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A DEGREE GROWTH STAGE (°GS) MODEL AND COLD ACCLIMATION
IN TEMPERATE WOODY PLANTS

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I. INTRODUCTION

Perennial woody species native to the temperate zone annually undergo rhythmic growth cycles that are synchronized with seasonal environmental changes. The timing, rate, and sequence of changes in bud growth and development are largely irreversible and induced by environmental signals (31,32,33) such as changes in temperature and daylength (6,9,38,39,46). The physiological model (Degree Growth Stage Model) is designed to numerically describe and predict the annual growth cycle and hardiness of vegetative buds of such species.

The literature on annual growth cycles and cold hardiness of trees and shrubs is too extensive to discuss in detail. Several good reviews on growth cycles (3,19,22,28,35,45,46,50,55,57,58,65,71,73,74,75,76) and hardiness (3,4,5,17,56,67,68,78,79,80) are available.

Attempts to relate growth stages to environmental factors have had limited precision because, to quote Sarvas, "there are no suitable, easily observable phases that can be accurately measured" (60,61). Improved techniques of identifying growth stages help overcome this problem (15,43,44,48,62,63). Progress is also inhibited because the terminology used to identify and describe growth phases is qualitative and often confusing (8,28,46,55,71,74); and because adjacent plant organs may be at different stages of development. The °GS model provides a quantitative means of describing distinct physiological stages of plant growth and development. For simplicity the terms used herein apply only to describing the physiological status of apical (terminal) buds.

In broad terms a living bud may either be growing or dormant (60,61). Growing buds characteristically elongate rapidly during the spring flush of growth, and more slowly as the summer progresses and environmental constraints and/or correlative inhibition by neighboring organs eventually cause the bud to stop growing. When a bud stops growing it is dormant. When all of the buds on a plant stop growing the plant is dormant. Growth cessation in autumn is a prerequisite to cold acclimation in most woody temperate zone species (79), and plants fully deharden when growth resumes in the spring.

A bud may be dormant for several reasons. At some stages of development a dormant bud will rapidly resume growth in response to changes in the physical environment. Dormant buds capable of resuming growth when the environment becomes favorable are dormant quiescent buds. Dormant buds which remain dormant in a favorable environment, but rapidly resume growth if neighboring organs (leaves, buds, etc.) are removed are dormant correlatively inhibited buds.

Dormant buds which remain dormant for prolonged periods even if the environment is favorable for growth and competitive/inhibitory organs are removed are dormant resting buds. Such internally inhibited buds normally require prolonged exposure to inductive chilling temperatures before they can be induced to grow. Figure 1 and 2 schematically illustrates this discussion.

Sarvas (60,61) developed an annual growth model for temperate zone tree species which could be used to mathematically predict the effects of temperature on plant development during the "active growth period" and during the "autumn and winter dormancy" periods. He had difficulty, however, in identifying specific starting and ending points ("point events"), and the intervening periods in plant development ("segment events"). Sarvas' models were well conceived and provided some of the

data and the conceptual basis for developing the °GS model. He attempted to relate cold hardiness development to tree growth (60,61), but this portion of his study was speculative, and not supported by experimental data.

Several other mathematical models have been developed to describe the breaking of winter dormancy in temperate plants (1,11,12,29,32,33,37,45,54) and to quantitatively express that portion of the annual growth cycle. All of these models assume that low temperatures (chilling) are needed to break rest, and that warm temperatures are needed to overcome quiescence.

There is a disagreement about the effects of chilling temperatures on breaking rest. Nooden and Weber (46) state that plant responses to temperatures varies widely among species, while Sarvas (60,61) suggests that it does not, and that similar chilling temperatures have the same effect on plants entering rest as in breaking rest (61). It is widely accepted that the onset of winter dormancy, and the duration of chilling (chilling units) required to overcome rest varies with genotype.

Mathematical models such as the Utah chill unit model (37,54) and heat unit models (60) do not accurately predict developmental stages in all environments (2,59), but in some locations they do provide good predictions. These models like Sarvas' do not identify and define physiological starting and ending "points events". They also do not measure physiological segment events and therefore, previous chill unit and heat unit models are not based on physiological processes. This is probably the reason that mathematical models work only in certain climates and with certain plants.

Various terms have been used to describe "point" and "segment" events during the annual developmental cycle of temperate zone woody species. Table 1 summarizes the terminology used in this paper, the sequence of point and segment events, and the corresponding °GS for a typical annual growth cycle. The ensuing discussion describes each event.

Point Events

1. Spring Bud Burst: When visible vegetative growth first appears from the dormant bud. Bud growth is not inhibited by short days, and it is not possible to induce cold acclimation at this stage.

2. Maturity Induction Point: When plants first become responsive to daylength or other environmental factors which promote development of vegetative maturity. In dogwood, growth of buds exposed to short days slows and stops. Growth of buds exposed to long days continues.

3. Vegetative Maturity: When leaf removal no longer stimulates dormant buds to resume growth. Prior to this point leaf removal stimulates correlatively inhibited dormant buds to begin growing within a few days. Whole plants artificially defoliated prior to this point suffer ultimately die-back and do not cold acclimate even in the absence of environmental

TABLE I. Bud growth and dormancy timing and terminology for point events and segment events during the seasonal cycle of development.

Developmental status	Point events	Degree growth stage (°GS)	Segment events
Growing	Spring bud break	0°	
Growing		0°-90°	Rapid growth phase
Growing	Maturity induction point	90°	
Growing/inhibited		90°-180°	Slow growth/correlative inhibition phase
Dormant	Vegetative maturity	180	Growth stops/end of correlative inhibition phase
Dormant		180-270	Deepening rest phase
Dormant	Maximum rest	270	
Dormant		279-315	Decreasing rest phase
Dormant	End of rest	315	
Dormant		315-360	Quiescent phase
Growing	Spring bud break/end of dormancy	360/0	

stress. Plants defoliated after this point survive prolonged storage and acclimate to freezing temperatures (Fig. 5) (15,43).

