SEED DORMANCY AND ITS RELATIONSHIP TO NURSERY PRACTICES

DALE E. KESTER
University of California, Davis

A seed may fail to germinate for three basic reasons. First, it may be non-viable and thus incapable of development. Secondly, it may be subjected to environmental conditions which are unsuitable for germination. Thirdly, the seed may be affected by specific internal conditions — either in the seed coverings or in the embryo itself — which prevent germination from taking place until such time as these conditions are removed. The latter cause of non-germination will be the subject of this paper.

CONCEPT OF DORMANCY

Dormancy refers to failure to grow or to germinate. It may be due to either environmental conditions outside the plant or seed or to conditions inside the plant or seed itself. To separate environmental and internal factors arbitrarily is difficult because the end result usually depends upon an interaction between both. That is, the effects of a specific internal condition within the seed which prevents germination may differ depending upon the environment in which the seed is placed.

On the other hand, the distinction between external and internal factors is usually made and dormancy in seeds has usually been used only in reference to conditions within the seed that prevent germination. Thus, the "normal" environmental requirements for germination are recognized as being a supply of moisture, a moderately warm temperature and a supply of oxygen. Failure of a viable seed to germinate because of the effect of some condition within the seed covering, the endosperm or in the embryo itself is considered to be seed dormancy. It has generally been recognized that such conditions have arisen through the evolutionary development of the particular plants because such characteristics have assisted survival during adverse periods of their natural environment.

CAUSES OF SEED DORMANCY

There are various conditions within seeds which cause dormancy and considerable information is available as to suitable methods of treatment. Much work concerning the problem has been carried out by the Boyce Thompson Institute of Yonkers, New York. Reviews of the work on seeds are available (3, 5, 17, 11). Attention should be called to the recent review by Dr Lela Barton at the 6th annual meeting of the Plant Propagators Society (2).

An outline of the various causes of dormancy and the general methods by which they can be overcome follow.

A CLASSIFICATION OF SEED IN RELATION TO TYPES OF DORMANCY WITH EXAMPLES

Seeds which have seed coats that are hard or impermeable to water

Species: *Acacia, Albizzia,* Amorpha, camellia, carob, *Ceanothus* (some species) chamise (*Adenostoma*), *Cytisus,* goldenrain tree

(*Koelreuteria*), honeylocust (*Gleditsia*), locust (*Robinia*), olive, *Parkinsonia, Rhus* (some species), *Sophora*.

Treatments: (1) Scarification: file or rub individual seeds with sandpaper, for large lots use mechanical scarifier.

(2) Sulfuric acid: place seeds in concentrated sulfuric acid for fifteen minutes to six hours depending upon species, follow by washing to remove the acid.

(3) Hot water: drop the seeds into hot water (180 to 212°F). Remove heat immediately and leave in gradually cooling water for six to twelve hours.

(4) Warm stratification: place seeds in warm, moist conditions to allow microorganisms to soften coats, may require several months.

Seeds which have a dormant embryo that responds to chilling

A. Those which require a single stratification period.

Species: a) fruit and nut trees. almond, apple, cherry, chestnut, grape, peach, pear, plum, walnut.

b) ornamental and forest plants: *Arborvitae*, alder (*Alnus*), *Amelanchier*, ash, barberry (*Berberis*), beech, birch, boxwood, *Chamaecyparis, Clematis* (some species), *Ceanothus* (some species), *Cercocarpus*, cypress, dogwood, Douglas fir, *Exochorda*, fir (*Abies*), *Garrya, Gaultheria*, hemlock (*Tsuga*), honeysuckle, larch, liquidamber, madrone, magnolia, *Mahonia*, maple (some species), *Myrica, Osmaronia, Photinia*, pine (some species), *Prunus*, pyracantha, *Rhamnus*, rose, spruce, sycamore, *Styrax, Viburnum* (some species), tulip tree.

Treatment: Stratify by holding the moist seeds at 32 to 50° F for one to as long as three to four months or more. May be fall planted or the pre-soaked seeds may be mixed in a moisture retaining material and stored out of doors in stratification pits or placed in metal (or plastic) containers and stored in commercial storage units.

B. Those requiring a warm period for root or embryo development prior to the chilling period.

Species: Some lilies, peony, a number of *Viburnum* species, wild ginger (*Asarum canadense*). Holly, fringe tree (*Chionanthus*), *Nandina* and ginkgo possibly should be listed here.

Treatment: Stratify at a warm temperature for several months followed by cold stratification for several months

C. Those requiring two consecutive chilling periods separated by a warm period.

Species: A few natives of temperate zone — *Trillium*, blue cohosh, lily-of-the-valley, solomon's seal, bloodroot, and false solomon's seal.

Treatment: Cold stratification for several months, followed by warm stratification of several months, followed by a second cold stratification.

Seeds which combine an impermeable seed coat with a dormant embryo

Species: *Arctostaphylos, Ceanothus* (some species). *Cotoneaster*, Dogwood (some species), elder (*Sambucus*), hawthorn (*Crataegus*), Halesia, holly (*Ilex*), honeysuckle (some species), juniper, linden (*Tilia*) mountain ash (*Sorbus*), *Rhus* (some species), *Symphoricarpus*.

