Temperature Control of Physiological Dwarfing in Peach Seedlings [1, 2]

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Physiological dwarfing of seedlings of many woody plants results when the embryo of a non-afterripened seed is permitted to germinate by excision of part of the seed coat. In this connection, the dwarfing of peach seedlings has received considerable attention, largely because the problem is associated with the embryo culture technique used in the breeding of early ripening varieties.

Dwarfing is of physiological interest because it is a manifestation of epicotyl rest, or dormancy, (5) and is considered by some authors (1, 3, 7, 10) to be similar to, if not identical with, the rest period in the buds of the mature tree. Dwarfing is characterized by the development of an abnormal shoot, with shortened internodes and deformed leaves. The root system, as well as any axillary bud which grows into a branch, is normal (7, 10, 20). Dwarf plants can be returned to the normal condition if they are chilled for at least one month (7, 20). In the absence of chilling, they have been reported to grow in the dwarf condition for as long as 10 years (7).

Much of the experimental work which has been reported has been based on the theory that dwarfing is the result of some growth inhibiting (or stimulating) compounds carried over from the seed or developed during afterripening (8, 9, 10). The literature contains on the one hand references indicating presence of growth inhibitors (3) and on the other hand references showing no significant inhibitors (9). Gross chemical analyses of dwarf plants provide no obvious clue to the mechanism (9). The dwarfing factor is neither altered by grafting nor transmissible to a normal plant by grafting (2, 10). Actually, two observations argue against the presence of a simple growth-inhibitor mechanism: A: The anatomical localization in the epicotyledonary axis, while the branches are normal, suggests the presence (or lack) of a factor which is transmitted only by cell division. B: The extreme persistence of the dwarf growth habit is incompatible with the presence of the normally recognized type of inhibitor which would be expected to be slowly metabolized or diluted out, at least in 10 years.

Several studies have been made of treatments to prevent or eliminate dwarfing. For example, photoperiodic treatments modify the dwarf condition but do not necessarily eliminate it (7, 13, 21). Several papers have been published suggesting gibberellin action (4, 7, 12, 19) but the effect has been shown to be transitory (7) or non-existent (15). Because there has been no simple way to eliminate dwarfing, workers have resorted to elaborate embryo-culture techniques (8, 22). However, in 1959, I reported that physiological dwarfing is actually determined by germination temperature and can be controlled at will (17). The effective temperature difference was very small, not more than 4 C between 23 and 27, and the sensitive period restricted to approximately the first week of germination. Experimental techniques used by other authors all have failed to control temperatures precisely in this range, and so this temperature sensitivity had been overlooked previously. The present paper provides further details on the temperature sensitivity of peach seeds and suggests a mechanism to account for the observed facts.

Materials & Methods

Peach seeds [*Prunus persica* (L.) Batsch, cv. Elberta] from the 1959 and 1960 crops were used in most of the experiments reported. The 1959 crop was taken from fruits which had dropped to the ground in the University of Delaware orchard. In 1960 stones were obtained from the processing line at a commercial cannery in southern Pennsylvania. Halehaven, Southland, Sullivan Elberta, and Redskin fruits were obtained from the U.S. Department of Agriculture orchards at Beltsville, Md. After collection, the stones were washed thoroughly, air-dried, and cracked, and the seeds stored at 10 C (50 % relative humidity) until used.

For germination, the seeds were placed in water overnight at 20 C and the seed coat and associated endosperm tissue was removed from approximately one-fourth of each seed at the hypocotyl end. These excised seeds were placed on filter paper in 9 cm petri dishes and germinated in plastic boxes immersed in constant temperature baths. In each case the bath temperature was adjusted to give the desired temperature in the petri dish. Dishes were covered loosely with aluminum foil, but no attempt was made to exclude light completely, since previous work (17) had

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[2] Some of the anatomical observations in this paper were made by students at the University of Delaware during preparation of the previous paper (17). Whitney R. Adams, Jr., now in the Biology Department, Princeton University, Princeton, N. J. counted the leaf primordia in the dry seeds. Melvin Fine, now in the Botany Department, Yale University, New Haven, Conn., originally observed fat in the abnormal area of dwarf leaves.

shown little light effect even at high light intensity. In experiments on afterripening, seeds were surface-sterilized and afterripened at 5 C as previously described (18).

