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Two Methods of Studying Rest: Temperature Alternation and Genetic Analysis

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Explaining the physiological basis of rest or endodormancy (23) in seeds and buds has been the goal of considerable research effort within the past 40 years. One of the most popular approaches has been to study hormonal control, based on the hypothesis that growth-inhibiting compounds accumulate in buds and seeds as growth slows or seeds mature, and that these are metabolized, or that growth promoters are synthesized, or both, during subsequent exposure to rest-breaking treatments (moist chilling, dry after-ripening, exposure to light, etc.)

Despite major advances since 1945 in the discovery of new hormones (gibberellins, cytokinins, and abscisic acid) and introduction of new methods of analysis, the mechanism(s) of dormancy release in cold-requiring seeds and buds of woody plants remains an enigma. Growth promoters have surprisingly little effect on intact seeds or buds during "deep" rest, and nonphysiologically high levels of ABA are required to inhibit the growth of seeds and buds after rest is broken (6). If their levels control response, why are they not more effective? One possibility is that the real "dormin" (the name originally given to abscisic acid) still remains to be discovered.

The major questions I will address are: a) Why should low temperatures favor a (chemical?) reaction (i.e., the breaking of rest), while high temperatures inhibit it?; and b) what genetic information about rest is available that might cast light on the mechanism of control? These two questions are not directly related, and I shall discuss them independently. Because the effects of temperature in breaking rest parallel in many ways its effects on vernalization of biennials, I will compare these two processes where appropriate.

Similarities between chilling of seeds and buds and vernalization

Chouard (4) differentiated clearly between vernalization and the breaking of dormancy (rest), defining "vernalization" as "the acquisition or acceleration of the ability to flower by a chilling treatment". The breaking of rest, on the other hand, "allows on active growth...but does not directly cause the formation of new kinds of organs". However, the similarities between the effects of low temperatures in breaking rest and in stimulating flowering of cold-requiring plants are well-known, and Schwabe (36) suggested that the two phenomena might be different manifestations of the same metabolic conditions. The process of vernalization was analyzed in detail in the 1950s and 1960s (see ref. 31). The optimum temperatures that hasten or induce flowering (≈7°C) in some species are similar to those that break rest in others [e.g., peach buds and seeds (9, 37)], and temperatures of 20° or higher can reduce or completely negate the effects of previous chilling (10, 11).

Despite these similarities, differences exist. Graft transmission of the vernalization effect has been demonstrated in several instances (see ref. 22), although doubts remain as to whether vernalization per se or merely the capacity to flower is transmitted. In contrast, little evidence exists for grafting effects in inducing or breaking rest (3, 29). Certain species (e.g., celery) have an obligate requirement for vernalization; in others (e.g., rye), low temperature only hastens flowering. In tree fruits, chilling is obligatory once rest is induced, although rest may be avoided by cultural practices (7, 8, 21).

Rationalization of the temperature effect

Several schemes, differing only in details, have been proposed to rationalize the effects of low and high temperatures on vernalization (24, 26, 27, 38). In the scheme (Fig. 1) proposed for winter rye by Purvis and Gregory (33), a precursor (A) is converted at low temperature to intermediates (A′ and B). Warm temperatures favor conversion of A′ back to A. Continued exposure to chilling permits the conversion of (A′) to (B) and thence to (C). Under the influence of long days (LD, spring), (C) is converted to (D), which stimulates flowering. Under short days, (C) is converted back to (B) and thence inactivated to (E). Short days will substitute for chilling, provided plants are subsequently exposed to LD. Intermittent exposure to temperatures of 18°C or higher during vernalization reduces response, the effect increasing with temperature (32).

To explain their results, Purvis and Gregory (33) proposed that the forward and the back reactions from (A) to (B) respond differently to temperature, the former being more rapid than the latter at low temperature and vice versa, resulting in a stimulation of flowering at low temperature and an inhibition at high temperature (Fig. 2). This proposal, though often quoted, has not been verified experimentally, chiefly because no one has yet determined the nature of the reactions (probably numerous) involved. Salisbury (34) described the theory as "a neat one, but...little more than a graphic representation of the experimental observations". Similarly, Chouard (ref. 4, p. 217) summarized the various schemes proposed as "handy to memorize", but providing "no more clarification than the authors' descriptions of their own results".

