posium is Dr. Bruce Pollock who is an outstanding authority on seed dormancy and storage.

DORMANCY AND PRETREATMENT

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This afternoon, in treating my assigned topic, "Dormancy and pretreatment," I face a difficult task. I am told that I must provide a "take-home" lesson. Unfortunately, most of you know far more about dealing with dormant seeds in practical propagation than I. Even more unfortunately, I have just completed two chapter-writing assignments on seed germination. At the conclusion of these assignments, I found myself depressed by the relative lack of scientific progress in the field during the last 30 years. If you review the scientific literature of the 1930's, you will find almost all the ideas we use today. Under these circumstances, I face the problem of providing a "take-home" lesson with some trepidation.

Therefore, instead of repeating old ideas which we all know are useful, I would like to speculate on newer ideas which I think might be important. Perhaps, at the close of the talk, some of you, from your intimate practical knowledge of seed germination, may be able to prove or disprove my speculations. After you leave, perhaps my speculations will help guide your observations in finding better ways for establishing seedlings from some of the species which are difficult to germinate.

The first point on which I would like to speculate is the importance of timing in seed germination. When we germinate seeds in the laboratory, we normally place the dry seeds under moist conditions at an "optimal" temperature and maintain that temperature continually until the seeds germinate, or until it becomes obvious that they will not germinate. In certain crops, the seed laws specify that this optimal temperature is a daily temperature alternation, but this is an alternation used continually from the beginning to the end of germination.

The thinking behind the use of constant "optimum" temperatures is based on the recognition that seeds respond to temperatures immediately during the period of exposure to the temperature in question. This is a direct type of environmental response.

Some years ago, I became interested in the phenomenon of physiological dwarfing in rosaceous seeds, particularly in

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peach. These seeds are dormant and require a period of low temperature after-ripening before germination becomes possible. If the seed coat and endosperm tissue surrounding the radicle are removed, the seed will germinate without after-ripening. However, the resulting seedlings are dwarfed, producing shortened internodes and frequently misshapened leaves. Such seedlings may continue to grow in the dwarf habit for as long as 10 years (3).