Treatment: (1) Treat by softening the seed coat followed by a cold stratification period.
(2) Give a warm stratification period of several months followed by a cold stratification period.
(3) Harvest the seeds when immature and do not allow them to dry before stratification

Seeds which contain inhibitors that prevent germination

Examples: A number of inhibitors have been identified in fruits and possibly may affect germination whenever a fruit part such as a hull, etc. is still retained on the seed. Presence of inhibitor affects germination in beet, pistache, guavule, a number of desert plants.

Treatment: Prolonged soaking in water to wash out the inhibitor.

Seeds which are dormant when freshly harvested but become germinable upon dry storage

Examples: Most grains, grasses, vegetables, many flower seeds

Treatments. This type of dormancy is difficult to classify since it is interrelated to specific environmental requirements. It is principally a problem of seed testers rather than propagators except in specific cases. Principal means of treatment include exposure to light, alternating temperatures, chilling and potassium nitrate. A number of such seeds germinate at 70-75° or less and become dormant at higher temperatures.

STRATIFICATION OF SEEDS

The group of seeds to be discussed in most detail are those which have a dormant embryo and which respond to stratification. *Stratification* refers to the procedure of mixing seeds with a moisture retaining medium, and holding them cold and moist for a prescribed length of time. During stratification certain internal changes take place which allow germination to proceed without hindrance. These changes have been referred to as "after-ripening" and, for want of a better term, it will be used here.

This pre-germination treatment is the commonest germination requirement for species of trees and shrubs found in the temperate zone. Of 444 species of plants listed in the Woody Plant Seed Manual 43 per cent have this requirement and an additional 17 per cent have dormant embryos combined with a hard seed coat, 60 per cent of the total species described (17). Seeds of practically all deciduous fruit tree species require stratification.

The general procedure for handling such seeds is reasonably well-known and probably has been recognized for centuries. On the other hand, the basic reason why such seeds are dormant is largely unknown although some of the biological changes that take place have been described (9).

After-ripening is a gradual, progressive change under proper environmental conditions of stratification. The seed becomes less and less dormant and more and more ready to germinate. Germination may then begin even at the low temperature of stratification. What may not be recognized as equally important is that the after-ripening reaction is reversible. If environmental conditions during stratification should change to that which will be discussed later, the degree of dormancy in the seed may increase rather than decrease.

Environmental Influences on Stratification

The four environmental factors which are necessary for the after-ripening reaction to be completed are moisture, low temperature, aeration, and a certain amount of time. The four factors will be considered in some detail.

Water. After-ripening does not take place in a dry seed but only after a certain amount of water has been absorbed. Thus, pre-soaking seeds in preparation for stratification is desirable, if not essential, to insure that sufficient moisture is in the seed at the beginning of the

