Quantifying Bud Dormancy: Physiological Approaches

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"Terms describing or identifying developmental stages of horticultural crops are not used consistently, thus the meaning of each term become ambiguous" (Watada et al., 1984).

A significant accomplishment of the ASHS Working Group on Plant Dormancy has been the workshops and publications on dormancy terminology that led to the adoption of the terms endo-, para-, and ecodormancy by the ASHS Publications Committee for classification of bud dormancy of temperate plants (Lang et al., 1985, 1987). These terms were adopted to reduce the ambiguities arising from the use of many terms for the same phenomena. These ambiguities may have contributed to our lack of understanding of dormancy processes (Lang et al., 1987). The adoption of the new terms of dormancy by our Society has improved communication and removed some of this ambiguity.

New terminology alone, however, probably will not have a major impact on research to improve our understanding of dormancy processes. Most terms that relate to developmental stages of plants are too general and overlook numerous physiological events between growth stages; thus, the usefulness of these terms is often limited. Their use can often lead to inaccuracies and ambiguities. For example, the statement that "application of compound 'X' during endodormancy increased the freezing resistance of..." does not indicate the physiological status of the plant; thus, the observed effect is often difficult to duplicate. The statement implies that either the development of endodormancy is static or application of chemical "X" at any time during endodormancy will result in the same effect. Neither implication is valid, and until we find better ways of classifying dormancy stages, this problem will continue.

The morphological and physiological status of woody temperate plants will vary according to the response of each plant/genotype to the changing environment. Morphologically changes occur from spring to summer to winter. For the plant to survive, its annual developmental cycle must be synchronized with the changing environment (Levitt, 1980; Sakai and Larcher, 1987; Sarvas, 1972, 1974; Weiser, 1970), especially with changes in photoperiod and temperature (Aitkens et al., 1995; Campbell and Sugano, 1975, 1979). Moving plants from these environments to other climates has often resulted in reduced productivity and growth and sometimes death (Heide, 1985; Weiser, 1970). In horticulture and forestry, the growing of plants outside their natural habitats depends on cultural practices to either modify the environment or the physiology of the plant. These practices are not always successful, and some of the problems can be attributed to our lack of understanding of the plant's physiological status. The possibility of climatic warming poses a threat to wild and native plants. High levels of CO₂ and higher temperatures will have an effect on growth, dormancy and hardiness of temperate trees (Cannell and Smith, 1986; Hanninen, 1991, 1995; Kramer, 1994b; Murray et al., 1989; D.T. Tingey, 1996, personal communication). Without quantitative data on the phenological cycle of temperate woody perennials, assessments of the impact of environment on physiological processes, as well as the effects of practices to prevent losses, are difficult.

With rapid advances made in computer, molecular and other technologies, the potential for quantifying developmental processes continues to improve. The benefits of developing and adopting a quantitative system of classifying dormancy development are to

improve 1) communication; 2) accuracy; 3) understanding; 4) impact of current practices, e.g., timing of defoliation, freeze protection measures, etc.; 5) predictive dormancy models; and 6) the ability to define and measure dormancy stages. This report will not include mathematical models for quantifying the annual stages of development in woody plants; for these see Cannell (1989, 1990), Campbell (1978), Fishman et al. (1987a, 1987b), Hanninen (1990, 1990a, 1990b, 1995), Hakkinen (1990), Hakkinen and Hari (1988), Hari (1968, 1972), Heide (1993a, 1993b), Kobayashi and Fuchigami (1983a, 1983b), Kobayashi et al. (1982, 1983), Kramer (1994a, 1994b), Landsberg (1974, 1977), Murray et al. (1989), Nizinski and Saugier (1988), Repo and Pelkonen (1986), Repo et al. (1990), Richardson et al. (1974), and Sarvas (1972, 1974).

QUANTITATIVE MODELS OF BUD DORMANCY

In horticulture, the principal method of determining the end points of endodormancy and ecodormancy is based on chill unit accumulation, but this does not take into account the physiological status of the plant. Because chill unit models are not realistic (i.e., not based on physiological processes), their accuracy in detecting end points may be confined to specific environments (Hanninen, 1995). Development of an accurate and realistic quantitative measure of dormancy stages will not be easy because "there are no suitable, easily observable phases that can accurately be measure" during endodormancy (Sarvas, 1972, 1974). There is no agreement on how to measure dormancy stages (e.g., rate of growth, rate of mitosis/meiosis); therefore, attempts to quantify developmental units (d.u.) are often based on arbitrary data; measurement of ontogenetic development in direct quantitative terms is impractical (Hanninen, 1990, 1995). The main purpose of phenological models has been to accurately predict the timing of various point events (e.g., time of vegetative or floral bud break) with less emphasis on modeling of physiological events in relation to environmental variables (Hanninen, 1995).