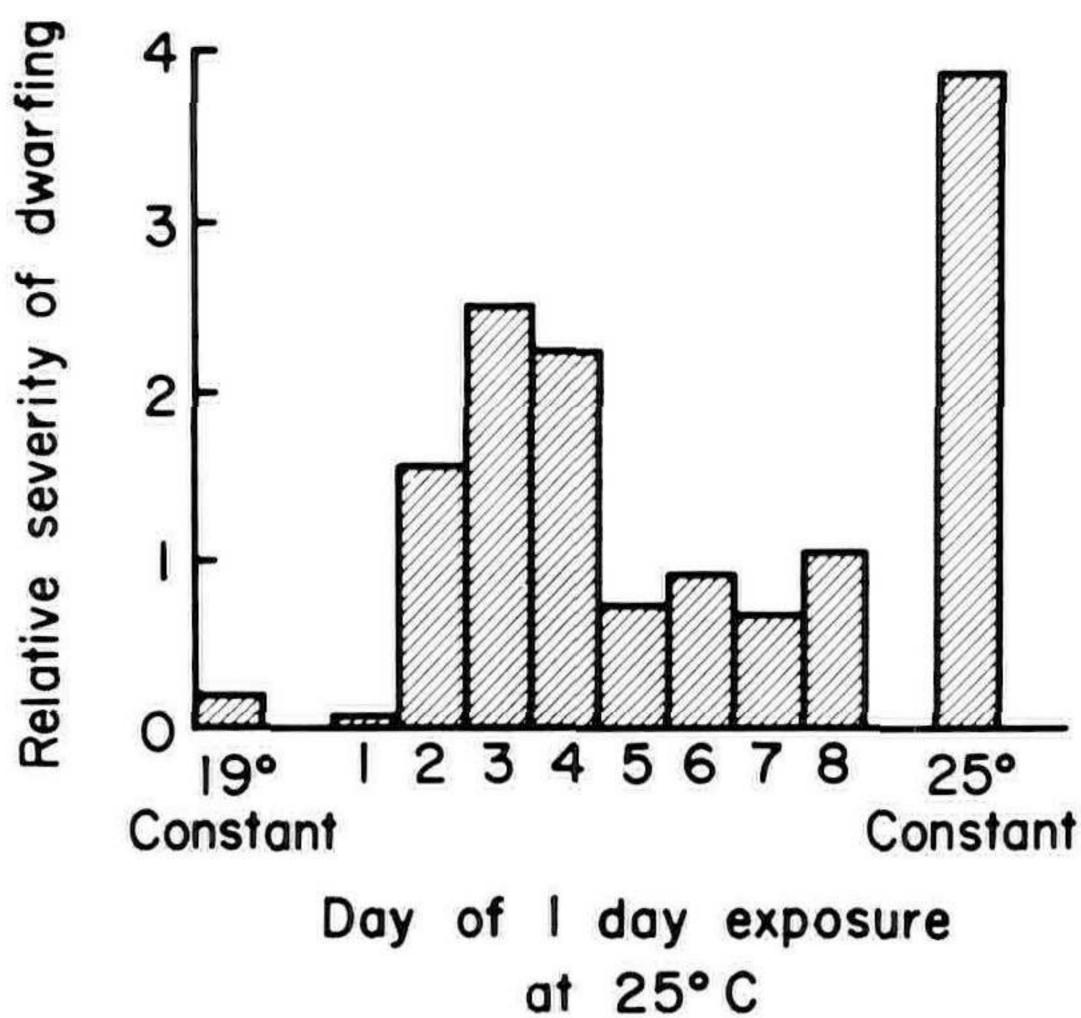
In studying this phenomenon, I found that dwarfing was a response to germination temperature (7). Seeds germinated at 27° C $(81^{\circ}$ F) or 23° C $(73^{\circ}$ F) produced dwarf seedlings, while seeds germinated at 19° C $(66^{\circ}$ F) produced normal seedlings (Fig. 1). More important for our purposes today, the response was time-specific, requiring an exposure of only one day at the high temperature for response. The one-day sensitive period occurred between the second and ninth day of germination (Fig. 2), at about the time that cell divisions begin in the apical meristem of the epicotyl.



Fig. 1.

Peach seedlings grown from non-after-ripened seeds, germinated for 8 days at the temperatures indicated and then grown 4 weeks at 25° C under a 16 hr. photoperiod.

This is an example of a delayed response to an environmental exposure, as contrasted with the direct type of response with which we are more familiar. In a delayed response, the plant may receive an environmental exposure at one time but not respond to that exposure until a later time. Obviously, such delayed responses may be very difficult to recognize when we encounter them in plant propagation.



Dwarfing of seedlings from non-after-ripened peach seeds as influenced by time of temperature exposure. The severity of dwarfing was estimated on a scale 0 (normal) to 4 (severely dwarfed).

This experience should have alerted me to the possibility that time-specific stages occur in other germinating seeds, but it did not. Later, quite by accident, we discovered that there is a tem-