After germination for the required period, seedlings were planted in Perlite (horticultural grade), one or two plants in a 4-inch glazed crock with a drainage hole. The plants were watered daily with Hoagland's nutrient solution. They were grown for 4 to 5 weeks in a growth room at a constant air temperature of 25 ± 1 C under a 16-hour day from standard cool white fluorescent lamps at an intensity of about 400 ft-c. Each experimental lot normally included seven or eight plants, and each experiment was replicated two or three times at intervals of several months.

Records were made as indicated in table I. In addition, root and shoot lengths at time of planting, date of emergence, and extent of branching were recorded, but showed no significant difference between lots and were, therefore, not utilized in interpreting results. The exact details of the experimental observations and their significance are discussed later.

Results

► Anatomical Localization. One of the most striking features of dwarfing is the anatomical localization of the affected organs. Hundreds of plants were examined, and in all but two the dwarfing symptoms were confined to leaves and stem produced from the apical meristem present in the seed. Branches, of which several thousand were observed, were always normal (fig 1 C). These same observations have been recorded previously (7, 20). In the two exceptions noted, the plant has been grown at an abnormally high temperature, 30 C constant, and some slight abnormality was observed in the uppermost branch which, immediately subjacent to the apical meristem, assumed apical dominance.

Although the dwarfing symptoms are confined to leaf primordia formed by the epicotyl meristem, they do not appear in leaves from all primordia in the seed. Sections of a mature seed show the presence of six to nine visible primordia most of which become scale leaves on the epicotyl (fig 2). Ledbetter (14) reported an average of 9.5 primordia per seed. Until approximately 12 primordia are produced, the leaf ar-