Although improved techniques for identifying growth stages and modeling dormancy processes have improved, methods of quantifying bud dormancy are still poor, because physiological events are difficult to quantify (Cannell, 1989, 1990; Dennis, 1987, 1995; Hakkinen and Hari, 1988; Hanninen, 1990, 1990a, 1990b; Hakkinen, 1990; Kobayashi and Fuchigami, 1983a, 1983b; Kobayashi et al., 1982, 1983; Lang et al., 1987; Lavender and Stafford, 1985; Lockhart, 1983; Luomajoki, 1986; Sarvas, 1972, 1974). Several attempts have been made to quantify developmental units during dormancy (Kobayashi and Fuchigami, 1983a, 1983b; Kobayashi et al., 1982, 1983; Sarvas, 1972, 1974). Sarvas used temperature response curves to predict the development of meiotic stages. The difficulty of expressing such stages quantitatively led him to use arbitrary d.u. (Sarvas, 1972, 1974). Although the model was not perfect, it suggested that changes in developmental unit stages (d.u.s) (e.g., meiotic stages) are physiological events controlled by the environment and, therefore, should be quantifiable. By arbitrarily measuring meiotic events and relating them to temperature, Sarvas was partly successful in quantifying d.u.s.

The accuracy and realism (e.g., based on actual physiological events) of dormancy (endodormancy and ecodormancy) models and their conceptual foundations have recently been compared and tested by Hanninen (1990, 1995) and Kramer (1994a, 1994b). In Hanninen's study, 96 hypothetical models were constructed by combining 14 original submodels. Some of the models were reformulations of previous ones but most of them were new. In general, many of these models accurately predicted the timing of bud burst for natural

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conditions, but not for simulated conditions (e.g., elevated temperatures). Interestingly, models with substantially differing assumptions were similar in accuracy. Kramer (1994a, 1994b), who tested 12 models, also reported similar accuracy with relatively simple models that had no relevance to ontogenetic events. Both, Hanninen and Kramer found high accuracy in models that included length of photoperiod as predictors. Hanninen concluded that "These experimental results demonstrate the importance of the concept of model realism" as proposed by Levins (1968). A model with high accuracy can have low realism and is, therefore, less accurate in situations where the model lacks precision in predicting realistic physiological processes (Hanninen, 1995). The models for bud burst phenology (chill unit models) of trees are examples of models with low realism that are generally based on long-term observations from natural conditions (Cannell and Smith, 1983; Hari and Hakkinen, 1991; Kramer, 1994a, 1994b) and not on physiological processes, and fail under certain environmental conditions (Hanninen, 1995). Accuracy can be achieved even when unrealistic factors are included in the model. Hunter and Lechowicz (1992) and Kramer (1994a, 1994b) reported similar findings. To find realistic and accurate phenological models, they must be subjected to a battery of varying experimental conditions. Hanninen (1995) found that testing seven of the most accurate models with experiments with drastic manipulations of environmental conditions was still insufficient for selecting a realistic model. Unfortunately, some models had about the same high degree of accuracy in spite of the wide range of environmental test conditions.

One of the problems with most models is that they are designed to test the timing of the endpoint event of the process (e.g., spring bud burst). Hanninen (1995) concludes that testing of models could be improved greatly if observations for the preceding point-events [e.g., d.u. or degree growth stage ($^{\circ}$ GS)] were available. For example, for endodormancy models, observations on point-events can be made directly by observing meiotic or mitotic changes in the flower or vegetative buds, respectively (Sarvas, 1972, 1974), or indirectly, by determining the rate and timing of budbreak in forcing experiments (Kobayashi and Fuchigami, 1983b). In the case of ecodormancy (=growth competence, Hanninen, 1990) only indirect observations are available (Hanninen 1990; Hanninen and Backman 1994; Kobayashi and Fuchigami, 1983a; Kobayashi et al., 1982; Sarvas, 1974). For the termination of paradormancy (photoperiodic or temperature induction phase of bud set) also only indirect observations are available (Renquist et al., 1978).