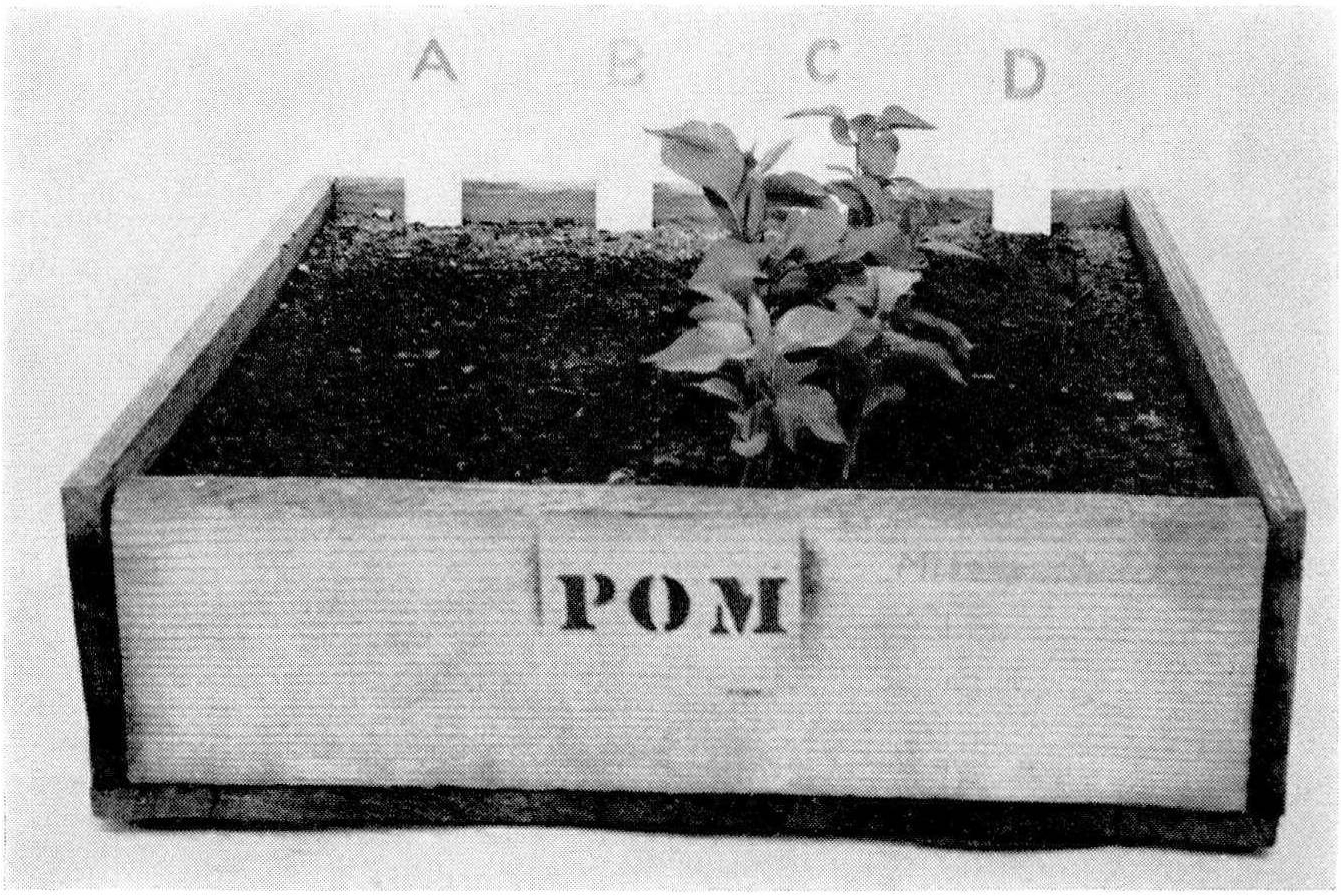

Figure 1.—Effect of environmental factors during stratification on germination of *apple seeds, A. unstratified seed, B. dry, 37° F, C. moist, 37° F, D. moist, 37° F, sealed container. Stratification time approximately 3 months.*

stratification period. Secondly, the seeds should not be allowed to become dry during stratification. If drying does occur, after-ripening ceases and, it is generally believed, will be reversed (12). On the other hand, some studies have indicated that reversal of after-ripening may not necessarily occur with drying (4, 13, 14, 16). This point should be clarified. If stratified seeds could be dried (under proper conditions) prior to sprouting, it would greatly facilitate planting.

Once the stratified seed begins to sprout, rapid absorption of moisture takes place and drying out at this point is decidedly injurious to the seedling.

Aeration. After-ripening requires air, presumably oxygen. That poor aeration can retard or stop the process can be easily demonstrated (see Fig. 1). Many years ago workers at the Boyce Thompson Institute showed that nondormant seed subjected to a carbon dioxide atmosphere become dormant and respond to stratification (6, 15). The principal point as regards stratification practices is to be sure that there is good aeration in the stratification containers.

Temperature. Temperature response is the most important difference between after-ripening and germination. A comparison of the temperature relationship of the two processes is shown in Fig. 2.

After-ripening takes place at cool temperatures from about freezing or slightly below to around 55 to 60 degrees F and ceases, and, at least in some cases, is reversed at higher temperatures. The temperature requirement for after-ripening has narrow limits for some kinds of seed. For instance, Barton (2) reports that *Rosa rubiginosa* seeds stratified for six months at a series of different temperatures germinated only after being stratifed at 41° F. On the other hand, seed of most species respond to a range of low temperatures although some temperatures are more favorable than others.

The range of favorable stratification temperatures has been established for many seeds (3). The effectiveness of different temperatures for after-ripening shown in Figure 2 is based upon detailed experimental work carried out recently in Europe on apple seed (1, 8, 14). Although comparable data of this detail is not available on other species, the relationship shown fits closely with present concepts of the phenomenon and should be expected to hold approximately for many, if not most seeds, requiring stratification.

Optimum temperatures for after-ripening in the case of apple are shown to be in the range of 37° F to 41° F. At temperatures lower than optimum, effectiveness becomes less but is still quite good at 32° F. It ceases somewhere around 5 to 7° F below freezing. As temperatures go higher than the optimum their effectiveness becomes less and less until a point is reached where the after-ripening process ceases. As temperatures go still higher than this point, after-ripening actually reverses itself and the seed becomes more and more dormant. In the experiment cited the "compensation temperature" (where after-ripening neither proceeded nor was reversed) was 17° C., slightly over 60° F.

Figure 2 also shows the effect of temperature on germination in the case of *nondormant* seeds of apple and radish. Both show basically

