors in January germ. 4% in March, but seeds given outdoor treatment from the time of collection in June germ. none the following spring. Treatment with GA-3 initiated germination, but to date the seedlings have been etiolated and died. The GA-3 treatment germ. 12% in 4th w at 70, 36% in 2-9 w for seeds that had been in alternating 70-40 cycles for two years, and 20% in 3-5 w for seeds that had been outdoors for 2 y.

P. grandiflora germ. 70(80% in 3-4 d) and 40(90% in 3rd w). Light had no effect. Seed DS 6 m at 70 germ. less, 70(2%) and 40(5%).

P. hybrid Lavender Lady germ. 70(50% in 3-7 d) and 40(50% in 3-5 w). Light or GA-3 had no effect.

P. sericea germ. 70(80-90% in 4-9 d) and 40(7%)-70. Light had no effect. This deleterious effect of sowing at 40 was observed on two independent samples.

Phellodendron (Rutaceae). *P. amurense* seed is enclosed in a black fruit and was WC for 7 d. After the WC and a one day drying, a thin pale tan husk falls off, and these were removed by placing in water where the husk floats and the seeds sink. Outdoor treatment of this seed germ. 75% in April from sowing in December. The six standard treatments germ. 0-1%, and these miniscule germinations occurred in the 2nd to 6th cycles. Attempts to conduct abrasion experiments were thwarted because of a tendency of the seed to crush.

Philadelphus (Saxifragaceae). *P. coronarius* germ. better after DS. Seed DS 6 m 70 germ. 70(58% in 5-25 d) and 40-70(57% in 3-20 d). Fresh seed germ. 70(2%)-40-70(41%) and 40-70(14%)-40-70. Seed DS 6 m 40 germ. 70(16%) and 40-70(68%) showing an intermediate behavior.

Phlomis (Lamiaceae).

P. fruticosa germ. 70D(2/6 in 5-10 d) and 40(2/6 in 4th and 12th w).

P. tuberosa germ. 70(3/6 in 3rd d). Light had no effect.

Phlox (Polemoniaceae). Phlox seed is hard to collect as there are only a few seed in each spherical capsule and these capsules roll away as soon as ripe. As a result seed of Phlox is not readily available except for the annual *P. drummondii*. In the perennial species germination was multicycle. The effect of DS ranged from a fatal treatment in *P. divaricata* and *P. bifida* to a favorable treatment in *P. glaberrima*. Taxonomy is particularly difficult in Phlox. In broadest terms Phlox *adsurgens*, *divaricata*, *paniculata*, *pilosa*, and *stolonifera* are reasonably distinct. Then there are a group of creeping Phlox in the Rocky Mountains, a group of creeping Phlox in Eastern U.S., and a group of June flowering Phlox from Southeastern U.S. centering around *P. glaberrima* and *P. pulchra*.

P. diffusa v. *longistylis* (*P. scleranthifolia* ?) germ. 70(1/4 in 7th w).

P. divaricata germ. 70-40-70(7%)-40-70(27% in 1-5 d) and 40-70(4%)-40(33% in 12th w)-70(18% in 2-3 d) using fresh seed. A second sample germ. 70-40-70(12%)-40(30%)-70(37% in 1-5 d)-40-70(3%) and 40(2%)-70(13%)-40(8%)-70(25% in 1-11 d). Germination is extended although details vary. DS is deleterious although a few seeds survive DS for 6 m at 70.

P. glaberrima germ. 70(27% in 4-11 w)-40-70(20%)-40-70(13%) and 40-70(11%)-40(9%)-70(16%)-40(2%). Seed DS 6 m at 70 germ. 70(50% in 5th w)-40-70(8%) and seed DS 6 m at 40 germ. 70(57% in 2-9 w)-40(3%)-70(3%) and 40-70(71% in 3-11 d).

P. hoodii germ. 70(1/6 in 4th w)-40(1/6 in 7th w) and 40-70(3/6 in 1-7 w). A second sample germ. 40-70(4/8 in 1-12 w) and 70-40-70(4/7 in 2nd d).

P. longifolia germ. 40(100% in 2-4 w, largely in 2nd w) and 70(24% in 7-10 w)-40(76% in 2nd w).

P. multiflora germ. 40(2/11 in 4th and 9th w) and 70(1/6 in 7th w).

P. paniculata germ. best in outdoor treatment. Seed sown in October germ. 96% in the following February and March. Germination was less in 40(66% in 12th w)-70(10%) and 70-40(40%)-70(20%). Note the predominance of germination at low T. Seed DS 6 m at 70 or 40 all rotted.

P. pilosa germ. 70(7%)-40(7%)-70(7%)-40(27%)-70(33% in 2-3 d) and 40-70(17% in 6-9 d) using fresh seed.

P. pulchra germ. 40-70-40(1/3)-70 and none at 70 using fresh seed.

P. pulvinata germ. 70(2/6 in 4th d) and 40-70(3/5 in 1-6 d).

P. speciosa germ. 40-70(2/5 in 3rd w). A second sample germ. 70-40(10/20 in 3-11 w) and 40(3/18 in 3-11 w)-70(5/18 in 1-12 w).

Phoenix (Palmaceae). It is a particular pleasure to be able to record an experiment performed sixty years ago when I was twelve years old. *P. dactylifera* is the edible date. The seeds (pits) were removed and washed after which they germ. in one to two months at 70.

Phoradendron (Loranthaceae). *P. flavescens* (mistletoe) germ. 70L(97% in 3rd w) and 70D(none). The seeds were WC 7 d to remove most of the gelatinous covering. The seeds are green in light and must be photosynthesizing. Germination consisted of sending out a green shoot equal in length to the diameter of the seed. Growth then stopped. It is possible that exogenous chemicals from the host are needed for further development, particularly development of the haustoria. This was not investigated. Other treatments such as 70D, 40-70L, and 40-70D were all fatal. Seed DS 6 m at 70 was damaged although 60% turned green on moistening at 40 or 70 and 3% germ. at 70.

Photinia (Rosaceae). *P. villosa* germ. 40(90% in 10-12 w)-70(10% in 1-7 d), 70D(none), and 95% in March and April when started outdoors in November. It is likely that germination at 40 would have been 100% if the time had been extended beyond 3 m. DS is detrimental. Seeds DS 6 m at 70 germ. 70-40(20%)-70(80% on 2nd d) and 40(36% in 6-9 w)-70-40(18%)-70(36% on 2nd d). Treatment with GA-3 did not change the pattern but reduced germination to 70-40-70(65%).

Phyllodoce (Ericaceae).

P. coerulea germ. 70(82% in 1-3 w). Light had no effect.

P. nipponica seeds received in January required light at 70, but this was removed by a preliminary 3 m at 40. The data are 70L(90% in 2-4 w), 70D(none), 40-70D(90% in 2-4 w), and 40-70L(90% in 2-4 w). A prior 4 w in 70D had no effect.

Physalis (Solanaceae). Light or GA-3 are required. Extending the period of WC from the usual 7 d to 2 w and even 4 w was beneficial. Seeds are in a berry in an inflated husk. DS is tolerated.

P. alkekengi germ. 70D GA-3(85% in 7th w) using seeds WC for either 3 or 7 d. In contrast germination in 70L was 43% for seed WC 2 w, 10% for seed WC 7 d, and none for seed WC 3 d. The data show that the inhibitors are not readily removed by WC and extended WC is beneficial. A prior 3 m at 40 had a small favorable effect. Seeds were viable for up to 3 y of DS.

P. virginiana germ. largely in light. Seed WC 5 w germ. much faster than seed WC only 7 d as shown by 70L(100% in 2-3 d) for the seeds WC 5 w and 70L(90% in 2-6 w) for the seed WC 7 d. Also the seed WC 5 w germ. a little in the dark as shown by 70D(5%) and 40-70D(48%) compared to none in 70D for seed WC 7 d. A prior 3 m at 40 had no effect. The seed was collected in December so that the seed can tolerate DS for some time in the berry.

Physaria (Brassicaceae).

P. alpina germ. in April from seed sown outdoors in January.

P. newberryi germ. 70(50% in 1-4 w) in either 70D or 70L and 40(40% in 4-11 w)-70(47% in 2-5 d).

Physocarpus (Rosaceae). *P. opulifolius* germ. 70(2%)-40-70(61%, ind. t 20 d, 20%/d)-40-70 and 40-70(11%)-40(7%)-70(9%) using fresh seed. Seed DS 6 m at 70 or 40 germ. 40-70(42% in 2-17 d) and 70(none).

Physoplexis (Campanulaceae). *P. comosum* germination was dramatically stimulated by GA-3, and the seedlings were normal and healthy. Seeds germ. 70D GA-3(82% in 3rd w), 70D(9% in 2-6 w), 70L(none), 40-70(none), and none in outdoor treatment. A prior 4 w in 70D or 70L had no effect, but a prior 3 m at 40 slowed down the rate and reduced the percent germination.

Physostegia (Lamiaceae). *P. virginiana alba* germ. 70(70% in 4-6 d) and 40-70(43% in 3-5 d).

Phyteuma (Campanulaceae). Seed of *P. charmellii*, *haemispherica*, *nigra*, and *scheuzeri* all germ. immediately at 70. In contrast *P. serratum* germ. only with GA-3. The data for *P. serratum* were 70D GA-3(50% in 3rd w) and none in 70D or 70L.

Phytolacca (Phytolaccaceae). *P. americana* seed was WC 7 d. Germination was best with seed DS 6 m at 70 or 40 in 40-70(70-80% in 5-16 d). Germination failed for seed sown at 70(1% in 5th cycle) or for fresh seed in either 70-40 or 40-70 treatment. Seed stored in the WC state or in the dried fruit gave the same results. GA-3 did not initiate germination at 70.

Picea (Pinaceae). There was a high percentage of empty seed coats.

P. abies germ. 70D(45% in 6-8 d), 70D GA-3(20%), and 40(9% in 9th w)-70(30% in 4-6 d).

P. excelsa seed collected in January germ. 70(18% in 6-8 d) and 40(1%)-70(11%). Light had no effect.

P. mariana germ. 70(14% in 5-10 d) and 40-70(14%). DS for 6 m at 70 or GA-3 also gave 14% germ. at 70, and outdoor treatment also gave 14% germination.

P. pungens germ. 70(4% in 3rd w) and seed DS 6 m at 70 germ. 40-70(10%). Other treatments gave no germination. These results are not in accord with the literature (ref. 31, Ch. 7).

P. rubra germ. 70(38% in 5-10 d), 40-70(80% in 5-12 d), and 3% in October from setting outdoors in September. In calculating percent germinations the 50% empty seed coats were not counted. DS for 6 m at 70 or GA-3 had no effect.

Pieris (Ericaceae). *P. japonica* germ. 70L(97%, ind. t 6 d, rate 20%/d), 70D(10% in 3rd w), and 40(14% in 9th w)-70D(none) using fresh seed. Seeds DS 6 m at 70 germ. 70L(86% in 2nd w), 70D(12% in 3rd w), 40(35% in 7-12 w)-70L(29%), and 40(35%)-70D(5%). This is similar to fresh seed.

Pimelea (Thymelaceae). *P. prostrata* germ. 40-70D(2/6 on 4th d) and none in 70D.

Pimpinella (Apiaceae). *P. anisum* germ. 65% in 5-11 d in either 70D or 70L, 40(41% in 3-6 w), and 34% in early April in outdoor treatment.

Pinellia (Araceae). *P. ternata* germ. 70(69% in 3-12 d) and 40-70(95% in 8-10 d). Seed DS 6 m at 70 or 40 gave similar results.

Pinguicula (Lentibulariaceae). *P. macroceras* required light as shown by 70L(73% in 3rd w) and 70D(2%). When the sample in 70D was shifted to 70L after 7 w, 78% germ. in 2nd w. A preliminary 3 m at 40 had no effect.

Pinus (Pinaceae). *P. canadensis*, *cembroides*, *contorta*, *coulteri*, *densiflora*, *echinata*, *excelsa*, *flexilis*, *insignis*, *koraiensis*, *lambertiana*, *monophylla*, *monticola*, *resinosa*, *rigida*, *sabiniana*, *strobis*, *torreyana*, *tuberculata*, and *virginiana* were reported to be 40-70 germinators (ref. 31, Ch. 7). Two m at 40 was sufficient for all except *P. excelsior* and *lambertiana* which required 3 m at 40 and *P. koraiensis* which required 5 m at 40. The southern pines *P. caribea*, *echinata*, *palustris*, and *taeda* were also reported to have germination increased by a preliminary cold cycle. A 40-70 pattern was also reported for *P. aristata*, *cembra*, *densiflora*, *koraiensis*, *parviflora*, *poderosa*, *pumila*, *radiata*, *sabiniana*, *thunbergii*, and *torreyana* (J H). *P. mugo*, *pinea*, and *roxburghii* were reported to germinate immediately at 70 (J H).

P. strobis germ. 70L(1/15)-40-70D(1/15), 70D(none), 40-70(1/32), and 1/43 in outdoor treatment.

P. sylvestris germ. 100% on 6th d at 70 using seed collected in January.

Piptanthus (Fabaceae). *P. nepalensis* germ. 70(3/3 in 1-8 w). It is likely that germination would have been immediate if the seed coat had been punctured.

Platanus (Platanaceae). *P. occidentalis* germ. best in outdoor treatment which germ. 34% in April from seed sown outdoors the preceding December. Seeds also germ. 40-70(28% in 1-12 d), 70L(8% in 2nd w), and 70D(1%)-40-70D(3%). Seeds DS 6 m at 70 or 40 germ. 70D-40-70L(5%) and 70D-40-70D(1%). Seeds were collected in December. Abundant chaff rendered seed counts inaccurate.

Platycodon (Campanulaceae). *P. grandiflora* germ. 70(68% in 5-6 d) and 40-70(100% in 2-4 d). Seed DS 6 m at 70 or 40 germ. 70(87% in 2-7 d) and 40(88% in 3-10 w). DS caused seeds to germinate at 40 as well as 70.

Pleuroginella (Verbenaceae). *P. brachyanthera* germ. one seed in April after a year outdoors.

Podophyllum (Berberidaceae).

P. hexandrum (*pentaphyllum*, *emodi*) seed is enclosed in a large red plum sized fruit. Germination was best with seed DS 6 m at 70 or 40 in 70(80-100% in 5-8 w) or 40-70(70-80% in 3-6 w). Germination with fresh seed was slower as shown by 70(33% in 6-12 w) and 40-70(80% in 4-11 w). If the 3 m at 70 is extended to 6 m, an additional 35% germinates. There was no difference in germination whether the seeds were WC for 7 d in water or WC for 5 d in water followed by WC for 2 d in aqueous detergent. Fresh seed germ. at 70 at a rate of 2.5%/d with ind. to of 26 d until

about 70% had germ. Then the germination rate suddenly became much slower being of the order of 0.3%/d, and this continued until a total of 98% had germ. The slower germination also followed zero order kinetics. It was as if there were two kinds of seed, 75% fast germinating and 25% slow germinating. The seedlings developed both cotyledons, but it takes 1-2 m at 70 for the cotyledons to develop after the radicle first appears. Treatment with GA-3 speeded up germination, and 100% germ. in 1-7 w. The seedlings were etiolated and died.

P. peltatum germ. 15% in April in outdoor treatment using seed that had been WC for 7 d. Germination dropped to 6% if the seed had been WC for 4 w. All other treatments failed. After 1-2 y some seeds would exert a radicle 1-3 mm., but such aborted seedlings would ultimately rot.

Polemonium (Polemoniaceae). The following germ. in 2-5 w at 70: *P. brandegii*, *haydeni*, *mellitum*, *pauciflorum*, and *pulchellum*.

P. acutiflorum germ. 70(8/15 in 4-17 d) and 40(2/21)-70(7/21).

P. coeruleum germ. 70(52% in 1-4 w) and 40(none).

P. coeruleum ssp *villosum* germ. 70D(82% in 2nd w), 70L(32% in 2nd w), and 40(8%)-70(4%). Modest differences such as this between 70D and 70L could possibly be a T effect as the seeds unavoidably heat up some because of light absorption.

P. delicatum self sows in sand beds here and is remarkably resistant to drought. Seeds DS 6 m at 70 germ. 40(50% in 3-5 w) and 70(40% in 1-3 w). Fresh seed germ. 40(48% in 2-10 w) and 70-40(10%)-70(8%)-40.

P. grayanum germ. 70L(25% in 3rd w), 70D(5%), and none in 70D-40-70L indicating that light promotes germination.

P. mellitum germ. 65% in 3-7 w in 70D.

P. pulcherrimum v. *calycinum* germ. 70L(56% in 2nd w), 70D(17% in 2nd w), and 40(32% in 2-7 w).

P. reptans germ. 70-40-70(5/13 in 2-28 d)-40(2/13) and 40-70-40(8/18 in 9-12 w)-70-40(2/18)-70 using fresh seed. Seed DS 6 m at 70 gave less than 2% germination. Light and GA-3 need to be tried.

P. vanbruntiae germination required either light or a preliminary 3 m moist at 40 as shown by 70L(57% in 1-11 w), 70D(2%), 40(6%)-70L(90% in 2-4 d), and 40(6%)-70D(90% in 4-8 d). Shifting the sample in 70D to 70L after 5 w germ. 96% in 1-16 d. Seed DS 6 m at 70 germ. 70L(95% in 1-3 w), 70D(none), 40-70L(95% in 1-12 d), and 40-70D(87% in 6-8 d).

P. viscosum germ. 70(42% in 4-10 d) and 40(19% in 3-8 w)-70. It is unusual for such a high alpine species to show immediate germination at 70.

Polygala (Polygalaceae). Seed is difficult to collect because it ripens over an extended period. The samples of seed were thus small. In view of the photoresponses in *P. calcarea* and *P. lutea*, the other species need photoexperiments although light had no effect on *P. brevifolia*.

P. brevifolia germ. 70-40-70L(2/7 in 1-3 w), 70-40-70D(2/5 in 2nd w), and none in 40-70D.

P. calcarea germ. 70L(1/13 in 5th w) and 70D-40-70D(1/11 in 5th w).

P. chamaebuxus germ. one seed in the 4th w at 70.

P. lutea germ. 40-70L(85% on 7th d), 40-70D(none), 70-40-70L(20% in 2nd w), and none in 70-40-70D. Seed DS 6 m at 70 rotted.

P. nuttallii germ. 70-40-70(50% in 2nd w) and 40-70(20%): Seed DS 6 m at 70 rotted.

Polygonatum (Liliaceae). The three species germ. hypogeally at 70 and form only a corm and branching root system at 70. When development of this is complete, the seedlings were shifted to 40. It was found that 3 m at 40 was insufficient to destroy growth inhibitors in the epicotyl. A 6 m period at 40 and a shift to 70 initiated stem and leaf formation in *P. biflorum* and *P. humile*, but not *P. glaberrimum*. A winter outdoors initiated stem and leaf development in all three.

P. biflorum seeds collected in October, WC 7 d, and placed outdoors germ. 90% in May-June. None germ. in 70L, 70D, or 40-70.

P. glaberrimum germ. 70D(33% in 3-8 w) and 40-70D(70% in 2 d-5 w). Seeds placed outdoors in April germ. 3/17 in July-October and 10/17 the following April.

P. humile germ. 70D((2/8 in 11th w).

Polygonum (Polygonaceae). *P. acre*, *acifolium*, *amphibium*, *aviculare*, *coccineum*, *hydropiperoides*, *lapathifolium*, *pennsylvanicum*, *scandens*, and *virginianum* were reported to be 40-70 germinators (ref. 44, Ch. 7).

P. cuspidatum germ. 70L(93% in 1-3 w), 70D(10% in 1-3 w), 40-70L(85% in 1-3 d), and 40-70D(97% in 1-3 d). The promotion of germination by light disappeared after 3 m at 40. It also disappeared on DS. Seeds DS 6 m at 70 germ. 70L(87% in 2nd w), 70D(70% in 1-3 w), and 40(70% in 4-11 w)-70D(20% in 2-3 d).

P. orientale germ. 4% in the 2nd w in either 70L or 70D. Puncturing the seed coats, outdoor treatment, or GA-3 failed to initiate germination. Are high T needed?

Poncirus (Rutaceae). *P. trifoliata* seed was removed from the fruit and WC 7 d. This seed germ. 70D(50% in 2-4 w) and 70L(none). This is one of the few examples of photoinhibition that was found in the present work. The sample in 70L was shifted to 70D after 5 w whereupon it germ. as if the 70L period had not occurred. If the undersize seeds are discarded, the percent germination is 80-90%. Seed started at 40 or outdoors largely rotted.

Popoviolimon (Plumbaginaceae). *P. turkomicum* germ. 40(1/3 in 3rd w) and 70(0/3). It is likely that there was only one viable seed and that the species is a D-70 germinator like the closely related *Acantholimons*.

Populus (Salicaceae). All species in the willow family are intolerant of DS.

P. gradidentata germ. 100% in 4-12 d using fresh seeds. The seeds rapidly deteriorate on DS. Percent germinations were 25% and 4% for seeds DS 2 w and 5 w at 70. The death rate is first order rate with half life of 7 d.