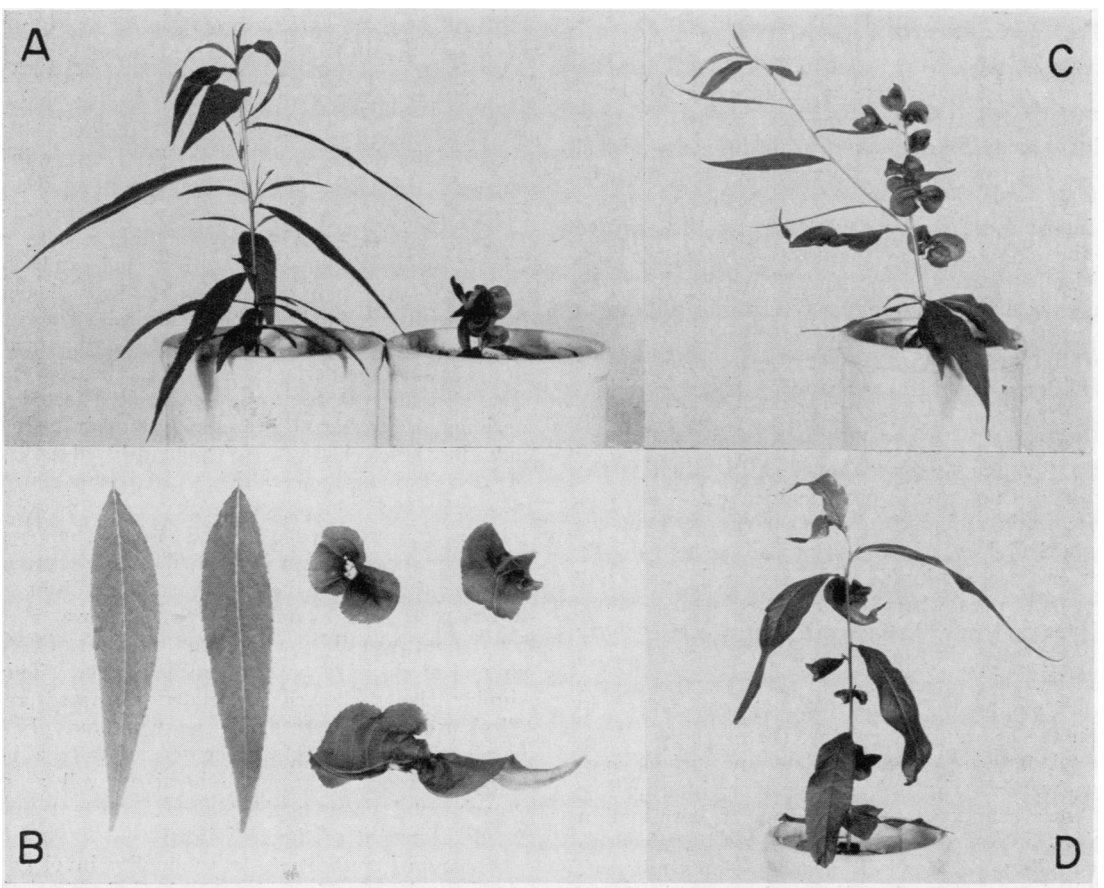


Fig. 1. A. Normal and dwarf Elberta peach seedlings developed from seeds germinated 8 days at 19 or 27 C and grown 4 weeks at 25 under a 16-hour day. B. Details of leaf abnormalities. C. Dwarf plant showing a typical normal branch. D. Dwarf plant showing skipped leaves.

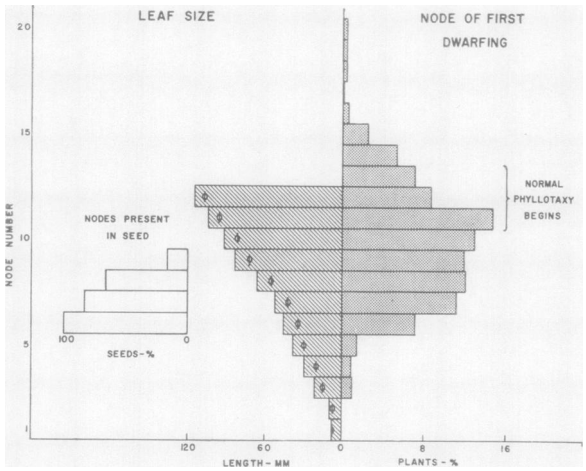


Fig. 2. Elberta peach seedlings position of first abnormal leaf, normal leaf size, and nodes differentiated in the seed. Nodes are numbered beginning with the first above the cotyledons. For leaf size, ϕ represents the negative 95 % confidence limit. Node of first dwarfing is based on 450 plants in several different experiments; nodes present in the seed are based on serial sections of 12 embryos.

rangement is irregular, with a tendency to develop a whorl of small leaves in the region of nodes 6 to 12. At higher nodes, a non-dwarf plant assumes normal phylotaxis, as does a slightly to moderately dwarfed plant; severely dwarfed plants may have such shortened internodes that the phylotaxis cannot easily be determined. A count of the node at which the first dwarf leaf appeared on the plants is shown in figure 2. It is clear that dwarfing can rarely appear in leaves at nodes which are well developed in the seed, at least up to node 6. By far the majority of the nodes with abnormal leaves are formed after germination. Because of the very few cases in which leaves were abnormal at nodes 1 to 5, these nodes were subtracted from the total on the plant to calculate the percentage of nodes with abnormal leaves.

Because the main axis always shows some evidence of a whorl of leaves in the region of nodes 6 to 12, it was easy to distinguish between main axis and branches in cases where the main axis died before emergence and growth resumed from a cotyledonary bud.

Considerable variability was noted in the degree of dwarf expression between individual plants and between the affected leaves. At the extremes of response, plants were either completely normal or completely dwarfed (fig 1 A). However, intermediate forms were common, particularly under germination conditions intermediate between those required to produce fully normal or fully dwarfed plants (fig 1 C, D). Typical moderately affected leaves (fig 1 B) were characterized by abnormal midrib development, in which the cells failed to elongate. At the same time, laminar development continued more or less normally; the unequal growth of midrib and lamina resulted in a twisted, deformed leaf. Frequently, the abnormal areas of the midrib were characterized by failure to develop chlorophyll. Hand sections of these abnormal areas revealed large numbers of Sudan-staining fat droplets in the cells, and hot ether or benzene extraction removed about 10 % of the dry weight of these areas.

In extremely severe dwarfing, the whole leaf was frequently reduced to a white, scale-like appendage. On the other hand, in slightly dwarfed leaves the midrib frequently was not involved; the abnormality appeared as a pinched area at one side of the midrib. In such plants the development of a few leaves of this type was frequently followed by the complete reversion to a normal growth habit. In the typically dwarfed plant all leaves were affected (fig 1 A). However, in many cases, particularly of moderately dwarfed plants, normal and dwarfed leaves could be found randomly distributed along the stem (fig 1 D).