4. **Maximum Rest:** The point at which buds require the longest chilling and/or exposure to the highest concentration of gibberellic acid (72) to resume growth.

5. **End of Rest:** When the chilling requirement is fully satisfied. Dormant buds will rapidly grow when exposed to favorable environmental conditions, or remain dormant (quiescent) if conditions are unfavorable.

Cold acclimation refers to the natural development of hardiness in the autumn and early winter. Deacclimation refers to the natural loss of hardiness in the late winter and early spring. In dogwood the first stage of acclimation in hardy species is normally induced by short days and warm temperatures after the photoreceptive point (90°GS), and the first evidence of acclimation appears at vegetative maturity (180°GS) (43),

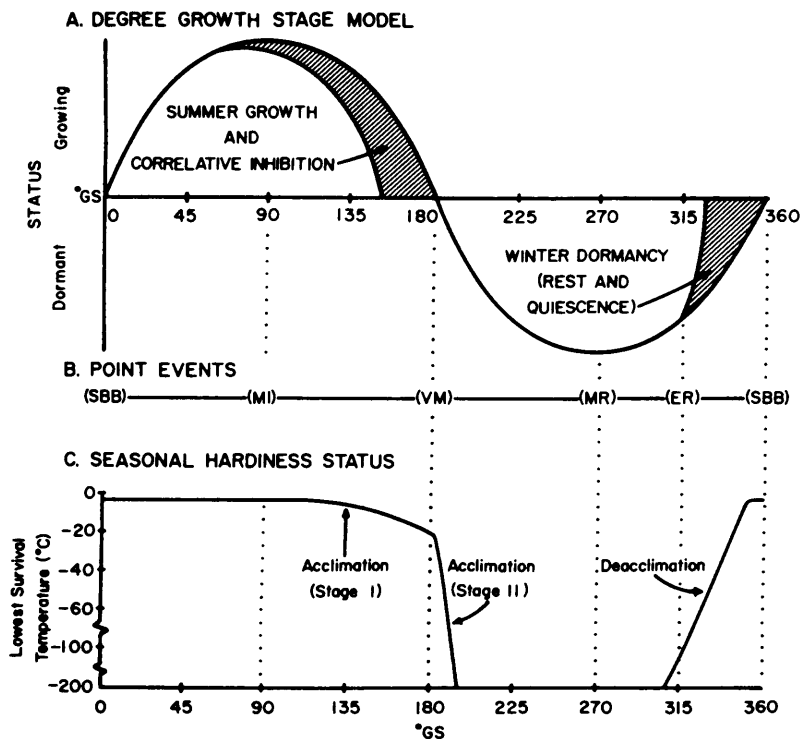


FIG. 1. Diagram of degree growth stage (°GS) model for identifying ontogenetic stages of development (A), point events (B), and hardiness (C) of vegetative buds of temperate woody plants. Point events are indicated: Spring bud break (SBB); Maturity induction point (MI); Vegetative maturity (VM); Maximum rest (MR); End of rest (ER); and End of dormancy/Spring bud break (SBB).

and the second stage by exposure to low temperatures after vegetative maturity (180°GS). Other environmental factors which cause growth cessation and promote development of vegetative maturity may also induce the first stage of cold acclimation. Spring deacclimation is largely dependent upon exposure to warm temperatures. Subsequent exposure to low temperatures may reverse the process (reacclimation) up until growth begins (0°GS).

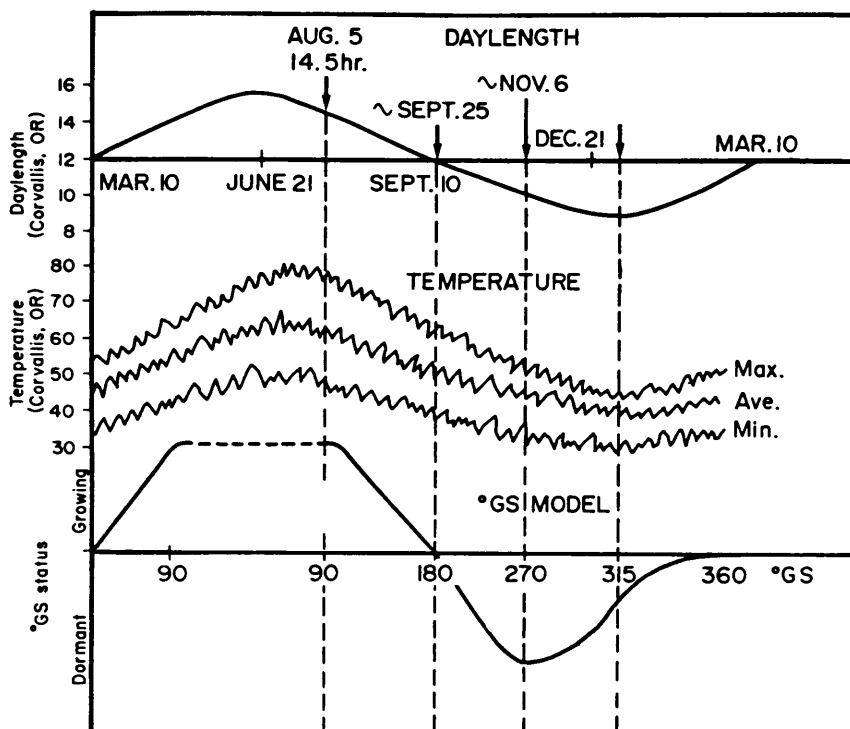


FIG. 2. The relationship of daylength and temperature changes to °GS. Based on studies of red-osier dogwood (Wayland, Massachusetts clone).