Although some of the recent models are more accurate in predicting major point events, e.g., time of bud burst, Hanninen (1995) claims that these models continue to lack realism of detecting actual physiological events. Until these models incorporate physiological processes in the equations, they may still suffer from erroneous predictions, particularly in climates that were not accounted for during the testing of the models.

Conceptual numerical model of bud dormancy: The $^{\circ}$ GS model

To 1) progress from the current dormancy terminology to one that more readily expresses the continuum of changes that occur within each dormancy stage, and 2) further improve communication, we propose that a conceptual model of the annual bud development of woody temperate plants be developed. This model should not be confused with the mathematical models discussed previously. By itself, the conceptual model of bud development (e.g., $^{\circ}$ GS model) (Fuchigami et al., 1982) is not dependent on mathematical equations. The numerical system used in the $^{\circ}$ GS model divides bud development into numerical units. Rather than a verbal description of bud development, numbers are used for simplicity and their potential for quantitating bud development. In the $^{\circ}$ GS model, the numbers (e.g., 0° GS) could be used to depict actual physiological (bud burst) and/or anatomical events (e.g., meiotic changes) and mathematical models could be developed to determine each $^{\circ}$ GS unit (Kobayashi and Fuchigami, 1983a, 1983b; Kobayashi et al., 1982, 1983; Renquist et al., 1978). The numerical conceptual model should 1) express bud development in numerical terms (which will allow for mathematical and computer modelling and imply that development is dynamic); 2) indicate that the

process is cyclic; 3) not be restrictive and allow for improvements in accuracy; 4) have readily recognizable numbers to depict major point events (e.g., onset of endodormancy = 180° GS, maximum endodormancy = 270° GS, bud burst = 360° GS, etc.); 5) be simple, clearly identifying the major point events, and include the major classifications of dormancy; 7) be usable by mathematical modelers for quantifying developmental units; and 8) improve communication and accuracy in defining the stages of plant development.

The $^{\circ}$ GS model provided a method of numerically expressing the annual ontogenetic bud development of woody temperate zone species (Fuchigami et al., 1982) and related growth competency and mathematical expressions of these events quantitatively (Kobayashi and Fuchigami, 1983a, 1983b; Kobayashi et al., 1982, 1983; Renquist et al., 1978). Previous terms and definitions of bud developmental stages were too general and lacked precision. A numerical framework was needed to express the growth competency of the plant daily, hourly and possibly more frequently, if necessary. Therefore, each number, e.g., 0° GS, refers to a specific developmental unit (or growth stage, GS). If greater accuracy is required in future models, each $^{\circ}$ GS could be further subdivided into minutes and/or seconds. A sigmoidal curve or circle was selected for the conceptual annual bud development model because of the cyclic nature of bud development (Fig. 1). The model divides the annual growth cycle into 360 units ($^{\circ}$ GSs) and the cyclical function passes through five major point events: 1) 0° GS = bud burst, 2) 90° GS = induction point, 3) 180° GS = bud set (vegetative maturity), 4) 270° GS = maximum endodormancy; and 315° GS = end of endodormancy. The major classifications of bud dormancy are expressed accordingly: 1) paradormancy = 0° to 180° GS, 2) endodormancy = 180° to 315° GS, and 3) ecodormancy = 315° to 360° GS. In previous publications (see Burr 1990; Dennis, 1995; Fuchigami and Nee, 1987; Fuchigami et al., 1982; Richie and Tanaka, 1990) the $^{\circ}$ GS model was described as a sine curve. We describe this model as a circle in this article to reduce the confusion that the sine curve may have caused. The changes in the shape of the sine curve were sometimes confused with the mathematical models used to determine the $^{\circ}$ GSs. [For further description and explanations of the components of the $^{\circ}$ GS conceptual model of bud development refer to Fuchigami et al. (1982), Burr (1990), and Richie and Tanaka (1990)]. The following paragraphs will discuss our attempts to incorporate mathematical models in the conceptual $^{\circ}$ GS model.