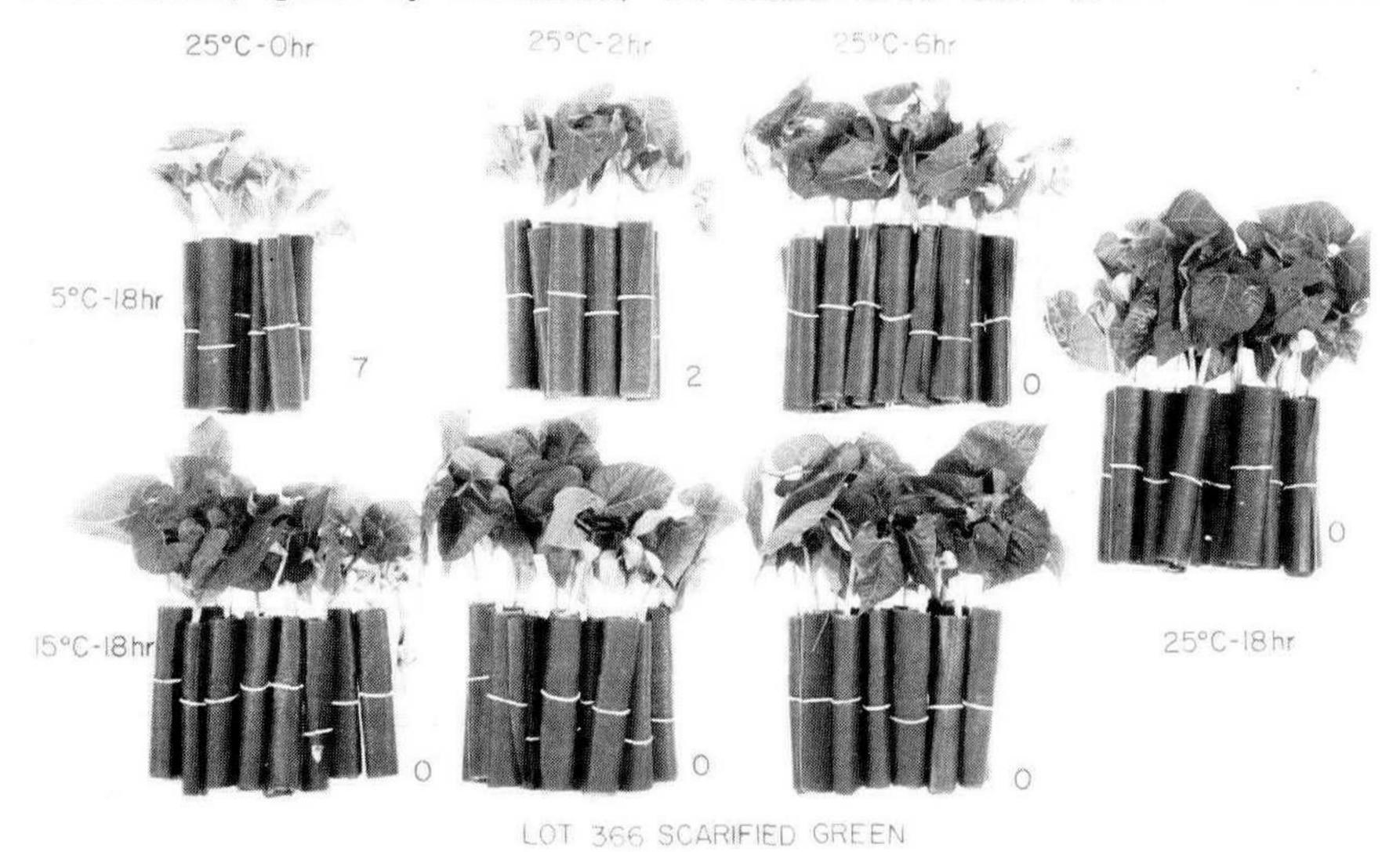
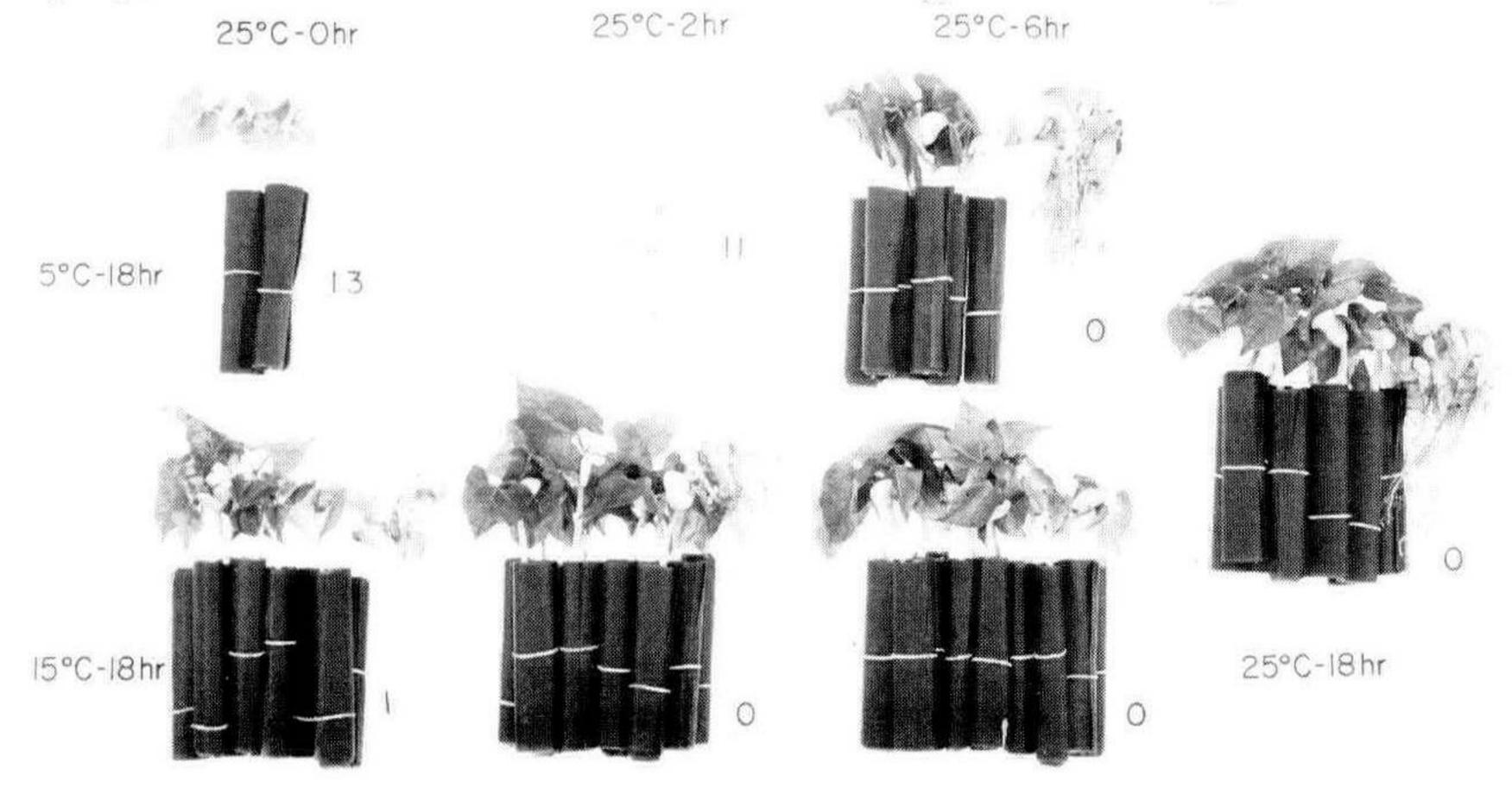