II. THE °GS MODEL

The °GS model is a conceptual numerical cyclical function for quantifying the annual ontogenetic development of vegetative buds of temperature zone woody species (Fig. 1A). The model divides the annual growth cycle into 360 degrees growth stages (°GS) and the cyclical function passes through the five distinct point events described (Fig. 1B). The sine curve illustrates the relative degree of development of the segment events between the point events. The segment events are 1) Rapid growth phase, 2) Slow growth/correlative inhibition phase, 3) Deepening rest phase, 4) Decreasing rest phase and 5) Quiescent phase (Table I).

The amplitude of the sine curve is unimportant, and simply illustrates whether growth is promoted or inhibited. Fig. 1c illustrates the seasonal changes in bud hardiness.

The portion of the sine function from 0 to 180°GS describes the growth period, and the function from 180 to 360°GS describes the dormant period.

Plant growth stages do not occur in a perfect sine function as depicted in Fig. 2. Normally, the curve is skewed, and the extent of skewing depends on environmental influences. Degree growth stages (°GS) represented by this model should not be confused with days of the year (Fig. 2).

One assumption on which this model is based is that under natural conditions the progression of bud growth and development stages are irreversible, e.g. "determination concept" (32). Buds may however reach plateaus of development (transition states) when there is essentially no developmental progress. This can occur when the environment is either non-inductive or inhibitory to development. In contrast cold acclimation and deacclimation are reversible, especially during deacclimation, suggesting that the loss of cold hardiness is a physical rather than a physiological process.

III. °GS MEASUREMENTS

°GS point events were established by experimentation using a clone of Cornus sericea L. (Wayland, Massachusetts Clone) as the test plant. The tests are relatively simple but time consuming. Faster and simpler techniques are needed. Tests that may someday prove useful for quantifying the °GS are described.

A. 0°GS Spring Bud Burst

0°GS spring bud burst was determined by visually observing terminal vegetative bud elongation, i.e. when the first green leaf tips emerge from the bud scales. The model is based on development of vegetative buds not flower buds. The environmental requirements for vegetative and reproductive bud development are different and vary greatly among genotypes (55). Microscopic observation to determine when stem elongation first begins before visible emergence may be useful for some applications (82). For simplicity we use visual observation.

B. 90°GS Maturity Induction Point

90°GS maturity induction point was determined by subjecting plants to short days and identifying when the least number of days needed to subsequently achieve the 180°GS occurred (Fig. 3). Dogwood plants grown under natural daylength, and at warm temperatures (15°-20°C), from 0°GS were placed in a short photoperiod (8 hr.) at a warm temperature at frequent predetermined intervals. Sub-samples from the short-day treatment were

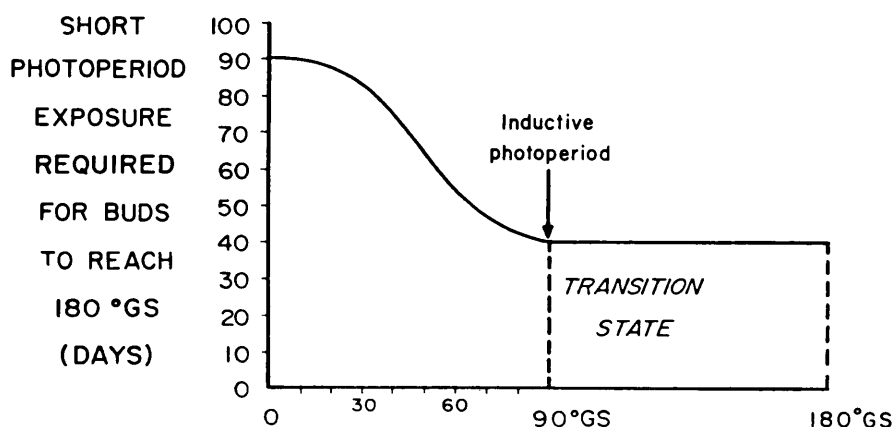


FIG. 3. Diagram illustrating the 90°GS test. Plants growing at 21°C are moved at frequent intervals from a long day environment to a short day environment, and then defoliated. The 180°GS is reached when buds which have become dormant in response to short days fail to resume growth in response to defoliation. The 90°GS is reached when further exposure to short days does not shorten the time required for buds to reach the 180°GS.

defoliated at regular intervals to determine when vegetative maturity occurred. The maturity induction point, 90°GS, was identified by plotting data to determine the earliest sampling date when the least number of subsequent days were required to acquire 180°GS. This test is time consuming and requires controlled environment capabilities and numerous test plants (Fig. 3). Simpler methods are needed.

In red-osier dogwood, about 40 days were required for buds to progress from 90°GS to 180°GS under short days at 21°C (53). Under field conditions in Corvallis, Oregon the Wayland, Massachusetts clone remained in a static transition phase at the 90°GS until the critical shortening photoperiod was reached (Fig. 2). Renquist et al. established by growth chamber and field studies that the critical photoperiod for this clone is about 14.2 hours (53), i.e. development of buds progressed from the 90°GS to the 180°GS in about 40 days at 21°C when plants were exposed to daylengths of 14.2 hours or less.

The maturity induction point is difficult to define and cumbersome to determine. In dogwood its determination is based on the fact that plants are not responsive to photoperiodic influences during the spring flush of growth (32), but later become responsive to photoperiodic stimuli. Many temperate

zone species behave this way, i.e. such plants reach a stage (90°GS) when they are induced by short photoperiods to proceed to the next phase of development. Nitsch (45) has described other types of plants which do not respond in this way including species that become dormant irrespective to daylength, and species that do not become dormant. He notes, however, that plants which eventually become dormant irrespective of photoperiod often become dormant faster under short days than long days. This suggests that under natural conditions most plants do respond to short photoperiods even though photoperiodic effects may be overridden by other environmental influences such as low temperatures, or be endogenous rhythmic processes (6,13,14,20,24,41,64).