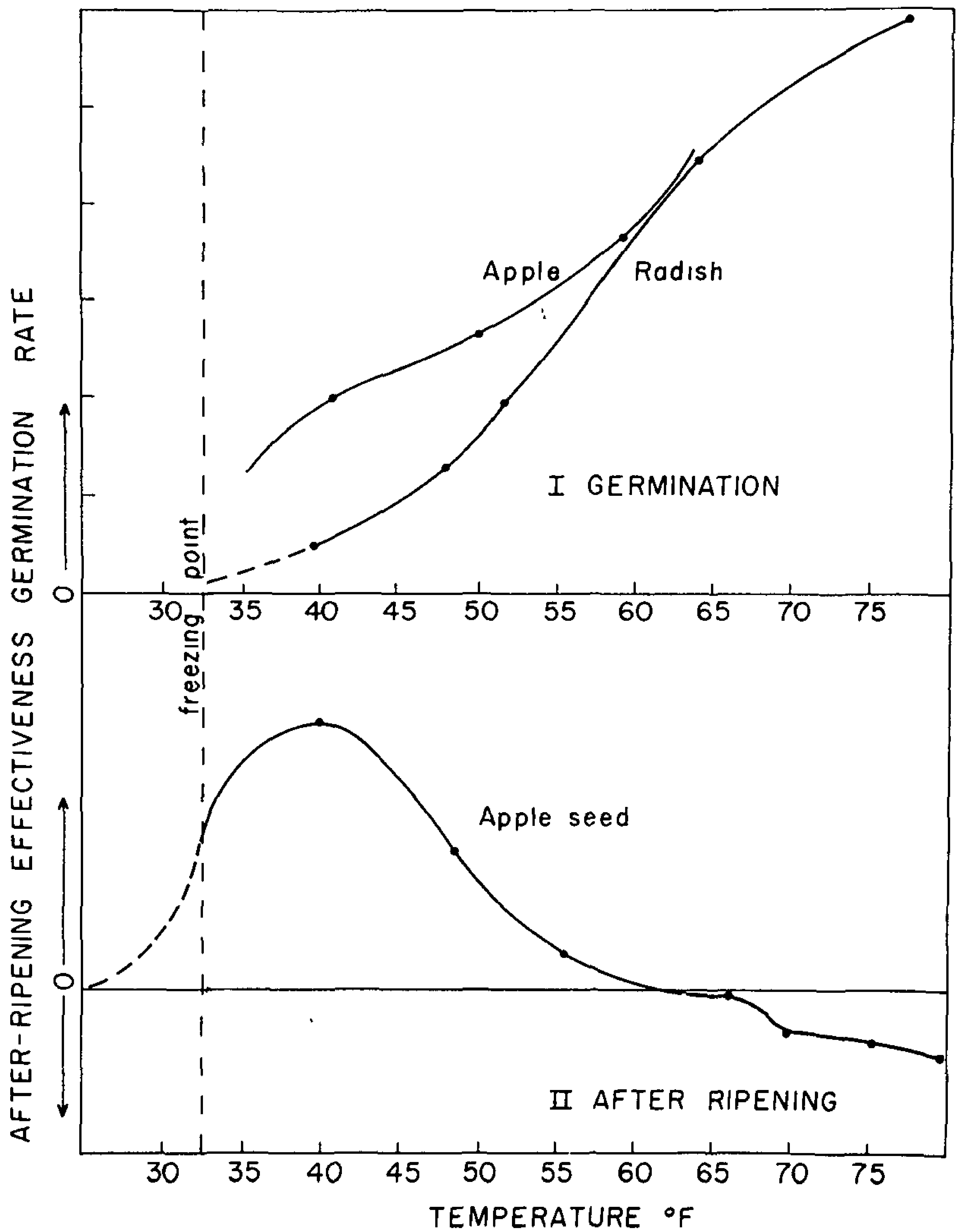

Figure 2.—Effectiveness of temperature of after-ripening (below) compared to its effectiveness on germination (above). Apple Data from Abbott (1) and Schander (14). Radish data from Figure 6-2 in Hartmann and Kester (11).

similar responses. The graph shows that at or near freezing temperatures, germination is either non-existent or very slow. As the temperature increases, the germination rate also increases. Optimum temperatures are somewhere around 70 to 80° F or higher depending upon the kind of seed.

In actual practice temperature does not affect the two processes — after-ripening and germination — separately as shown in Figure 2 but involves the two processes simultaneously Figure 3 shows experimental germination data which parallels conditions that can exist in nursery practice. The seed — again apple — were stratified at 37° F for 65 days and then germinated at the temperatures indicated in the graph (8).

Germination occurred most rapidly at 60° F but only a portion of the seeds germinated. In other words, at the higher temperature where germination was most favored, some of the seeds remained dormant Such seeds may not only fail to germinate but may develop secondary dormancy and require a second stratification period. Thus, if relatively high soil temperatures occur after planting — for instance, if planting is delayed or if unseasonably warm temperatures prevail early in the season — poor stands may result. This situation has apparently occurred some years in our nursery at Davis Such unsprouted seeds remain in the soil all summer and sometimes have been observed to sprout in large numbers the folowing year. Also, in breeding programs for stone fruits at Davis, California, seeds are stratified in controlled cold storage at 36° F and germinated in the greenhouse where relatively high daytime temperatures can occur. It has generally been observed that unless a seed is actually sprouting at the time of planting, it will probably not germinate in the greenhouse even though it is viable, has been stratified for the prescribed length of time and others of the lot are sprouting

Germination of stratified seed of Eastern Hemlock (*Tsuga canadensis*) has also been shown to be inhibited by warm temperature (13). The optimum temperature was 62° F

Seeds planted at 50° F took slightly longer to germinate but higher percentage of germination resulted although not enough to produce a complete stand. At temperatures of 45° F the germination was still more delayed but complete germination of all of the seeds took place. In other words, the temperature was cool enough for after-ripening and warm enough for germination to take place with no inhibition. This situation probably occurs in the open when seeds either are planted in the fall or are planted early in the spring when temperatures are cool. Good stands can result even though the seeds are not completely stratified at the time of planting.

