REST, POSTDORMANCY, AND WOODY PLANT SEED GERMINATION[1]

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Abstract. A phenomenon of significance to propagation by seeds having dormancies is the postdormancy as hypothesized by Vegis (12). Seeds of two cotoneaster species were used to test this hypothesis and both showed the postdormant condition. These results are discussed in relation to other work and practical considerations of afterripening and germination response of woody plant seeds. Length of moist-chilling, conditions on planting, fall planting, and implications to model systems, are discussed in relation to the postdormant condition of many woody plant seeds.

INTRODUCTION

Seeds of temperate zone woody plants, which develop during the summer, have produced mechanisms to prevent germination at inappropriate times in the fall. These mechanisms consist of internal conditions, called true dormancy (12), rest (9), or endo-dormancy (6), which prevent germination even though external conditions may be favorable. These mechanisms are usually modified by a period of moist-chilling (stratification) which, in the natural environment, is received by seeds during the winter. This can also be done by placing the seeds in moist material under refrigeration (3). Models have been developed (10) for dormancy modification as to chill units needed to satisfy the chilling requirement. After sufficient chilling is given, seeds would be expected to germinate at optimum germination temperatures.

A phenomenon of considerable practical significance but little understood by those developing terminology (6), or data for models (10), is the concept of postdormancy developed by Vegis (12). This concept can be simply stated as: after a period of moist-chilling that overcomes rest, seeds will germinate and grow at a narrow temperature range, but higher or lower temperatures will prevent germination. As more chilling time is given, the temperature range for germination and growth increases until after a long period of chilling the range is near the maximum and minimum for all growth processes. Although Vegis presented three scenarios for this phenomenon, the one perhaps most appropriate for temperate zone woody plants is that germination starts at an intermediate temperature range which continues to widen towards a maximum and minimum as longer periods of moist-chilling are given. This concept is graphically presented in Fig. 1. The reason that this phenomenon

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is not better understood is the magnitude of Vegis's article (12) published over 20 years ago, the way he presented his graphs, and the lack of subsequent experiments to directly test his hypothesis.

Experiments were designed to test this hypothesis using seeds of two species, *Cotoneaster apiculatus* and *C. divaricatus*. The reasons for selecting these species are given by Meyer (7).