Fig. 3.
Lima bean (*Phaseolus lunatus* L. 'Thorogreen') seeds imbibed for 18 hr at 15° C (59° F) preceded by varying periods of imbibition at 25° C (77° F). After imbibition, all seeds were germinated and grown for 7 days at 25° C. The number at the right indicates the number of seeds which decayed from a 15-seed sample. Green seeds in baby limas are high vigor seeds. Figures from *Plant Physiology* 41: 221-229, 1966.

perature-sensitive stage at the very beginning of the imbibition stage in germination of lima and garden bean seeds (8, 10). Imbibition at a low temperature results in death of many seeds and reduces the size of the surviving seedlings (Fig. 3). As little as two hour imbibition at a higher temperature (25° C), is enough to reduce or eliminate chilling injury, which is much more severe in low vigor seeds (Fig. 4).



LOT 366 SCARIFIED BLEACHED Seedlings from low vigor (bleached) seeds in the same experiment as those in

Figure 3. 100 15° IMBIBITION DECAY 25° IMBIBITION 20 INITIAL SEED H20 (F.W. BASIS)

Fig. 4.

Fig. 5. The effect of initial seed moisture on decay of lima bean seedlings as influenced by imbibition temperature. Figure from Plant Physiology 44: 907-911, 1969.

In further study of this time-specific temperature sensitivity, I discovered that sensitivity is a function of seed moisture at the time of planting (9). Increasing seed moisture to above 12% eliminates temperature sensitivity (Fig. 5, 6).