P. tremuloides germ. 100% in 5-7 d at 70 and 100% in 4-6 w at 40. Germination dropped to 10% after DS 2 m at 70 and 25% after DS 2 m at 40 showing the more rapid death rate at 70 relative to 40. Seed DS 6 m at 70 or 40 was dead.

Potentilla (Rosaceae). *P. atrosanguinea*, *P. rupestris*, and *P. megalantha* germinations were stimulated by light and by GA-3. In *P. rupestris* this light or GA-3 requirement was removed by 3 m at 40. *P. recta* was complex with light, GA-3, 3 m at 40, and DS all having effects. *P. argrophylla*, *crantzii*, *cuneata*, *eriocarpa*, *fruticosa*, *nuttallii*, and *salesoviana* germ. in 70D and did not require light or GA-3.

P. atrosanguinea germ. 70L(34% in 2nd w), 70D GA-3(33% in 2nd w), 70D(10% in 2nd w), 40-70L(36% in 4th d), and 40-70D(none).

P. cuneata germ. 70D(74% in 2-6 w) and 70D GA-3(55% in 2nd w).

P. eriocarpa germ. 100% in 2nd w in either 70L or 70D. A prior 3 m at 40 was fatal.

P. fruticosa pumila germ. 70(100%, ind. t 5 d, 10%/d) and 40-70(100% in 6-8 d).

P. megalantha germ. 70L(65% in 2nd w), 70D GA-3(50% in 4th w), 70D(7%), 40-70L(100% in 4th d), and 40-70D(none). These seeds had been DS for 6 m. There was evidence that DS for a y removed much of the light requirement.

P. recta germ. 70D GA-3(60% in 3-11 w), none in 70D or 70L, 40-70L(5%), and 40-70D(none) using fresh seeds. Seeds DS 6 m at 70 germ. 70L(60% in 2nd w), 70D GA-3(60% in 2nd w), and 70D(5% in 2nd w). The DS for 6 m at 70 converted the seeds from requiring GA-3 to requiring either GA-3 or light.

P. rupestris germ. 70L(70% in 2-4 w), 70D GA-3(63% in 2-5 w), 70D(12% in 2-5 w), 40-70L(77% in 3-4 d), and 40-70D(59% in 4-11 d).

P. salesoviana germ. 70(78% in 5-11 d) and 40(41% in 5-11 d). This species is sometimes placed in the genus *Comarum*.

Primula (Primulaceae). The discovery of a photorequirement in *P. kisoana* and dramatic stimulation of germination by GA-3 in *P. sieboldi* and *P. japonica* suggest that these treatments need to be tried on more of the species.

Five books deal solely with this genus: *The Cultivated Species of Primula* by W. Blasdale, *Pictorial Dictionary of the Cultivated Species of the Genus Primula* by the American Primrose Society, *Asiatic Primula* by R. Green, *Primulas of Europe and the Americas* by G. Smith, B. Burrow, and D. Lowe, and *The Genus Primula* by J. Halda. The older classification of 26 sections is used instead of Wendelbo's eight sections. The twenty-six sections are relatively well defined, but there is a plethora of species names, particularly in the *Farinosa* section. After the name of each species, the section to which it belongs is indicated by an abbreviation in parentheses. The abbreviations used are A for *Auricula*, B for *Bullatae*, Cap for *Capitata*, Cor for *Cortusoides*, Can for *Candelabra*, Cun for *Cuneifolia*, D for *Denticulata*, F for *Farinosa*, Fl for *Floribundae*, Mal for *Malacoides*, Min for *Minutissima*, Mus for *Muscoides*, N for *Nivalis*, O for *Obconica*, P for *Parryi*, R for *Rotundifolia*, Sik for *Sikkimensis*, Sol for *Soldanelloides*, and V for *Vernales*.

The majority of *Primulas* have seed that survive DS and germinate in 2-8 w at 70. Species that fit this pattern as judged by qualitative experiments are *P. cuneifolia* (Cun), *ellisiae* (P), *gambeliana* (R), *maguerei* (P), *malacoides* (Mal), *minutissima* (Min), *nutans* (*flaccida*), *obconica* (O), *reidii*, *rotundifolia* (R), *rusbyi* (P), and *suffrutescens* (Cun).

Auricula, germination in this group extends over at least three months and usually more. Commercial and seed exchange DS seed of the following germinated at least some in 3-10 w at 70: *P. auricula*, *calycina*, *clusiana*, *glutinosa*, *integrifolia*, *marginata*, *minima*, and *viscosa*. *Candelabra*, most of these germinate immediately at 70, but *P. japonica* was strictly a 40-70 germinator. Although *P. japonica* sets seed abundantly and self sows in our marsh, the other species do not seem to set seed naturally and they die out. The following gave at least some germination in 2-5 w at 70 in qualitative experiments: *P. anisodora*, *aurantiaca*, *chungensis*, *cockburniana*, *helodoxa*, *poissoni*, *prolifera*, *serratifolia*, and *wilsoni*. *Capitata*, a number of samples of DS seed of *P. capitata* germinated immediately at 70. *Cortusoides*, this group is well suited to conditions in eastern U.S. and should be be grown more as they are

beautiful floriferous plants. This group is subdivided on the basis of pinnate or palmate veining in the leaves. In my experience this distinction fails because both kinds of leaves and intergradations can be found on the same plant and seeds labelled *P. geraniifolia*, *heucherifolia*, *jesoana*, and *polyneura* intergrade, possibly because of hybridization in cultivation. Farinosa, this large group is composed of several diverse clusters of species. *P. farinosa* is circumpolar in both hemispheres, and there is a plethora of species names for every geographical variant. The following are *P. farinosa* variants and DS seed germ. in 2-6 w at 70: *P. algida*, *auriculata*, *darialica*, *farinosa*, *halleri*, *laurentiana*, *modesta*, *scandinavica*, and *scotica*. Nivales, these species tolerate DS well and DS seed of the following germ. abundantly in 3-6 w at 70: *P. chionantha*, *melanops*, *sinoplantaginea*, *sinopurpurea*, *stuartii*, and *tshuktschorum*. Glorious plants have been bloomed from seed, but the group is decimated by root aphids and fungal diseases in our hot summers. Petiolares, It has been documented many times that this group cannot tolerate DS. Sikkimensis, these species tolerate DS well and germ. immediately at 70. DS seed of the following germ. in 3-7 w at 70: *P. alpicola*, *alpicola violacea*, *firmipes*, *florindae*, *ioessa*, *reticulata*, *secundiflora*, *sikkimensis*, and *waltoni*. It is unfortunate that this group does not prosper in eastern U.S., but the loss is diminished by the fact that they resemble the Vernales Group which do prosper. Vernales, these generally have long extended germinations. It seems to be primarily a matter of low rates of germination rather than any specific cycle requirement.

P. apocrita (Mus) germ. well in 3rd w at 70.

P. spectabilis (A) germ. 70(1%)-40-70(22% in 3rd w) and 40-70(17% in 1-3 w) with DS seed.

P. beesiana (Can) from two sources gave different behavior. One germ. 70(90%, ind. t 5 d, 3%/d) and 40(90%, ind. t 23 d, 2%/d). The other sample germ. 70-40-70(90% in 4-6 d) and none at 40 after three cycles.

P. bulleyana (Can) germ. 70(50% in 3-12 w) and 40(18%)-70(70% in 1-3 w).

P. burmanica (Can) germ. 70(88% in 4-6 d) and 40(10%)-70(90% in 4-6 d).

P. buryana (Sol) showed a mild promotion of germination by light. Seed received in November from Nepal germ. 70L(100% in 8-17 d) and 70D(65% in 8-24 d). The sample in 70D did not germinate further. A prior 3 m at 40 injured the seed as shown by 40-70(8%). Two collections of unidentified species from the same region germ. the same including the injurious effect of 3 m at 40.

P. cockburniana (Can) germ. 70(53% in 1-4 w) and 40(56% in 8-12 w)-70(11% in 1 d).

P. cortusoides (Cor) germ. at least 50% in all six standard treatments. Fresh seed germ. 70(70%, ind. t 10 d, first order rate, half time 3 d) and 40-70(92%, ind. t 1 d, first order rate, half time 1.5 d). Seed DS 6 m at 70 germ. 70(68% in 7-9 d) and 40(67% in 3-6 w). Light had no effect. Seed DS 6 m at 40 germ. 70(71% in 3-7 d) and 40(65% in 2-6 w). A sample of wild collected seed germ. 70(100% in 5-7 d) and light had no effect. Note the effects of DS on increasing the rate of germination at 40.

P. denticulata (D) germ. 70(75% in 3-11 d) and 40(15%)-70(80-90% in 4-5 d) for either fresh seed or seed DS 6 m at 70 or 40.

P. elatior (V) gave about the same pattern of germination for either fresh seed or seed DS 6 m at 70 or 40. Germination extended over many cycles and was still

continuing after 18 m. Typical patterns were 70(2%)-40(26%)-70(18%) and 40(9%)-70(2%)-40(4%)-70(9%).

P. elliptica (F) germ. 55% in 1-3 w when sown at 70. When sown at 40 or outdoors no germination ever occurred even after a year.

P. erosa (D) germ. immediately at 70.

P. flexuosa (F) germ: 40(1/14 in 8th w) and 70D(none).

P. florindae (Fl) germ. 70L(95% in 4-9 d), 70D(73% in 4-11 d), and 40(18% in 3-8 w)-70(82% in 4-6 d).

P. forrestii (B) germ. 70L(3/5 in 3rd w), 70D GA-3(3/7 in 4th w), and 70D(2/7 in 2nd and 6th w).

P. frondosa (F) is the most vigorous of the farinosa variants. Fresh seed germ. 70(46% in 2-5 w) and less than 1% at 40. Seed DS 6 m at 70 germ. 70-40-70(42% in 5-9 d) and none at 40. Seed DS 6 m at 40 germ. 70(10%) and 40(25%).

P. geraniifolia (Cor) germ. 70-40(13%)-70(87% in 2-3 d) and 40(31%). Seed DS 6 m at 70 or 40 gave less than 2% germination in one sample and less than 10% germination in another indicating that DS is not tolerated.

P. heucherifolia (Cor) germ. in 2nd w at 70.

P. iljinski (F) germ. 70L(2/4 in 3rd w), 70D(1/20 in 2nd w)-40-70D(1/20 on 8th d), and 40-70(1/8 in 2nd w). It is suspected that the seeds had been DS for several years.

P. intercedens (F) is another farinosa variant. The best germination was with seed DS 6 m at 70 in 40-70(43% in 6-10 d). Fresh seed or seed DS 6 m at 40 gave low germination under all conditions.

P. involucrata (F) germ. 70(95% in 4-18 d) and 40(13% in 9-11 w)-70(86% in 4-10d). Seed sown outdoors in November germ. 100%, part in November and the rest in April.

P. japonica (Can) is largely a 40-70 germinator. Fresh seed germ. 70-40-70(100% in 2-4 d), 70 GA-3(45% in 2nd w), and 40-70(50%). Seed DS 6 m at 70 or 40 germ. 70(1%)-40-70(50%) and 40(30%)-70(70%). The increasing effect of DS at 70 was shown by DS for 0, 1, 3, and 6 m. The respective germinations were 40-70(50%), 40(1%)-70(97%), 40(20%)-70(80%), and 40(30%)-70(70%). The longer the DS at 70 the faster the germination at 40. However, seed DS at 70 for 2 y was dead.

P. juliae (V) germ. a few immediately at 70.

P. kaufmanniana (Cor) germ. abundantly in 3-6 w at 70 in two separate samples from Russian Botanical Gardens. However a third sample germ. only 70(10%)-40-70(3%) which possibly suggests that the samples differed in time of DS and that DS may be deleterious.

P. kisoana (Cor) germ. in only two procedures. It germ. 70D GA-3(70% in 2nd w) using fresh seed or in 70L with DS seed. Seeds DS 2 y at 70 germ. 70L(80% in 1-3 w) and seeds DS 6 m at 70 germ. 70L(16% in 2-6 w)-40-70L(17% in 2-4 w)-40-70L(37% in 1-4 w). The seedlings from GA-3 germination were normal. Germination was under 2% in all other treatments. *P. kisoana* has been a special project here (ref. 43). It is reported to be extinct in the wild.

P. denticulata (D) germ. 70(75% in 3-11 d) and 40(15%)-70(80-90% in 4-5 d) for either fresh seed or seed DS 6 m at 70 or 40.

P. luteola (F) germ. 70(50% in 1-4 w) and 40-70(30%). A number of samples of seed failed to germinate. The sample for which data is cited was from a nursery that grows this species well.

P. macrophylla (N) failed to germinate under all treatments with two independent samples, and it is possible that DS is not tolerated.

P. modesta (F) germ. some at 70, but better germination was obtained by sowing outdoors in March with germination in May.

P. muscarioides (Mus) germ. well in 3rd w at 70.

P. pamirica (F) germ. best with seed DS 6 m at 70 in 70(90% in 1-4 w). Fresh seed germ 70-40-70(80% in 1-5 d) indicating that DS is beneficial although unfortunately the data were not taken on the same set of seeds. Light had no effect.

P. parryi (P) germ. best in a 40-70 pattern as shown by 40-70(32% in 4 d-6 w) and 70(2%)-40.

P. polyneura (Cor) germ. abundantly in 2-8 w at 70 using commercial seed. Fresh seed germ. 70(90%, ind. t 10 d, first order rate, half time 5 d)-40(5%) and 40(62% in 6-12 w)-70(30% in 1-5 d). Seed DS 6m 70 or 40 germ. 70(92% in 5-9 d) and 40(96% in 3rd w).

P. pulvurea (N) germ. 70L(3/12) and 70D(2/27).

P. pulverulenta (Can) germ. 70(100% in 1-3 w) and 40(35% in 4-20 d)-70(65% in 4-8 d).

P. rosea (F) does not tolerate DS and large amounts of seed are distributed dead. Fresh seed germ. 70(50%, ind. t 6 d, 40%/d). Unfortunately this species is susceptible to fungal disease and attack by a small black insect in the heat of summer here. In cool summers large stands can be grown.

P. rotundifolia (R) germ. 70D GA-3(88%), 70L(71%), and 70D(11%) all in 2nd w.

P. sieboldi (Cor) germ. 70D GA-3(54% in 3rd w), 70D-40-70D(62%), and 40-70-40(none). Seeds DS 6 m at 70 or 40 were dead.

P. veris (V) is one of the few Primulas that sets seed naturally and self sows here. Although DS is not essential for germination, it improves germination. The DS occurs naturally to some extent as the seeds are retained in the capsule long after the capsule has dried. For example a sample collected in November germ. 70D(95% in 1-4 w), 70D GA-3(76% in 2nd w), and 40(80% in 3-9 w). A sample collected in August germ. in a more extended manner, 70(30%)-40(46%)-70(20%) and 40(45%)-70(25%). When this latter sample was DS 6 m at 70, it germ. 70(40%)-40(20%)-70(10%) and 40(100%), and when DS 6 m at 40, it germ. 70(22%)-40(27%)-70(7%) and 40(100%).

P. vernaes hybrids (V) were hybrids with possibly all four species of the vernaes section involved. Germination at both 40 and 70 was stimulated by GA-3. Seeds germ. 70 GA-3(82% in 1-3 w), 70(41% in 1-7 w), 40 GA-3(95% in 2-4 w), and 40(86% in 3-8 w). There have been various recommendations involving hot water and other treatments, but in view of the satisfactory germinations at 40, none of these claims were investigated.

P. verticillata (FI) germ. 70L(90% on 8th d), 70D GA-3(90% on 8th d), 70D(none), and 40-70D(2%).

P. vialli (Mus) germ. 70(90%, ind. t 2 d, 25%/d) and 40(3%)-70(11%).

P. violacea (Mus) germ. 70(5%)-40-70(87% in 6-8 d).

P. warshenewskiana (F) germ. 70(80% in 2-4 w). This species seems to tolerate DS better than the closely related *P. rosea*. Light had no effect.

P. yargongensis (F), numerous samples of DS seed germ. immediately at 70.

Prinsepia (Rosaceae). *P. sinensis* is the first example found to date of a seed with an impervious seed coat enclosed in a fleshy fruit. Presumably there are no germination inhibitors in the flesh of the fruit. After washing off the pulp for 14 d (largely for convenience), the seeds were subjected to four comparative treatments: (a) control, (b) the seed coats were squeezed in a vice until the seed coats cracked, (c) the seed coats were removed, and (d) the seed coats were removed and after two days of soaking in water the testa were removed. The optimum treatment was (b) where 7/8 germ. in 8-14 d, and the seedlings all developed normally. In the control (a), 6/24 germ. in the 5th w and there was no further germination over the next month. In treatment (c) and (d) germination started in the 8th d, but there was extensive rotting so that only 6/19 developed normally in (c) and none in (d). It is evident that the seeds are very susceptible to rot and that the testa provides a barrier and protection against rotting organisms. In treatment (c) presumably minor nicks were made in the testa inadvertently which initiated rot. After 2 m the controls were subjected to the barely cracking technique whereupon and additional 7 germ. in the 3rd w with the remaining 11 rotting. A prior 3 m at 40 or DS for 6 m at 70 had no effect.

Prunella (Lamiaceae). *P. webbiana* germ. in 4-8 w at 70.

Prunus (Rosaceae). All seed was WC for 7 d.

P. allegheniensis WC and placed outdoors in October germ. a few 3 y later.

P. armenica seed coats can be cracked open without damaging the kernel by a tap with a hammer on the edge. The data are for such free kernels. Germination was 70(100% in 5-9 w) and 40(25%)-70(75%). Seed placed outdoors in June also germ. 100% in 2-4 m. Germination was extended in uncracked seeds. Germination is hypogeal, and the stem and leaves develop within 7 d of germination.

P. avium var. *juliana* germ. 70-40-70(10%)-70-40(40% in 11th w)-70(3%) and 40-70-40-70(5%)-40-70(5%). Seeds DS for 6 m at 70 were dead.

P. serotina germinations were extended, occurred at 70 (and not at 40), and were better when started at 40 (instead of 70). Seeds DS 6 m at 70 or 40 germ. the same as fresh seed. The seeds expand slightly in a cycle at 40 causing the seed coats to fall away, but only about half of such naked seeds germinate in the next cycle at 70. Germination was 40-70(18%)-40-70(66% in 1-5 d) and 70-40-70(23%)-40-70.

P. serrulata germ. 70-40(2%)-70(15%)-40(15%)-70(15%)-40-70(15%)-40-70(8%) and 40(4%)-70(7%)-40(7%)-70(27%)-40-70(29% in 4-11 d)-40-70(4%). Seed WC and DS 6 m at 70 or 40 gave results similar to fresh seed.

Pseudomertensia (Boraginaceae). *P. nemorosa* germ. in 9-14 d at 70.

Pseudotaenidia (Apiaceae). *P. montana* seed DS 6 m at 70 germ. 70(2/20) and none at 40.

Pseudotsuga (Pinaceae). *P. menziesii* germ. 70D(4/11 on 4th d) and 70L(none) using seeds taken from current year cones that were just starting to turn from green to brown. Seeds DS for a y outdoors germ. 70L(4/21 in 1-3 w), 70D(1/21), 40-70(2/22), and 2/22 in March in outdoor treatment.

Psychrogeton (Asteraceae). *P. andryaloides* germ. 70(100%, ind. t 5 d, 8%/d) and 40-70(90% in 3-30 d).

Ptelea (Rutaceae). *P. isophylla* and *trifoliata* were reported to be 40-70 germinators (ref. 22, Ch. 7).

Ptilotrichum (Brassicaceae). *P. macrocarpum* germ. 40(95% in 8-10 d) and 70(70%, ind. t 4 d, 2%/d). Seed DS 6 m at 70 gave markedly lower germination.

Pulsatilla (Ranunculaceae). The following species germ. in April from seed sown outdoors in winter: *P. ambigua*, *bungeana*, *grandis*, *occidentalis*, *pratensis*, *sulphurea*, and *vernal*.

P. albana germ. 70(90% in 3-20 w) whereas DS seed germ. in a more extended manner as shown by 70-40-70(53%)-40-70(10%)-40(17%).

P. campanella germ. 70(2/6 in 2-5 w) and 40(2/6 in 12th w).

P. patens germ. in 3-5 w at 70.

P. turczaminovii germ. 70D(15% in 6th w).

P. vulgaris germ. at the same rate at 70 as at 40. Seed DS 6 m at 40 and fresh seed germ. 70(91% in 2-5 w) and 40(18%)-70(72% in 2-30 d). Seed DS 6 m at 70 germ. in lower percentage as shown by 70(17% in 3rd w) and 40-70(50% in 1-5 w).

P. vulgaris v. *zimmermannii* germ. 70D(20% in 5th w).

P. wallichianum germ. 70(6/8 in 3-5 w) and 40(2/12).

Punica (Punicaceae). *P. granatum* was reported to germinate if the seeds were first soaked for 12 hours in water (J H).