At temperatures approaching freezing after-ripening continues but the germination is much delayed Thus as stratified seed nears the stage where sprouting will begin and if planting is to be delayed, the seeds can be shifted to colder temperatures and held for some time to delay sprouting. Work in Germany (7) indicated that the seeds can be held effectively at temperatures as low as 28° F. They also report that if apple seeds are air dried at this low temperature they can be held for a long period of time without losing their readiness to germinate

Time Time is closely related to temperature. The after-ripening reaction requires a certain amount of time to complete (as already indicated) but the requirement varies with temperature. The shortest time is required at optimum temperatures. As the temperature deviates from optimum the stratification requirement becomes longer and longer

An important aspect of the stratification problem is that individual seeds within a given lot have different time requirements. Figure 4 illustrates this fact with cherry seed in that the percentage capable of germinating increases with time. Similar results are shown with *Abies* in Figure 5 which shows germination at warm temperatures following different periods of stratification time. In this species, as in many conifers (3) some germination can occur even without stratification but the results are erratic and germination is very slow. Increasing the length of stratification thus can increase not only the percentage of germination but also the rate of germination. It can reduce the effects of the high temperature inhibition shown in Figure 3.

The variability of time requirement in individual lots creates an important practical problem. Thus, if the time to remove seeds from stratification is established by the time that the first sprouting occurs, then many of the seeds will still be dormant. On the other hand, if one waits until all seeds of the lot have sprouted to indicate that the stratification period in all seeds is complete, then many will be over

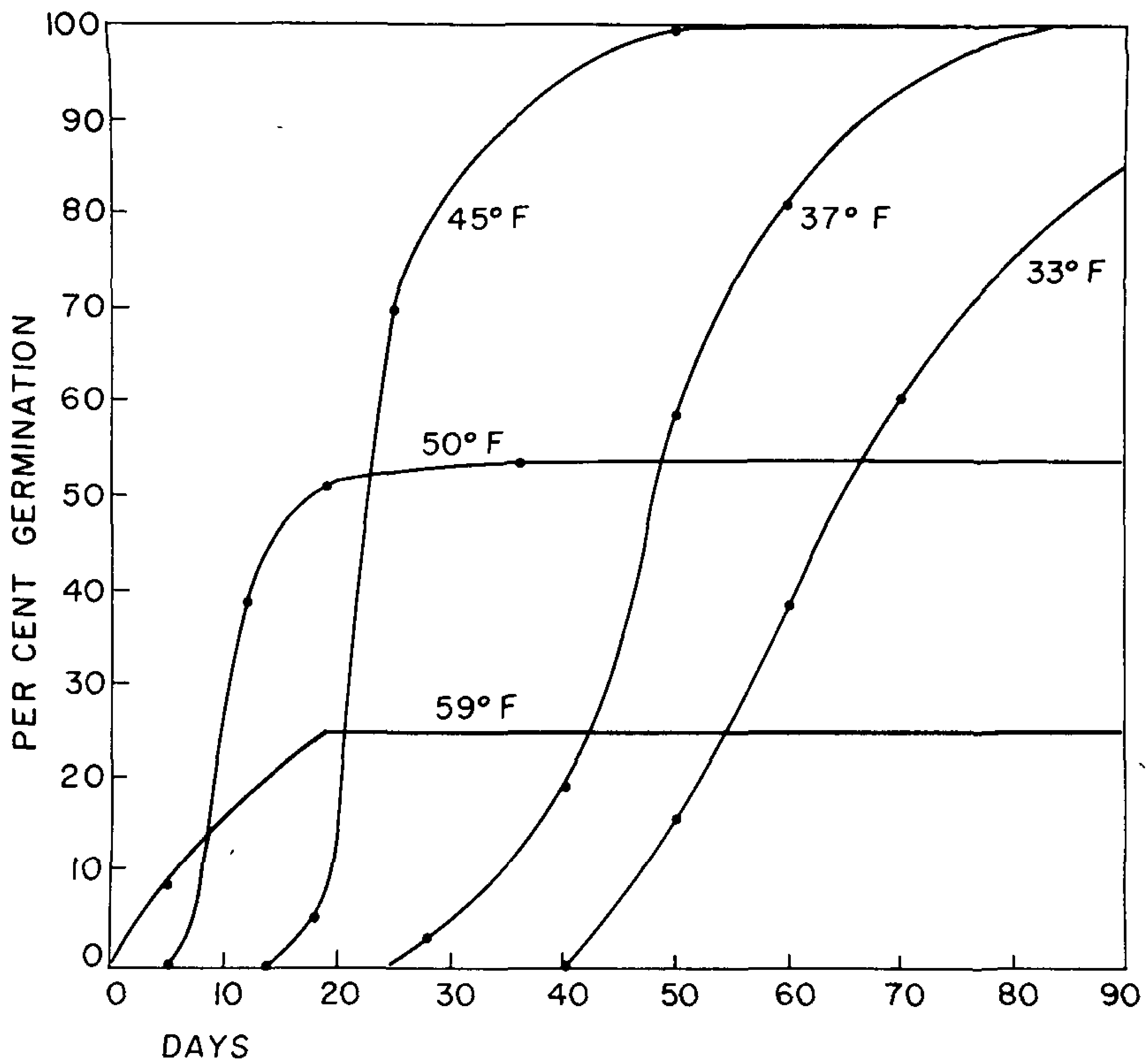

Figure 3.—The effect of temperature on germination of apple seeds that had been previously stratified for 65 days at 37° F. The abscissa is the days following stratification From De Haas and Schander (8).