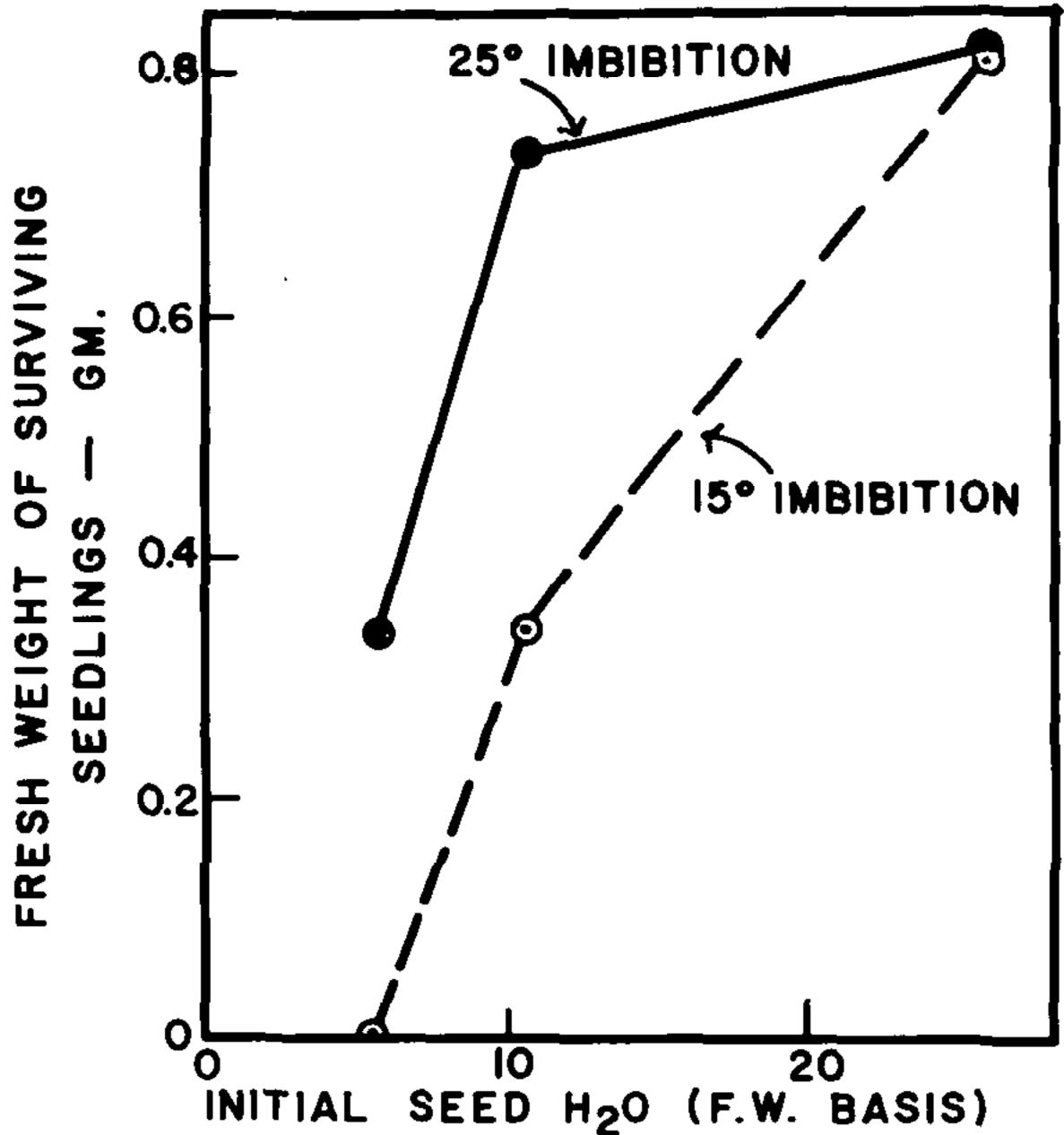


Fig. 6. INITIAL SEED H₂O (F.W. BASIS)
The effect of initial seed moisture on the size of surviving lima bean seedlings.
Data from experiment shown in Figure 5. Figure from *Plant Physiology* 44: 907-911, 1969.