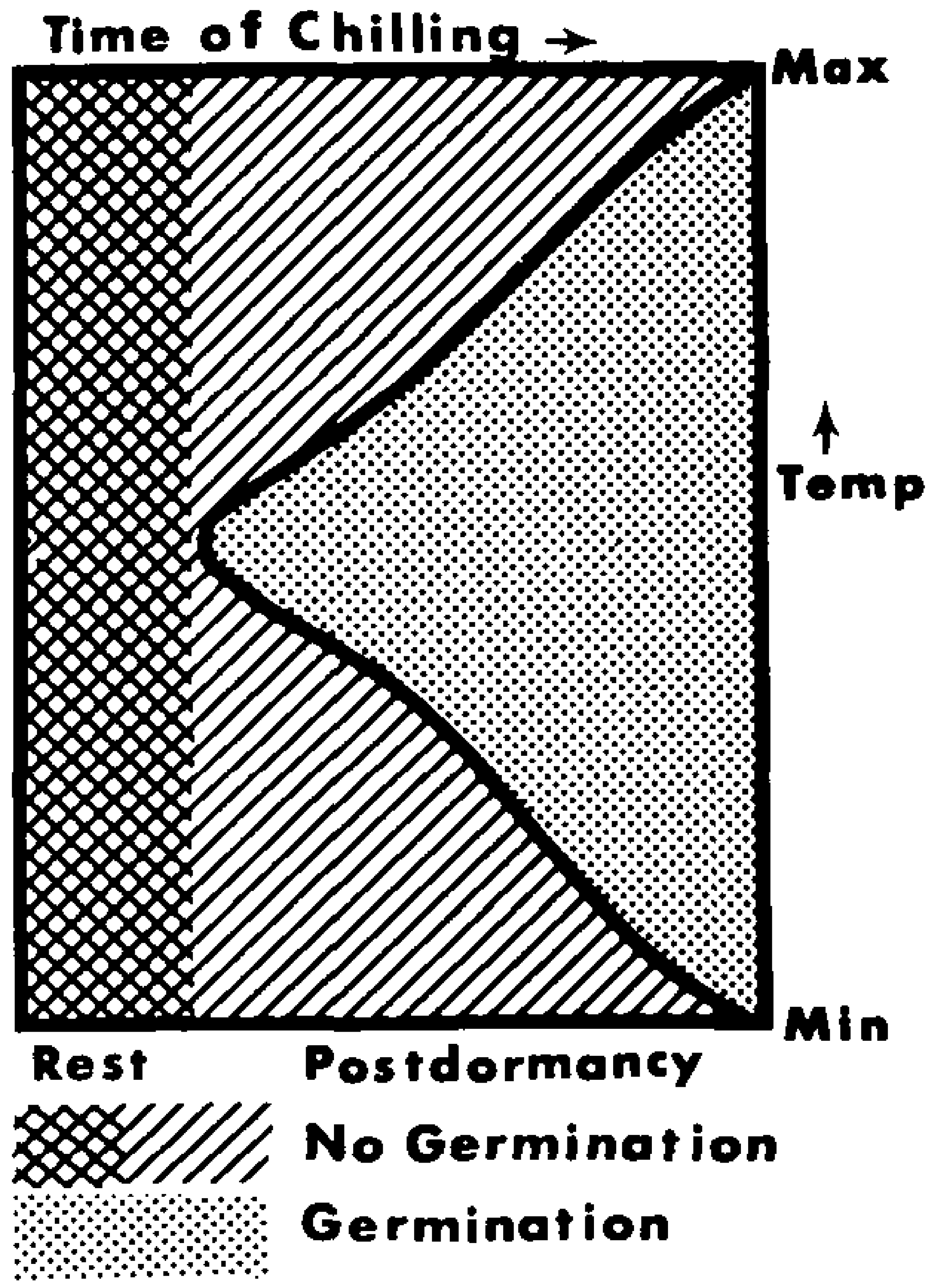

Figure 1. The postdormant condition hypothesized by Vegis which is relevant to woody plant seeds and buds where germination or budbreak starts at an intermediate temperature and widens as more chilling is given. Redrawn, with permission, from Annual Review of Plant Physiology, Vol. 15 © 1964 by Annual Reviews Inc.

MATERIALS AND METHODS

Seeds of these two species were collected on the University of Illinois campus in late September, extracted from the fruit, dried at 26°C, and stored dry at 2°C until used, but not over 130 days. At approximately 4 week intervals, lots of seed were treated for 90 min in concentrated H_2SO_4 (acid:seed, 2:1 v/v) maintained at 28 to 30°C and washed in running water for 4 hours. Seeds were then placed in moist vermiculite in lots of 50 seeds and maintained at 2°C until the germination treatments. Seeds were sown on steam pasteurized soil in 9×9×6 cm pots and covered 1.5 cm with moist vermiculite. The pots were placed in controlled temperature greenhouse compartments at 10, 15.6, 21, 26.7°C and in a cold storage at 4.4°C with light at 50 μmol s^{-1} m^{-2} for 16 hr days provided by cool white fluorescent lamps. There were 5 replicates of 50 seeds each for the storage germination treatments. The number of seedlings emerged were counted after 4 weeks.

RESULTS AND DISCUSSION

Both the chilling time and germination temperatures caused highly significant differences in germination percentage (Table 1). There was a highly significant interaction of these two factors, which can be predicted by the hypothesis of Vegis (12) for the post-dormant state. The data in Table 1 would appear to fit the hypothetical graph of postdormancy presented in Fig. 1 as seeds of both species showed greater temperature ranges for germination as the length of chilling increased.

Table 1. The influence of length of moist-chilling and germination temperature on seed germination during post dormancy of two cotoneaster species.

Cold treatment (Days at 2°C)	Germination temperature				
	40 4.4	50 10	60 15.6	70 21	80°F 26.7°C
	Percent germination[z]				
	C. divaricatus				
0	0	0	0	0	0
30	0	0	0	0	0
58	0	0.8	0.8	0	0
87	10.4	57.2	43.6	30.4	10.4
116	70.8	82.8	80.4	72.0	77.6
	C. apiculatus				
0	0	0	0	0	0
30	0	0	0	0	0
58	0	12.0	7.6	0.8	0
87	0	36.4	36.8	15.2	2.4
116	20.4	29.2	31.2	28.0	11.2

[z] Analysis of variance showed a very high significance ($p < .001$) for days storage (D), germination temperature (T) and D × T interaction.