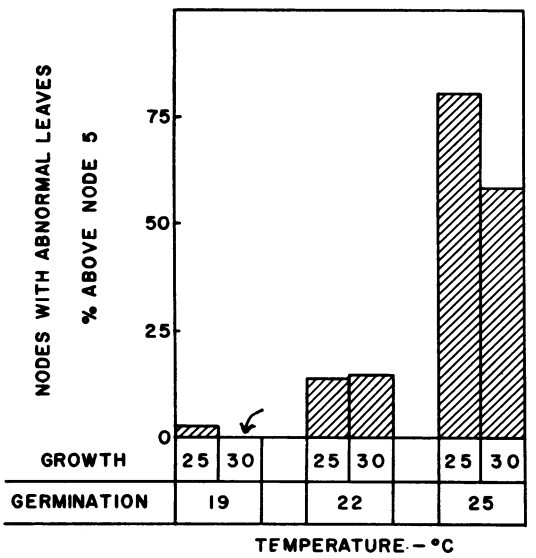
Internode shortening, resulting in rosetting, was a common feature of the severely dwarfed plants (fig 1 A), but was frequently absent from moderately affected individuals (fig 1 C, D). Preliminery data and information in the literature (2, 7) suggest that light intensity or daylength may influence the degree of internode, involvement, but this aspect was not studied and all experiments were performed under a 16-hour photoperiod.

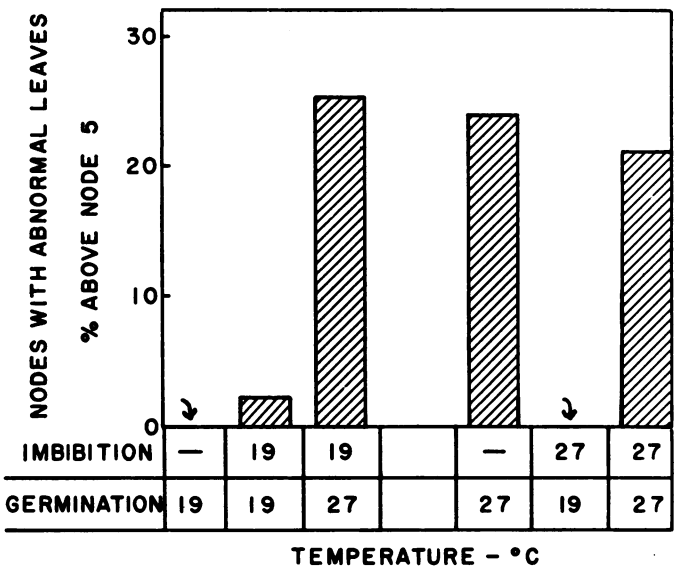
► Variability; Measuring Methods. Although superficially the degree of variability between individuals seemed high, closer observation showed that individuals tended to fall in three well-defined classes: A: Normal plants, with no dwarfing symptoms. B: Lightly dwarfed plants, with a few moderately dwarfed leaves, alternating normal and dwarf leaves, or leaves with only laminar abnormalities. These plants might after a period of growth lose the dwarfing symptoms altogether. C: Severely dwarfed plants, with all leaves moderately to severely affected. Experimental treatments altered the number of individuals in these classes. Conspicuously absent, however, were individuals which shifted from normal to severely dwarfed (class A-class C) or severely dwarfed to normal (class C-class A). The degree of dwarfing shown by an individual was approximately constant throughout the entire period of observation; in one case, a moderately dwarfed plant was observed for 6 months until it had reached a height of about 70 cm and produced 60 to 70 abnormal leaves. This and similar plants showed no tendency toward gradual dilution or loss of the dwarfing symptoms. In other words, the degree of dwarfing seemed to be a quantitative character of an individual as well as of an experimental group and remained constant through the development of the individual.