Preliminary studies indicate that the square wave patterns generated by an oscilloscope when probes are placed in plant stems may provide a simpler way for determining the maturity induction point (66). Square wave patterns observed during winter dormancy in red-osier dogwood persisted into the spring flush of growth before assuming a different shape (66). Further research is needed to determine whether the change in square wave pattern coincides with the maturity induction point.

C. 0° to 90°GS Rapid Growth Phase

Segment developmental phases between the 0° and 90°GS point events were not measured experimentally by our group, but Sarvas's (60) technique for determining period units (p.u.) during the active period of pollen mother cell meiosis and catkin development is worthy of mention. His major conclusion was "that the regression of the rate of progress of the active period on temperature is the same for all the genera, species, individual trees and the different parts of the active period." "In all the phases of the active period, the rate of progress of the active period depends in the same manner on temperature . . ." Sarvas developed equations based on these conclusions to predict the following point events (or °GS's) during the ontogenetic development of temperate tree species. His equations which are based on observations of plant development, overcome the limitations of models based on heat units and day-degrees. When Sarvas's equations are adapted to the °GS model we have:

$$^{\circ}\text{GS}_1 \rightarrow ^{\circ}\text{GS}_2 = v(T) (t_2 - t_1) \quad (1)$$

where °GS₁ and °GS₂ are equivalent to Sarvas's period units, p.u. and $v(T)$ is the rate at which the physiological processes proceed at temperature T between time t_1 and t_2 .

The variable $v(T)$ apparently changes at each °GS as latter discussion will illustrate. $v(T)$ can be determined experimentally in controlled environment studies. Such studies give rise to the following relationship:

$$v(T) = v(T)_p \times \frac{hp}{ht} \quad (2)$$

where $v(T_p)$ is the rate of development at temperature T_p . hp is the time (hours) required for the cycle to pass through a given °GS interval at the base temperature T_p . ht is the time (hours) required for the cycle to pass through a given °GS interval at temperature T .

When equation (1) is adapted to an environment with fluctuating temperatures we have:

$$^{\circ}\text{GS}_1 \rightarrow ^{\circ}\text{GS}_2 = \int_{t_1}^{t_2} v(T(t)) dt \quad (3)$$

in which $T(t)$ is the temperature at a particular time t and $v(T)$ the rate of progress at temperature T .

For practical purposes equation (3) may be written in the form:

$$^{\circ}\text{GS}_1 \rightarrow ^{\circ}\text{GS}_2 = \sum_{i=1}^n v(T_i) t_i \quad (4)$$

in which i is the i 'th temperature measurement when the time lapse from °GS₁ to °GS₂ is divided into n equal parts.

Landsberg (31,32,33) used these and similar equations, which he developed independently based on arbitrary "development units" to quantify several readily observed phenomena. He, like Sarvas (58), recognized that the major problem of quantifying growth processes is the identification of accurate developmental stages of plant differentiation or point events, which occur as a result of some stimulus (i.e. daylength). Controlled experiments involving responsiveness to daylength as previously discussed are useful for describing the segment events occurring between the 0°GS and 90°GS point events. As previously noted plants cannot be cold acclimated, either naturally or artificially, during this growth phase (13,70).

D. 180°GS Vegetative Maturity

180°GS vegetative maturity was determined experimentally by defoliation studies (15,16,62,63). Buds are vegetatively mature when no bud regrowth occurs following complete manual defoliation (Fig. 4).

Seibel et al. (61) found that 180°GS coincided with the transition from correlative inhibition (summer dormancy) the onset of rest. This test is simple and straightforward, but it cannot be used to quantify the "segment events" between 90°GS and 180°GS.

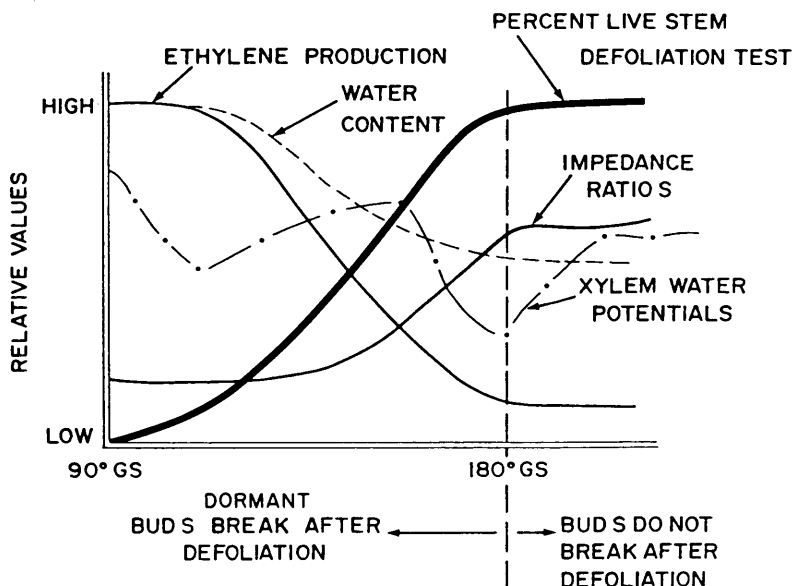


FIG. 4. Test for 180° GS. Relationship of several tests to measure 180° GS from 90° GS. Relative units derived from references 15, 16, 43, 44, 53, 63 and 66.

Other tests (Fig. 4) that have been used with limited success to determine vegetative maturity (180° GS) include ethylene production from nodal stem sections (62), xylem water potential (44), stem water content (44), electrical impedance ratios (44,48), square-wave patterns (48,66) and starch accumulation (61). Results tend to verify that the 180° GS is a distinct stage of development, but none, as yet, provide as precise a measure of vegetative maturity as the defoliation and regrowth test.