Some further corroborative evidence (which led to the above work) for the existence of the postdormant state of woody plant seeds can be seen in Fig. 2. This is a graphic presentation of work of DeHaas and Schander (1) on temperature and germination of apple seeds presented in the 2nd and 3rd editions of Hartmann and Kester's textbook (3). This work shows the widening range of temperature for germination when the seeds are germinated at temperatures which are also appropriate for moist-chilling (10). The lower the germination temperature the longer the chilling requirement before the seeds will germinate at that temperature. The post-dormant state is also apparent in the work of Greisbach and Voth (2) with daylily seed, but the intermediate temperature at which germination begins is higher than in the above two cotoneaster species.

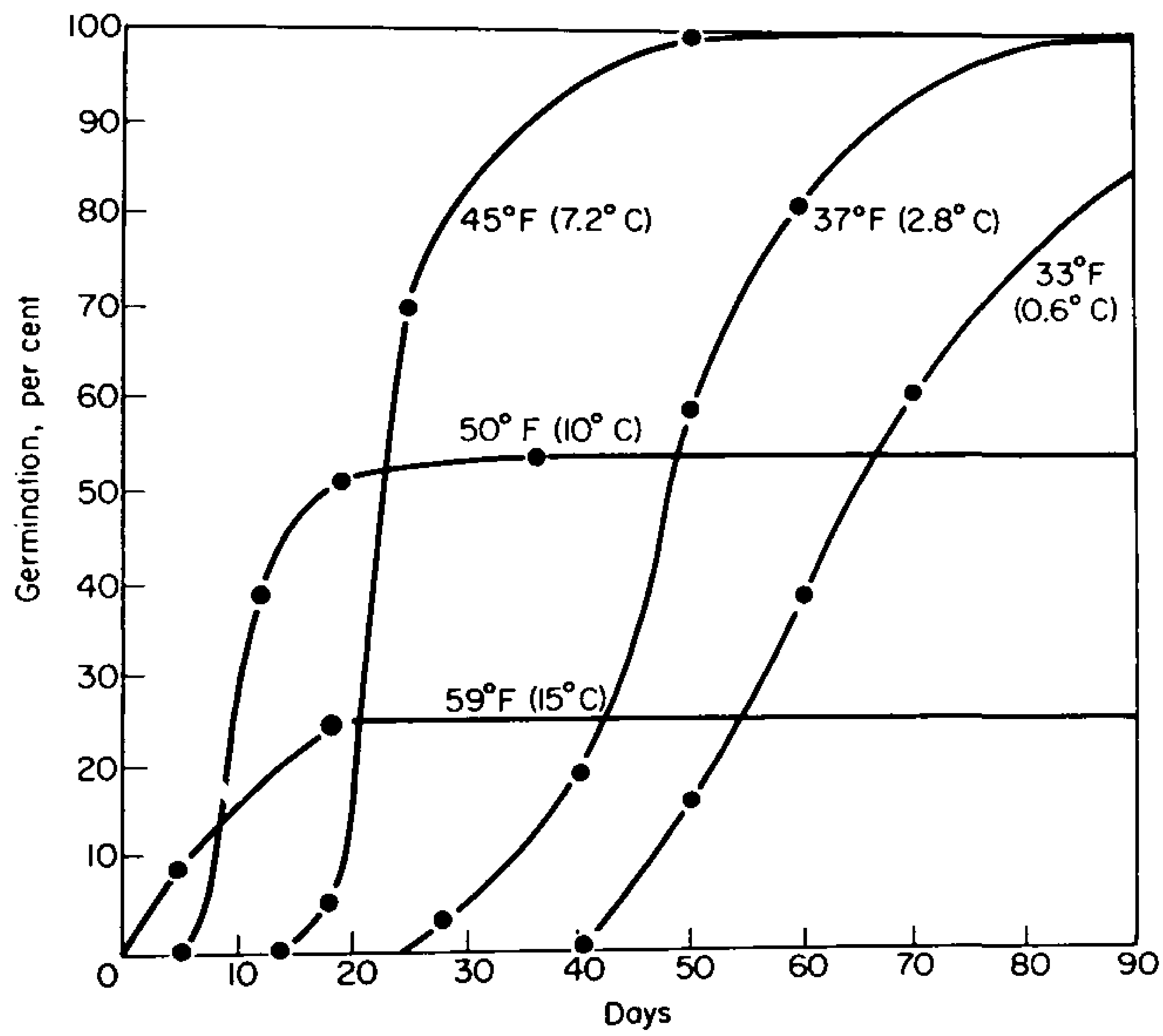

Figure 2. The effect of temperature on germination of apple seeds previously moist-chilled for 65 days at 3°C. Data from (1). When germination temperatures also induce afterripening, germination occurs when sufficient chilling overcomes the postdormant condition as can be seen in the lower part of Fig. 1. Reprinted from Hartmann and Kester (3) with permission from Prentice-Hall, Inc. © 1975.