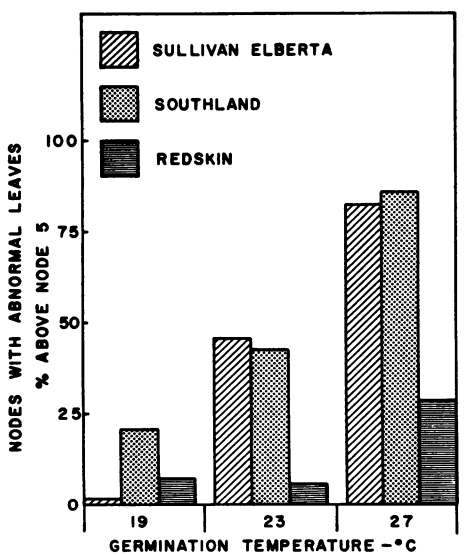
Recognizing the type of variability involved, one of the major problems in this investigation was to provide a quantitative measure of dwarfing. Other workers have expressed data as either proportion of

plants dwarfed (20, 22) or "normal", "semi-dwarfs", and "dwarfs" (9). The actual syndrome involves plant height, number of nodes per plant, number of nodes with abnormal leaves, severity of leaf distortion, and percentage of plants affected. These symptoms all tend to change in the same direction as a result of temperature treatment, i.e., high-temperature treatment decreases plant height and number of nodes but increases the number of leaves affected, the severity of symptoms shown by each leaf, and the number of plants affected. Unfortunately, the relationship between these individual symptoms varies from plant to plant; no obvious simple method has been found to weight all symptoms so that they may be combined to give a strictly quantitative measure of dwarfing.

Complete data on several different measurements from one experiment are presented (table I) together with a measure of variability. In addition to the objectively measurable observations, a subjective estimate of severity of dwarfing was made on a numerical







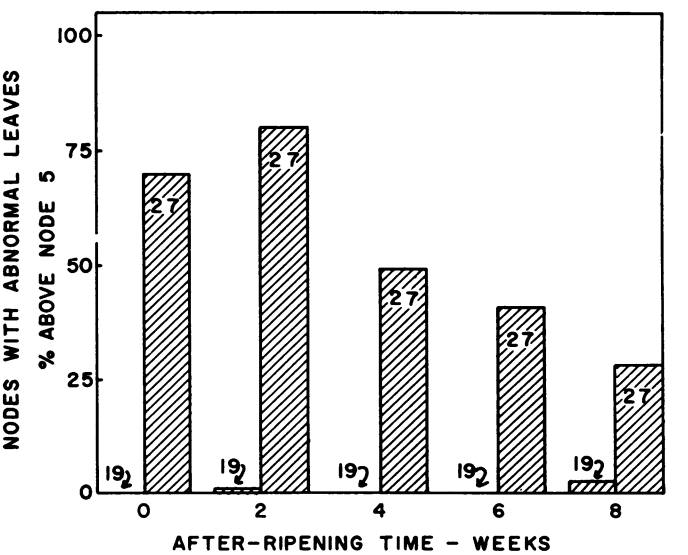


Fig. 3 (*Upper left*). Effect of 25 and 30 C growing temperatures on dwarfing of Elberta peach seedlings, 1960 crop seeds, germinated for 9 days at 19, 22, and 25 C.

Fig. 4 (*Upper right*). Relationship between 9 days imbibition at 19 or 27 C and subsequent germination temperature of 19 or 27 C on development of dwarfing symptoms in Elberta peach seedlings, 1959 crop.

Fig. 5 (*Lower left*). Varietal variations in dwarfing development resulting from 8-day germination at the temperature indicated.

Fig. 6 (*Lower right*). Effect of after-ripening at 5 C on development of dwarfing symptoms following germination for 8 days at the temperatures indicated. Elberta peach seedlings, 1960 crop.

scale from 0 to 4. By each of these measurements, the variability tended to be much lower under extreme conditions (19 & 22 vs. 25 constant) than under intermediate conditions (daily temperature alternation). According to each measurement the temperature effect was toward the limits noted at the morphological extremes; however, the variability within any one character tends to be too high to handle by simple statistical treatment. Therefore, because of the similarity of results by the various parameters measured, most data presented are in terms of percentage of nodes above number 5 which showed any dwarfing symptoms whatsoever, i.e., percentage of potentially dwarfed nodes actually showing symptoms. The one case where this measure did not approximate the degree of dwarfing is noted separately (fig 7).