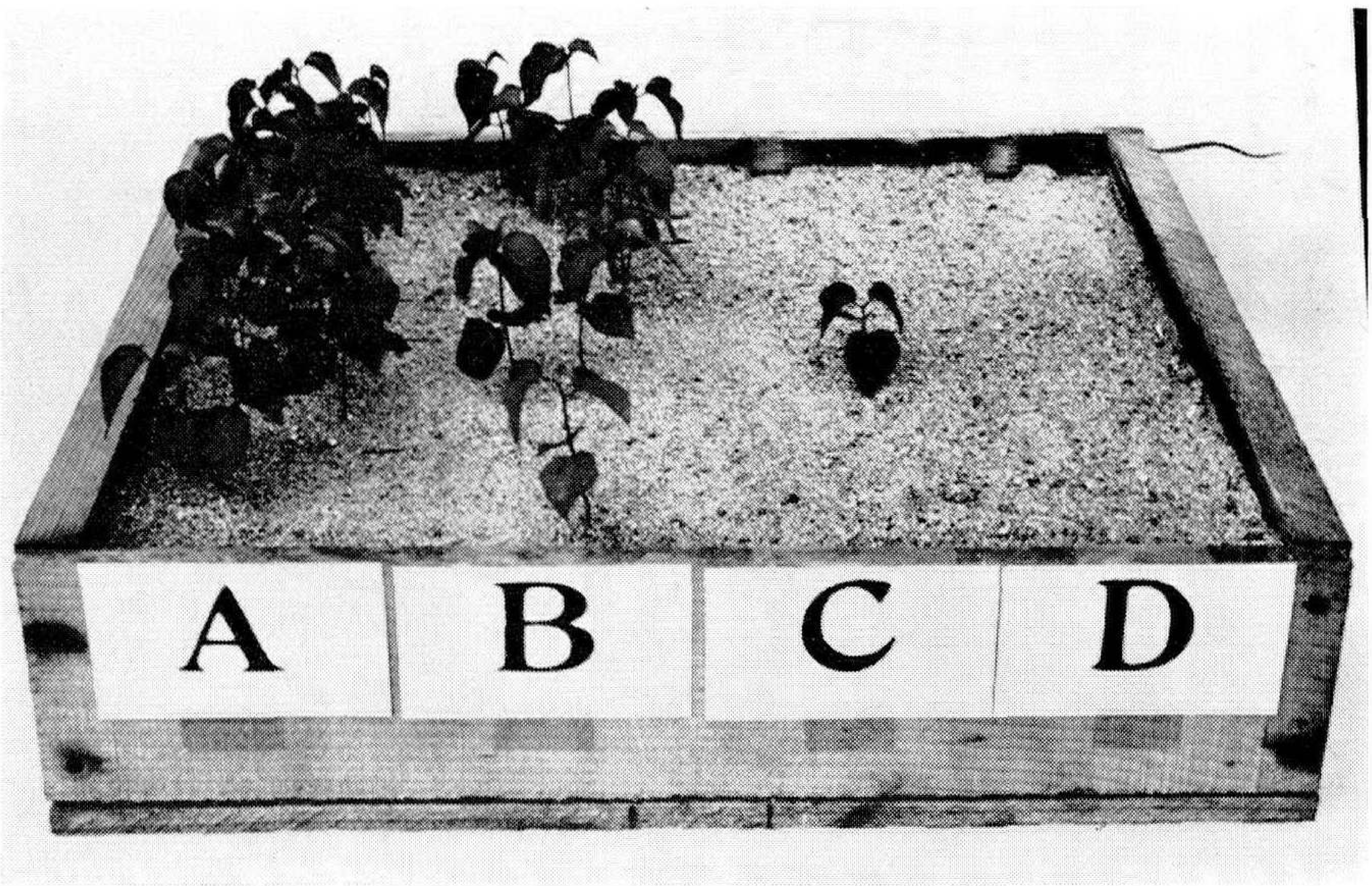

Figure 4.—The effect of stratification time on germination in Mahaleb cherry seeds. A. stratified 127 days. B. stratified 89 days, C. stratified 39 days, D. unstratified. Temperature of stratification was 32° F. Reprinted from Hartmann and Kester (11).

sprouted and injury during planting is likely to occur.

Differences in time requirement also exists between diffrent species as indicated by the time requiremnt for the following common fruit tree species.

American plum	5-6 months	Pear	1½-3 months
Almond	3-4 weeks	Peach	1-3 months
Apricot	3-4 weeks	Myrobalan plum	3-4 months
Apple	2-2½ months	Mahaleb cherry	3-4 months

Differences can also exist among varieties of a species and among different seed sources.

Methods of Stratification

Fall planting of seeds requiring stratification is a widely used and an adequate method of handling seeds. It relies on the subjection of the seeds to natural winter chilling. Certain problems are involved, for example, the control of weeds, rodents, moisture, etc. In view of the previous discussion it is likely that the environmental conditions of temperature and moisture, both during the winter and during the spring, could have a great bearing on its success.

Outdoor stratification pits have been widely used in nursery practice. This procedure involves the stratification of the moist seeds in outdoor pits between layers of sand or other media. The same environmental problems as in fall planting would likely occur. Inadequate sanitation of the seeds could also be a problem.