E. 90° to 180° GS Slow Growth and Correlative Inhibition Phase

Segment developmental events between 90° and 180° GS can be characterized by the defoliation test. In that test (15) plants are completely defoliated manually during the summer and fall, and any resultant regrowth of leaves from previously correlative inhibited buds is removed daily. Bud break and stem and bud survival is observed the following spring, and plotted against the initial time of defoliation. Figure 5 shows the curve that resulted when red-osier dogwood survival in Corvallis, Oregon was studied (15). The earliest autumn defoliation date which resulted in 100% survival the following spring is the time of the 180° GS.

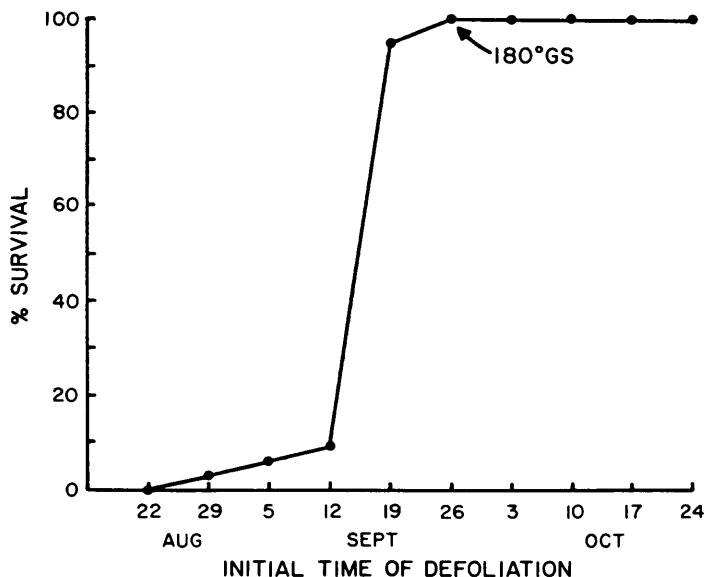


FIG. 5. Percent stem survival test for determining vegetative maturity (180°GS) development. Plants are defoliated in the fall, and % stem survival is determined the following spring. The 180°GS is reached when defoliation results in no stem dieback. Data from Fuchigami et al. (15).

As previously noted a critical shortening daylength had to be reached in red-osier dogwood (14.2 hrs. for the Wayland, MA clone) before bud development progressed beyond the 90°GS (15,53). Temperature effects on the rate of development from 90°GS to 180°GS to within ± 4 days for field grown dogwood plants (51).

The equations developed by Sarvas (60,61) are useful for improving the accuracy of the model in predicting bud development between 90° and 180°GS , i.e. temperature effects established in growth chamber studies (53) were used to compute $^{\circ}\text{GS}$ using Equation 4. As noted previously, the rate of development at each $^{\circ}\text{GS}$ is not a constant (27). This increases the complexity of the model, but must be considered to accurately predict developmental events (27).

In summary this growth phase is characterized in dogwood by its response to a critical short-day stimulus which triggers buds to develop beyond the 90°GS (7,15,53). Other environment variables such as temperature (15,53), mineral nutrition

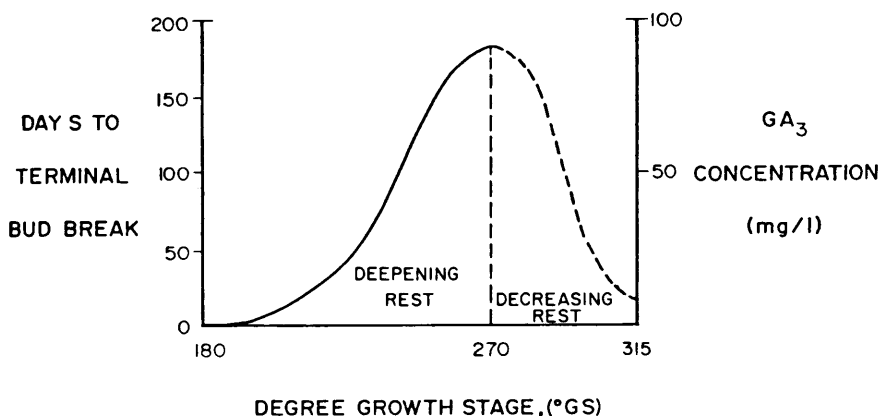


FIG. 6. Regrowth test for 270° GS. Days of exposure to warm temperatures (25°C) and long days required before dormant terminal buds begin growing, or concentrations of GA_3 required to stimulate bud growth.

(16,49,81), and water (81) also influence the rate of development at this stage. Such variables were controlled in this study. Temperature appears to be the most important of these other variables within normal ranges of mineral nutrition and water availability.

F. 270° GS Maximum Rest

270° GS maximum rest can be determined by either of two standard physiological tests (7,15,21,72). The depth of rest can be established by subjecting excised stems to various gibberellic acid concentrations and observing regrowth in a favorable environment (7,20,70). When buds are at the point of maximum rest (270° GS) they require the highest concentration of gibberellic acid (GA_3) to resume growth (7,21,72).

The depth of rest can be established by simply holding intact plants with resting buds in a warm (25°C) environment under long days, and observing how long it takes before buds resume growth. Under such conditions resting buds will eventually begin to grow even though they have been exposed to insufficient chilling. The length of time for growth to resume is proportional to the depth of rest. Maximum rest (270° GS) is the point at which the most time is required before regrowth begins (Fig. 6). In the Wayland, MA dogwood clone almost 200 days were required for regrowth at 270° GS (15,27).