► Temperature Sensitivity. In the previous paper (17), it was shown that seeds from the 1958 Elberta seed crop were strongly dwarfed when germinated for 7 days at 27 C, but were normal when germinated at 19° for the same period. Germination at 23 produced very slight dwarfing in some plants. In some experiments (fig 4, 5, 6) in the present study, a temperature range in 4° steps (19, 23, & 27) was also used. However, the degree of dwarfing at 23 was somewhat variable, and in later experiments a 3° range at 19, 22 and 25 was used (table I, & fig 3, 7). In each case, 19° resulted in plants almost 100 % normal, while 25 or 27 resulted in severely dwarfed plants. The intermediate temperature (22 or 23) gave somewhat variable results. Since no temperatures between 23 and 25 were tried, it is clear that the effective temperature span resulting in normal or dwarf plants is not more than 3°, and may be somewhat less. That this temperature sensitivity does not extend beyond germination is shown in figure 3. In this experiment, two lots of seeds were germinated for nine days at 19, 22, and 25°. After planting, one lot was grown under the normal 25° growing conditions while the other was grown at an air temperature of 30 under identical light and daylength. While evaporation from the growing medium reduced its temperature about 2°, the plants in the 30° room should have been dwarfed if they were sensitive.

Seeds do not become sensitive to temperature until after the seed coat is removed (fig 4). In this experiment, seeds were held imbibed for 8 days at temperatures which should have caused the seedlings to be either normal or dwarf and then excised, and lots were placed at each temperature. In each case, only the germination temperature was important in determining dwarfing; there was no aftereffect of imbibition temperature.

Most work was done with the Elberta variety. However, four other varieties showed the same type of response, although modified slightly as to degree and precise temperature of response. In figure 5, the variety Redskin is shown to respond less and at a higher temperature than Southland and Sullivan Elberta. The Halehaven variety, which is not shown in this figure, has a sensitivity similar to Elberta.

Since the temperature-sensitive period does not extend beyond the first 8 or 9 days of germination, the exact amount of temperature exposure required is of interest. In table I, an 8 hr daily exposure to 25 C, alternating with 16 hours at 19°, produced very little dwarfing; 12- and 16-hour exposures produced progressively more severe dwarfing, but even 16 hours did not produce as severe symptoms as germination at a constant 25°.

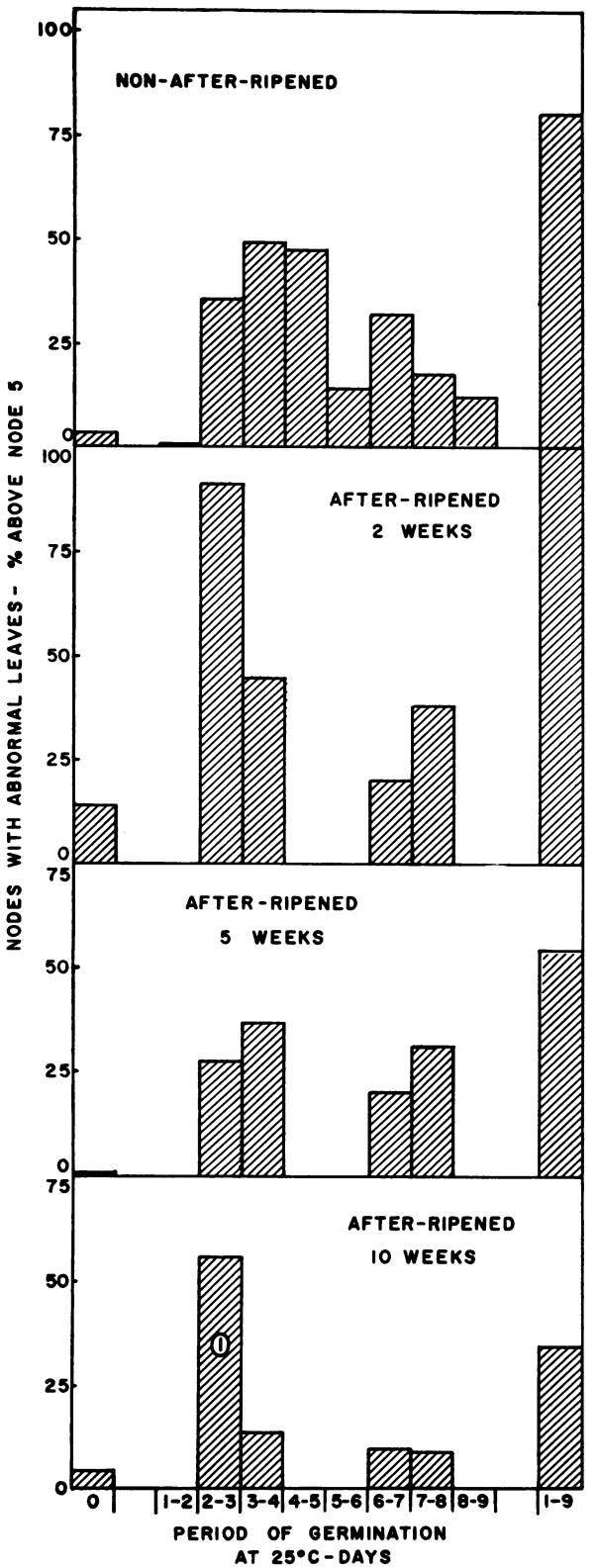
To determine if sensitivity varies throughout the germination period, a 2-day exposure at 25 C was given at various times during 9 days of germination at 19 (fig 7, top). Although the 2-day period was not enough to produce maximum dwarfing at any time during the week, apparently the seed was not sensitive at all during the first day or two of germina-