Puschkinia (Liliaceae). *P. scilloides* was collected over three years (1988-1990), but only the collection from May 1989 gave any germination. This germ. 70-40(56% in 6-8 w) for seed with no WC and 70-40(26% in 8th w) for seed WC 7 d. The seedlings were susceptible to rotting of the radicle. Probably they should grow at low T. Outdoor treatment needs to be tried. Seed DS 6 m at 70 was dead.

Pycnanthemum (Lamiaceae). *P. incanum* germ. 70D GA-3(58% in 3-12 d), 70L(30% in 2-8 w), 70D(2%), 40-70L(47% on 4th d), and 40-70D(none). Seeds placed outdoors in November germ. 48% in April.

Pyracantha (Rosaceae). *P. lalandi* germ. 70(70%, ind. t 4-6 d, 14%/d) and 40(70%, ind. t 30-40 d, 5%/d) using fresh seed or seed DS for 6 m at 70 or 40. The seed was WC for 7 d before sowing or DS. Many of the plants of this species are vegetatively propagated from sterile clones so that little if any seed is set despite a great show of berries. The most viable seed that was obtained was collected in a junk yard where the plants arose from bird sown seed.

Pyrus (Rosaceae). *P. calleryana* germ. 40(100% in 7-12 w) and less in 70(3%)-40(74% in 8-12 w) and outdoor treatment (78% in March) using either fresh seed or seed DS 6 m at 70.

Pyxidantha (Diapensiaceae). *P. barbulata* seed collected in June and sown immediately germ. 70(27% in 7-9 w) and 40(1%)-70(34% in 3-75 d). Light had no effect. Seed DS 6 m at 70 germ. less and the seedlings seemed weaker.

Quercus (Fagaceae). *Q. borealis*, *macrocarpa*, and *velutina* were reported to be 40-70 germinators (ref. 28, Ch. 10). In the present work *Q. borealis* germ. 70(4/13 in 3-7 w)-40(1/13)-70(2/13), 40-70(33% in 2nd w), and 20% in March in outdoor treatment. The seeds that failed to germinate were found to have been largely destroyed by grubs. A stem with true leaves develops within 1-2 m after germination.

Q. alba germ. 80% at 70, 40, or outdoor conditions when started October 1. The 20% that failed to germinate were infested with grubs so that germination was 100% for seeds free of grubs. Germination at 70 occurred in 1-3 w, and a stem with true leaves (hypogeal) developed in 1-2 w after germination. Outdoor treatment was essentially equivalent to sowing at 70 because the weather was warm through October. The rate of germination at 40 is only slightly slower than at 70 and requires 1-5 w for completion.

Q. borealis germ. 40-70(100%, ind. t zero, first order rate, half life 2.5 d) and 70(10%)-40(80% in 8-10 w). The seedlings developed a 4-6 inch radicle followed by a stem with true leaves (hypogeal) all within a month. Soaking the seeds for a week, making a hole in the seed coats, or removing the seed coats had little effect. Unfortunately the outdoor experiments were terminated by mice eating the acorns.

Q. coccinea germ. best in 40-70(61%, ind. t 4 d, 7%/d). It also germ. 70(8%)-40-70(28% in 2nd w). Only the 50% with densities greater than one were viable.

Q. phellos germ. 70-40-70(1/13 on 2nd d).

Ramonda (Gesneriaceae). *R. myconi* germ. best with seed DS 6 m at 40 in 40-70(37%) and less in 70(19%). Other seed germ. less as shown by 70(4%) and 40-70(none) for fresh seed and 70(11%) and 40-70(none) for seed DS 6 m at 70.

Ranunculus (Ranunculaceae). Germination was remarkably varied.

R. acris germ. largely in a 40-70 pattern. Fresh seed germ. 70-40(3%)-70(93% in 2-3 d) and 40-70(41%)-40(3%)-70(48%)-40-70(6%). Seed DS 6 m at 70 or 40 germ. 40(21%)-70(67% in 2-3 d). Seed DS 6 m at 70 or 40 and sown at 70 germ. over five cycles. The overall germination was 65-90%. Photoexperiments need to be tried in view of the results with *R. repens*.

R. adoneus germ. 70L(6/16 in 1-10 w) and 70D(1/16).

R. gramineus germ. 40(58% in 6-12 w)-70(9% in 4-12 d)-40(7%), 70-40(60% in 3-7 w), and 30% in late April and May in outdoor treatment. Light had no effect. Seeds treated with GA-3 were killed.

R. hispidulus germ. 70(10%)-40(22%)-70-40(27%) and 40(2%)-70(2%)-40(11%)-70(16%). Germination in either a 70 or 40 cycle occurs throughout the cycle. Seed DS 6 m at 70 or 40 was dead.

R. illyricus germ. 70D(6% in 3-6 w)-40(6%) and 40(8% in 7th w). Light or GA-3 had no effect. Seeds placed outdoors in November germ. 1/26 in April.

R. lyallii is the famous Mt. Cook "lily" of New Zealand. Much difficulty has been reported in trying to germinate seed. It was thus a great pleasure to find that GA-3 is a requirement for germination. In retrospect it is obvious that the ecology of this plant is similar to the rosulate violas and other GA-3 requirers. Fresh seeds germ. 70 GA-3 (22% in 5-7 w). A prior 3 m in 70D had no effect. Seedlings were normal.

R. repens required light. The seed can be started in light at 70 or shifted to light anytime during at least five cycles. Germination is 85% in the 2nd w using fresh seed or seed DS 6 m at 70. Germination in the dark is under 3% after five cycles.

R. sp. Kashmir germ. immediately at 70.

Ratibida (Asteraceae). *R. columnifera* germ. 100% in 6-8 d in either 70D or 70L and 40(50% in 4th w)-70(50% on 2nd d).

Rebutia (Cactaceae). Seed of hybrids germ. in 4-6 w at 70.

Rhamnus (Rhamnaceae). Seed is enclosed in a black berry and was WC.

R. caroliniana germ. 40-70(98% in 4-7 d) using fresh seed and 40-70(50%)-40-70(50%) using seed DS 6 m at 70 or 40. None germ. in 70-40-70. It is remarkable that an initial 3 m moist at 70 is so completely fatal. Outdoor treatment germ. 50% in April. Germination is hypogeal with the true leaf developing in 2nd w after germination.

R. cathartica germ. 70(90%, ind. t 9 d, 6%/d) and 40-70(90-100%, ind. t 2 d, 12%/d) for either fresh seed or seed DS 6 m at 70 or 40.

R. fallax germ. 70D(1/10 on 5th d) and 1/9 in May in outdoor treatment. All other treatments failed on samples of the same size including treatment with GA-3.

Rheum (Polygonaceae). Germination was immediate at both 70 and 40.

R. altaicum germ. 70(8/8 in 3-4 d) and 40(5/7)-70(2/7).

R. ribes germ. 70(2/4 in 4-6 d) and 40(4/4 in 2nd w).

R. tibeticum germ. 70(4/4 in 3-4 d) and 40(4/4 in 4th w).

Rhexia (Melastomaceae). Both of the species studied required light.

R. mariana germ. 70L(96% in 4th w) and 40-70L(73% in 2nd w). None germ. in 70D or 40-70D. When the sample in 70D was shifted to 70L after 6 w, 95% germ. in 1-3 w showing that the 6 w in 70D had no effect. The seed was received in February and had experienced about 6 m DS showing that DS is tolerated. Seed that had been given an additional DS 6 m at 70 germ. similarly.

R. virginiana requires light and either DS or 3 m at 40. Germination in 70L was 72%, 37%, and zero for seed DS 6 m at 70, seed DS 6 m at 40, and fresh seed. Seeds also germ. 40-70L(80%) for seed DS 6 m at 70 and 40-70L(54%) for fresh seed. None germ. in any dark treatment.

Rhinopetalum (Liliaceae). DS seed of *R. bucharica* and *R. stenantharium* germ. in April from seed sown outdoors the month before in March.

Rhodiola (Crassulaceae).

R. atropurpurea germ. 70L(30% in 4-8 d), 70D(10%), and 40-70D(1%).

R. heterodonta germ. 70(1) and 40(1)-70(6). Equal samples were used so that relative numbers have significance.

R. sp. Ladakh germ. 70(21 in 1-10 w) and 40(25 in 2-10 w). Equal samples were used and absolute numbers are given. It is interesting that the germination rate was the same at 40 as at 70.

R. sp. Ladakh germ. 70(302 in 1-5 w) and 40(280 in 1-5 w). These last two are probably the same species and the comments under the first apply to both.

R. sp. Nepal germ. 70(100% in 2nd w) and 40(20% in 4th w)-70.

Rhododendron (Ericaceae). Usually light was required for germination.

R. anthopogon germ. 70L(6/8 in 4th w) and 70D(2/11 in 3rd w). The 70D sample was shifted to 70L after 4 w, but no further germination occurred. A prior 3 m at 40 was fatal. The samples were so small that the experiments need repeating.

R. catawbiense hybrids germ. 70L(80-85% in 1-3 w) and less in 70D(5-25%) or 40-70D(15%). A prior 3 m at 40 had little effect. Outdoor treatment ultimately germ. 73%, but germination extended from May to August and is inconvenient. Fresh seed and seed DS 6 m at 70 or 40 gave identical results in all treatments.

R. lepidotum from Kashmir germ. best in 70L(30% in 5-10 d). Germination was reduced to 4% if the seed were kept just 3 w in 70D before shifting to 70L. Seed also germ. 40-70L(2/7) and 40-70D(1/6). The promotion by light was confirmed with a sample from Nepal which germ. 70L(85% in 10-15 d) and 70D(26% in 3rd w). After 4 w the sample in 70D was shifted to 70L whereupon 40% germ. in 3rd w. However another sample from Nepal germ. 100% in 3rd w in either 70L or 70D. The identifications are obviously in question, but the results do confirm the general tendency for germination in *Rhododendron* to be promoted by light.

R. maximum germ. only at 70. Sowing fresh seed at 70 germ. 50% with ind. t 11 d and a first order rate curve with half time 3 d, but the fit was not exact with the rate faster than first order in the early stages. Germination was lower for seed DS 6 m at 70 or 40, and germination was always lower when the cycle at 70 was preceded by 3 m at 40. Photoexperiments are needed.

R. mollis hybrids are probably derived more from southeastern U.S. species than from *R. mollis*. Seed sown at 40 germ. predominantly at 40 and seed sown at 70 germ. predominantly at 70, a curious contrast. Difficulties in counting seeds is the reason for expressing germination in absolute numbers, but the results can be compared because equal samples of seed were used in all experiments. Fresh seed germ. 70(87) and 40(44)-70(8). Seed DS 6 m at 70 germ. 70(18)-40-70(3) and 40(124)-70(8). Seed DS 6 m at 40 germ. 70(20)-40-70 and 40(86). Germination at 70 occurred largely in 2nd w and germination at 40 occurred largely in 4-10 w. Photoexperiments are needed.

R. schlippenbachii germ. 90% in 2nd w when sown at 70 in either dark or light.

R. sp. Nepal required light as shown by 70L(50% in 3rd w) and 70D(none). After 4 w the sample in 70D was shifted to 70L whereupon 50% germ. in 3rd w.

Rhodolirion (Amaryllidaceae). *R. montanum* germ. 40(3/7 in 4th w) and 70(1/9 in 3rd w). The seeds that germ. at 40 were shifted to 70 one week after germination whereupon they grew strongly, stronger than those that germ. at 70. The remaining seeds soon rotted.

Rhodophiala (Amaryllidaceae). Although some species germ. at 70, the general pattern in this genus is for germination to be best at 40.

R. advena germ. 100% in 1-5 w at 70 and 100% in 8-11 w at 40.

R. andicola germ. 40(8/12 in 6-10 w) and 70-40(3/21 in 7-10 w)-70(2/21).

R. araucana germ. 40(50% in 6-10 w) and 70-40(22% in 4-12 w)-70(6%, 4th d).

R. elwesii germ. 40(100% in 2-12 w) and 70(42% in 1-4 w)-40(19% in 5-10 w).

R. pratensis germ. 40(100% in 13th w) and 70(66% in 1-3 w)-40(5%)-70(10%).

R. sp. (Archibald's 12288) germ. 40(6/7 in 2-4 w) and 70(1/7 in 3rd w). The seeds that germ. at 40 were shifted to 70 one week after germination whereupon they grew strongly whereas the seeds that germ. at 70 were weak. The remaining seeds soon rotted. Sowing at 70 appears to be detrimental, and there is some indication of this in the closely related *Rhodolirion* described above.

Rhodotypos (Rosaceae). *R. tetrapetala* gave multicycle germination with germination occurring at both 70 and 40. Seeds collected in January germ. 70-40(44%)-70(16%)-40(12%) and 40(14%)-70(24%)-40-70(14%)-40(11%)-70(3%). Seed DS 6 m at 40 germ. 70-40-70(47%)-40(25%) and 40(57%)-70(17%)-40-70(2%)-40. Seed DS 6 m at 70 germ. 70-40-70(43%)-40(28%) and 40(65%)-70(16%).

Rhus (Anacardiaceae).

R. canadensis germ. over many cycles as shown by 70-40(8%)-70-40-70(23%) and 40(4%)-70(8%)-40-70(61% in 4-7 d). Seeds that were abraded to form a hole in the seed coat quickly rotted. This behavior contrasts strongly with that of *R. typhina*.

R. trilobata was reported to have an impervious seed coat (J H).

R. typhina is one of the few species other than legumes where grinding a hole through the seed coat is necessary for germination. Seed so treated germ. 100% in 11-13 d at 70 for fresh seed or seed DS 6 m at 70 or 40. The 50% empty seed coats were not counted. The berry and inner casing were removed by soaking and WC as this facilitates the grinding. The seed is enclosed in a dryish berry covered with soft red hairs. These hairs contain ascorbic acid which is the basis for sumach tea.

Ribes (Saxifragaceae). All seed was WC for 7 d.

R. americana is native on the property and germ. best if WC and placed outdoors in September. These germ. 35% in April. This sample also germ. 70 GA-3(6% in 2nd w) and 70D(none). Other samples germ. 40-70L(9% in 2-9 w) and 40-70L-40-70L(10% in 2nd w). The seeds are difficult to clean as a membrane adheres tightly and the seeds float.

R. cereum was received in the red berried form and the orange berried form. Gibberelins are a natural germination requirement for this species, and the survival value of this is discussed in Chapter 12. The GA-3 treatment was varied in an effort to optimize the production of healthy seedlings. The seeds were exposed to the GA-3 for 1, 3, 5, and 8 days before removal and the GA-3 was used as described in Chapter 12 and in a dosage about 1/10 as much. The percent germinations for the normal GA-3 dosage were 90%, 29%, 61%, and 49% respectively and 30%, 35%, 42%, and 56% respectively for the 1/10 dosage. Only the lighter dosage gave healthy seedlings. The number of days of exposure did not seem to matter. The behavior of the orange berried form paralleled that of the red berried form except germination was lower. Seeds of the red berried form placed outdoors in December germ. 1% in April and an additional 2% in April a year later. Seeds of the orange berried form placed outdoors in December germ. 16% in April and an additional 25% the following April. All other treatments gave less than 1% germination over 2 y.

R. grossularia was reported to be a 40-70 germinator (ref. 22, Ch. 7). Although some germination can be obtained this way, outdoor treatment is better. Fresh seed germ. 40-70(19% in 1-12 w)-40-70(2%), none in 70-40-70, and 26% in April-May in outdoor treatment. Note that the 70-40-70 treatment is fatal.

R. lobbia seeds WC for 7 d germ. 70-40-70-40-70(30% in 1st w), 40-70-40(10%)-70(20%), and 55% in April 15 m after placing outdoors in December. Seeds DS 6 m at 70 in the dried berries and WC for 7 d germ. 70-40(30% in 8-12 w)-70-40 and 40-70-40-70(none). Treatment with GA-3 has not stimulated germination.

Robinia (Fabiaceae). *R. pseudoacacia* is one of the legumes where grinding a hole through the seed coast is essential for good germination. Seed so treated whether fresh or DS 6 m at 70 germ. 100% in 2-3 d when sown at 70. Sowing at 40 and DS 6 m at 40 germ. less than 50% because of increased rotting. Untreated seed did give some germination, but after 3 m it was still below 20%. Exposure of the seed to 20 and 40 minutes in water at 140 deg. F increased germination to 20% and 60% respectively, but the germination extended over 1-6 w.

Rodgersia (Saxifragaceae). Germination was predominantly at 70. DS seed of *R. pinnata*, *pinnata alba*, *pinnata superba*, and *sambucifolia* germ. 70(50-75%, ind. t 5 d, 13%/d for the *pinnata* and 21%/d for *sambucifolia*) and 40-70(12-15%). Sowing at 40 is harmful. *R. tabularis* behaved differently with DS seed giving 70-40(10%) and none at 40. A sample labelled *Astilboides tabularis* is presumed to be *Rodgersia tabularis*. However, its germination differed from the earlier sample and resembled more the germination of the first three *Rodgersias*. It germ. 70(50% in 4-10 d) and 40-70(13% in 3rd w).

Romanzoffia (Hydrophyllaceae). *R. sitchensis* germ. 70L(8% in 2nd w) and 70D(none). Another sample germ. in April from seed sown outdoors in March suggesting that this may be another species that germinates either under light or oscillating temperatures.

Romneya (Papaveraceae). *R. coulteri* germ. 70D GA-3(62% in 1-4 w) and none in 70D, 70L, or 40 using seeds that had been DS for 12 m. There have been some weird myths about germinating this species. The truth is that it is another cold desert plant that requires GA-3 for germination.

Romulea (Iridaceae). Both *R. bulbocodium* and *R. luthicii* germ. at 40 but not 70. J. Forrest reported that *R. hantamensis* germ. 96% in winter using his own fresh seed whereas fourteen samples of imported DS seed failed to give a single germination.

Rosa (Rosaceae). Germination occurs largely at 40 and extends in an erratic manner over several cycles. All seed was WC 7 d. Although the seed coat is hard, grinding a hole through it did not initiate germination. In view of the results with two of the four species, outdoor treatment should be tried on the other two.

R. amurensis germ. 2/33 in March from seed started outdoors the previous October. No other treatment gave any germination.

R. avchurensis germination was much extended. Seeds germ. 70-40-70(8% in 1-6 d)-40-70(5% on 5th d), 40-70(3% on 3rd d)-40-70(3% on 5th d)-40-70(18% in 1-4 d), and 7% in April and 3% the following November from sowing outdoors in October. Seed DS 6 m at 70 germ. 70-40-70(7%) and 40-70(1% on 3rd d)-40-70(24% in 1-15 d). Grinding a hole in the seed coat had no effect.

R. hybrid seed germ. 70-40(2/12)-70(1/12) and 40(4/12)-70-40(1/12).

R. multiflora germ. best in 40(26% in 5-7 w)-70(3%)-40-70. Germination is less in 70(8%)-40-70(3%)-40-70(3%) and less in seed sown outdoors (6% germ. in April). Seed DS 6 m at 70 or 40 was all dead.

R. virginiana germ. 70D-40-70D(80% in 2-8 d). Germination was not stimulated by GA-3.

R. webbiana did not germinate so that after 6 m the samples were shifted outdoors in January. These germ. 3/21 in April.

Roscoea (Liliaceae). *R. alpina* germ. 70(70% in 3rd w) and 40-70(100% in 10-12 d). Germination is hypogeal. The true leaf develops in 2nd w after germination.

Rosmarinus (Lamiaceae). *R. officinalis* germ. 21% in 1-5 w in either 70L or 70D, 40(25% in 3-12 w), and 34% in late April and early May in outdoor treatment.

Rubus (Rosaceae). *R. argutus* and *R. occidentalis* are native on the property, set fruit abundantly and self sow, but germination has been low.

R. argutus germ. 40-70(1%) using fresh seed. All other treatments have failed, but extended outdoor treatment needs to be tried.

R. occidentalis has germ. in only two treatments. In one the seed was collected in July 1989 and WC for 7 d. It was then DS for 6 m at 70 in the WC state, sown at 40, and shifted to outdoors on January 9 of 1991 (18 m after collection). This germ. 33% in April-May. The second was the same seed but sown outdoors immediately after WC. This seed germ. 3% the following April-May and an additional 29% the following April-May a year later. Seed DS 6 m at 70 and sown January 1 germ. 1/90 in June. Probably more will germinate with time. This is the first species to show the need for two winters outdoors. All other treatments failed with *R. occidentalis* including light and GA-3. The seedlings open their cotyledons within 2 w of germination.

R. odoratus germ. 1/3 in 70L and none in 70D with or without GA-3 treatment. The sample was so small that there is no assurance that there were viable seeds in all treatments.

R. parviflorus germ. 70 GA-3(25% in 4-7 w), 70D(none), and 40-70D(6%). Eugene Zielinski communicated that it germ. in April in outdoor treatment.

Rudbeckia (Asteraceae). *R. hirta* hybrids germ. 90-100% under all treatments. Germination at 70 was in 6-8 d and germination at 40 was much slower occurring in 3-12 w and sometimes germination ran over into the following cycle at 70.