Table 1.... Effect of initial seed moisture on emergence of early planted garden bean seedlings.

Variety	Lot No.	Seed moisture, percent	Emergence, percent
White-Seeded			
Tendercrop	70-1	8.8	38.3
		13.1	70.5
, ,	70-2	8.7	17.7
		13.2	54.2
Kinghorn Wax	70-5	8.6	33.2
		11.2	55.7
, ,	70-6	8.7	31.0
		11.7	68.0

This year, in early spring planting of garden beans, my colleagues, Mr. Joseph Manalo and Dr. Eric Roos, found that increasing the seed moisture prior to planting approximately doubled plant establishment (Table 1).

Thus it is clear that, for the bean varieties studied, there is a time-specific temperature-sensitive stage at the very beginning of imbibition. Pretreatments which increase initial seed moisture above a critical level eliminate this sensitive period. These results have been extended by others to include soybeans (5), sorghum (6), and cotton (1). In the case of cotton, there are actually two temperature sensitive periods; the beginning of imbibition as described above and the period 18-30 hours of germination at 31° C.

Although many seeds are routinely germinated under a daily alternation of temperatures, the rules of seed testing (4) do not specify the initial temperature to be used. Recently Elkins, Hoveland and Donnelly (2) found that the initial temperature in an alternation is important in certain species and genetic crosses of *Vicia*. There are two responses: (A) Using an alternating $4.5-21^{\circ}$ C ($40^{\circ}-70^{\circ}$ F) cycle they found that an initial low temperature greatly reduced the emergence in *Vicia sativa* and crosses of this plant type, possibly by the imbibition temperature sensitive mechanism previously described for beans. (B) In a $21-32^{\circ}$ C ($70^{\circ}-90^{\circ}$ F) alternation, when the 32° C temperature was first, germination of *V. angustifolia* was delayed, although in the end this treatment had no effect on total germination.

Based on these observations, I would like to speculate that time-specific, environment-sensitive processes are common in seed germination. Because the responses to these processes are delayed responses, I suspect that many otherwise anomalous cases of plant behavior may be the result of this type of phenomenon.

In terms of practical seed germination technique, this means that we must be very careful to avoid introducing unrecognized and hence uncontrolled variables. One such variable is the temperature of the medium into which seeds are planted. For example, seeds to be placed at an after-ripening temperature of 5° C (41° F) might frequently be planted in a germination medium at room temperature and then placed in a refrigerator. However, because of the length of time required for the germination medium to reach 5° C, such a procedure means that the actual imbibition temperature is much higher than 5° C. In Figure 7 I have plotted the rate of change in the temperature at the center of a plastic box $2.5 \times 12 \times 12 \text{ cm}$ (1 inch $\times 4\frac{1}{2}$ inch x 4½ inch) filled with moist sand. You can see that it took approximately two hours to cool from 25° C to 5° C (77° F to 41° F). This period is long enough to obscure the existence of imbibitional temperature sensitivity. In the case of dormant seeds which require a low temperature after-ripening period, as far as I know we

have no information available on the effect of initial imbibition temperature on subsequent plant response. However, it may well be of importance.