Table I

Effect of Constant & Alternating Germination Temperatures on Subsequent Development of Dwarfing in Elberta Peach Seedlings, 1960 Crop*

Germination temp (°C)	Height (cm)	Total nodes per plant	Nodes with abnormal leaves	% Nodes above node 5 with abnormal leaves	Severity of dwarfing**	Plants (dwarf/total)
19 (constant)	14.4 ± 2.8	17.8 ± 1.6	0.6 ± 1.0	5.1 ± 10.0	0.3 ± 0.2	2/7
22 (constant)	16.3 ± 1.9	19.4 ± 2.1	0.3 ± 2.1	1.9 ± 4.5	0.1 ± 0.2	1/7
25 (8 hr) +19 (16 hr)	15.3 ± 2.0	19.0 ± 1.5	1.4 ± 2.7	11.2 ± 20.6	0.6 ± 1.0	2/7
25 (12 hr) +19 (12 hr)	14.0 ± 4.3	19.3 ± 6.1	3.4 ± 3.1	29.1 ± 35.5	1.8 ± 1.6	4/7
25 (16 hr) +19 (8 hr)	12.0 ± 3.9	17.1 ± 3.2	3.7 ± 2.0	36.4 ± 23.3	2.1 ± 1.5	6/7
25 (constant)	7.6 ± 1.2	12.1 ± 1.8	5.0 ± 0.9	73.5 ± 17.6	4.0 ± 0.0	7/7

* Variability expressed as ± 95 % confidence limits.
** Subjective scale from 0 to 4.



tion. The data suggest that days 3, 4, and 5 might be more sensitive than days 6 through 9 but confirmation would require precise measurements.

In one experiment, the seeds were exposed to gibberellic acid at concentrations of 2×10^{-7}, 2×10^{-5}, and 2×10^{-3} M and temperatures of 19, 23, and 27 C during the sensitive period. Although the plants later showed increased elongation from the gibberellin, abnormal leaves were produced in the normal manner as long as the terminal bud survived.

Temperature sensitivity declines with afterripening at 5 C (fig 6, 7), but there is no evidence that the sensitive period is shortened (fig 7). Both of these experiments suggest that the initial effect of afterripening is actually to increase temperature sensitivity and amount of potential dwarfing. In a closely related plant, *Prunus cerasus* L., the first weeks of afterripening apparently involve cell divisions continued from seed maturity (18). A similar observation has been made for *Lindera benzoin* (16).

In neither of the experiments recorded in figures 6 and 7 did afterripening completely eliminate dwarfing in response to temperature. The total chilling requirement of the seed for germination is 2 to 3 months, but depends on germination temperature. However, as afterripening is completed the seed will germinate at 5 C; seeds completely afterripened could grow past the temperature-sensitive stage at 5° and thus make it impossible to show a complete relation between the elimination of the dwarfing response and breaking of the rest period.

Discussion

The data presented in this paper are difficult, if not impossible, to explain on the basis of the presence of growth-inhibiting or stimulating compounds. In addition to the problems of localization and persistence previously noted, present data show that dwarfing is not an obligatory stage in the development of the seedling. The shoot apex of the non-afterripened epicotyl seems to be capable of existing in one of two relatively stable growth habits. A temperature-sensitive process apparently results in a relatively permanent conversion of a self-duplicating system within the meristem cells; this self-duplicating system then controls processes of cellular growth leading to the normal or dwarf habit. It is, of course, possible that the seed contains a sensitizing agent in the non-

Fig. 7. Leaf abnormalities of Elberta peach seedlings following germination at 19 or 25 C for 9 days, or for 7 days at 19 and 2 days at 27 with the 2-day period at 27 at the time specified. After-ripening at 5 C. 1960 crop. The lot indicated by (1) was not as severely dwarfed as the percent of nodes would indicate; leaf symptoms were much milder than normal and a rating of severity of dwarfing would place this lot about equal to the others after 10 weeks after-ripening.

afterripened condition, but this would not be the same as a direct growth inhibitor.