Ruellia (Acanthaceae). *R. humilis* requires either a period at 40 or GA-3 to effect germination at 70. Using the 40-70 procedure, the maximum 100% germination is achieved only if the time at 40 is 14 w. Shorter and longer times at 40 give reduced germination. For times at 40 of 0, 4, 6, 8, 10, 12, 14, 18, and 22 weeks the respective percent germinations on shifting to 70 were 0, 2%, 6%, 27%, 29%, 47%, 100%, 75%, and 88%. Germination is complete in 2-5 d after the shift to 70. Fresh seed and seed DS 6 m at 70 gave similar results. With GA-3 germination is 71% in 5-9 d at 70. Without the GA-3 treatment, sowing the seed at 70 is detrimental as shown by 70(4%)-40-70(17%) for fresh seed and 70-40-70(2%) for seed DS 6 m at 70 or 40.

Rumex (Polygonaceae). *P. obtusifolius* requires light, GA-3, or outdoor conditions for germination. Seeds germ. 70L(89% in 7-12 d), 70D with GA-3(10% in 5-12 d), 70D(none), 40-70L(6/ in 6- d), and 40-70D(none). Seeds placed outdoors in November germ. 50% in April.

Sabal (Palmaceae). *S. minor* was reported to be a 40-70 germinator (J H).

Sabatia (Gentianaceae). *S. kennedyana* germ. 70(42% in 2-5 w)-40-70(30% in 6-8 d) and none at 40 even after 3 cycles showing that sowing at 40 is fatal.

Salix (Salicaceae). *S. cascadiensis* germ. 70L(4/18 in 1-3 w), 70D(all rotted), and 40-70L(9/19 in 5-8 d). Most of the ungerminated seed in 70L or 40-70L remained green and photosynthesizing for an additional month but failed to develop a radicle or open the cotyledons and ultimately rotted.

Salpiglosis (Solanaceae). *S. hybrids* germ. 70(100% in 2nd w) and 40(100% in 7-9 w). Light or GA-3 had no effect.

Salvia (Lamiaceae).

S. argentea germ. 70L(16% largely in 1-2 d), 70D(4%), 40(6% in 7-9 w)-70(2% in 2nd d), and 1% in outdoor treatment.

S. candidissima germ. 70L(59% in 3-14 d), 70D(43% in 3-14 d), 40-70(none), and 58% in outdoor treatment.

S. cyanescens germ. 70L(11% in 3-14 d), 70D(2%), 40(4% in 4-8 w)-70(18% in 2-10 d), and 26% in outdoor treatment.

S. dumetorum germ. 70(30% in 1-6 d), 40(7% in 3-8 w)-70(8% in 2-10 d), and 21% in outdoor treatment. Light had no effect.

S. glutinosa germ. 70L(22% in 8-9 d), 70D(12% in 12-15 d), 40-70(26% in 4-7 d), and 27% in outdoor treatment.

S. hians germination may be promoted by light. Seeds germ. 70L(3/12 in 5-6 d), 70D(none), and 40-70D(1/3).

S. huberi germ. 40(10% in 7th w), 20% in outdoor treatment, and none in 70D or 70L.

S. moorcroftiana germ. best with seed DS 6 m at 70 in 70(59% in 2-6 d) and 40(60%)-70(1%)-40-70. Fresh seed gave a more extended germination as shown by 70(29%)-40-70(10%)-40 and 40(10%)-70(26%)-40(4%)-70(2%). Seed DS 6 m at 40 gave an intermediate behavior. The data indicates a D-70 pattern, and it is possible that longer DS would have given higher germination.

S. officinalis (sage) germ. 92% in 5-12 d in either 70L or 70D, 40(74% in 5-12 w), and 94% in April in outdoor treatment.

S. repens germ. 70(60% in 2-12 d), 40(46% in 2-6 w)-70(none), and 40% in March in outdoor treatment.

S. sclarea (60 cm. form) germ. 70L(46% in 2-12 d), 70D(31% in 2-12 d), 40(1%)-70(2%), and 40% in outdoor treatment.

S. sclarea (180 cm. form) germ. 70L(61% in 2-6 d), 70D(43% in 2-7 d), 40(41% in 7-12 w)-70, and 27% in outdoor treatment.

Sambucus (Caprifoliaceae). *S. canadensis* germ. 70D GA-3(85-90% in 2nd w). This was a remarkable discovery because all other treatments had failed to germinate a single seed in 2-3 y. It is likely that *S. canadensis* requires fungal products for germination under natural conditions. The seedlings were healthy and vigorous. Seeds were WC for 7 d. A variety of prior treatments had no effect on germination in 70D GA-3. There is a report in the literature that *S. canadensis* is a 40-70 germinator (ref. 18, Ch. 10). This must be in error. *S. racemosa* was also found to germinate only with GA-3 and germ. 70D-40-70 GA-3(2/8 in 8th w). Large samples of *S. pubens* failed to germinate and GA-3 needs to be tried on this species.

Sandersonia (Liliaceae). *S. aurantiaca* germ. 70L(1/6 in 4th w) and none in other treatments despite the seed remaining firm through many cycles.

Sanguinaria (Papaveraceae). *S. canadensis* germ. 62% in October from seed sown in July. After the radicles developed to a length of two inches, they began to rot and all the seedlings ultimately perished. Other treatments gave less than 2% germination and again the seedlings died. DS is fatal. This species self sows here, but the critical factors are a mystery. A report in May 1993 Horticulture that fresh seed germinates immediately at 70 is entirely contrary to the experience here.

Sanguisorba (Rosaceae).

S. minor germ. 90% in 3-6 d in either 70L or 70D and 87% in 4th w at 40.

S. officinalis germ. 70L(45% in 2nd w), 70D(15% in 2nd w), 70 GA-3(36% in 2nd w). Data are for only the first six w.

Saponaria (Caryophyllaceae). *S. caespitosa* germ. best with seed DS 6 m at 70 or 40 in 40(87% in 9-12 w). Germination was low and extended in all other treatments as shown by 70(1%)-40(1%)-70 for DS seed and 70-40(14%)-70(19%)-40(1%) and 40(4%)-70(2%)-40(9%)-70(1%) for fresh seed.

Sarracenia (Sarraceniaceae).

S. alabamensis germ. 40-70L(86% in 2-4 w), 40-70D GA-3(94% in 3rd w), 40-70D(23% in 5th w), 70D GA-3(5%)-40-70(47% in 4th w), 70L-40-70L(10%), and 70D-40-70D(2%). Seedlings from GA-3 treatment were normal. The seedlings are very cute and send up their first tiny pitcher within a month.

S. flava germ. 40-70L(1/21 in 2nd w), 40-70D GA-3(2/10 in 4th w), 70D(none), 70D GA-3(none), and 70L(none). The pattern appears to be like *S. alabamensis*.

S. purpurea was subjected to four dark cycles before being placed in 70L where it germ. 6%. Obviously 40-70L and GA-3 should have been tried.

S. sp. germination was reported by Larry Mellichamp of the Univ. of North Carolina at a meeting of the Am. Rock Garden Soc. Seeds were sown at 35 and samples shifted to 70 every week. Germination maximized with seed kept the full 10 w at 35 and significant germination did not occur until after exposure to 7 w at 35. It seems likely in view of my results with *S. alabamensis* that the seeds were exposed to light after the shift to 70. The rates of germination followed first order kinetics.

Sarcoccca (Buxaceae). *S. saligna* seed was collected in midwinter, WC, and sown at 70. Germination was 70(4/6 in 14-16 d).

Sassafras (Lauraceae). *S. verifolium* has failed to germinate under a variety of treatments despite the fact that the seed was wild collected and contained a normal sized seeds on opening the seed coats.

Satureia (Lamiaceae).

S. discolor germ. in 3rd w at 70.

S. hortensis germ. 100% in 2-4 d in either 70L or 70D, 100% in the 3rd w at 40, and 100% in late March in outdoor treatment.

S. vulgaris required light or GA-3 for germination. Seeds germ. 70L(48% in 1-8 w), 70D GA-3(54% in 2nd w), 70D(none), 40(6%)-70L(80% in 4 d-3 w), and 40(6%)-70D(2%) using either fresh seeds or seeds DS 6 m at 70.

Saxifraga (Saxifragaceae). The stimulation of germination by GA-3 in *S. oppositifolia* and the stimulation by light in other species suggest that GA-3 and light should be tried on all species in this genus.

S. caesia germ. 70D(1/19 in 6th w).

S. flagellaris germ. 70-40-70(62%) and 40(4%)-70.

S. hirculus germ. 40(2/10 in 2nd w) and none at 70.

S. hostii germ. in April from seed sown outdoors in January.

S. latioptalata germ. in 5th w at 70.

S. aff. nanella germ. 70L(2/11 in 2nd w) and none in 70D, 40-70D, or 40-70L.

S. oppositifolia germ. 70D GA-3(75-80% in 3rd w), 70L(12% in 3rd w), and 70D(6% in 3rd w). A prior 4 w in 70D or 70L had no effect. The seedlings from GA-3 treatment were etiolated and survival was low, and this needs more study.

S. paniculata germ. 70D or 70L(60% in 2-4 w), 40-70L(25% in 4th w), and 40-70D(none) using seed DS 6 m at 70. Fresh seed germ. 70(23% in 4th w) and 40-70D(none).

S. sp. Nepal germ. 70L(2/3 in 3rd w) and 70D(none). The sample in 70D was shifted to 70L after 4 w whereupon 1/4 germ. in 3rd w.

S. spinulosa germ. 70L(50% in 3rd w) and 70D(none).

S. tricuspidata germ. in 2nd w at 70.

Scablosa (Dipsacaceae). *S. caucasica* germ. 70(50% in 1-4 w).

Schisandra (Schisandraceae). *S. chinensis* germ. 40-70(2/2 in 2-6 d) and 70-40-70(0/2). The seeds swell and show signs of germinating near the end of the cycle at 40. The two cotyledons are slow to develop.

Schizanthus (Solanaceae). Both species had germination inhibited by light. The survival benefits of this are discussed in Chapter 11. The commercial hybrids did not show this behavior.

S. grahamii germ. 70D(41% in 2 d-6 w) and 70L(none). The seeds in 70L were shifted to 70D after 4 w whereupon 3% germ. showing that even such a short treatment in 70L was fatal. A prior 3 m at 40 is also deleterious with one sample failing to give any germination on shifting to 70D and the other giving 14% germination in 3-5 w at 40 and no further on shifting to 70D. The above data is on seed that had been DS for 4 m at 40. An additional two samples were received that had been DS at 40 for 6 m. These germ. 70D(30%) and 70L(7%) and 70D(18%) and 70L(2%) respectively. Although the differences between 70D and 70L were not as large, it was still evident that light inhibits germination. It is possible that the effect of light could gradually disappear on further DS, but this was not tested. For optimum germination the seeds should either be buried a half an inch to insure being in the dark or the seeds should be germ. in towels in the dark and planted as soon as they germinate.

S. hookeri germ. 70D(57% in 2-14 d) and 70L(none). The seeds in 70L were shifted to 70D after 4 w whereupon 27% germ. on the 8th d. The seeds also germ. 40(25% in 3rd w). Like *S. grahamii* the seed is deteriorating both in 70L and at 40, although not as fast as with *S. grahamii*. The above data is for seeds DS 3 m at 40. A second sample that had been DS for 6 m at 40 germ. 70D(63%) and 70L(3%) confirming the inhibitory effect of light.

S. hybrids Disco germ. 80% in 3rd w in either 70D or 70L and 40(80% in 7th w). Treatment with GA-3 was fatal.

Schoenolirion (Liliaceae). *S. bracteosa* germ. 40(9/9 in 7-10 w) and 70D-40(8/9 in 9th w).

Sciadopitys (Pinaceae). *S. verticillata* germ. 53% in 1-9 w in either 70L or 70D and 40-70(75% in 10th w). This agrees with a report in the literature (ref. 22, Ch. 7). A peculiar result was that 40% of the seedlings lacked chlorophyll although the cotyledons developed to normal size. The remaining seedlings were healthy in every respect. Seeds started in outdoor treatment in December (same starting time as the other treatments) did not start to germinate until July and germ. 97% in July and August. This result is similar to the 40-70 treatment. A tree of this species sets many cones and fat seeds, but as has been noted by others, seeds from isolated trees are usually not viable despite their promising outward appearance.

Scilla (Liliaceae).

S. bifolia germ. best with seed DS 6 m at 70 in 40(70% in 2-4 w)-70(6%)-40(2%). The seedlings must remain at 40 for the full 3 m cycle. If shifted to 70 too quickly, the cotyledons fail to develop. Curiously, germination failed completely if the DS seed were sown at 70. Fresh seed gave a different pattern and a more extended germination as shown by 70-40(64%)-70(21%)-40-70(2%)-40-70(2%) and 40-70(1%)-40(76% in 2-4 w)-70(2%). Seed DS 6 m at 40 gave an intermediate behavior as shown by 70-40(34%)-70(11%)-40-70 and 40(52%)-70(22%)-40-70.

S. campanulata germ. best in 70-40(60-75% in 3-11 w). Germination was the same for fresh seed or seed DS 6 m at 70 or 40. A prior 3 m at 40 not only gave lower germination, but germination extended over 3 cycles as shown by 40(7%)-70-40(70%)-40 for fresh seed and 40(7%)-70(5%) for seed DS 6 m at 70 or 40.

S. hispanica germ. best in 40(32% in 10th w) using fresh seed. Germination is hypogeal. The seedlings need to be kept at 40 for 1-2 m after germination and until the true leaf starts to emerge in order to get proper development on the shift to 70. Germination failed completely for fresh seed sown at 70 or for seed DS 6 m at 70 or 40 sown at either 70 or 40.

S. natalensis was reported by James Forrest to germinate immediately from his own fresh seed whereas imported DS seed always failed.

S. rosenii germ. best in 40(15%)-70(20%)-40(50%). Cotyledons developed in 7 d after the germination in the 3 m cycle at 40 and the shift to 70.

S. scilloides germ. 70(99% in 4-8 d) and 40(86% in 6-8 w).

S. sibirica germ. best in 70(22%)-40(65%) or 40(58%)-70(3%)-40(24%). Seed DS 6 m at 40 germ. well although two samples gave different behavior, 70-40(53%)-70(12%) and 40(38%)-70(1%)-40(21%) for one sample and 70(60%)-40(25%) and 40-70(7%)-40(70%) for the other. Seed DS 6 m at 70 germ. less as shown by 40(11%)-70-40(31%)-70(2%) and none when sown at 70. The seed deteriorates in DS.

S. tubergeniana germ. 70-40(100% in 3-5 w) and 40(80% in 8-12 w) using DS seed. Light had no effect on germination.

Scleria (Poaceae). See Chapter 22

Scoliopus (Liliaceae). *S. bigelovii* germ. best in 70-40(47% in 12th w) and none when started at 40 even after a year of alternating cycles. Such seed remained firm and unrotted. Light had no effect. The radicle forms at 40, and the cotyledon develops in the first w after the shift to 70. Seed DS 6 m at 70 all rotted. Seed DS 6 m at 40 germ. 70-40(50%), but the seedlings looked weak.

Scutellaria (Lamiaceae). The seven species studied all germinated in 6-9 d at 70 in the following percentages: *S. adenostegia* 70%, *S. haematochlora* 37%, *S. intermedia* 20%, *S. microdasys* 14%, *S. pontica* 20%, *S. rubicunda* 50%, and *S. subcaespitosa* 29%. Light had no effect. A preliminary 3 m at 40 had little effect on the germination at 70 of *S. adenostegia* and *S. intermedia*, but it lowered the germination of *S. haematochlora*, *S. intermedia*, and *S. microdasys* to 0-10%. Outdoor treatment gave no advantage and seed placed outdoors in January germ. in March. Germinations for the first four and the last species were 10%, 30%, 60%, 15%, and 0% respectively. *S. novae-zealandiae* germ. 70D(1/10 in 5th w).

Securinega (Euphorbiaceae). *S. suffruticosa* germ. 30-40% on the 10th d in either 70L or 70D and 40-70(61% in 5-11 d). Ungerminated seed rotted within 2 w.

Sedum (Crassulaceae). All *Sedums* tolerated DS and germ. largely at 70. Germination in *S. pilosum* and *S. pulchellum* was promoted by light.

S. kamschaticum germ. 70(50-90% in 1-4 w) and 40-70(1-5%) using fresh seed or seed DS 6 m at 70 or 40.

S. lanceolatum germ. 70(30-40% in 1-8 w) and 40(3%)-70(56% in 1-10 d) using seed DS 6 m at 70 or 40. Fresh seed germ. less in 40(13%)-70(53%) and even less and more extended when sown at 70 indicating that the species is D-70.

S. pilosum is monocarpic and exists as a self sowing colony here. The only germination so far was 70L(2/18 in 2nd and 4th w). Both 70D and outdoor treatment failed using both both fresh seed and seed DS 6 m at 70. GA-3 has not yet been tried.

S. pulchellum germ. 70L(100% in 2nd w) and 70D(5%) using seeds DS for 6 m at 70 or 40. Germination on fresh seeds was not tested.

S. spectabile germ. 70(90-100% in 1-6 d) and 40(90-100% in 2-4 w) using seed DS 6 m at 70 or 40 and 70(90% in 2-12 d) and 40(75%)-70(25%) using fresh seed.

S. stelleforme germ. 70(100% in 3-5 d). Light and GA-3 had no effect.

S. subulatum germ. 70(30% in 11-20 d) and 40(5%)-70(10%). Seed sown outdoors in November germ. 22%, partly in November and partly in February during a warm spell.

S. telephioides germination was promoted by light and GA-3. Seeds germ. 70D GA-3(100% in 10-19 d), 70L(24% in 1-4 w), 70D(5%), 40-70L(20% in 2nd w), and 40-70D(none) for either fresh seeds or seeds DS 6 m at 70.

Selinus (Apiaceae). *S. tenuifolium* germ. 70(30%)-40-70 and 40(8%)-70(2%)-40(1%)-70(1%) using seed DS 6 m at 70 or 40. Fresh seed gave lower and more extended germination; 70(10%)-40(9%)-70(22%)-40(2%)-70(3%) and 40-70-40(14%)-70-40-70(1%).

Sempervivum (Crassulaceae). *S. sp.* germ. 70L(20% in 1-3 w), 70D(1%), 40-70L(1%) and 40-70D(none).

Senecio (Asteraceae). *S. harbouri* and *S. holmii* germ. 70D(100% in 5-7 d) and 40(100% in 6-9 w). *S. nudicaulis* germ. 25% in 3-6 d in 70L or 70D and 25% in 4-6 w at 40.

Sequoia (Pinaceae). *S. gigantea* was reported to be a 40-70 germinator (ref. 44, Ch. 7).

Sequoiadendron (Pinaceae). *S. giganteum* germ. 70D(22% in 2-4 w) and 40(none). GA-3 had no effect.

Shortia (Diapensiaceae). *S. galacifolia* requires exogenous chemicals for germination. Seeds germ. in 70L in New Jersey Pine Barren Sand and in 70D or 70L when treated with GA-3. The data for the New Jersey Sand are presented in Chapter 12. The exogenous stimulant in the sand cannot be GA-3, because the substance in the sand stimulated germination only in 70L whereas the GA-3 stimulated germination in either light or dark with germination in 70D(60% in 3rd w) being significantly greater than the germination in 70L(12% in 3rd w). The seedlings from GA-3 treatment appeared to be normal. There must be much complexity to the chemistry of these interactions. The seeds die quickly under moist or dry non-germinating conditions.

Sibbaldia (Rosaceae). *S. procumbens* germ. 70L(67% in 3-5 d), 70D GA-3(52% in 5-11 d), and 70D(14% in 7-9 d).

Sicyos (Cucurbitaceae). *S. angularis* seeds WC for 2 w and placed outdoors in October germ. 64% in April. Seed DS 6 m at 70 and placed outdoors in March germ. 13% in April. All other treatments germ. under 10% indicating that outdoor treatment is required.

Sideritis (Lamiaceae). *S. hyssopifolia* germ. 70(82% in 3-4 d) and 40(20% in 12th w)-70(27% in 4-6 d). Light had no effect.

Silene (Caryophyllaceae). While many *Silene* germ. at 70 like typical Caryophyllaceae, complex patterns and photoeffects were found in some species. DS seed of the following species germ. in 2-5 w at 70: *S. acaulis*, *californica*, *ciliata*, *compacta*, *douglasii*, *elizabethae*, *guntensis*, *hookeri*, *keiskii*, *nutans*, *pusilla*, *saxatilis*, *saxifraga*, and *vallesia*.

S. agraea germ. 70(44% in 3-4 d) and 40(75% in 5th w)-70(10%).

S. armeria germination was affected by both light and DS. Seeds DS 6 m at 70 germ. 70D or 70L(75% in 2-4 d), 40(12%)-70L(20%), and 40(12%)-70D(1%). Fresh seed germ. 70L(70%), 70D(10%) and none in 40-70L and 40-70D.