Plants may be triggered to develop maximum rest by defoliating plants prematurely between vegetative maturity (180° GS) and natural maximum rest development (270° GS). Leaves appear

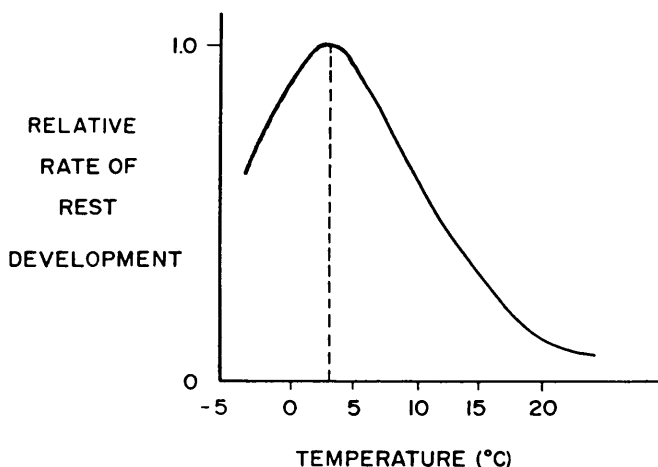


FIG. 7. Temperature effects on the relative rate of rest development in buds. Relative rates for temperatures below 5°C from Sarvas (57); relative rates for temperatures higher than 5°C from Kobayashi (26).

to possess growth promoters that delay maximum rest development. Under natural conditions low "chilling" temperatures are responsible for stimulating leaf senescence thus reducing the supply of growth promoters (27).

These two tests, or modifications (11), are accurate and useful but both require environmental controls, sufficient material for frequent periodic sampling, and a long time (from 2 to 29 weeks) to evaluate results. There are no other effective chemical, electrical or physical tests for measuring rest.

G. 180 to 270°GS Deepening Rest Phase

The tests described (7,15,21,27,72) above can be used to experimentally quantify the °GS segment events that occur between 180° and 270°GS (Fig. 6). Rest is quantitative, as illustrated by the sigmoid curve that results (Fig. 6) when either concentration of gibberellic acid (21,72) or days to terminal bud break (15,27) is plotted between 180° and 270°GS. The rates ($\dot{v}(T)$) at each °GS may be determined experimentally as a function of temperature. Sarvas (61) reported that the minimum, optimum, and maximum temperatures for promoting deepening rest during this phase of development were -3.5, 3.5 and 10°C, respectively (Fig. 7). Other workers have reported similar results (1,12,27,30) and have suggested that high

temperatures, above 21°C , cause negation of low temperature effects (12,77).

In the $^{\circ}\text{GS}$ model we used Sarvas's data at temperatures below 5°C , and expanded the model to 21°C as shown in Fig. 7. Temperatures above 21°C and below -3.5°C are given a value of zero, and considered to be ineffective in promoting rest development in buds. It is also assumed that bud development is irreversible (32). A computer model based on these data and assumptions has been developed by Kobayashi (27). The model has predicted maximum rest (270°GS) in red-osier dogwood within ± 1 day.

H. 315°GS End of Rest

315°GS end of rest occurs in buds when their chilling requirement has been satisfied. Experimentally this point may be determined by placing either excised branches or whole plants in a favorable warm environment for growth, and observing the time required for bud break ($^{\circ}\text{GS}$). Rest is ended when further exposure to inductive chilling temperatures no longer shortens the time for buds to begin growing in a warm environment favorable for growth. Bud break is normally observed after some predetermined time (5 to 8 days), or recorded as the time required for 50% of the buds to break because it takes awhile for bud growth to become visible (12,72). In our tests we have arbitrarily determined the end point by plotting the regressions of the days to bud break against time of sampling. Two regression equations are produced, one which indicates the rapid loss of rest in response to chilling temperatures, and the other which indicates the slow change in bud development during the quiescent period (Fig. 8). The point where regression lines intersect is considered the end of rest, 315°GS .

I. 270 to 315°GS Decreasing Rest Phase

Regrowth tests described previously to determine the 315°GS are also used to determine the segment developmental events ($^{\circ}\text{GS}$'s) between 270° and 315°GS . A reverse sigmoid curve is obtained when days to bud break or GA concentration is plotted against $^{\circ}\text{GS}$ during this period (Fig. 9). This indicates that the rate of decrease in rest ($U(T)$) is different at each $^{\circ}\text{GS}$. This can be verified experimentally in controlled temperature tests. Sarvas's (59) equations (1,2,3,4) may then be employed to determine the various $^{\circ}\text{GS}$.

The low temperature which satisfy the chilling requirement, and ultimately terminate rest during the 270° to 315°GS phase are identical to the temperatures required to promote rest during the 180 to 270°GS phase (Fig. 9). The same procedures are used to quantify rest status in the deepening rest and the decreasing rest phases (27).

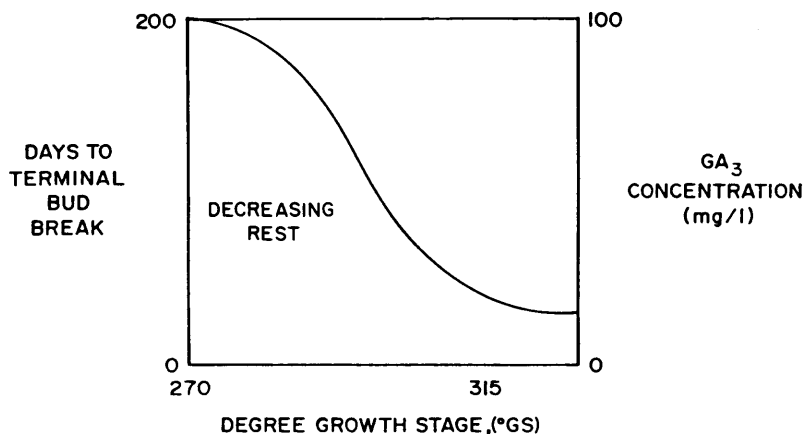


FIG. 8. Test for 315°GS. Determination of rest completion by locating the point of intersection of two linear regression lines plotted through a growth curve in which days to terminal bud break is plotted against °GS.