Promotive effects of intermediate temperatures

Extensive experiments by Erez and co-workers (9–11) with intact potted trees and with rooted or nonrooted cuttings of peach have indicated that intermediate temperatures (e.g., 15°C), which are

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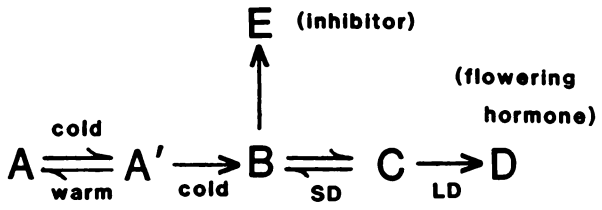

Fig. 1. Scheme proposed to explain the effects of temperature and photoperiod on the vernalization of 'Petkus' winter rye (32, 33). See text for explanation.

ineffective alone in breaking rest, often promote budbreak when alternated in diurnal cycles with chilling temperatures (e.g., 6°), even though the buds are exposed to fewer total chilling hours (Table 1). In contrast, temperatures of 20° or above counteract the effects of chilling provided exposure time is greater than 4 hr/day (5, 9–11). Intermediate temperatures are generally most effective when applied during the final third of the chilling period.

Gilreath and Buchanan (15), also using rooted peach cuttings, reported that the breaking of rest of flower buds was hastened when diurnal temperatures alternated between 7° and 15°C, thus supporting the observation of Erez et al. (Table 1). Again, the effect was observed only late in the chilling process (650 hr at 7°).

Erez and Couvillon (9) proposed a modified version of Gregory and Purvis's scheme to explain their results (Fig. 3). Intermediate temperatures permit more rapid conversion of (B) to (C), thus increasing the efficiency of low temperature in breaking rest. In contrast, temperatures of 20°C and higher, when interspersed with chilling temperatures, presumably favor conversion of (B) back to (A).

Erez and Couvillon (9) do not attempt to explain what A, B, and C might be, and their curve (Fig. 3) for promotion can be faulted for not coinciding with "c" below 10° and "b" above 10°. Nevertheless, their proposal is of interest as a working model. I have found in the literature no reference to promotive effects of intermediate temperatures (e.g., 15°) on vernalization, although prolonged exposure to 20° can sometimes hasten flowering or prevent the negative effects of subsequent exposure to high temperatures (14).

Do intermediate temperatures promote budbreak in species other than peach? Felker and Robitaille (13), using cuttings of sour cherry (*Prunus cerasus* L.), observed that alternating temperatures during chilling affected subsequent bud swell in different ways, depending on the time of treatment (Table 1). When cuttings were treated for 400 hr before forcing at 27°C, alternating temperatures (5°/15°) had little effect on nonchilled buds or on partially chilled buds collected

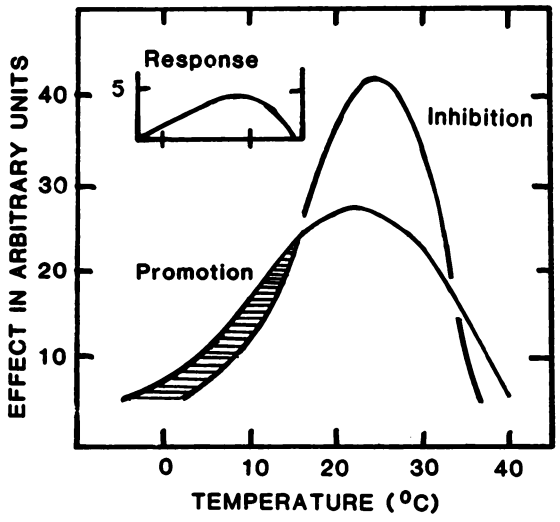

Fig. 2. Presumed effects of temperature upon the relative rates of conversion of A to A′ (promotion) and of A′ back to A (inhibition) (see Fig. 1). (**Inset**) Temperature-response curve of vernalization (promotion minus inhibition) resulting from differences between rates of two reactions (adapted from refs. 22 and 34.)

from the orchard in late December. However, when treatment was continued for 2000 hr (= 1333 hr at 5°), bud swell was equal to that following 2000 hr at a constant 5°. However, mean bud stage on forced cuttings seldom exceeded a value of 2 ("half green"). In a separate experiment, buds on trees in containers exposed to alternating temperatures were as far advanced ("green tip") after exposure to 1600 hr at 5° as were those on trees chilled continuously at 5° for 2400 hr, and grew at the same rate when trees were moved to a greenhouse. In contrast, buds on trees held continuously at 15° failed to grow on transfer to 21° to 25°.