S. caroliniana germ. in April from seed sown outdoors in January.

S. dioica germ. 70(32%)-40(2%)-70(6%) using fresh seed.

S. laciniata germ. 70D(81% in 3-9 d) and 40-70(53% in 2-15 d). Light and GA-3 had no effect.

S. pendula germ. 70D(100% on 3rd d). Light and GA-3 had no effect.

S. pennsylvanica seed collected in June and placed outdoors germ. 1% in August and 37% in March and April. Seeds DS 6 m at 70 and placed outdoors in February germ. 20% in March and April. All other treatments gave germinations under 5% after many cycles. Oscillating temperatures are required.

S. ruprechtii germ. 70(28% in 3-7 d)-40-70 and 40(4%)-70.

S. polypetala germ. at 70 but only after 3 m.

S. regia germ. at 70 but only after 3 m. Jan Midgley (MD) reported 95% germination in 2-10 d at 70 if the seed were first put outdoors in January for 3 w.

S. schafta germ. 70(9%)-40(18%) using fresh seed. Fresh seed sown at 40 and DS seed sown at either 70 or 40 germ. only 0-3%. Photoeffects should be studied.

S. sp. Kashmir germ. 70(36% in 4-9 d)-40-70(57% in 2-4 d).

S. virginica germ. 70-40-70(2%)-40-70 and 40(2%)-70 with fresh seed and 40(3%)-70(2%) with seed DS 6 m at 40. Other treatments gave no germination. Photoeffects should be studied.

Sisyrinchium (Iridaceae). Light and outdoor conditions should be tried.

S. angustifolium germ. 70L(40% in 6-9 w), 40-70L(15%), and none in 70D or 40-70D. GA-3 did not stimulate germination.

S. bellum placed outdoors in September germ. 2/4 in November 14 m later.

S. campestre placed outdoors in June (fresh seeds) germ. 10% in April and 25% the next April (22 m later). Seeds DS 6 m at 70 and placed outdoors in December germ. 26% in the April 16 m later. Other treatments including light and GA-3 gave germinations less than 0.5%.

S. demissum album germ. 70L(15% in 1-4 w), 40-70L(57% in 2nd w), and none in 70D and 70 GA-3.

S. inflatum germ. 40(70% in 8th w) and none in 70D or 70L.

S. mulcronatum seeds placed outdoors in January germ. 30% in April. None germ. in other treatments including light and GA-3, but the expts. are only 6 m old.

Skimmia (Rutaceae). *S. japonica* collected in May and WC germ. 70(21% in 12-15 d) and 40(28% in 3-8 w). The seed that did not germinate rotted quickly suggesting internal infection. The seedlings produce only the two cotyledons in the first year.

Smilacina (Liliaceae). *S. racemosa* germ. 40-70(90% in 4-11 w) and 70-40-70(5%) using seed DS 6 m at 70 or 40. Fresh seed ultimately germ. 50-82%, but germination was much extended as shown by 40-70(25%)-40-70(25%) and 70(10%)-40-70(14%)-40-70(3%)-40-70(55% in 4-6 w). Both DS and fresh seeds germ. far better when sown at 40 with DS seed best. Germination is hypogeal. The radicle was allowed to develop to its full three inches at 70. Shifting to 40 for 4 m and back to 70 caused stems and leaves to develop in 25% of the seedlings, but the remaining 75% did not develop and most of these ultimately died by rotting of the terminal bud. More work is needed in determining conditions for destroying the growth inhibitors in the terminal bud. Treatment with GA-3 blocked germination.

Smilax (Liliaceae).

S. ecirrhata is difficult to germinate and many samples remained firm and unrotted through several years of moist treatments. The only significant germinations were with seeds DS for 6 m at 70 or 40, given a year of alternating cycles moist, and placed outdoors in April. Germination took place in June to the extent of 20-70% in four separate samples. A three inch radicle with branching rootlets formed, but a variety of treatments involving various cold, warm, and outdoor cycles have not as yet induced formation of stem and leaves even after 18 m. The best recommendation at present is to plant these germinated seeds outdoors. Why the germinations occurred so reproducibly in June is a further puzzle. It is possible that temperatures significantly above 70 are needed for germination. GA-3 did not stimulate germination.

S. ferox germ. 70L(2/2 in 13th w), 70D(2/3 in 16th w). and 40-70-40(2/4 in 4th w)-70-40-70(1/4). A true leaf (hypogeal) developed 4 w after germination.

Solanum (Solanaceae).

S. dulcamara germination was complex. The length of time for the WC was a factor and seeds WC for 7 d, 12 d, or 4 w germ. 70L(55% in 2-5 w), 70L(93% in 2nd w), and 70L(97% in 2nd w) respectively. None germ. in 70D, but seeds WC 7 d germ. 70D GA-3(86% in 1-3 w). The requirement of light for germination is largely eliminated by either DS or 3 m at 40. Seeds WC for 12 d or 4 w germ. 40-70L(100% in 2-4 d) and 40-70D(60%), and seeds DS for 6 m at 70 germ. 70L(98% in 3-10 d) and 70D(43% in 2-4 d). Outdoor treatment was in effect like a prior 3 m at 40 and 98% germ. in spring. DS for more than 6 m might have removed the photoresponse completely.

S. melongena is the eggplant. Commercial seeds germ. 70L(100% in 2-8 d), 70D GA-3(94% in 1-5 w), 70D(50% in 1-5 w), 40-70(75% in 4th w), and 40 (GA-3)-70(60% in 4-8 d). Both light and GA-3 showed small effects.

Soldanella (Primulaceae).

S. montana germ. in 3rd w at 70.

S. hungarica germ. 70(100% in 2nd w) and 40(4%)-70(68% in 3rd w). Light had no effect.

Solidago (Asteraceae).

S. caesia is a 40-70 germinator for fresh seed and a D-70 germinator for DS seed. Fresh seed germ. 70(5%)-40-70(95%) and 40-70(100%). Seed DS 6 m at 70 or 40 germ. 70(100%, ind. t 4 d, 11%/d) and 40(6%)-70(94% in 2-13 d).

S. canadensis collections contained great amounts of chaff. Seed DS 6 m at 70 or 40 germ. in 2nd w at 70. All other treatments germ. none.

S. spathulata germ. 70(100% in 3-9 d) and 40(100% in 7-12 w). It is likely that DS was beneficial if not necessary.

Sophora (Fabiaceae).

S. japonica seed was collected November 1. It was still soft and green, and it was feared that it was immature. However, the seed pods were soaked and washed in water for several hours to remove the seed capsule and the sticky syrup covering the seed. This washed seed germ. 70(100% in 6-20 d). Without the washing the seed germ. 70(6/10 in 10-12 d) and 40-70(6/12 in 1-2 d) showing that the washing was advantageous. If the seed is DS at 70 for 3 m, the seed coat becomes impervious. Now it germ. 100% in 3-6 d, but only if a hole had been ground through the seed coat. Untreated seed germ. only 1/15 in 3 m.

S. moorcroftiana germ 70(1/1 in 4th w).

Sorbus (Rosaceae).

S. aucuparia requires oscillating temperatures. Fresh seeds placed outdoors in November germ. 80% in March and April. Seeds DS 6 m at 70 and placed outdoors in May germ. 80% the following April. All other treatments gave under 1% germination. *S. aucuparia* was reported to be a 40-70 germinator (ref. 31, Ch. 7) and Nikolaeva (ref. 7, pp. 41-44) reported that all species are 40-70 germinators. My results are not in agreement with these literature claims, and I wonder if the other workers had used outdoor conditions, and when the seeds germ. in spring, they assumed it had been a 40-70 pattern. Treatment with GA-3 was tried with little effect. Sterile clones of *S. aucuparia* are extensively planted here. These set vast numbers of orange fruit none of which contain seed.

S. caucasica germ. 40-70(3/5 in 2nd w) and 70D(all rotted). Light or GA-3 did not stimulate germination.

Sphaeralcea (Malvaceae). It is likely that all species would have germ. in a few days at 70 if a hole had been made in the seed coat. This was tested only with *S. parvifolia*.

S. coccinea seed DS 6 m at 40 germ. 70(1/2 in 4th w) and 40-70(1/3 on 1st d). Both fresh seed and seed DS 6 m at 70 failed to germinate.

S. grossolariaefolia germ. 70(1/3 on 9th d) and 40(1/2 on 12th d).

S. parvifolia germ. 70(100% on the 2nd d) if a hole was ground through the seed coat. Untreated seeds germ. 70(4%)-40-70(4%) and 40(4%).

Spigelia (Loganiaceae). *S. marilandica* germ. 1/3 in May from placing outdoors February 1. Other treatments failed, but the samples were small. Germination is hypogeal.

Spiraea (Rosaceae). Some required light.

S. alba germ. 70D(100% in 2nd w) and 40-70(100%) using seed DS 6 m at 70. Fresh seed germ. 70-40-70(a few) and 40-70(100%).

S. betulifolia requires light for germination. Fresh seed or seed DS 6 m at 70 germ. 70L(100% in 1-4 w), 70D(1%), 40-70L(100% in 1-4 w), and 40-70D(none).

S. canescens germ. 70D or 70L(100% in 3rd w) and 40(6%)-70(70%).

S. japonica requires light for germination. Fresh seed or seed DS 6 m at 70 germ. 70L(100% in 3rd w), 70D(none), 40-70L(100% in 1-3 w), and 40-70D(none). Seed DS 6 m at 70 germ. in the same pattern, but the percentages were much lower.

Spraguea (Portulacaceae). *S. umbellata* germ. best in 70D-40-70L(90% in 5-6 d) and less in 70L(1/4)-40-70L(2/4), 70D(10%)-40-70D(25%), and 2/9 in outdoor treatment. This is an unusual behavioral pattern.

Stachys (Lamiaceae). *S. macrantha* requires outdoor treatment. Seeds DS for 6 m at 70 placed outdoors on March 1 germ. 31% in April and 14% the following December-March. Other treatments gave less than 5% germination.

Stanleya (Brassicaceae). *S. pinnata* germ. 50-100% in the first cycle in all procedures with DS seed. Germination at 70 occurred in 4-7 d and germination at 40 occurred in 5-8 w. Light had no effect.

Stellaria (Thymelaceae). *S. chamaejasme* germ. 50% over 3 cycles whether started at 70 or 40 using seeds DS 6 m at 70 or seeds DS 2 y at 40.

Sternbergia (Amaryllidaceae). *S. candida* was received in March in a DS state. After 18 m in alternating cycles between 40 and 70, the three seeds were placed outdoors in October whereupon 2/3 germ. in the 4th w. More studies are needed, but the meagre data do suggest that oscillating temperatures are needed.

Stewartia (Theaceae). Germination occurs only under the oscillating temperatures of outdoor conditions. *S. koreana* sown outdoors in January germ. 1/12 in April and 1/12 in March over a year later. *S. pseudocamellia* sown outdoors in October 1990 germ. 6/10 in March 1992 over a year later. The seedlings develop cotyledons and grew strongly.

Stipa (Poaceae). See Chapter 22

Stokesia (Asteraceae). *S. laevis* germ. at 70.

Strangweia (Liliaceae). *S. spicata* germ. exclusively at 40 as shown by 40(2/2 in the 4th w) and 70-40(3/3 in 3rd w). The germ. seeds can be shifted immediately to 70 whereupon they produce a true leaf (hypogeal) in a few weeks.

Stylophorum (Papaveraceae).

S. diphyllum germ. best in 40-70-40(4%)-70(65%, ind. t zero, 36%/d, exact zero order) and less in 70-40-70(10%)-40-(2%)-70(2%). All DS seed was dead. This one of the rare four cycle germinators, and it is remarkable that the germination fit zero order kinetics so exactly after three cycles.

S. lasiocarpum sown outdoors in June germ. the following April.

Styrax (Styracaceae).

S. japonica germ. 70-40-70-40-70(60% in 2-6 d). The seeds that germ. split in the previous cycle at 40. The seedlings develop their cotyledons in 2-3 w after germination and grow on strongly. There were two remarkable features of this germination. Exactly the same rate and the same percentage germination occurred in seeds that been filed throught the tip, filed through the base, and sawn through the side showing conclusively that producing a hole in the seed coats had no effect. Germination had not occurred after two years of outdoor treatment. Presumably germination will ultimately occur because the species self sows abundantly here.

S. obassia germ. 40(1/7)-70(2/7 in 5-7 d).

Swertia (Gentianaceae). *S. fedtschenkoana*, *marginata*, and *shugnanica* gave a few germinations in spring after being 6-18 m outdoors.

S. perennis germ. 70(6% in 3rd w) on a small sample. Light had no effect.

Symphoricarpos (Caprifoliaceae). *S. orbiculata* germ. 40-70-40-70(1/13)-40(1/13)-70(5/13)-40(1/13)-70(1/13) using fresh seeds WC for 7 d. Seed WC and DS 6 m at 40 germ. 70-40(3/9)-70(1/9)-40(2/9)-70-40. Seeds DS 6 m at 70 were dead.

Symphyandra (Campanulaceae).

S. hoffmannii best in 70-40-70(56% in 2nd w) and less in 40-70(9%) using seeds DS 6 m at 40. Germination was also less in 70(16%)-40-70 and 40(3%)-70(6%) using seeds DS 6 m at 70 and 70(6%)-40-70(14% in 3rd w) and 40-70(14%)-40-70 using fresh seeds.

S. tianschanica germ. 70(90% in 7-12 d) and 40(60% in 6-12 w).

S. wanneri germ. in 4th w at 70.

Symplocarpus (Araceae). *S. foetidus* germ. 40-70(60% in 1-3 w)-40-70(8%) using fresh seeds WC for 7 d. Only roots developed at 70. The seeds act like small corms and roots develop from the top and turn down as in a mature plant. On shifting to 40 for 3 m and back to 70 vigorous root development commenced and some leaf development. It is suspected that leaf development would have been more vigorous at lower temperatures. Seeds started at 70 did not germinate over six cycles. At the end of the 6th cycle, half of the seeds were shifted to 70L whereupon 3/6 germ. in 3rd w (however they did not develop normally). The whole problem of photoresponse and optimum T for development of leaves must be reinvestigated. Seeds DS 6 m at 70 or 40 failed to germinate, although the seeds remained firm and unrotted for a number of cycles.

Synthyris (Scrophulariaceae). *S. pinnatifida* germ. 70(3%)-40(17% in 5-10 w)-70(6%) and 40(8%)-70(5%)-40-70(11% in 4th d).

Syringa (Oleaceae).

S. amurensis germ. 70(90%, ind. t 35-45 d, 4%/d) and 40-70(25-60%) using fresh seed or seed DS 6 m at 70 or 40. Curiously seed sown outdoors in December when collected germ. none, again showing that sowing at 40 is detrimental.

S. pekinensis germ. 70(65% in 6-12 d) and 40(69% in 8-11 w).

S. vulgaris seed was collected late in November. Fresh seed germ. 70(90%, ind. t 7 d, 6%/d)-40(4%)-70(2%) and 40-70(97%, ind. t 2 d, 5%/d). Seed DS 6 m at 40 germ. 70(89%) and 40(44%)-76(32%), and seed DS 6 m at 70 germ. 70(67%) and 40(32%)-70(29%) which shows some deterioration on DS.

Talinum (Portulacaceae). Sowing at 40 was better than sowing at 70.

T. calycinum germ. 40-70(17% and 50%, 2 samples, in 2-10 d) and none at 70..

T. okanoganense germ. 40(48% in 10-12 w)-70(36% in 2-16 d) and none at 70..

T. spinescens germ. 70(9%)-40-70(2%) and 40(2% in 10-12 w)-70(10%).

T. sp. 12" germ. 40-70D(12% in 2nd w) and none in 70D, 70L, or 70 GA-3.

T. teretifolium required both light and a prior 3 m at 40 for fresh seed as shown by 70L(1%), 70D(none), 40-70L(47% in 3-5 d), and 40-70D(1%). Seed DS 6 m at 70 germ. 70L(27% in 2nd w), 70D(none), 40-70D(5%), and 40-70L(90% on 4th d).

Tamus (Dioscoreaceae). *T. communis* germ. 70-40(2/9 in 11th w)-70(2/9 on 6th d). Germination is hypogeal.

Tanacetopsis (Asteraceae). *T. subsincks* germ. in 4th w at 70.

Tanacetum (Asteraceae).

T. capitatum germ. 70(100% in 5-9 d) and 40(100% in 4-8 w).

T. dolichophyllum germ. 70(100%, ind. t 3 d, 30%/d) and 40-70(100% in 2-6 d).

T. gracile germ. 70(70% in 3-9 d)-40-70(10%)-40-70(3%).

T. sp. (coll. by J. Halda in Tadzhikistan) germ. 70D(8/8 on 4th d).

Taraxacum (Asteraceae). *T. officinale* germ. 70(76% largely in 3-5 d) for fresh seed, 70(90% in 4-5 d) for seed DS 6 m at 40, and 70(53%) for seed DS 6 m at 70. Germination was much lower for seed sown at 40. Typical is 40(15%)-70(2%) for fresh seed. But who wants to grow dandelions.

Taxodium (Pinaceae). *T. distichum* was reported to require one m at 40 followed by a shift to 70 (ref. 44, Ch. 7).

Taxus (Taxaceae). *T. baccata* had some of the most extended germinations yet observed rivaling the Juno and *Oncocycclus Iris*. Seeds were WC for 7 d. Fresh seeds germ. 70-40-70(1%)-40-70(28% in 2nd w) and seeds DS 6 m at 70 germ. 70-40-70(10%)-40-70-40-70(35% in 2nd w). Seeds started at 40 gave comparable patterns, and outdoor treatment gave equally extended germinations. Most of the seed was still firm and might germinate in further cycles.

Telesonix (Saxifragaceae). *T. jamesii* required light and germ 70L(38% in 3rd w)-40-70L(9%), 70D(none), 40-70L(17% in 1-3 w). Seeds kept in 70D for 3 w were dead.

Tellima (Saxifragaceae). *T. grandiflora* germ. 70L(72% in 2-6 w), 70D(none), 40-70L(20%), and 40-70D(none). When the seed in 70D was shifted to 70L after 6 w, 83% germ. in 1-4 w showing that the 6 w in 70D had no effect. Seed also germ. 25% in April and May in outdoor treatment.

Tephrosia (Fabaceae). *T. virginiana* germ. 100% in 4-6 d at 70 if a hole is ground through the seed coat using either fresh seed or seed DS 6 m at 70. Untreated fresh seed germ. 100% over 1-10 w, but untreated seed that had been DS 6 m at 70 germ. only 16% over 3 w showing that DS makes the seed coats more impervious.

Teucrium (Lamiaceae).

T. sp. Turkey germ. 70D(3/5 in 10-14 d) and 40-70-40-70(0/5). Seeds of a second species from Turkey germ. 40(4%)-70(4%)-40 and 70-40(5%)-70(15%).

Thalictrum (Ranunculaceae). Germination in this genus was found to be dramatically stimulated by GA-3. The seedlings are normal and healthy. This is a great benefit because otherwise germination is low and much extended in most of the species. In general DS is not tolerated. Light was not used in this genus.

T. aquilegifolium germ. 70(21% in 2nd w), 40(23%)-70(21%), and 50% in outdoor treatment using DS seeds started February 1.

T. dioicum requires GA-3. Seeds germ. 70 GA-3(100%, zero order rate, ind. t 14 d, and rate 4%/d), 70-40-70(1%)-40(2%), 40-70(all rotted), and 5% in April in outdoor treatment. Seeds DS 6 m at 70 were dead.

T. kemense germ. 40-70 GA-3(5/7 in 2nd w) and none in other treatments. The initial 3 m at 40 may not be necessary.

T. petaloideum germ. 70(51% in 12-15 d) and 40(3%)-70(32% in 2-4 w). This seed was received from Manchuria in April and had been DS for at least 6 m.

T. rochebrunianum requires GA-3 or outdoor treatment. Seeds germ. 70 GA-3(81% in 2nd w) and 40-70 GA-3(95% in 2nd w). DS 6 m at 70 had no effect. The seedlings from GA-3 treatment were normal. Seeds placed outdoors in September germ. 95% in April. All other treatments failed.

T. speciosissimum germ. 70(32% in 1-2 w)-40(5%)-70(41% in 3rd w) and 40(33% in 9th w).

T. sp. Afghanistan germ. 70(3/7 on 9th d) and 40(7/8 in 5th w).

T. tuberiferum germination is stimulated by GA-3. Seeds germ. 70 GA-3(63% in 3rd w), 40-70 GA-3(76% in 2nd w), and 70-40-70 GA-3(88% in 3rd w). As indicated the GA-3 was applied after the shift to 70. Untreated seeds germ. 70D-40-70D(15% in 2nd m), 40-70D(none), and 1% in outdoor treatment. Removing the seed coat had no effect. The seedlings from the GA-3 treatment were normal.