The concept of postdormancy has considerable practical significance to the plant propagator. The postdormant state explains some of the controversy found in the literature regarding germination requirements. Recommended moist-chilling times for a single species of cotoneaster vary by as much as 60 days (11). This can be readily explained by considering the postdormant state. The researchers may germinate the chilled seeds at different temperatures, which will indicate that different lengths of chilling are needed (Fig. 1). A propagator who stratifies seeds of a woody plant species for comparable times in two different years, may find that the seedling crop is considerably better in one year than the other. This person might assume that one seed lot was poor. An alternate explanation could be that one year's seeds were planted during a warm spell with higher soil temperatures and some seeds were still in the postdormant condition.

The postdormant phenomenon may be related to the incomplete chilling that leads to dwarfism in seedlings, but may be present only towards the maximum temperature part of the response. Pollock (8) demonstrated that lower germination temperatures after incomplete chilling prevented dwarfism in peach seedlings. This obvious part of the postdormant phenomenon may be shown to be significant in the recommendations of Heit (4,5) that seeds of certain hardwood and conifer species germinated and grow better the first year when fall-planted rather than moist-chilled and planted in the spring. This may mean that the extended natural chilling and the gradual warming of the soil in the spring as the seeds are germinating prevent dwarfism associated with the postdormant state. In this case, the seeds go from chilling temperatures gradually through the intermediate temperatures where there is the least requirement of the postdormant state.

Another problem in storing stratified seeds is that the minimum germination temperature decreases over time in the postdormant state and eventually the germination temperature equals the stratification temperature resulting in immediate germination as seen in Fig. 2. Both species of cotoneaster showed this phenomenon at the 4.4°C germination temperature. Seed lots which had received shorter chilling times and had not germinated 4 weeks after planting at 4.4°C continued to be observed for another 3 months. These seed germinated at approximately monthly intervals respective to the time of chilling initiation. The postdormant phenomenon is why seeds cannot be stored moist for long periods of time or until the following season. Seeds stored under these conditions will eventually germinate right in the bag at refrigerator temperatures.

The embryo's sensitive response to slightly different temperatures in the postdormant state is difficult for the biochemist or molecular biologist to explain, but still is demonstrably present. The development of terminology for physiological research on dormancy by Lang et al. (6) that does not take into full account postdormancy is missing a significant practical concept. The development of data for chill units for fruit tree seeds (10) that uses only one germination temperature will lack a significant factor in using the model to explain the germination of seeds outside the laboratory. The understanding of postdormancy as advanced by Vegis (12) and presented in this paper has considerable significance in understanding the moist-chilling and germination response of many temperate zone woody plant seeds.

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RALPH SHUGERT: Just a comment. If you have fresh seed of *Picea Pungens* 'Glauca', fall sown in the U.S. Midwest with a mulch and seed germination occurs under the mulch, your crop will be dead the following spring.

DICK JAYNES: What effect does temperature have during the cold stratification period?

MARTIN MEYER: With apple seeds, there is not much difference between 2 and 6°C. However, since it is a biological process, 0°C or below should shut it down. Therefore, it would be satisfied better between 2 and 6°C than closer to 0°C.

MARK WIDRLECHNER: I can agree with your model for all the plants you mentioned which are all in the rose family.

DAVE BAKKER: What can I do to cause *Syringa reticulata* seeds to germinate in June instead of around Labor Day?

BILL BARNES: *Syringa* embryos, and many other Oleaceae species, have an immature embryo and are what we call summer dormancy. The seeds require a period of afterripening at warm temperature, after which a cold period will satisfy the dormancy requirement.

DAVID VANSTONE: We found that 2 months at 5°C followed by 2½ months at 20°C will produce prompt spring germination.