Thus, in two species at least, moderate temperatures appear to enhance the effects of chilling temperatures in breaking the rest of buds, provided they are applied at the appropriate time, i.e, late in the chilling period.

Is there evidence for promotive effects of intermediate temperatures in breaking rest in seeds? The seeds of certain species [e.g., Bells of Ireland (*Molucella laevis* L.)] require alternating temperatures (10° or 15° alternating with 20°C) for optimum germination (16, 17). However, the low temperature need not be in the "chilling" range. Preliminary work with peach seeds indicates that sub-

Table 1. Effects of alternating[z] vs. constant temperatures (°C) on breaking of rest.

Species and cultivar	Effect	Ref.
Peach leaf buds		
Redhaven	6°/15° >> 4°	10
Redskin	6°/15° > 4°	10
Redhaven	4°/15° >> 4°	5
	4°/15° = 4°	5, 9
	6°/15° = 6°	9
	6°/9°, 6°/11°, 6°/13° and 6°/15° > 6°	9
Cornet	0°/15°, 4°/15°, and 6°/15° >> 0°, 4°, or 8°	9
Peach flower buds		
Redhaven	4°/15° = 4°	5
	4°/15° > 4°	9
Sungold[x]	6°/9°, 6°/11°, 6°/13° and 6°/15° ≥ 6°	9
Sour cherry flower buds	7°/15° > 7°[y]	15
Montmorency		13
Peach seeds	5°/15° > 5°[y]	
Halford	5°/10° > 5°	1
	5°/15° < 5°	1
Siberian C.	5°/10° > 5° or 10°	(A. Mahhou, unpublished data)
	5°/15° < 5°	

[z]All 18 hr at low and 6 hr at high temperature except for 'Sungold' nectarine (14/10 hr).
[y]Effective only during latter part of chilling period.
[x]Nectarine.

Table 2. Growth and germination characteristics of four genotypes of *Arabidopsis thaliana* (adapted from refs. 18, 20, and 21).

Genotype	Phenotype	Requirements for seed germination
Wild type (AAGG)[z]	Normal	Chilling plus light or storage
Mutants		
GA-deficient (AAgg)	Dwarf; GA stimulates stem elongation	Fails to germinate regardless of conditions unless GA supplied
ABA-deficient (aaGG)	Wilts readily	Germinates in absence of light, chilling, or GA
GA- and ABA-deficient (aagg)	Same as AAgg; wilts readily	Same as aaGG

[z]"A" represents a dominant gene for ABA synthesis, "G" a dominant gene for GA synthesis (these symbols were not used in papers cited).

sequent germination is promoted when stratification temperatures are alternated between 5° and 10°, but usually inhibited by 5°/15° (ref. 1; A. Mahhou, unpublished data). Thus, peach seeds appear to differ from buds in their temperature thresholds for promotion/inhibition. That for buds is ≈18° (10, 11), whereas the value for seeds appears to lie between 10° and 15°. In peach buds, the negative effect of high temperature is eliminated on long cycles; the longer the cycle, the less inhibitory the effect (11). This change suggests a "fixation" of B, preventing conversion back to A, in the scheme proposed by Erez and Couvillon (Fig. 3). Data for peach seeds support this observation (A. Mahhou, unpublished data).

Additional experiments (A. Mahhou, unpublished data) indicate that holding peach seeds at 5°C for 6 weeks, followed by 3 weeks at 10°, is as effective in promoting germination as are alternating cycles of 16 and 8 hr at 5° and 10°, respectively, for 9 weeks; 15° is just as effective as 10° using this system, yet inhibits germination when used in a daily cycle (Table 1). Holding seeds at either temperature during weeks 4 through 6 is also effective, but both treatments inhibit germination when applied during weeks 1 through 3 in a 9-week experiment (total of 6 and 3 weeks at low and high temperature, respectively).