T. tuberosum germ. 40-70(1/4 on 6th d) and 70-40(4/4 in 8-11 w).

T. uchiyamai experiments are only 2 w old. Seeds are germinating at 70 with or without GA-3.

Thlaspi (Brassicaceae). DS seed of *T. bulbosum*, *montanum*, and *rotundifolia* germ. in 6-8 w at 70, and DS seed of *T. stylosum* germ. in 2-4 w at 70.

Thermopsis (Fabaceae).

T. alpina is another legume which germ. 100% in 2-3 d if a hole is made through the seed coat. Untreated seed germ. very slowly.

T. alternifolia germ. 70(71% in 2nd w) if a hole was ground through the seed coat. Without the hole the seed germ. 70(7% in 1-2 w).

T. caroliniana has an impervious seed coat. The seeds are small and producing a puncture without injuring the seed is difficult. The best results were obtained by placing the seed between two pieces of sandpaper and grinding without rotating the seed. Seeds so treated germ. 75% in 4-18 d whereas controls germ.

70(2%)-40-70(9%). Seeds DS 6 m at 70 gave identical results.

Theropogon (Liliaceae). *T. pallidos* germ. 100% in 70L or 70D.

Thuja (Pinaceae). *T. occidentalis* germ. 100% in 12-14 d in 70L or 70D. A prior 3 m moist at 40 or treatment with GA-3 had no effect, but DS for 6 m at 70 lowered germination to 35%. Seeds placed outdoors in September germ. 86% in April. *T. gigantea*, *occidentalis*, and *orientalis* were reported to be 40-70 germinators (ref. 22, Ch. 7).

Thymus (Lamiaceae).

T. incertus germ. 70D or 70L(100% on 4th d) and less in 40-70(30%).

T. vulgare germ. 70D or 70L(100% in 2-4 d), 40(100% in 3rd w), and 75% in early March in outdoor treatment. A caution about the outdoor treatment, a drop in T to 15 in mid-March caused the seedlings to all die.

Tiarella (Saxifragaceae). In the two species studied germination required light and DS was fatal.

T. cordifolia germ. 70L(67% in 3-7 w), 70D GA-3(75% in 2-4 w), 40-70L(74% in 2-7 w), and none in 70D or 40-70D. The seedlings from GA-3 treatment all died. Seed DS 6 m at 70 was dead.

T. wherryi germ. 70D-40-70L(62% in 5-9 w). Germination would presumably have been high in 70L and 70D GA-3 in view of the results with the closely related *T. cordifolia*. Seeds DS 6 m at 70 were dead.

Tigridia (Iridaceae). *T. pavonia* germ. 70L(78% in 2-5 w), 70D(50% in 2-6 w), 40(22% in 10-12 w)-70(35% in 1-4 w), and 4/6 in May in outdoor treatment..

Tilia (Tiliaceae).

T. americanum was reported to germinate only after the fruit coats were removed, the seeds treated with sulfuric acid, the seeds given a period of warmth, and finally subjected to outdoor treatment (ref. 28, Ch. 10 and ref. 31, Ch. 8).

T. cordata sets a great many seed capsules, but in State College typically 80% of these are slightly undersized. These rot in 2 w after encountering moisture at 70 and were not counted. It is convenient to remove the outer coating after 2 w moist. The only germinations to date with fresh seeds have been 70-40-70(1/28 on 2nd d)-40-70(1/28) and 13% in April (17 m after placing seeds outdoors in November). The only germinations with seeds DS 6 m at 70 were 40-70-40(1/7 on 12th d)-70(1/7). Puncturing the seed coat did not initiate germination.

Townsendia (Asteraceae). This genus is composed entirely of D-70 germinators. The time required for DS may be short as in *T. eximia* and *T. formosa* or 4-6 m as in *T. parryi*. DS seed of the following germ. within 2 w at 70: *T. florifer*, *glabella*, *grandiflora*, *hirsuta*, *hookeri*, *montana*, *rothrockii*, *sericea*, *tomentosa*, and *wilcoxiana*.

T. eximia germ. 70(90-100% in 4-12 d) using either fresh seed or seed DS 6 m at 70 or 40. Fresh seed germ. 40(33%)-70(57%) and seed DS 6 m at 40 or 70 germ. 40(100% in 3-7 w) showing the speeding up effect of DS.

T. exscapa germ. 70(100% in 7-10 d) and 40-70(100% in 7-10 d).

T. formosa germ. 70(90-100% in 2-5 d) and 40(20%)-70(78% in 2-3 d) using fresh seed or seed DS 6 m at 70 or 40.

T. incana germ. 70(100%, ind. t zero, 5%/d).

T. mensana germ. 70(100%, ind. t 6 d, 10%/d).

T. sp. Idaho germ. 70(100%, ind. t zero, 10%/d).

T. parryi germ. best with seed DS 6 m at 70 in 70 (90-100%, ind. t 2 d, first order rate with half time of one d). All other treatments gave lower germination.

Trachelium (Campanulaceae). *T. rumelicum germ.* best in 70L(82% in 1-3 w) and less in 70D(7%) and 40(5%)-70(5%). Seeds treated with GA-3 were killed.

Tradescantia (Commelinaceae).

T. longipes self sows here, but the only successful germination was fresh seed in 40-70(1/14)-40-70(1/14). Photoexperiments and outdoor treatment need to be tried.

Trichosanthes (Cucurbitaceae). *T. cuspidata germ.* in the 1st w at 70.

Trichostema (Lamiaceae).

T. dichotomum germ. 70D GA-3(88% in 2nd w), 70L(none), 70D(none), 40-70 GA-3(70% in 2nd w), 40-70L(31% in 2nd w), and 40-70D(none). Seeds placed outdoors in November germ. 10% in April.

T. setaceum germ. 70-40(4%)-70(40% in 1-3 w), 40-70(30% in 1-3 w), and 40% in April from sowing outdoors in October using fresh seed. Seed DS 6 m at 70 germ. 70(1%)-40-70(15%) and 40-70(4%). Seed DS 6 m at 40 germ. 70(5%)-40-70(6%) and 40-70(4%). Treatment with GA-3 must be tried.

Tricyrtis (Liliaceae). DS seed of the following were sown outdoors in February and germ. in May: *T. flava*, *formosana*, *latifolia*, *macrantha*, and *puberula*. Light stimulated germination, although the effect could be complex. Attention is called to the problem of a tiny grub attacking the seedlings (see Chapter 14). The effect of sowing at 40 is complex. In some species this was found to be fatal despite the fact that 70L-40-70L germ. seeds in both cycles in 70L. In other species there was significant germination at 40 (in the dark).

T. affinis germ. 70L(50% in 4th w) and none in 70D. A second small sample germ. 70L(1/1 on 11th d) and 40(2/2 in 3rd w).

T. bakeri germ. 70L(30% in 3rd w). It also germ. in May from seed placed outdoors in February. A second sample germ. 70L(10/11 on 11th d), 70D(none), and 40(5/7 in 7th w)-70L(1/7). A third sample germ. 70L(8/20 in 2-6 w)-40-70L(4/20 in 2nd w), 70D(none), and 40-70L(none). When the seeds in 70D were shifted to 70L after 6w, none germ. in the following 6 w, but after shifting to 40 for 3 m and returning to 70L, 8/14 germ. in the 3rd d. All of this is a bit confusing, but there does seem to be a photorequirement for germination although germination occurs sometimes at 40.

T. dilitata requires light. Seeds germ. 70L(41% in 3rd w)-40-70L(14%) and 40-70L(14%)-40-70L in one sample and 70L-40-70L(93% in 2nd w) and 70L-40-70L(63% in 2nd w) in two other samples; and none in 70D or 40-70D. When a sample in 70D was shifted to 70L after 4 w, none germ. showing that the seed rapidly dies in 70D. None germ. in any dark treatment.

T. flava germ. 70L(5/9 in 3rd w) and 40(none).

T. formosana germ. 70L(25% in 2nd w), 70D(none), and 40-70D(15% in 2nd w).

T. hirta requires light. Seeds germ. 70D-40-70L(100% in 8-12 d), 40-70L(100% in 2nd w), 40-70D(14%), 70D-40-70D(none), and 15% in April and May in outdoor treatment. It is likely that DS would reduce the photorequirement as in *T. hirta alba*. Direct sowing in 70L needs to be tested.

T. hirta alba germ. 40-70L(100% in 6-8 d), 70D-40-70L(65%), none in 40-70D or 70D-40-70D, and 23% in outdoor treatment.. Seed DS 6 m at 70 germ. 70L(68% in 11-16 d), 70D(49% in 3rd w), and 40(71% in 8-12 w)-70D(29% in 2-6 d). DS for 6 m at 70 largely eliminates the photorequirement, and it is possible that longer DS times might completely eliminate the photorequirement.

T. latifolia germ 40-70L(29% in 10-16 d) and none in 70L, 70D, or 40-70D. Seed DS 6 m at 70 failed to germinate.

T. macrantha germ. 70L(4%)-40-70L, 70D-40-70D(none), and 40(30%)-70L-40-70L(20%). The sample of seed had low viability, and all that can be said is that its germination is similar to *T. hirta*.

T. macropoda germ. differently with different samples which is attributed to the seeds being received after varying amounts of DS. One sample germ. 70L(18% in 3rd w), 40-70L(84% on 8th d), and 70D(none). Another sample germ. 70L(5% in 2nd w)-40-70L(28% in 2nd w), 70D-40-70L(45% in 2nd w), and 40-70L(none). Seeds also germ. in May from seed placed outdoors in February.

T. nana germ. 40-70L(86% in 1-4 w) and none in all dark treatments using freshly collected seed. When the sample from 40-70D was shifted to 70L after 4 w in 70D, none germ. Seed DS 6 m at 70 is dead.

T. perfoliata germ. 70L(6/8 in 2nd w) and 40-70L(none).

T. pilosa germ. 40-70(2/10 in 8-12 d) and none at 70.

T. puberula germ. 70L(30% in 2-4 w)-40-70L(4%), 70D(14% in 2-6 w)-40-70L(14% in 2nd w), and 40-70L(none). If the sample in 70D is shifted to 70L after 8 w, and additional 10% germ. A second sample germ. 70L-40-70L(28% in 2nd w), 70D-40-70L(50% in 2nd w), and 40-70L (none).

T. stolonifera germ. 70L(60% in 2-6 w)-40-70L(8%), 70D(3%)-40-70L(3%), and 40-70L(none).

Trifolium (Fabaceae).

T. dasyphyllum germ. 70(6/16 in 6-12 w) and 40(2/10 in 2-9 w)-70(1/10).

T. pratense germ. 70D(1% on 3rd d). The remaining seeds rotted.

T. virginiana germ. 70(100% in 3rd w) and 40(85% in 9th w) using fresh seed.

Trillidium (Liliaceae). *T. govianum* germ. 70D(GA-3)-40-70D(2/4 on 2nd d). This sample had been subjected to 3 m moist at 70 followed by outdoor conditions from February to September before GA-3 treatment. Treatment with GA-3 is promising.

Trillium (Liliaceae). Gibberelins are at least desirable if not requisite for both germination and the production of healthy seedlings. More work is necessary before an optimum procedure can be recommended. The GA-3 treatment was tried with fresh seeds of *T. grandiflorum* and *T. tschonoski*. With *T. erectum*, *T. flexipes*, *T. luteum*, and *T. ovatum* the GA-3 was applied after the seeds had undergone 2-4 y of other treatments. The GA-3 stimulated germination in all six species, and the seedlings developed better than the occasional seedling obtained in other treatments. It is apparent that extensive experiments are needed on treating *Trillium* seed with GA-3.

Germination in *Trillium* is epigeal despite the delayed development of the cotyledon and its ovate shape. Each year a single leaf emerges until enough strength is stored to produce a stem with the characteristic three leaflets. Flowering usually occurs the following year, and the whole process to flowering takes 4-6 y.

DS 6 m at 70 is largely fatal to seed of all species with the exception of *T. rivale* (communication from Fred Case) and DS 6 m at 40 is largely fatal. The extended nature of the germination would allow the seed to be distributed in moist paper towels in polyethylene bags and commercial sources and seed exchanges will have to adapt to such procedures. As it is now all seed that is distributed has been in effect subjected to DS and is largely dead.

The seeds have an attached aril, and the seeds are dispersed by ants and perhaps other insects. The pulp of the seed capsule is sweet, and it is more in the nature of a fruit in the common sense than a seed capsule. There have been suggestions that the aril inhibits germination and that its removal would benefit germination. The following results make this doubtful although it is a convenience. A few preliminary experiments indicated that light has no effect in this genus.

T. albidum germ. 40-70(100% largely on the 3rd d). The seedlings require about a month at 70 to complete development of the radicle and tuber after which they are shifted to 40. After 1-2 m at 40 the cotyledon begins to draw out of the seed coat. It is best to keep the seedlings an additional month or two at 40 before shifting to 70. On shifting to 70 development of the cotyledon is completed in a week or so. All other procedures either fail to give any germination or the seedlings are weak and never fully develop the cotyledon.

T. erectum seeds that had been in outdoor treatment for 4 y were treated with GA-3 whereupon 4/7 germ. in the 5th w and 2 more germ. two cycles later. The seedlings appear normal. Up to 4 y of various other treatments had failed to give a single germination.

T. flexipes seeds that had been in outdoor treatment for 2 y were treated with GA-3 after which 84% germ. in 4-9 w. All other treatments gave germinations below 5%, and the seedlings failed to develop. This species is sometime confused with *T. grandiflorum*. In *T. flexipes* the flowers are horizontal instead of tilted upwards, the seed capsule is maroon red instead of light green, the aril is deep yellow instead of white, and the pollen is white instead of yellow.

T. grandiflorum germ. 70 GA-3(74% in 7-11 w) and 70D(none). Although the cotyledons were starting to expand, the seedlings were placed at 40 at the end of the 12th w. They continued to show a little growth so that after 4 w at 40, they were placed at 60 whereupon they gradually opened their cotyledons over the next 3 m. It was thus possible to get the first leaf within 6 m of seed collection. More work is needed to define the optimum treatment. Earlier samples germ. 70(22%)-40-70-40-70(24%)-40(3%) and 40-70(42%)-40(31%) without GA-3, but the cotyledons failed to develop suggesting that gibberelins are required for healthy seedlings.

T. luteum seeds that had been in various treatments for 2 y were treated with GA-3 whereupon 100% germ. in 7-10 w. After 3 m at 40, the seedlings developed a healthy cotyledon on shifting to 70.

T. nivale germ. 40-70(40%)-40-70-40(14%)-70(24%)-40(2%) with fresh seed. The cotyledons did not develop normally. Studies with GA-3 are needed.

T. ovatum germ. 70D(4/9 in 2-8 w) and 40(1/8)-70-40-70. The seeds were received in moist towels and one had already germ. at 70. The seeds started at 40 were treated with GA-3 after a y of alternating cycles whereupon 6/7 germ. in 4-8 w.

T. pusillum germ. 40-70-40-70-40(82%).

T. tschonoski germ. 70 GA-3(80% in 8-10 w) and 40-70 GA-3(50% in 7th w) using fresh seeds. None germ. in other treatments. Development of the corm and radicle takes another 2 m. On shifting the seedlings to 40 the cotyledons slowly expand. A full 3 m at 40 is required. It would probably be best to slowly raise the temperature, most conveniently by planting outdoors in April.

T. vaseyi germ. better with seed WC for 3 w compared to seed WC for only 7 d. The former germ. 40-70(24% in 10-16 w) and the latter none. Another sample WC 2 w germ. 70(30%)-40(12%)-70-40(6%) and 40-70(45%)-40(3%). However, cotyledon development was unsatisfactory so that again gibberelins may be required.

Triteleia (Liliaceae). *T. laxa* germ. best in 40(92% in 3-6 w) and less in 70(8% in 2nd w)-40(40% in 3-8 w).

Tritoma (Liliaceae). This genus is also called *Kniphofia*. *T. hybrids* germ. 70D(80-90% in the 3rd w) and 40(60% in 6-11 w)-70(38% in 2-6 d). Light or GA-3 had no effect.

Trollius (Ranunculaceae). Nikolaeva (ref. 10) reported that several species had germination stimulated by GA-3. Robert and Brigitte Stewart and myself have confirmed these results with several species. However, the seedlings decline in vigor after producing a true leaf or two so that at present GA-3 cannot be recommended for the production of *Trollius* plants.

T. acaulis germ. 70(7%)-40-70(60% in 1-3 w) and 40-70(70% in 6-10 d).

T. altissimus germ. 1/30 in outdoor treatment. The rest rotted.

T. asiaticus germ. in April from seed sown outdoors in January.

T. chinensis germ. 40(6% in 3rd m) and none at 70.

T. dschungaricus germ. in April from seed sown outdoors in January.

T. laxus germ. in April in outdoor treatment with 40% for fresh seed and 25-35% for seed DS 12 m at 40. Seed sown in other treatments germ. 0-10% over several cycles, and seed DS 6 m at 70 failed to germinate. Experiments were conducted on abrading the seeds by rubbing between sandpaper for different amounts. There was no increase in germination.

T. ledebouri germ. 70 GA-3(38% in 3rd w), none in 70D or 70L, and 40-70(6%)-40(16%). A prior 3 m at 40 or a prior 70-40 cycle had no effect on the germination in 70 GA-3. Seeds placed outdoors in October germ. 6% in November and 14% in April. The outdoor treatment is recommended, see general comments on *Trollius*.

T. pumilus germ. 70(5/9 in 12-20 d), 40-70(2/9), and 4/7 in outdoor treatment. A second sample of *T. pumilus* collected in the wild in Nepal had much finer seed and a different behavior. This latter sample required light and germ. 70L(100% in 2-4 w), 70D(none), 40-70L(100%), and 40-70D(none). After 4 w the 70D sample was shifted to 70L whereupon 100% germ. in 3rd w. The two sample are presumably different species as judged by the difference in size of their seeds. It does show that photoeffects must be tested in *Trollius*.

Tropaeolum (Tropaeolaceae). Although they have not been exhaustively studied, the best germinations were obtained by giving the seeds 4 w at 70 and shifting to 40. Germination at 40 occurs in the 3rd w, but the seedlings must be kept at 40 until the stem begins to emerge (hypogean). Several of these species are hardy in England if the tuber is below frost line. Young plants need to be grown under milder

conditions until is tuber is large enough to place below frost line. It remains to be seen if deep planting of the tuber can effect hardiness in Eastern U.S.

T. azureum germ. best if given 4 w at 70 and then shifted to 40. These germ. 62% in 3rd w after the shift to 40. Seeds also germ. 70D(1/10) and 40(3/10).

T. polyphyllum germ. 5/5 in 3rd w at 40 if given a prior 4 w at 70. When sown directly at 40 1/3 germ. in the 4th w. If after 6 w at 40 the seed was given 4 w at 70 and then back to 40, the remaining 2/3 germ. in the 3rd w.

T. sessilifolium germ. 4/4 in the 3rd w at 40 if given a prior 4 w at 70. When sown directly at 40, only 1/3 germ. in the 4th w. If after 6 w at 40 the seed was given 4 w at 70 and shifted back to 40, the remaining 2/3 germ. in the 3rd w in a behavior identical to that of *T. polyphyllum*.

Tsuga (Pinaceae). *T. canadensis* germ. 40(68% in 12th w)-70(11% on 2nd d), 70(GA-3)-40(70% in 2-12 w), 70L(2%)-40(7%)-70(43%), and 70D-40(2%)-70D(11%). Seeds placed outdoors in October germ. 74% in April.

Tulipa (Liliaceae). Germination takes place either at 40 or after a 3 m period at 40. Preliminary results indicate that the seedlings must grow at low temperatures as a quick shift to 70 generally led to rotting starting at the tip of the radicle. Outdoor treatment needs to be tried not only for the germination but also for the cotyledon development. GA-3 probably has no effect in this genus.

T. clusiana germ. 70-40(1/3) and 40-70(none).

T. sp. Darwas germ. 40(95% in 4-7 w) and none in 70 or 70 GA-3.

T. stellata germ. 70-40(6/7 in 6-10 w) and 40(7/7 in 4-6 w).

T. tarda germ. 40(3%)-70(75%) and 70-40(28%)-70(32%) using seed DS 6 m at 70. Another sample germ. 40(9%)-70(23%)-40(9%). Fresh seeds germ. 40(8%)-70(1%)-40(6%) and 70-40(3%)-70(3%)-40(12%)-70(3%). Light had no effect on germination.

T. turkestanica germ. best in 70-40(50% in 3-8 w) and 40(30%)-70(30%) using either fresh seed or seed DS 6 m at 70 or 40. When sown at 40 germination was less convenient as it extended over two cycles.

Tussilago (Asteraceae). *T. farfara* was unusual for a composite in that seed DS 6 m at 70 or 40 was totally dead. The seed matures in early May and is quickly wind born. In this it resembles *Populus* and *Salix* which are also notoriously intolerant of DS. Fresh seed germ. 70(100% in 2-3 d) and 40(100% in 7-12 d).

Typha (Typhaceae). *T. latifolia* produces large amounts of brown powder on the outside of the cat tails, but it has proven to be difficult to recognize or count the viable seeds. Seeds germ. 70L and 40-70L and none in all other treatments.