Controlled temperature storage is probably preferable to the other procedures if available. At the Department of Pomology, Davis, California, pre-soaked seeds are mixed with a half sand-half peat mixture (dampened only to the extent that water can just barely be squeezed out) and placed in five gallon egg cans covered with heavy paper that has been perforated. These containers are placed at 36° F until they begin to sprout. If planting is delayed, the containers are shifted to 32° F until planting.

Polyethylene plastic bags have proven particularly satisfactory as stratification containers The plastic holds moisture but allows aeration It is transparent so that the beginning of sprouting can be noted

Aseptic stratification of seeds in sterile water and glass flasks is the method used almost exclusively at Davis, California, for seeds to grow seedlings in breeding work on stone fruits. The method, worked out by Gilmore (10) is particularly useful for small lots of valuable seed The method could possibly be extended to other species. The procedure consists of sterilizing the dry seed in a 50 per cent alcohol solution of

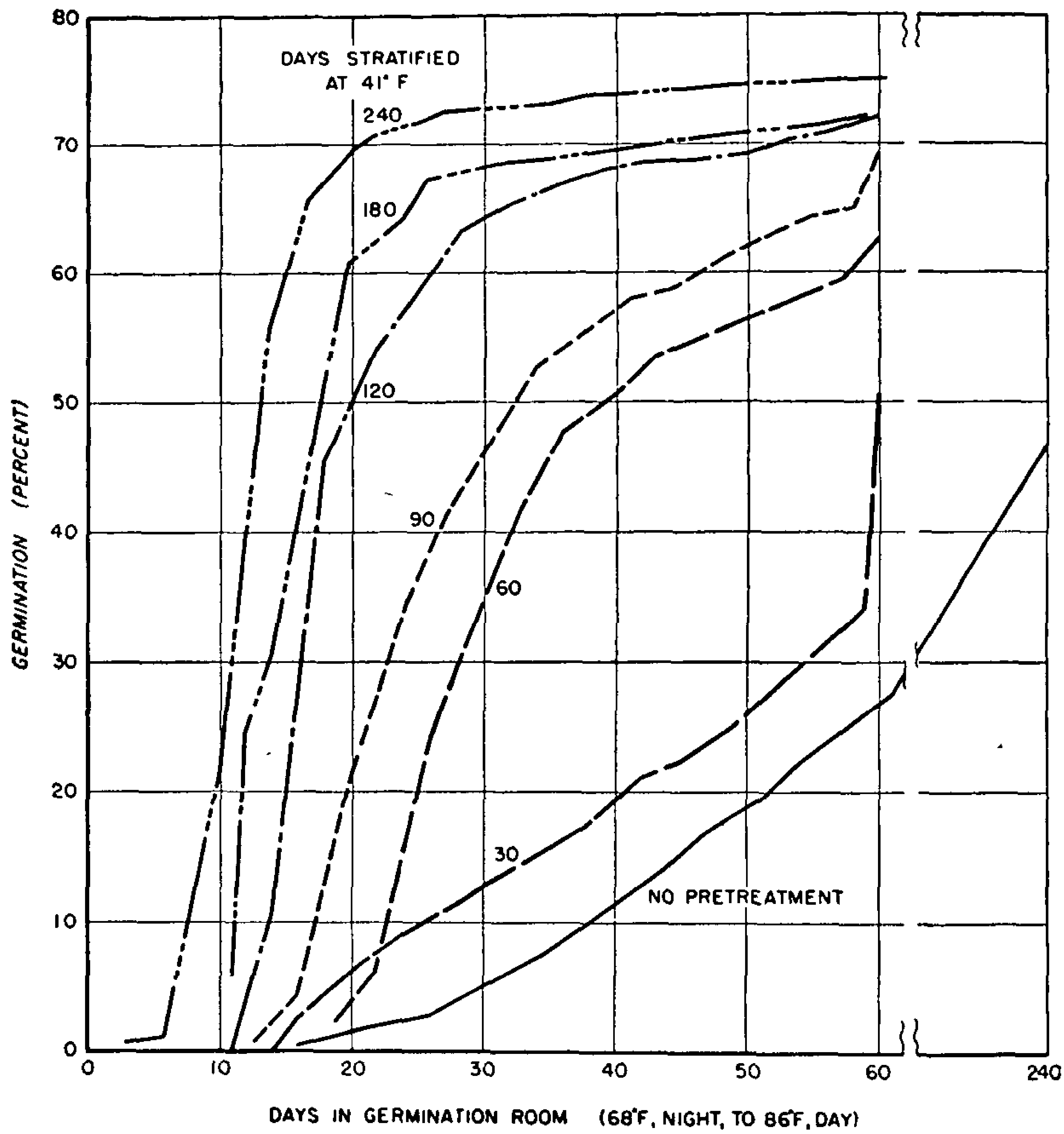

Figure 5.—Effect of length of stratification on germination of Abies seed. From Woody Plant Seed Manual (17).

merthiolate 1:2000 for five minutes followed by a five minute washing with sterile water. The seeds are stratified in sterilized glass flasks covered with inverted cotton lined beakers.