What conclusions can be drawn from these observations? As previously noted, the major difference between vernalization and the breaking of rest is that chilling induces subsequent morphological changes (flowering) in the former, whereas it merely permits growth to occur in the latter. Buds and seeds can begin growing when partially chilled, whereas flowering is an after-effect of chilling. Therefore, transferring partially chilled buds or seeds to temperatures of 10° to 15°C may stimulate growth. This may or may not be reflected in germination/budbreak during treatment. I suggest, therefore, that intermediate temperatures do not hasten the breaking of rest, but merely stimulate growth in partially chilled organs. Treatment is ineffective in the early part of the rest period because growth cannot occur at that time. Unfortunately, in most of the published data, budbreak is reported only after exposure to temperatures of 20° or higher; this limits confirmation of the hypothesis.

Brown's (2) study on apricot buds is of interest in this regard. He noted that bud development became increasingly responsive to growing temperatures as rest was broken, and suggested that "the total number of chilling hours required to break the rest might be reduced" by such growing temperatures, whereas "the time required to effect the break...could be longer than with more intense, high efficiency chilling". This statement, of course, does not explain why temperatures of 20°C and above are inhibitory. Pollock (30) demonstrated that nonchilled peach embryos produced normal seedlings when held at 20° or below during the first few days of germination; dwarfs developed at higher temperatures. A similar process could control development in partially chilled buds. Direct transfer from chilling temperatures to 20° or above may permit growth of only those buds that have begun to expand; intermediate temperatures may allow a larger number of buds to begin developing prior to transfer.

Saure (35) proposed another explanation for the promotive effects of intermediate temperatures. His scheme, resembling that proposed by Vegis (40) for seed germination, assumes that response to temperature shifts as chilling is prolonged. The temperature range effective in breaking rest is relatively narrow in nonchilled organs, but widens as chilling is prolonged; that for inhibition simultaneously narrows. This would explain why intermediate temperatures become more effective in breaking rest as chilling proceeds. Additional data are needed to differentiate between this hypothesis and that involving the direct effect of higher temperatures on germination per se. For example, prevention of germination by osmotica during the stratification of seeds might permit separation of the effects of temperature on rest vs. germination.

Genetic aspects of rest

A knowledge of the genetic basis of rest might provide clues to its physiological control. Considerable progress could be made by using genotypes in which rest is controlled by a few genes, for this would permit concentration of effort on a few critical reactions. Unfortunately, control of rest in most species appears to multigenic. However, the genetics of rest has been investigated in a few species, and some important breakthroughs have occurred within the past few years.

Let us first briefly review the genetic basis of vernalization in some selected species. A cautionary note is necessary here. I will refer to a "single gene" as an hereditary unit that appears to be indivisible on the basis of data obtained from controlled crosses. It could, however, include several genes in close proximity.

Reciprocal crossing of spring and winter strains of 'Petkus' winter rye (diploid) demonstrated that the vernalization requirement was controlled by a single gene, the spring form being dominant (31).

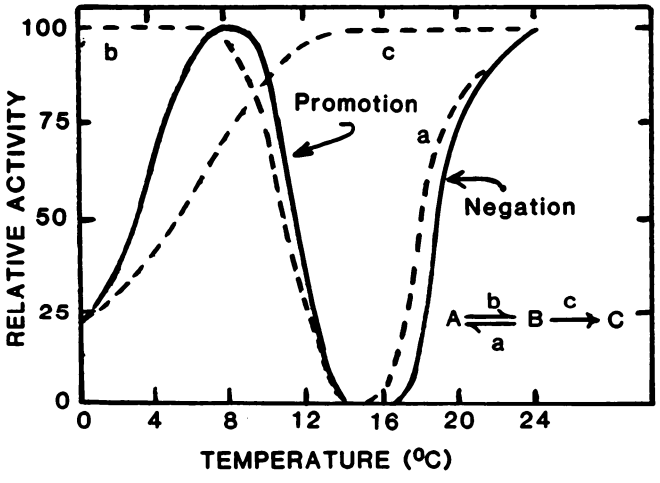

Fig. 3. Observed effects of temperature in breaking bud rest in peach (solid line below 16°C) and in negating the effects of chilling (solid line above 16°), and presumed effects upon relative rates of hypothetical reactions a, b, and c (**inset**) (adapted from ref. 9).