Ulmus (Ulmaceae). Fresh seed of *U. glabra* germ. 70(96% in 4-6 d) and 40(56% in 2-4 w). Seed DS 6 m at 70 germ. 70(14%) and 40(73%). Seed DS 6 m at 40 germ. 70(65%) and 40(20%)-70(46%).

Umbilicus (Cupressaceae). *U. rupestris* germ. 70(5% in 3rd w) and none in 70L or 40-70D.

Ungernia (Amaryllidaceae). *U. victoris* germ. 70(70% in 8-10 d) and 40(70% in 3rd w). Light had no effect.

Uvularia (Liliaceae). *U. grandiflora* germination is two step and hypogeal. Fresh seed sown outdoors in August as soon as it was ripe germ. 32% in May and June of the next year. Other treatments germ. under 10%. So far the seedlings have not developed properly and GA-3 needs to be tried. This species self sows here.

Vaccinium (Ericaceae).

V. macrocarpum germ. 70L(95% in 1-3 w), 70D GA-3(95% in 1-3 w), 70D(10% in 5th w), and 40-70D(50% in 1-4 w). Although the seeds are enclosed in a fruit, they are not in contact with the juices of the fruit and WC had no effect.

V. nummularia germ. 20% in 4-6 w in 70L or 70D and 40-70(none).

Veratrum (Liliaceae). *V. californicum* germ. 40-70 GA-3(2/3 in 5th w), 40-70(none), and 70-40-70(3/4 in 1-10 w).

Verbascum (Scrophulariaceae).

V. blattaria requires light. Seed DS 6 m at 70 or 40 or DS 12 m at 70 germ. 70L(100% in 4-5 d) and 70D(3%), and a prior 3 m at 40 had no effect. Fresh seed germ. less in 70L(70% in 1-3 w).

V. phoeniceum germ. 70(100% in 3-4 d) and 40(38% over 3 m). Light had no effect.

Verbena (Verbenaceae). *V. hastata* germ. 40-70L(100% in 3-5 d), 70D GA-3(54% in 5-25 d, mainly in 5-10 d) and none in 70D or 70L using either seeds collected in November or seeds collected in September and DS 6 m or 12 m at 70. Fresh seeds collected in September gave lower germination in 40-70L. Other treatments failed. The rate of destruction of inhibitor was studied. Seeds DS 12 m at 70 were held at 40 for 4 w, 8 w, and 12 w before shifting to 70L. Germinations were 2%, 100%, and 100% showing that 6-8 w were required.

Vernonia (Asteraceae). *V. novaboracensis* is one of the very few Asteraceae that is not a D-70 germinator. One sample of fresh seeds germ. 40-70D(100% in 2-4 d), 70 GA-3(100% in 2nd w), and 70D(5%)-40(1%)-70D(28%). DS for 6 m at 40 had no effect, but seeds DS for 6 m at 70 germ. 40-70D(100% in 2-4 d) and 70D(33%)-40(3%)-70D(23%). A second sample was studied a y later to determine the effect of GA-3. This sample gave a somewhat different behavior and germ. 70 GA-3(100% in 3rd w), 40-70L(100% on 4th d), and none in 70D, 70L, or 40-70D. After 6 m DS at 70, this second sample germ. 70L(54% in 3rd w), 70 GA-3 (100% in 3rd w), and 70D(none).

Veronica (Scrophulariaceae).

V. aphylla germ. 70L(2%)-40-70L(15% in 2nd w), 70D-40-70D(none), and 40(30% in 5-9 w).

V. bellidioides germ. 70L(57% in 6-20 d), 70D(54% in 2-7 w), and 40-70(13% in 2nd w).

V. caespitosa germ. 40-70(3/4 in 2-60 d) and none at 70.

V. fruticulosa (black seeds) germ. 70D(4/4 in 4-7 d), 70L(4/4 in 4-7 d), and 40(4/5 in 4-8 w). *V. fruticulosa* (light brown seeds) germ. 40(33% in 4-7 w) and none in 70L or 70D. The seeds are so different in appearance and germination behavior that it is likely that they are different species, but which is the true *V. fruticulosa*.

V. nipponica germ. 70L(1/1 on 6th d), 70D(2/2 in 6-10 d), and 40-70(none).

V. nummularia germ. 70L(31% in 2nd w), 70D-40-70L(74% in 2nd w), 70D-40-70D(16% in 2nd w), and 40(32% in 4-6 w)-70(7%). The behavior is complicated, but stimulator of germination by light is evident.

V. ponae germ. 70L(100% in 2nd w), 70D(47% in 2nd w), and 40-70D(30%).

V. tauricola germ. 70(4/7 in 2nd w) and 40(4/7 in 9-12 w).

Viburnum (Caprifoliaceae). Viburnums divide into two groups. The first group germ. in a 40-70 pattern. The cotyledons develop within a week or two after germination. This group is adapted to germination in spring and immediate leaf development and growth. The second group germ. in a 40-70-40 pattern with extension into a 40-70-40-70-40 pattern. Germination takes place in a cycle at 40. The seedlings must be kept at 40 for two to three months after radicle development is complete in order for the cotyledons to develop properly on shifting to 70. Puncturing the seed coat had no effect in three species. All seed was WC for 1-2 w. Germination was stimulated by GA-3 in *V. opulus* and *V. trifolium*, and this needs more study.

V. acerifolium germ. 70-40(1/13)-70-40(4/13)-70(1/13) and 40-70-40(2/21)-70-40(5/21) using fresh seed collected in October. Seed DS 6 m at 70 or 40 gave lower and more extended germination. The cotyledons failed to develop on the shift to 70, but this was before it was recognized that the 3-4 m at 40 was needed.

V. burkwoodi is a 40-70 germinator. Fresh seed or seed DS 6 m at 70 or 40 germ. 40-70(75-80% in 5-10 w) and 70(none). The cotyledons develop within a week or two after radicle emergence. Grinding a hole through the seed coat had no effect. Fresh WC seed germ. similarly, but seed collected in February gave lower germination.

V. dentatum germ. 70-40-70(1%)-40(48% in 3-12 w)-70(3%), less in 40(12%)-70(3%)-40(9%), and none (all rotted) in outdoor treatment. Seed DS 6 m at 40 germ. 40(3/8 in 2-7 w) and all rotted when started at 70. The seedlings were kept at 40 for 2 m after radicle development was complete after which the cotyledons developed normally on shifting to 70. Seed DS 6 m at 70 was dead.

V. dilatatum seed collected in early December and DS 6 m at 70 in the WC state germ. 70-40-70-40-70(71% in 10-14 w) and 40-70-40(5%)-70-40-70-40(80% in 3rd w). After radicle development was complete (3 m), the seedlings were shifted to 40 and samples periodically shifted to 70. Only after 4 m at 40 did the cotyledons develop.

V. lantana germ. 40-70(86% in 2nd m)-40-70(5%) and less in 70(47%)-40(28%)-70(3%) using seeds collected in December and WC or WC seed DS 6 m at 70 or 40. The cotyledons opened in 2nd w after germination.

V. opulis germ. 70-40(3%)-70-40(62% in 2-8 w) and 40-70-40(18%)-70(3%)-40(16%)-70-40(14%) for fresh seed, 70(15%)-40-70-40(4%)-70-40(52% in 3-12 w) and 40-70-40(4%)-70-40(70% in 4-11 w) for seed DS 6 m at 70, and 70-40-70(2%)-40-70-40(37% in 3-11 w) and 40-70-40(2%)-70(2%)-40(48% in 4-11 w) for seed DS 6 m at 40. Seed WC and sown outdoors in December delayed germination until the following October and November when 33% germ. However these seedling were killed by winter and this outdoor treatment is not recommended. The radicle and root system form at 40, and it is best to keep the seedlings at 40 for 2 m after radicle development is complete in order for the cotyledons to develop on shifting to 70.

V. prunifolium is native on the property and large amounts of fruit are set. However, 80-95% of the seed coats are empty shells. Seeds WC for 5 w germ. 40-70-40(20% in 4-8 w) and 70-40-70-40(18% in 3-7 w). When this WC seed was DS for 6 m at 70, it germ. 40-70-40(36% in 4-10 w)-70-40(10%) and 70-40-70(26% in 4-10 w)-40(7%). The cotyledons developed quickly after the shift to 70. When the seeds were WC for 7 d instead of 5 w, none germ. This was one of the rare examples where the extent of WC made a big difference. Seeds all rotted in outdoor treatment.

V. rhytidophyllum germ. 40-70-40-70(23% in 2-8 w) and 70-40-70-40-70(7%). The seedlings develop a root system at 70. The cotyledons will not develop until after 3 m at 40 and a return to 70.

V. sargentii germ. 70(92% in 8-12 w) and 40-70(90%). The seedlings develop a root system at 70. The cotyledons will not develop until after 3 m at 40 and a return to 70.

V. setigerum germ. 70-40(12%)-70(1%)-40(72% in 2-10 w)-70(4%)-40(4%) and 40-70(3%)-40(78% in 3-12 w)-70-40(13%)-70(6%) using seed collected in November and WC or this same WC seed DS 6 m at 70 or 40. Puncturing the seed coat had no effect. The seedlings must be kept at 40 until radicle development is complete plus an additional 2 m in order for the cotyledons to develop normally on shifting to 70.

V. sieboldi germ. 70-40-70(15% in 2 d-11 w)-40(1%), 40-70(13%)-40(6%)-70(38% in 2-21 d), and 14% in March and April in outdoor treatment. Only the radicle and root system develop at 70, and a 3 m at 40 and shift back to 70 are needed to develop the cotyledons. Seed DS 6 m at 70 or 40 largely rotted, but outdoor treatment of seed DS 6 m at 40 germ. 27% in March and April a year after being placed outdoors in April. It was not checked whether the seeds in outdoor treatment developed cotyledons in the same spring as germination.

V. tomentosum germ. 70-40-70(70% in 1-42 d) and 40(2%)-70(50% in 1-26 d) using seed collected in July and WC 7 d. Cotyledons develop in 2 w at 70. Seeds DS 6 m at 70 or 40 were dead.

V. trifolium germ. 70 GA-3(64% in 8th w), 70D(none), and 40-70(65% in 11-15 w). The seedlings require 3 m at 40 before they will develop their cotyledons at 70.

***Vicia* (Fabaceae).**

V. americana like many legumes germ. 100% in 2-6 d if a hole is ground through the seed coat. Germination is still good without this pretreatment in both fresh and DS seed, although germination extends over 1-3 cycles, and runs around 50-75%.

V. cracca germ. 95% in 3-5 w at 70 using fresh seed and 70(10%) using seed DS 6 m at 70. Puncturing the seed coat had no effect.

***Viola* (Violaceae).** Although the results were complex, it is certain that at least in some species germination requires light and/or GA-3 (or other fungal products). An extreme example are the rosulate *Violas* of the Andes where germination (at 40) was 60-70% when treated with GA-3 and absolutely none in all other treatments. The survival value of this exogenous chemical requirement is discussed in Chapter 12.

Many *Viola* species are short lived. They survive by abundant self sowing. Seed is difficult to collect and in a period of several days the seed capsules go from an immature state to the day when the capsule explodes throwing the seeds for distance of 10-20 feet. The answer is to enclose the ripening capsule in aluminum foil or some other contrivance to catch the seed. What happens is the seed is usually collected before it is mature and such seed largely rots. This is one reason why germinations were generally poor. DS is not tolerated well, and DS seed rotted or germ. weakly except for *V. rugulosa*, a prairie species. Possibly other prairie and dry land species would also tolerate DS. Many species produce a first crop of seed that ripens in June or July from sexually fertilized flowers and a second crop of seed from cleistogamous flowers that ripen in the fall. Experiments were conducted on both types of seed.

V. altaica germ. 70(70% in 1-6 w) and 40(25%)-70(30%).

V. appalachensis germ. 70L-40-70L(70% in 5-6 d) and 60% in April in outdoor conditions. None germ. in 70D-40-70D, 40-70L, or 40-70D. Seed DS for 6 m at 70 was dead.

V. biflora received in October promptly rotted on contacting moisture. This is mentioned because it is a further example of intolerance to DS in this genus.

V. canadensis germ. 40-70-40(9% in 4th w)-70(2%) and 12% in March-April in outdoor treatment. All other treatments failed including 40-70L and 70-40-70L. Seed DS 6 m at 70 was dead.

V. cornuta germ. 70D(35% in 1-7 w) and 40(14% in 5th w). This latter sample had five seeds still unrotted after a year of alternating cycles. It was then treated with GA-3 in a 70 cycle whereupon 4/5 germ. on the 5th d.

V. cucullata germ. 70L(51% in 1-8 w)-40-70L(9%), 70D GA-3(92% in 5-7 d), and 70D(1%)-40-70D(21% in 3-16 d). The GA-3 seedlings were normal.

V. dactyloides germ. 70L(94% in 1-4 w), 70D(11%), and 40-70L(68% in 1-3 w).

V. delphinantha seed was received in December and quickly rotted on encountering moisture indicating that it was dead. It is likely that DS is not tolerated.

V. fimbriatula germ. 70D GA-3(85% in 5-18 d), 70L(6%)-40-70L(37% in 1-3 w), 70D-40-70D(3%), 40-70L(37% in 1-7 w), and 40-70D(5%). Seeds placed outdoors in September germ. 27% the following April. The GA-3 seedlings were normal.

V. incisa germ. 70L(72% in 6-11 d), 70D(none), and 40-70L(86% in 1-3 w). Curiously the period in 70D was fatal even when the period was only 2 w in duration.

V. labradorica germ. 70L(16% in 4-10 w), 70D GA-3(10% in 3rd w), and 70D-40-70D(10%).

V. montana failed to germinate in seven alternating 3 m cycles. However the seed remained firm and when shifted to 70L, 2/12 germ. in the 8th d. The two seedlings grew strongly. Light, GA-3, and outdoor conditions need to be tried.

V. palmata collected in June germ. 56% in late March and early April in outdoor treatment. The same seed can be given 70-40-70 and shifted to outdoors January 1, and this gave 32% germination in late March. Other treatments gave little germination except that light gave a small stimulation as shown by 70L-40-70L(7%) compared to 70D-40-70D(none) and 40-70L(5%) compared to 40-70D(none). Seed collected in September from cleistogamous flowers germ. 40-70(2/17) and 70-40-70(none). All DS seed rotted and DS is a fatal treatment.

V. papilionacea collected in June germ. 54% in March in outdoor treatment. Another sample was given 70-40-70 and then shifted to outdoors January 1. This germ. 68% in March. The seeds expand and split a week or two before the radicle starts elongating. Germination was low in other treatments although there was a small stimulation by light as shown by 70L-40-70L(3/8 on 6th d), none in 70D-40-70D, 40-70L(8%), and 40-70D(2%). Seed collected in September from cleistogamous flowers germ. 40-70(1/11) and all rotted in 70-40. Seed DS 6 m at 70 was dead.

V. pedatifida germ. 70D GA-3(5/8 in 3rd w), 40-70D(1/8), and 70D-40-70D(30% in 6th d). Seeds placed outdoors in October germ. 7/9 in April. Light had no effect.

V. pubescens germ. 70D GA-3(62% in 2-6 w)-40-70(15%), 70D-40-70D(40% in 1-3 w), and 70L(none). Outdoor treatment germ. 6%. Seed DS 6 m at 70 was dead.

V. (rosulate species) were obtained in eight different collections by the Archibalds and three different collections by J. Andrews, all in the Chilean Andes. None germ. in any treatment over 1-2 y until treated with GA-3. Germination occurs only at 40 in the GA-3 treatment. The Archibald seeds germ. 62% in 4th w at 40 after 6 m or 12 m of other treatments. It did not seem to make much difference what the previous treatment had been. The Andrews seeds germ. 63% in 4th w at 40 after 6 m of other treatments. The seedlings seem etiolated although I am not familiar with the appearance of normal seedlings. However, they did survive and develop true leaves. Panayoti Kelaidis reported to me that he had succeeded in germinating several species using a combination of GA-3 with cytokinins.

V. rugulosa germ. 9% in March and April in outdoor treatment. If this seed from outdoor treatment is shifted to 70L on April 1, there seems to be some promotion of germination and 15% germ. over the next two weeks. The seeds expand and split a week or two before the radicle starts elongating. Other treatments germ. only 0-1%. In the 40-70 treatments the seeds expand and split, but the radicle did not develop. It was as if part of the inhibition was removed. Seeds DS for 6 m were dead.

V. sagittata germ. 40-70-40-70-40-70L(5/38 in 3rd w) and 55% in early April after being outdoors for 19 months. More photoexperiments are needed.

V. sheltoni germ. 40(2/5 in 11th w) and 70D or 70L(none).

V. sororia alba germ. 70(16%)-40-70(3%) and 40(8%)-70(13%)-40-70. All cleistogamous seed and DS seed rotted. Photoexperiments are needed.

V. striata germ. 70D GA-3(62% in 2-6 w), 70D(none), 70L(19% in 5-10 w)-40-70L(50% in 7-9 d), 70D-40-70D(1/6), 40-70L(none), and 55% in April in outdoor treatment. A sample started at 40 in August was shifted to outdoors January 9 whereupon 67% germ. the following April. Seed from cleistogamous flowers and all DS seed rotted and was dead.

V. tricolor germ. 70L(72% in 4-10 w), 40-70L(10% in 4-7 w), 40-70D(none), and 70D(1%). A preliminary 3 m at 40 is deleterious. All DS was dead.

Vitis (Vitaceae).

V. vinifera germ. 70(47% in 10-14 d)-40-70(47% in 3-6 d) and 40-70(100% in 1-3 d) using fresh WC seed. Seed DS 6 m at 70 or 40 germ. 70-40-70(85-90% in 2-6 d) and 40(20% in 11-12 w)-70(70% in 2-3 d). This is one of the few examples where anything approaching induced dormancy was observed.

V. vulpina germ. 40-70(76% in 4-6 d), 70 GA-3(30% in 4th w), and 70(none) using seeds collected in either October or January and WC 7 d. All other treatments including DS gave under 20% germination and usually none germ.

Waldheimia (Asteraceae).

W. glabra germ. 70(100%, ind. t 6 d, 3%/d) and none at 40.

W. stoliczkai germ. 70(100%, ind. t 4 d, 6%/d) and 40(100% in 1-9 w)

W. tomentosa germ. 70(100%, ind. t 6 d, 8%/d) and none at 40.

Waldsteinia (Rosaceae). *W. fragrarioides* requires light. Seeds germ. 70L(95% in 4-14 w with a sharp maximum in rate in the 11th w), 40-70L(58% in 2-5 w with a maximum in the rate in the 3rd w), and none in any dark treatment.

Washingtonia (Palmaceae). *W. filifera* seeds germ. 100% in 2nd w if punctured and 75% in 3rd w otherwise. The seed coat impedes germination, but the effect is not as striking as in most examples of impervious seed coats.

Weigelia (Caprifoliaceae). *W. florida* required light or GA-3. Seeds germ. 70L(82% in 5-18 d), 70D GA-3(95% in 5-14 d), and 70D(3%).

Wisteria (Fabiaceae). *W. sinensis* germ. under all treatments. Fresh seed germ. 70(90-100%, ind. t 5-8 d, 8-17%/d) and 40(100%, ind. t 2-4 d, 1.3-1.9%/d). The range of values given reflects the fact that three forms of this species were studied including the alba form, and there was some variation in the ind. t and rates. Seed DS 6 m at 70 or 40 germ. 70(100%, ind. t 4 d, 6%/d) and 40(100% in 1-9 w).

Wulfenia (Scrophulariaceae). *W. carinthiaca* required light or GA-3. Seeds germ. 70L(90% in 8-10 d), 70D GA-3(90% in 9-15 d), 70D(none), 40-70L(86% in 4-6 d), and 40-70D(none)..

Wyethia (Asteraceae). Samples were small, and differences between GA-3 treated seeds and the controls are not regarded as significant. As with some other Asteraceae, GA-3 treatment did not significantly stimulate germination and in some species it killed the seed.

W. arizonica germ. 70(2/12 in 3rd w) and 70D GA-3(7/8 in 3-20 d), and 40(7/15 in 5-10 w)-70(5/15 in 1-3 d).

W. amplexicaulis germ. 70(3/9 in 3rd w) and 40(2/13 in 10-11 w)-70(5/13 in 1-3 d). All rotted when treated with GA-3.

W. helianthoides germ. 70(1/9 in 10- d) and 40(4/10 in 9-11 w)-70(2/10 on 2nd d). All rotted when treated with GA-3.

Xeranthemum (Asteraceae). *X. annuum* germ. 70D(2%) and 40-70(none).

Xeronema (Liliaceae). *X. callistemon* germ. 40(8% in 4th w)-70(5% in 2nd w) and none in 70D-40 with or without GA-3 treatment.

Xerophyllum (Liliaceae). *X. asphodeloides* germ. 62% in March and April in outdoor treatment. All other treatments germ. under 10% and DS seed was dead. Light did not promote germination.

Xylanthemum (Asteraceae). *X. pamiricum* germ. 70D(100% in 2-6 d) and 40(60%)-70(40%).