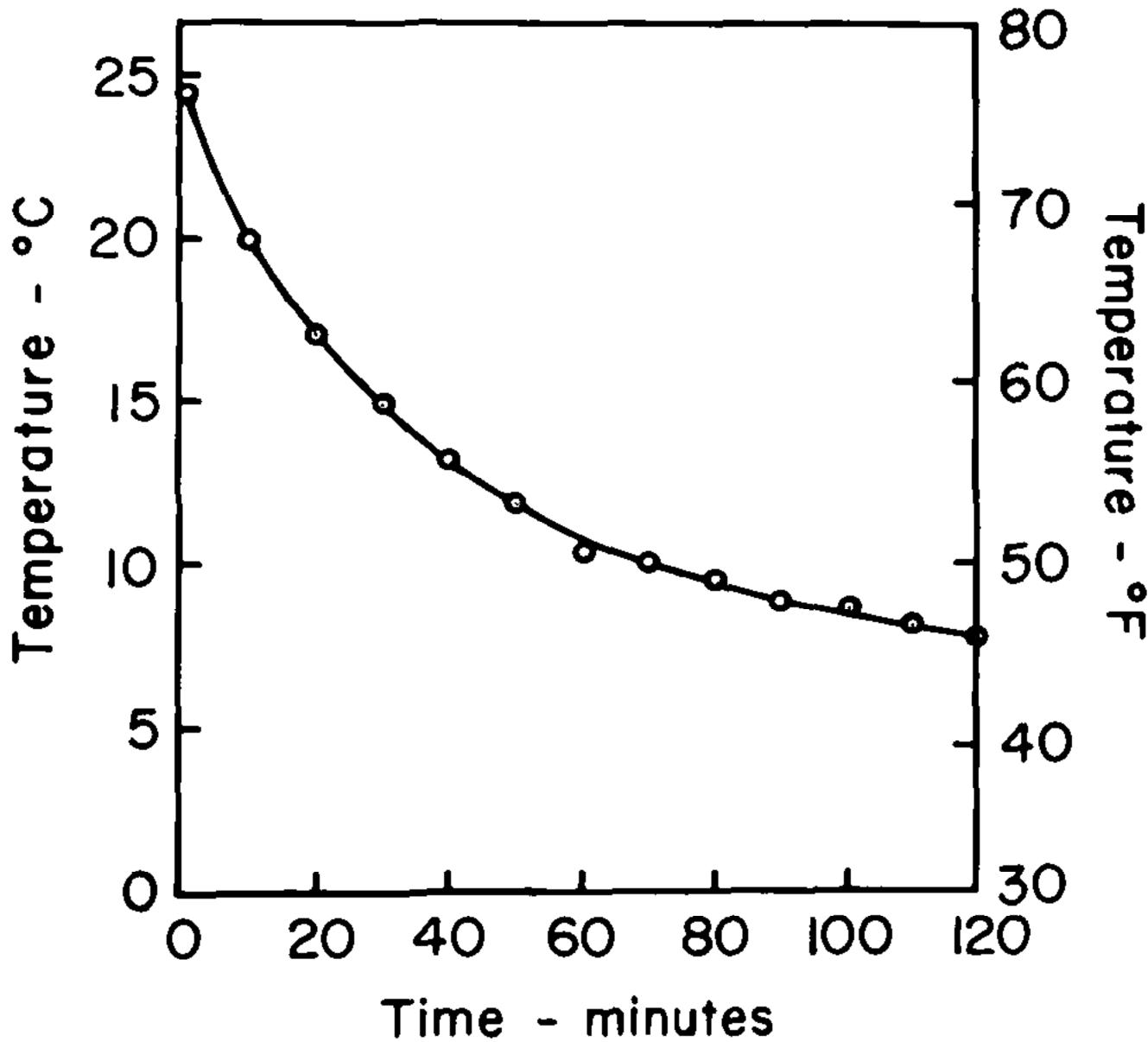


Fig. 7. Change of temperature in a box of moist sand 2.5 x 12 x 12 cm (1 in x $4\frac{1}{2}$ in x $6\frac{1}{2}$ in) following transfer from 25° C to a 5° C cold room.

With this speculation on the possible importance of time-specific environment-sensitive periods, I would like to return to speculate on the general topic of dormancy. In so doing, I would like to return to the question of peach dwarfing. One of the symptoms of dwarfing is abnormal leaf development which is marked externally by the formation of white "knots" of abnormal leaf tissues (Fig. 8). One of my former students (now Dr.) Melvin Fine examined these abnormal leaf areas and discovered that they are full of fat globules. The peach plant normally produces such high quantities of fat only in the tissues of developing cotyledons. Therefore, this observation suggests that the abnormal leaf areas are functionally cotyledon tissue.