In wheat and barley (tetraploid), at least two genes appear to be involved (see ref. 31), although some investigators have reported evidence for single gene control in barley (38). The vernalization requirement of *Arabidopsis thaliana* (L.) Heynh varies with strain; none has an absolute requirement and some require no chilling (27). Napp-Zinn (27) concluded that four different genes were involved. Given the characteristics of this species (see below), much might be learned about the physiological bases of vernalization from genetic analysis of the various response types.

Until recently, little was known about the genetic control of rest that can be broken by chilling, although several genetic studies have been made of other types of dormancy (see ref. 39). However, recent experiments with *Arabidopsis* have provided some new insights.

Freshly harvested, mature seeds of *Arabidopsis thaliana* require light and a brief (1 week) exposure to low temperature (4° to 6°C) in order to germinate (20). Dry storage for several months at room temperature eliminates the need for chilling. Seeds of ABA-deficient mutants (aaGG, Table 2) are nondormant (18, 20). Additional monogenic recessive mutants fail to germinate under optimum conditions for germination of the wild type (20). Seeds of one group of such mutants can be induced to germinate by application of GAs, and continued application is necessary for normal stem extension. These mutants are assumed to lack the capacity to synthesize GAs (AAgg, Table 2). A chemical mutagen and backcrossing were used to obtain plants that were both ABA- and GA-deficient (aagg); their seeds germinated in the absence of GA but still produced dwarfs (20). These data suggest that GA is required for germination only when ABA is present, in contrast with the scheme proposed by Khan (19), which assumes no germination in the absence of both hormones. However, limited production of GA by "leakage" may explain this contradiction. I know of no data as to the effects of light and/or chilling on GA or ABA content of wild-type seeds.

Data from reciprocal crosses suggest that the ABA content of the embryo, rather than the seed coat, is the primary factor limiting germination (18). Nevertheless, hybrid seeds developing on wild-type plants require a longer period of dry storage to break dormancy than do similar seeds from ABA-deficient plants (18), suggesting a seed coat effect.

Are these data, obtained with an herbaceous species, relevant for studies of rest in woody plants? Crosses made between poplar ecotypes with varying response to photoperiod suggest multigenic control of "summer dormancy" (28). However, Thompson et al. (39) have provided evidence that a single recessive gene may control bud rest in filbert (x = 11). Analysis of data for 55 progenies that contained both dormant and nondormant seedlings indicated that many commercial cultivars are heterozygous for this gene. Chi square values were consistent ($P < 0.05$) for 3:1 (dormant : nondormant) ratios in 51 progenies, indicating single gene control. Ratios in the remaining four progenies gave significant χ^2 values for two-gene control (7:1 ratio for dormant : nondormant seedlings) (M. Thompson, personal communication). The author noted that other fruit and nut crops could possess similar genes; nondormant mutants could easily be eliminated inadvertently by cold injury in breeding programs conducted in the temperate zone. Rest generally has been considered a complex phenomenon involving multigenic control. Control in filbert also is probably multigenic, but one controller gene may set the process in motion. Thompson et al. (39) state: "...here is a single gene that regulates a pivotal process for the normal expression of other genes. Perhaps the mutant affects the photoperiodic receptor system in leaves...or a translocatable phytohormone which may transmit the message to other plant tissues".

I began this review with some skeptical comments concerning the roles of plant hormones in rest. However, the data for *Arabidopsis* certainly provide strong support for such roles. One of the difficulties faced in working with woody plants is the multitude of genes that may be involved in controlling rest. *Arabidopsis* has been proposed as an ideal experimental plant for studies of physiological genetics for several reasons, including its few chromosomes (x = 5), short generation time (4 to 5 weeks), and the number of known mutations available (25). The genetic diversity in *Arabidopsis thaliana* with regard to vernalization is likewise of interest, as noted above. Should we wait until all the facts are in on *Arabidopsis* before proceeding with studies of rest in trees? I think not. But we might make more rapid progress by combining forces with plant breeders and geneticists.