Yucca (Liliaceae).

Y. glauca germ. 70(90% largely in 5-9 d) and 40-70(80-90% in 2-4 d) with either fresh seed or seed DS 6 m at 70 or 40.

Y. filamentosa seed can be collected from October to March as the seed is held in the upright capsules through most of the winter. Germination is increased by DS. Seed DS 6 m at 70 or 40 germ. 70(57%, ind. t 2 d, first order rate, half time 20 d)-40-70(43%, ind. t 2 d, first order rate, half time 1-2 d) and 40(11%)-70(85%, ind. t 2 d, first order rate, half time 2 d). Note the much faster rate of germination in a 70 cycle which was preceded by a 40 cycle. Fresh seed germ. at lower rates and lower percentages. Seed collected in March approached the higher rates and better germination of DS seed since overwintering outdoors in the seed capsule is equivalent to DS.

Y. navajoa germ. 70D(95% in 3-9 d); 40-70(100% in 3-5 d), and 60% in April in outdoor treatment. Possibly seed was killed by low T in the outdoor treatment.

Y. whipplei germ. 70(40-50% in 2-4 w) with either fresh seed or seed DS 6 m at 70. Germination dropped to 3% when sown at 40 even after four cycles.

Zaluzianskya (Scrophulariaceae). *Z. capensis* germ. 70(90% in 3rd w) and 40(60% in 6-11 w). Light or GA-3 had no effect on the rate or percent germination.

Zantedeschia (Araceae). *Z. ethiopeca* seeds are enclosed in a green photosynthesizing capsule. This capsule appears to secrete a germination inhibitor. Seeds removed from the capsule and rinsed with water germ. 100% in 4th w in 70D. Germination was delayed for seeds left in the capsule although the capsule soon rotted. Light and a prior 3 m at 40 had no effect on the germination.

Zauschneria (Onagraceae).

Z. arizonica germ. 70(75% in 2-30 d) and 40(80% in 11-15 d)-70(2%).

Z. garrettii germ. 70(59% in 2-8 w) and 40(93% in 2-4 w).

Zephyranthes (Amaryllidaceae):

Z. atamasco germ. 70(3/4 in 10-15 d).

Z. rosea germ. 70(100% in 4-7 d). Germ. is hypogeal and true leaf develops in a w after germination.

Zigadenus (Liliaceae).

Z. elegans germ. 70(100% in 11-15 d) and 40(100% in 6-8 w). Light had no effect.

Z. fremonti germ. 40(92% in 6-10 w), 70-40(50% in 3-5 w), and 12% in outdoor treatment. The species may have not been sufficiently hardy and some were killed by cold in outdoor treatment.

Zizia (Apiaceae). *Z. aurea* germ. 70D GA-3(100% in 12-15 d) and none in 70D and 70L. A prior 3 m at 40 had no effect. The seedlings were normal. Seeds DS 6 m at 70 germ. in the same pattern but the percent germination was reduced to 60%.

Ziziphora (Lamiaceae). *Z. bungeana* germ. 70(83%, first order rate, ind. t 2 d, half life one d) and 40(16%)-70(1%). Light had no effect.

CHAPTER 21. THE ORCHIDS (ORCHIDACEAE)

In this family the germination of seeds and the growing on of the seedlings is a highly specialized field. Propagation of hardy temperate zone orchids has been achieved in the past few years, both by meristem methods and from seeds. The following summary is based on presentations at a symposium sponsored by the Brandywine Conservancy and held March 11-12, 1989, at the Brandywine Museum in Chadds Ford, Pennsylvania.

First a plea to refrain from purchasing collected native orchids and to refrain from personally collecting them unless one is willing to make the requisite commitment to studying their culture. Only a few species (*Cypripedium andrewsii*, *calceolus*, and *candidum* for example) will grow in neutral garden loams and even these are susceptible to fatal viral and fungal diseases. Paul Keisling in Mass. has had the most success, and he uses special microclimates and plenty of fungicide. At present there are only two commercial establishments in the U.S. that purport to propagate their own orchids and both operations are more in the nature of cropping natural populations on their own lands. It would be possible to propagate hardy temperate zone orchids from either seeds or meristem techniques on a commercial basis. However, I suspect that after an initial burst of popular enthusiasm, any market would decline as the home gardener encountered repeated failures.

Orchids are fertilized by insects and often the orchid requires a specific species of insect. There is the famous example of the orchid with a ten inch spur for which Darwin predicted a moth pollinator with a ten inch tongue. The moth was discovered later. There are several *Orphrys* where the lip becomes bulbous and intricately marked to resemble a female bee. The male alights and attempts copulation which fertilizes, not the bee, but the flower.

Orchid seed is the smallest of all seeds with only a few hundred cells in each seed. A capsule of *Cypripedium* will contain ten to twenty thousand seeds. These are dispersed by wind which is aided by a thin membrane in which the seed is embedded. Survival is by massive numbers of dispersed seed with a minutely few maturing.

A successful cycle in the wild starts with a fungal invasion of the seed. The mycelia of the fungi invade the orchid seed, but the orchid seed contains chemicals that kill the mycelia but only after they have made considerable growth. The dead fungal mycelia provide the nutrient for the orchid seedling and possibly necessary metabolites that the orchid cannot make for itself. This is termed symbiotic germination but in fact seems to benefit only the orchid. The orchid cells grow and divide to produce a protocorm. With species like *Calopogon* the protocorm is nearly spherical but with others an irregular shape develops with roots ultimately emerging. With saprophytic orchids the plant does not progress beyond this stage underground and flowering stems emerge directly from this protocorm. Even with non-saprophytic orchids, the first growth above ground is either a flowering stem or a mature true leaf.

It was a great breakthrough in 1922 when L. Knudson developed agar gel compositions in which a variety of tropical orchids would germinate and grow to mature plants. One of the key ingredients was common sugar, sucrose. Currently propagation by meristem culture dominates, but the Knudson method was the source of market supply for many years. The Knudson method was tried many times with

temperature zone orchids, always with failure until recently.

In the eighties a second breakthrough occurred when several investigators reported the propagation of hardy orchids from seed using agar gel compositions of 20-30 components coupled with introduction of certain fungi. This is termed symbiotic germination. Germination and growth will occur without the fungi, but at present the fungi give much superior results. Geoffrey Hadley has tested a variety of fungi and so many were successful as to suggest that orchids are not species specific for the fungi, although it can hardly be expected that any fungal species will work. Vivid evidence of success was presented by W. W. Ballard, James Coke, Ian Donovan, Geoffrey Hadley, Robert B. Mitchell, Warren Stoutamire, Carson Whitlow, and Robert A. Yannetti. Yannetti exhibited a small glass jar with a screw type cover in which four *Arethusa bulbosa* were growing on a half inch thick layer of gel with two of the four having a perfect flower and the other two in bud. This species is nearly saprophytic as the green stem has only a few bracts and most of the nutrition must come from non-photosynthetic sources. Generally the seeds were disinfected with a 0.5% NaOCl (sodium hypochlorite) prepared by diluting commercial bleach 1:10. The seeds float and Coke described evacuating a vacuum chamber which removed the air from the seeds after which the seeds would sink in water to which surfactant had been added. An easier technique was described by Mitchell. This was to disinfect the seed capsule just before it splits and to handle the seed under sterile conditions.

When everything is optimum, true leaves appear in 6-18 months and flowering was achieved in 2-6 years. Extensive losses can occur on transferring the seedlings with leaves out of the agar gel, but this is a problem of culture. Although the fungi are requisite and beneficial to the germination and development of the seedlings, it is not evident that they are necessary to mature plants except for saprophytes. Fungal mycelia invade only the outer half of the long roots and the infections come and go. Regular treatments with fungicide as practiced by Paul Keisling is not only beneficial but virtually requisite suggesting that the mature plants do not require the action of fungi.

Orchid seed is long lived in dry storage. Stoutamire reported that three year old seed of *Cypripedium reginae* and ten year old seed of *Cypripedium acaule* germinated as well as fresh seed. There is some evidence that dry storage is required for good germination. The following recent references deal with germination of hardy orchids and were selected from an exhaustive bibliography that was distributed at the Brandywine Symposium. A. B. Anderson, *Wildflowers: Canada's Natl. Mag. Wild Flora* **1**, 23 (1985); J. Arditti, *J. Orchid Biology: Rev. and Perspectives II*, Cornell Univ., New York 1982, p. 243; *Am. J. Botany* **142**, 442 (1981); *Am. Orchid Soc. Bull.* **50**, 162 (1982); J. Arditti and A. Oliva, *Bot. Gazette* **145**, 495 (1984); W. W. Ballard, *Am. Orchid Soc. Bull.* **56**, 935 (1987); W. Frosch, *Am. Orchid Soc. Bull.* **55**, 14 (1986); J. E. Henrich, *J. Am. Soc. Hort. Sci.* **106**, 193 (1981).

Since the Symposium there has been continued activity in this field. A recent paper by Ben Linden (*Ann. Bot. Fennici* **29**:305-313, 1992) describes various techniques for improving germination. These include treatments with disinfectants, intermittent vacuum to introduce water into the testa, one week soaking in water in a rotary shaker, and enzyme treatment to degrade the cell walls. This paper summarizes the latest techniques including the components of the medium.

CHAPTER 22. THE GRASSES (POACEAE)

The family name Poaceae has been adopted in place of the older Graminae for the reasons given in Chapter 16. The data on this family has been placed in a separate Chapter for several reasons. No data on this family was included in the First Edition. Until the recent burst of enthusiasm grasses had not played a prominent role in horticulture. Even now their culture tends to be restricted to a limited group of enthusiasts. Finally it had been presumed that most if not all of the species would be D-70 germinators and not very interesting to investigate.

Twenty-one of the most popular ornamental species have now been examined. Germination was always hypogeal. All but one (*Setaria glauca*) were D-70 germinators. Light or GA-3 had no effect. The data were *Andropogon gerardii* 70(76% in 3-6 d) and 40-70(35% in 2-11 d), *Andropogon scoparia* 70(50% in 4-9 d) and 40-70(62% in 2-11 d), *Bouteloua curtipendula* 70(100% in 3-6 d) and 40-70(97% in 2-4 d), *Bouteloua gracilis* 70(100% in 3-6 d) and 40(93% in 5-8 w), *Briza maxima* 70(90% in 5-9 d) and 40(74% in 6th w), *Bromus macrostachys* 70(80% in 5-8 d) and 40(20% in 6th w), *Calamagrostis acutiflora* 70(27% in 2nd w) and 40-70(20% in 4-7 d), *Eleusine coracana* 70(50% in 5-6 d) and 40-70(none), *Festuca glauca* 70(100% in 5-8 d) and 40(86% in 3rd w), *Festuca mairei* 70(60% in 6-9 d) and 40(50% in 8-12 w)-70(30% in 2-6 d), *Festuca ovina* 70(65% in 5-9 d) and 40(60% in 1-5 w), *Festuca novae-zealandiae* 70(90% in 3rd w) and 40(7%)-70(75% in 4-11 d), *Hystrix patula* (5% in 4th w) and 40-70(31% in 2-12 d), *Koeleria glauca* 70(100% in 4-8 d) and 40(100% in 6th w), *Lagarus ovatus* 70(100% on 3rd d) and 40(100% in 5th w), *Melica ciliata* (95% on 3rd d) and 40(100% in 6th w), *Miscanthus hybrid* 70(55% in 3-9 d), *Panicum violaceum* 70(100% on 2nd d) and 40(40% in 6th w)-70(6%), *Panicum virgatum* 70(80% in 3-9 d) and 40-70(80% in 2-6 d), *Pennisetum alopecuroides* 70(95% in 2-5 d) and 40(70% in 7-12 w), *Pennisetum villosum* 70(100% in 4-9 d) and 40-70(30% in 4-6 d), *Setaria glauca* 70(25% in 4th w)-40-70(75% on 6th d), *Stipa capillata* (1/6 on 9th d), and *Stipa pennata* (1/7 in 8th w).

The above data is interesting in showing that some species germinate at 40 as well as 70, other germinate only on shifting from 40 to 70, the 3 m at 40 is deleterious to many, and the 3 m at 40 benefitted *Hystrix*. In general there is no advantage to sowing the seeds at 40. Eight of the above were placed outdoors in October and all had rotted by spring so that outdoor treatment is not recommended.

CHAPTER 23. LIST OF DONORS OF SEEDS

Many botanic gardens, individuals, and botanical expeditions contributed seeds for the studies. It is a pleasure to acknowledge these invaluable contributions now. A particular debt is owed to John and Janet Gyer, Don Hackenberry, Gwen and Panayoti Kelaidis, and my wife Ginny. These people not only went out of their way to collect seeds, but they understood the work and were a source of encouragement. James Wilson of the Television Series Victory Gardens gave valuable editing advice. Unusually generous supplies of seeds were received from James Forrest in New Zealand, Leon Glicenstein in California, Barry Glick in West Virginia, Doris Goldman in Pennsylvania, and Ron Ratko in Washington. John Gyer conducted several critical experiments. I am also indebted to all of my old colleagues in the field of physical organic chemistry. We had wonderful years opening a new field.

Botanic Gardens

Czechoslovakia: National Botanic Garden

Republic of China:

Beijing Botanic Garden, Beijing

Nanjing Botanical Garden, Nanjing

Italy: Parco Nazionale Gran Paradiso

Mongolia: Hortus Botanicus Mongolia

Japan: Nippon Shinyaku Institute for Botanical Research

Sweden: Goteborg Botanic Garden, Goteborg

United States:

Denver Botanic Garden, Denver, Colorado

Mount Cuba Botanical Garden, Pennsylvania

New York Botanic Garden, New York, New York

U.S.S.R.:

Hortus Botanicus Tallinnensis (Tallinn, Estonie)

Khorog Botanic Garden, Khorog

Leningrad Botanic Garden, Leningrad

Moscow Botanic Garden, Moscow

Sverdlovsk Botanic Garden, Sverdlovsk

Tashkent Botanic Garden, Tashkent

Tbilisi Botanic Garden, Tbilisi

Finland: Hortus Botanicus Hauniensis

Seed Exchanges

American Rock Garden Society, British Alpine Society, Scottish Rock Garden Club

Seed Companies

Burpee Seed Co., Pennsylvania; Jelitto Seeds, Germany; Thompson and Morgan, Ipswich, England

Source of Gibberelic Acid-3

Abbott Laboratories Agricultural Research Division, Long Grove IL, gave a generous sample of gibberelic acid-3. Special acknowledgement is given to Dr. Roland Carlson and Dr. Michael Meyer of Abbott Laboratories.

Seed Collecting Expeditions

Archibald, Jim and Jenny: Rocky Mountains U.S. and Eastern Turkey and Iran
 Barr, Claude: Central U.S.
 Chadwell, Chris: Kashmir and Ladakh in India; Nepal
 Halda, Josef: Pamir Mountains and Siberia
 Kelaidis, Gwen and Panayoti: Rocky Mountains U.S.
 Plestl, Vaclav: Czechoslovakia
 Walker, Sally: Southwestern U.S. and Mexico

Individuals

Alexander, Anita		Allen, Emmy Lou	Ashland OR
Avent, Tony	Raleigh NC		
Bartolomei, Robert P.	New York NY	Beatty, George	Lemont PA
Beckwith, Ronald	Southampton MA	Behmlander, Doris and Harold	Saginaw MI
Berginiec, Ted	Milwaukee WI	Brinckerhoff, Ellie	West Redding CT
Burnett, Tig	Boalsburg PA	Burrell, Mrs. Clark	WY
Butler, Harry	Spring Valley OH		
Case, Fred and Roberta	Saginaw MI	Clark, Doroyth	Stamford NY
Clinebell, Richard	San Francisco CA	Cobb, Ray	
Collins, Mary	NJ	Colvin, Mina	Nashville IN
Cooke, Charles	Corning NY	Correvon, Henry	SWITZERLAND
Critz, Richard	Rosemont PA		
Deno, Bina	Berwyn PA	Deno, Don	Lennox MA
Desmond, Sally	Mackeyville PA	Deurbrouck, Al	Pittsburgh PA
Drake, Jack	SCOTLAND	Driscoll, Thomas	Ambler PA
Driver, Lloyd	State College PA	Duchacova, Olga	CZECHOSLOVAKIA
Elkins, Harry	Grosse Point Park MI		
Fenderson, G. K.	South Acworth NH	Fingerut, Joyce	Fort Washington PA
Flook, Marnie	Chestertown MD	Forrest, James	Tauranga, NEW ZEALAND
Foster, Linc	Falls Village CT		
Gehenio, Carl	Tarentum PA	Gevjan, Roxie	Newtown Square PA
Glattstein, Judy	Wilton CT	Glicentein, Leon	Salinas CA
Glick, Barry	WV	Goldman, Doris	Waynesboro PA
Goplerud, Robert	Livonia MI	Goroff, Iza	East Troy WI
Graham, Paul	Corning NY	Guest, Stephen	Charleston WV
Gyer, John and Janet	Clarksboro NJ		

Hackenberry, Don	Reedsville PA	Haines, Ben	NB
Hamilton, Robert	State College PA	Harkness, Bernard	NY
Harper, Pamela	Seaford VA	Hartell, Tam	Philadelphia PA
Haumont, Frieda	Wyoming	Hawkins, Judith	Rockmart GA
Healy, Trudy		Heapes, Robert	Parker CO
Hildebrandt, George	State College PA	Hull, Catherine	Manchester MA
Jacobs, Don	Decatur AL		
Kammereck, Ursel	Cashmere, WA	Keisling, Paul	Boylston MA
Kelaidis, Gwen and	Panayoti Denver CO	Kistler, Anita	West Chester PA
Kline, Boyd	Medford OR	Knapp, Joann and Fred	Locust Valley NY
Leamy, Bodil	British Columbia	Lighty, Richard	PA
Lippitt, Kathie	Scotia NY	Long, James	Marion VA
Lutz, Lois	Boalsburg PA		
MacPhail, James	BC, CANADA	McDermott, Robert	Pittsburgh PA
Means, Joan and Robert	Georgetown MA	Mech, Betty Ann	Minneapolis, MN
Mellichamp, Larry	NC	Mineo, Baldassare	Medford OR
Nickou, Nicholas	Branford, CT		
Palomino, Paul	Seaford NY	Patten, Bill	PA
Pfeiffer, Howard	Mansfield CT	Plestl, Vaclav	CZECHOSLOVAKIA
Ratko, Ron	WA	Redfield, Richard	Hampton CT
Redos, Michael	Renovo PA	Roback, Helen	King of Prussia PA
Sauer, R. E.	Oialla WA	Schick, Peter A.	WA
Skrocki, Ed	Southington OH	Smith, Don and Hazel	NJ
Spingarn, Joel	West Reddomg CT	Stoutamire, Warren	Akron OH
Summers, Alan	Westminster MD		
Tietjens, Marie and Max	Blue Bell PA	Tindall, Tom	Mars PA
Tressler, Martha	State College PA	Tuomey, Ann	Wexford PA
VanderPoel, Waid	Barrington IL		
Way, Robert	Kennet Square PA	Weydahl, Christen	NORWAY
Whittemore, Evelyn	Penrose NC	Williams, Margaret	Sparks, NV
Wister, Mrs. John C.	Swarthmore PA	Wurdack, John	Beltsville MD
Yelton, Ernest	Rutherfordton NC	Zabkar, Paulette	Pittsburgh PA
Zielinski, Eugene	Milesburg PA	Ziehl, Dianne	Tawas MI

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CHAPTER 25. DIGEST OF SYMBOLS AND ABBREVIATIONS

Letters

- DS dry storage with the temperature (40 or 70) given after the DS
WC washed in water and cleaned daily usually for a period of seven days
GA-3 is gibberelic acid-3.
d days
m months
y years
T temperature in degrees Fahrenheit
t time

Numbers

- D-70 A species in which the seed requires dry storage before the seeds will germinate at 70.
40-70 means that the seeds were subjected to 3 m at 40 followed by germination at 70. This system can be extended indefinitely.
70-40-70-40 means that the seeds were subjected to 3 m at 70, 3 m at 40, 3 m at 70, and shifted to 40 whereupon germination began.
70D means that the seeds were in the dark.
70L means that the seeds were in the light as described in Chapter 3.
70 GA-3 means that the seeds were treated with GA-3 as described in Chapter 3.
40% In referring to germination this means 40% of the normal sized seed coats germinated. Some attempts were made to discard and not count undersize seed coats, seed coats that readily crushed and were obviously empty, and overly thin seed coats that were empty of endosperm.
in 6-10 w Referring to germination this means that germination started at the end of the 6th week and ended at the end of the 10th w.

Abbreviations

- ind. t is the induction time, which is the time between the seeds being shifted or started in a particular cycle and the time the seeds start to germinate in that same cycle.
25%/d means that 25% of the seeds germinate in each day once germination starts.
half life This is the time for half of the seeds to germinate again starting from the time germination starts
zero order rate This is a rate in which a constant amount germinates in each time period
first order rate This is a rate in which a constant fraction germinates in each time period
germ. germinated