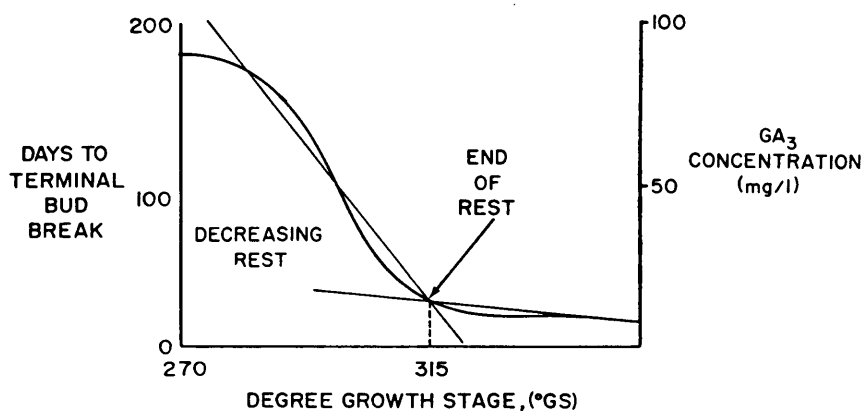


FIG. 9. Determination of time for terminal bud break under LD-warm temperature environment and concentration of GS₃ required to stimulate bud break.

J. 360°GS

It is the same as the 0°GS (A).

K. 315 to 360°GS Quiescent Phase

The progression of bud development during this phase is promoted by warm temperatures favorable for growth. The tests described by Sarvas to determine $v(T)$ catkin development during the active period may be used (60), and his adapted equations (1,2,3,4) can then be employed to determine $^{\circ}\text{GS}$ during this period. Spring bud break signals the end of this phase and the beginning of a new growth cycle (0°GS).

IV. RELATIONSHIP OF COLD ACCLIMATION TO $^{\circ}\text{GS}$

The general relationship of cold hardiness to $^{\circ}\text{GS}$ has been shown in Fig. 2. Kobayashi, et al. have developed a model to predict hardiness levels based on environmental factors and the degree Growth Stage Model (27). General concepts which will provide the basis for modelling cold acclimation and deacclimation in red-osier dogwood include the following:

Cold acclimation does not begin before growth cessation at 90°GS (15,43), and deacclimation is complete when growth begins at 360°GS (27). In nature the maximum hardiness levels are achieved when plants pass through two or three point events or distinct stages of hardiness as hypothesized by Weiser (78,79) and Tumanov (66,68,69). Landsberg states that before plants can respond to a given stimulus, cells must be in a state in which they are "competent" to act (32). Competence may be either an "all or nothing" state or a quantitative state. For example, in hardiness development, if plants are subjected to cold temperatures before they have acquired the first stage of acclimation induced by short days and warm temperatures (13,15) they will not acclimate as rapidly or to the maximum level (13,20,26,70). Experimental evidence suggests that this period begins at 90°GS and ends at 180°GS (13,15). Similarly, plants exposed to long days (LD) after the first stage of acclimation (between 90° to 180°GS) will not be "competent" to respond to low temperatures, which trigger the second stage of cold acclimation, and may take many days longer to acclimate (6,13,24,26). Apple trees exposed to long days and warm temperatures in a greenhouse were observed to cold acclimate a few degrees in the autumn in spite of the non-inductive environment (24). Some plants may respond to endogenous biological rhythms (6,13,14,20,24,41,64), or have redundant overriding mechanisms for triggering cold acclimation and enhancing the potential for survival (79). In short the sequence of stimuli is important. Plants exposed to an inductive stimuli, such as low temperature

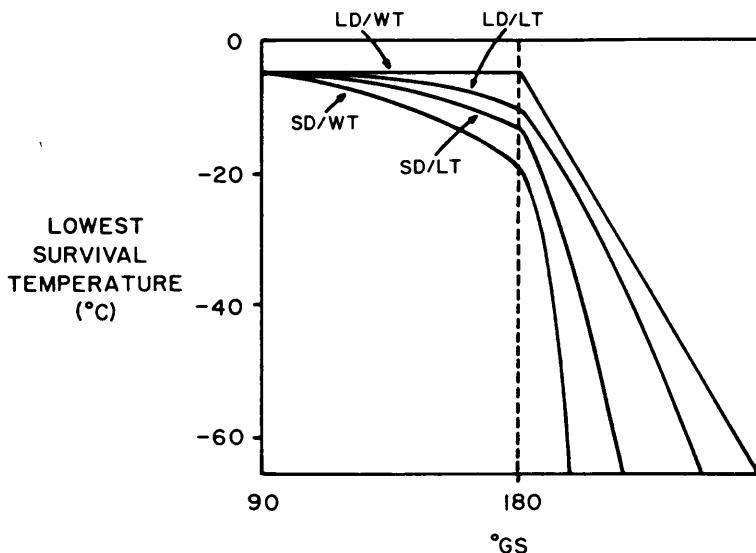


FIG. 10. Effects of daylength and temperature on cold acclimation before and after 180°GS. LT is low temperature; WT is warm temperature; SD is short daylength; and LD is long daylength. Exposure to LT regime after 180°GS.

before they are competent to respond will acclimate, but not as effectively.

Native temperate woody species normally become fully "competent" and achieve the 180°GS in response to shortening photoperiod. This is not always true of cultivated species and man-made hybrids which are native or adapted to other regions. Such plants are often injured because they fail to achieve 180°GS and the first stage of acclimation (to 20°GS in red-osier dogwood) before lethal freezing conditions occur.