From our current understanding of biochemistry, we know that the formation of fat requires the participation of a number of highly specific enzymes. These enzymes are likely to exist in quantity only in cells which synthesize storage fat. To synthesize an enzyme, the cell needs information on the structure of the enzyme; this information is encoded in the DNA (deoxyribonucleic acid) of the gene. However, most genes are inactive at most times. Before the cells can use their genetic information to produce fat-synthesizing enzymes, the appropriate genes must be "turned on."



Fig. 8.
Leaves from normal (left) and dwarfed (right) peach seedlings. Figure from Plant Physiology 37: 190-197, 1962.

The "turning on" of genes during plant development is something we are just beginning to understand. We know from a variety of data that the process exists and that it is basic to the work of the plant propagator. For example, the changing of stem cells to produce root initials, the key process in rooting of cuttings, must involve the "turning on" of "root" genes in the cells. However, we know little of the details of the "turning on" process, nor how that process is controlled.

Similarly, the change from seed development to seed germination must involve a "turning off" of seed development genes and a "turning on" of seed germination genes. Seed development is primarily concerned with the synthesis of nutrient reserves in the storage cells of the seed. In peach, this means the synthesis of storage fat, and requires the participation of fat-synthesizing enzymes and hence requires that the genes providing information for fat-synthesizing enzymes be turned on.

These are speculations. However, I believe that most plant biologists would accept them as valid speculations on which to plan experiments. The importance of these speculations, coupled to the fat-synthesizing activity in the abnormal areas of leaves of peach seedlings grown from non-after-ripened (dormant) seeds is this: it suggests to me that some of the seed-development genes were not turned off during germination. Further, it suggests that dormancy itself may occur in seeds in which the development genes have not been turned off and the germination genes turned on.

If this is true, then all seeds must pass through a dormant, or resting, stage between development and germination. We can look

across the spectrum of seeds, (A) from tree seeds which require long periods of low temperature after-ripening to break dormancy, to (B) grains which are dormant at maturity but which after-ripen in dry storage, to (C) many seeds which are dormant during development but which are capable of germination immediately after separation from the mother plant. From your own experience, I believe that you can name species to fit at all points in this spectrum.

This is speculation. However, I believe that it may be valuable in providing a unifying concept for our thinking and practices in handling dormant seeds. It may serve to focus our attention on what happens between the time that the seed reaches "physiological maturity" and the time that the new seedling is established. It provides a basis for appreciating the possible critical nature and long-term delayed effects of the time-specific processes of which I spoke earlier. I hope that you may find these speculations useful in your daily contact with seed germination problems.

MODERATOR HESS: Thank you very much, Bruce: You are truly an expert in your area.

The next paper was to have been presented by Mr. Brian Humphrey of the Great Britain and Ireland Region, but Mr. Humphrey was not able to be with us because of an unfortunate accident in his immediate family and his paper will be presented by Mr. Richard Martyr.

DICK MARTYR: Mr. Chairman, ladies and gentlemen, I know Mr. Humphrey is a very disappointed man today. He is one of the oldest members of the Society from Britain, having joined well before the G. B. and I. Region was organized and he had looked forward to coming over here and meeting with you.

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THE LARGE SCALE RAISING OF NURSERY PLANTS BY SEED PRODUCTION IN ENGLAND

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THE PAST

Apart from the nationally-owned Forestry Commission which operates several large nurseries mainly oriented toward seed production and the privately-owned forestry nurseries similarly organised, production by seed in most English nurseries has not reached an advanced stage of development or sophistication.

It is difficult to be certain of the reasons for this situation but some contributory factors can be isolated. In broad terms the monetary value of items raised from seed is not so high as clonal forms or rare species produced by vegetative propagation. This has an influence on the owner or management who perhaps erroneously imagines that the higher priced items are the most profitable. Most of the nurseries in England are small in physical size and turnover and also they are heavily biased towards the retail trade. This type of business has few resources for large scale seed production in terms of finance or land. The main requirements are for clonal forms to satisfy the retail trade and the policy, naturally enough, has been concentrated upon purchasing from abroad seed-raised items for use as understocks, etc., rather than attempting to produce them at home. The large and highly efficient seed production nurseries of Holland, Northern Germany,