Workers in Germany have described a method of handling apple seeds which deserves recognition (7). Its success depends upon proper manipulation of the factors of moisture, temperature and time previously discussed There are two stages involved in the procedure. The first stage is the normal stratification treatment at 36° F, the second stage involves the period between the end of stratification and the time of planting. During the second stage the seeds are separated from the stratification medium and air dried at 28 to 31° F. Once the seeds are dry they can be stored for a considerable period of time without their sprouting and without altering the internal state of dormancy of the seed. The dry seeds can then be machine planted. Prompt uniform germination is reported to result.

LITERATURE CITED

1 Abbott, D L Temperature and the dormancy of apple seeds, 1955 *Rpt 14 Int Hort Cong*, pp 746-753

2 Barton, Lela V Gathering, stratification and sowing seeds 1956. *Proc 6th Ann Mtg Plant Prop Soc.* pp 95-107.

3 Crocker, W *Growth of Plants* 1948 New York Reinhold, Chap. 3

4 ______________, and L V Barton After-ripening, germination and storage of certain rosaceous seeds 1931 *Contrib Boyce Thompson Inst* 3 385-404

5 ______________, and ______________. *Physiology of seeds* 1953 Waltham, Mass · Chronica Botanica

6 Davis, W E Primary dormancy, after-ripening and development of secondary dormancy in embryos of *Ambrosia trifida* 1950 *Amer Jour Bot* 17·58-76

7 DeHaas, P G Neue Beitrage zur Samlingsanzucht bei Kernobst 1955. *Rept. 14th Int Hort Cong* pp 1185-1195.

8 ______________, and Schander, H Keimungsphysiologische Studien an Kernobst I Kamen and Keimung 1952 *Zeitschr f. Pflanzenzuchtung*, 31, Heft 4

9 Flemion, F Physiological and chemical changes occurring prior to, during, and subsequent to germination of some rosaceous seeds 1955 *Rpt. 14th Int. Hort. Cong* pp 1197-1200

10. Gilmore, A E A technique for embryo culture of peaches 1950. *Hilgardia* 20· 147-169

11 Hartman, H T, and D E Kester *Plant Propagation· Principles and Practices.* 1959. Englewood Cliffs, N J Prentice-Hall

12 Haut, I C The influence of drying on after-ripening and germination of fruit tree seed 1932 *Proc Amer Soc Hort Sci* 29·371-374.

13 Olsen, J S, F W Stearns, and H. Nienstaedt Eastern Hemlock Seeds and seedlings. 1959 *Conn Agr Expt. Sta Bul* 620

14 Schander, H Keimungsphysiologische Studien an Kernobst II Untersuchungen uber die Temperaturbedurnisse der Samen wahrend der Vorkeimung und Keimung 1955 *Zeitschr f. Pflanzenzuchtung* 34·421-440

15 Thornton, N C Importance of oxygen supply on secondary dormancy and its relation to the inhibiting mechanism regulating dormancy 1945 *Contrib. Boyce Thompson Inst* 13, 487-500

16 Visser, T Some observations on respiration and secondary dormancy in apple seeds 1955 *Proc Koninkl. Nederl. Akad van Wetens*, Series C, 59 325-334.

17 United States Dept of Agriculture, *Woody Plant Seed Manual.* 1948 Miscellaneous Publication No 654. Washington D C: U. S Government Printing Office.

CHAIRMAN HERB FOWLER In the stratification of cherry seeds, Mahaleb and Mazzard, is it desirable to store the seeds moist after harvest?

DR. KESTER: Apparently, cherry seeds have some problems in germination, more so than some of the other fruit species. It goes back to the long stratification time that is required. There is little question that if you dry seeds out, you do not reduce viability, with cherry or any other of the fruit tree seeds that are normally stratified. Now there is also experience of some people that if you keep them moist, you can increase percent germination. I think this goes back to the question of stratification time. However, holding seeds moist creates the problem of storage. If you could dry them and stratify them at the proper time, it would be much simpler handling for the nurseryman. Cherry seeds require three or four months, at least, for stratification, possibly more and I think it is a matter of giving a required length of time.

CHAIRMAN FOWLER: Is it possible to lower the temperature to slow down germination?

DR. KESTER: Yes, once they start to sprout, you can shift the seeds to lower temperature and slow down germination. We have done this in our own experience.

Chairman Stoutemyer introduced Mr Dennison Morey, Director of Research, Jackson and Perkins Company of California, Pleasanton, California, who discussed seed stratification procedures with special regard to roses.

SEED STRATIFICATION TECHNIQUES, WITH EMPHASIS ON ROSES

DENNISON MOREY

Jackson and Perkins Company of California
Pleasanton, California

Several of my more sophisticated friends in the trade have asked me what I felt this new society was going to accomplish. I think this is a fair question I doubt that there is anyone who does not have trouble finding the time to get things done Few of us have time for frivolous affairs. I cannot blame anyone for wanting to be sure we are going to amount to something before investing much time in this embryonic society. Unfortunately, I must confess to them that I don't know what we are going to accomplish. I do know what I think we can do and should accomplish. Frankly, I believe this group can contribute a great deal to the stability and profitability of the nursery business

There are two primary reasons for my view. The first is that the more dependable and economical propagation becomes, the more predictable and profitable production becomes. The second reason is my belief that only through cooperative development of knowledge and techniques can we hope to advance our methods fast enough to keep pace with the social and political structure in which we operate and in which we often find ourselves at a serious disadvantage.