The second stage of hardiness occurs in response to low temperatures after the 180°GS (27,43,83). After 180°GS the rate of acclimation becomes a function of temperature as shown in Fig. 10, 11. Frosts are not necessary for the second stage of acclimation as once thought (78,79), but exposure to frost does increase the rate of acclimation at this stage (29,47,67, 68,69,78,79). Even temperatures as high as 20°C induce plants to acclimate between 180° and 315°GS (Fig. 11), and the upper limit of the acclimation promoting temperature range may extend above 20°C (27). Studies of red-osier dogwood (27) and Douglas fir (Timmis, unpublished data) suggest that it does in these species.

Equipment limitations have prevented us from investigating the low temperature end of the acclimation promoting temperature range. Sakai (56) has reported that temperatures between

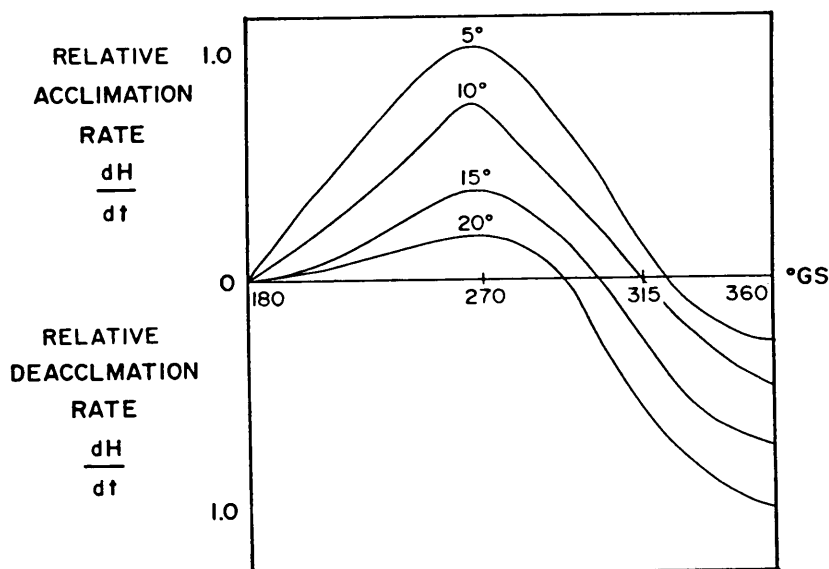


FIG. 11. Relative rates of cold acclimation and deacclimation in relation to temperature between 180° and 360°GS. dH/dt is the rate of hardness change in relation to temperature.

0 and -5°C were best for acclimating plants at this stage and states that temperatures below this range were less effective.

Kobayashi (27) observed that the rate of acclimation increases between 180°GS and 270°GS. In addition, he found that temperatures from 5° to 20°C all caused acclimation in red-osier dogwood, with effectiveness increasing with decreasing temperature. None of the temperatures studied caused deacclimation between 180° and 270°GS (Fig. 10,11). This implies that the Landsberg (32) concept of irreversibility and "determination", may apply to cold acclimation during this phase of development. Temperatures higher than 20°C , which we have not investigated, may cause loss of hardness (10,18,23, 25,36,51,52). Maximum acclimation rate occurs at 270°GS (Maximum Rest) (27). Between 270° and 315°GS plants continue to acclimate, but the rate of acclimation decreases from 270°GS to 360°GS.

Deacclimation first occurred in dogwood between 270° and 315°GS, and soon after the 315°GS a stage is reached when temperatures as low as 5°C promote deacclimation as shown in Fig. 11 (27). The rate of deacclimation increased with increasing temperatures and the deacclimation rate at each temperature increased from 300°GS to 360°GS.

After 360°GS (0°GS) when the vegetative buds break plants loses hardiness completely. From this growth period to 90°GS the plant can not acclimate under natural conditions and plants continue to grow even at low temperatures and short photoperiods (34). Within a few weeks of rapid growth buds attain "competence" at 90°GS to acclimate once they are exposed to the critical short photoperiod which is genotype specific (79).

V. DISCUSSION AND CONCLUSION

Annual ontogenetic "point" and "segment" events during the annual cycle of bud development are defined and expressed numerically in the degree growth stage (°GS) model. "Point events" were identified at 0°GS, 90°GS, 180°GS, 270°GS, and 315°GS. A sine curve can be drawn through these points from 0° to 360°GS. Sarvas's (60,61) equations were used to quantify point events and segment events. These equations could be refined further to account for environmental factors other than temperature and photoperiod that influences bud development, but they are useful in their present form, and each has a physiological basis that can be experimentally established. Greater detail will ultimately be required to identify °GS between point events. Computers can be used effectively to determine the rate change ($v(T)$) occurring at each °GS in relationship to temperature (27).

The °GS model is not mechanistic. Hence other physiological processes and environmental factors such as nutrition and moisture were not considered. These were assumed to be important and were controlled during experimentation. Limitations or excesses of these factors affect bud development, and will be considered as sub-routines in future refinements of the model.

The GS model should provide a basis for estimating hardiness levels in plants. Previous attempts to predict hardiness via computer models (40) have failed because the developmental status of plants were undefined, and the models were not based on physiological processes. Kobayashi and others (27) have developed a hardiness model based on the °GS model. This model is quite accurate and illustrates the importance of relating hardiness rates to specific growth stages.

Kobayashi's studies (27) have shown that the rate of acclimation and the effects of temperature on the process changes, between 180° and 360°GS. A bell-shaped curve describing these relationships is generated when the rate of hardiness in response to temperature (dH/dt) is plotted against °GS (Fig. 11). Deacclimation was not observed until about 300°GS in the decreasing rest phase of bud development. Acclimation has been observed in dogwood after 300°GS, indicating that reacclimation can occur after deacclimation (27). The ability to

reacclimate decreases rapidly after 300°GS because of the increased rate of deacclimation at progressively lower temperatures. Similar observations have been reported for other species (19,23,25,29,36,42,51,56).

In addition to its predictive potential the numerical $^{\circ}\text{GS}$ model can help clarify the subjective and complex nomenclature and used to describe developmental events which occur during the annual cycle of temperate woody plants.

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