CONCLUSIONS

a) The effective temperature range for the breaking of dormancy in cold-requiring seeds and buds closely parallels that for vernalization of biennials.

b) Exposure to high temperatures during the course of low-temperature treatments counteracts the effects of the latter on both processes.

c) Evidence for the suggestion that two antagonistic reactions are involved, one favored by low temperature, the other by high temperature, remains tenuous, but the hypothesis provides a framework for further experiments.

d) Intermediate temperatures (e.g., 10° to 15°C) appear to increase response to low temperature in breaking rest of both buds and seeds of several species. Such temperatures do not appear to have a similar effect on vernalization.

e) Previous investigators have suggested that alternating temperatures stimulate the process of rest-breaking per se. However, other data suggest an effect on growth (budbreak and germination).

f) The genetic control of the chilling requirement for flowering and the breaking of rest vary greatly within and among species. Although vernalization is controlled by a single gene in some species, multigenic control is the rule. Only recently have mutants been found in which rest is controlled by a single gene. Their existence suggests that similar cases may exist in other species.

g) The time appears ripe for research involving physiological genetics (and genetic engineering?) to determine the basis of rest in both seeds and buds.

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Apical Dominance

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None of the physiological events in plant growth and development is truly independent. Photosynthesis, flowering, and mineral transport are sharply focused areas of research; yet these phenomena are not separable from other metabolic events in the plant. This feature of interdependence may be called correlations (26) or growth correlations (49, 50). The control exerted by the growth zone emanates from a meristem; these meristems include the root or shoot apex, cambium, flowers, fruit, pollen on stigma, and the ovule or seed in a fruit.

In the 20th century, individual growth correlations have become special areas of investigation (e.g., shoot growth or fruit growth) without regard for their influence over other correlations. Apical dominance is one such correlation that has been studied extensively this century, and it has become a defined area of plant growth research. In apical dominance, the shoot apex can prevent lateral bud growth, and the root apex can prevent lateral root formation (68). The degree of dominance is a function of genetic loci, environmental factors, physiological processes, and plant age. Apical dominance can mean a) complete or nearly complete control of lateral buds by the apex, b) dominance of one growing shoot over another, and c) the apex influence on the orientation of branches and leaves.

It is probable that the term apical dominance stems from the early studies by Thimann and Skoog (85, 86). Experimenting with the herbacious annual *Vicia faba* L., they reconfirmed that apex removal led to growth of lateral buds that previously were not growing. Continued apex removal led to bushy growth in a plant that otherwise would have produced a dominant central stem.

The problem in the exact meaning of apical dominance arose when application of this term was transferred from an annual plant directly to perennials. Brown et al. (13) clarified the issue and presented a solution; refer to their paper for a complete analysis. In their system, apical dominance concerns the apex influence over lateral buds on a single branch, whereas apical control concerns the influence of the main growing point on all branches on a perennial plant. An excurrent tree, like an arborescent gymnosperm, has a strong central leader and exhibits strong apical control, whereas polyaxial fruit trees have a weak central leader and weak apical control—all branches tend to grow equally. Many fruit trees exhibit strong apical dominance of individual branches growing from the main trunk and yet weak apical control over the entire tree. To resolve this issue clearly, one must see each branch separately on the polyaxial fruit tree and not view the tree in total. Each branch on the polyaxial fruit tree is expressing strong apical dominance, which is why a central leader will not occur without judicious, annual pruning. Because no single apex controls the form of the fruit tree, the natural unpruned shape is many-branched and clearly polyaxial. When some genera are pruned annually, they will form a central leader. Once pruning is stopped, however, the upper portion of the tree will immediately return to the polyaxial form.

Apical dominance has significance in agriculture, particularly as we might envision its control by human beings. Apical dominance expression has direct relationships with plant form and subsequent potential for yield. In tomato and tobacco, a strong central growing point would enhance yield. In cereals, ornamental flowers, and young fruit trees, however, growth of lateral branches would enhance yield. Valuable reviews on apical dominance are found in Andus (7), Brown (13), Hillman (38), McIntyre (55), Philips (68), and Rubinstein and Nagao (72).

The purpose of this review is to take a historical perspective, emphasizing the environmental factors that influence the degree of apical dominance expressed; to describe the initial events that occur in a lateral bud released from apex control; to discuss the hypotheses for apical dominance mechanism involving hormonal control; and to finish the review by offering an alternative hypothesis for testing.

No attempt has been made to cover all the possible literature on