The sensitive period is limited approximately to the time between first visible root growth and the first shoot elongation; there is at present no obvious explanation for this limited period of sensitivity.

Some physical mechanism must operate to direct the anatomical localization of the dwarfing symptoms. The work of Dermen with mature peach trees (6) offers some possible explanations. In a study of cytochimeras Dermen reported that the apical meristem has three important cell layers. The outer two layers contribute to all structures of the leaf except the inner portion of the midrib; the third layer contributes mostly to the inner portion of the midrib of the leaf. The third layer may or may not appear in the buds produced by the apical meristem. The location of the layers is not rigid; a degree of plasticity within the developing organs allows for some shifts in cell position. Unfortunately, Dermen's data apply mostly to more mature trees; this same type of data is needed for epicotyl development.

If we assume that A: peach dwarfing is controlled by self-duplicating units in a specific layer of cells of the meristem, B: these units are transmitted only by cell division, and C: in the early plant development there is a regular relationship between cell layers and axillary bud development, then many of the present observations might be explained. Furthermore, we may assume that each self-replicating unit can exist only in either the normal or the dwarf condition, and that, within the effective temperature range, increasing exposure increases the number of cells in the dwarf condition. If this is so, there would be little or no chance for a strongly dwarfed plant, with most meristematic cells in the dwarf condition, to recover. However, a slightly or moderately dwarfed plant might produce a few normal leaves, or many slightly abnormal leaves, simply because in some developing primordia the dwarf cells might be overgrown or pushed aside.

According to this hypothesis, the real measure of the dwarfing response must be related to the number of affected cells in the meristem, and the location of these cells, not to the leaves or stem resulting from their division. Ledbetter (14) and Holmsen (11) studied the anatomy of dwarf stems, noted that the shortened stems are primarily due to a reduction in cell division, and suggested (14) that the factor controlling stem development comes from the leaves above. The proposal made here is in line with these observations, but directs primary attention to the apical meristem. The relationship between dwarf leaves and stem could be investigated by using moderately dwarfed plants to study internode length relative to the severity of leaf abnormality.

The data in the present paper do not bear directly on the problem of mechanism controlling the rest period of buds. However, the similarities between dwarfing and the rest period of buds have been noted. If such a comparison is valid, then it may be necessary to consider that bud rest also may be due to mechanisms other than those associated with simple growth inhibitors.

Summary

► Physiological dwarfing in peach seedlings from non-afterripened seeds has been considered by others to be the result of a growth inhibitor persisting from the resting seeds. However, this dwarfing factor never enters the axillary buds nor does it appear to be degraded or diluted during seedling growth. The present study was made using resting peach seeds [*Prunus persica* (L). Batsch. cv. Elberta] permitted to germinate by removal of part of the seed coat and associated endosperm tissue.

► The expression of dwarfing symptoms during growth was found to be controlled by germination temperature during the first 2 or 3 to 8 or 9 days. Within this period, germination at 22 C produced almost entirely normal plants; germination at 25 resulted in severe dwarfing. Almost all of the affected organs were formed during or after the germination period. Other peach varieties responded in the same general way. Daily alternation between 25 and 19 C (12 or 16 hr & 12 or 8 hr), or 2-day exposure at 25° during a 9 day germination period at 19°, produced plants with less severe symptoms than those germinated at a constant 25°. Treatment with gibberellin during germination did not alter temperature sensitivity. Imbibed seeds did not become temperature sensitive until removal of part of the seed coat permitted germination to begin; no sensitivity could be shown beyond the 9 day germination period. Afterripening seeds at 5 C reduced the severity of dwarfing resulting from 25° exposure, but did not shorten the sensitive period.

► The physiological and anatomical aspects of dwarfing suggest control by a self-duplicating system localized in a limited region of the apical meristem and transmitted only by cell division. This system is temperature sensitive during only a limited period of plant development.

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