Quantitative models to determine degree growth stages

In the development of a quantitative measure of the ontogenetic events in the annual cycle of woody temperate plants the following assumptions were made: 1) the ontogenetic changes are dynamic and based on physiological processes (e.g., active events); 2) these changes

Fig. 1. Degree growth stage model.

can be divided into d.u.s or growth stages (e.g., °GS); 3) the rate of change from one d.u. to another d.u. depends on environment; 4) the change in d.u.s can be quantified; 5) the change in d.u.s is irreversible; 6) the effects of environmental factors on changes in d.u.s are genotype- and stage-dependent; 7) the change in d.u.s can be measured phenotypically and/or physiologically; 8) changes in d.u.s of tissues and/or organs can occur independently (e.g., in endodormancy the dormancy of each bud is independent of other buds, while in paradormancy the development of axillary buds depends on the terminal bud and/or leaves); 9) several environmental factors may have either an abrupt or subtle effect on d.u.s; 10) the development of quantitative models for species with determinate (e.g., most conifers and some deciduous species with fixed number of nodes within buds vs. node counts not fixed) and indeterminate (most deciduous species) may vary; and 11) a universal quantitative assessment of the annual development of temperate woody plants is possible and important.

The use of mathematical models to predict °GSs was first attempted by Renquist et al. (1978); Kobayashi and Fuchigami (1983a, 1983b) and Kobayashi et al. (1982, 1983) continued this work. Renquist et al. (1978) reported on the development of the short day-inductive phase of dormancy in red-osier dogwood (*Cornus sericea* L.) from 90° to 180°GS. This study helped to establish the critical photoperiod and temperature for the onset of endodormancy (maturity induction phase or bud set). The critical photoperiod was determined for the Massachusetts dogwood clone by using the temperature models developed from controlled growth chamber studies and temperature and bud set records from natural conditions [e.g., from bud set (180°GS) the model predicted the critical photoperiod (90°GS) by working backwards, 180°GS to 90°GS]. The critical photoperiod was then tested and confirmed experimentally by daylength studies. In some species, e.g., apples *Malus domestica* Borkh. and other Rosaceae, bud set induction depends on temperature and not photoperiod. Determination of the inductive phase (90°GS) in these species may be less definitive; however, a similar strategy may be used for temperature models have been developed for bud set. In species with determinate bud development, e.g., many conifers and some deciduous species, the maturity induction point (bud set = determination of 180°GS) may be a greater challenge. This difficulty may explain some of the discrepancies among models (Hanninen, 1990, 1995; Kramer, 1994). In determinate species, other phenological or physiological indices must be developed for determination of the 180°GS starting point.

Although no apparent visible change in bud phenology occurs during endodormancy and parts of ecodormancy, the development from 180° to 360°GS requires metabolic processes (Fuchigami et al., 1982). Therefore, the rate of physiological change is temperature and growth stage-dependent. Within the acceptable temperature range for bud development, physiological changes are continuous. The optimum temperature for the breaking of endodormancy is near 3.5 °C. The optimum temperature for endodormancy development is not well-defined, perhaps because of genotype × temperature differences (Erez and Couvillon, 1987; Fishman et al., 1987a, 1987b; Hanninen, 1990, 1995; Kobayashi and Fuchigami, 1983a; Kobayashi et al., 1982; Kramer, 1994a, 1994b; Sarvas, 1972, 1974). Kobayashi and Fuchigami's models were based on the time to bud burst in a standard warm environment. In photoperiod-sensitive species, long photoperiods can have an effect on the time to bud burst during early endodormancy (e.g., between 180° and 210°GS). Some researchers report photoperiod enhancement of bud burst at much later stages of dormancy (Hanninen, 1995; Kramer, 1994a, 1994b; Lavender, 1985). This effect may, in part, be due to photosynthetic influences on development (Kramer, 1994a, 1994b). To avoid photoperiod and/or photosynthetic effects, the standard test environment should be short days (e.g., 12-h day and 12-h night) and warm conditions (e.g., 25 °C day and 20 °C night). Under these conditions, beginning at 180°GS and ending at 315°GS, a bell-shaped response curve (typical of all biological systems) is generated by plotting days to bud burst vs. time. The slopes of the curve depend on the temperature during the breaking of endodormancy (e.g., at 3.5 °C the slope of the curve is greatest, and at temperatures above or below 3.5 °C the slope is less). Kobayashi et al. (1982) determined the effects of various temperatures at several growth stages on rate of bud development as measured by time to bud

burst. The rate of development was slow immediately after 180°GS (lag phase), increased at later stages (e.g., 220 to 260°GS, exponential phase) and leveled off near maximum endodormancy (270°GS). During the breaking of rest (between 270 and 315°GSs) the rate was slow immediately after 270°GS and increased thereafter (exponential phase) during the bud release phase (270° to 315°GS). The GS was arbitrarily determined from these growth models and assigned values based on the results obtained for the bell-shaped curve (e.g., 180° was assigned to bud set stage and 270° was assigned to maximum rest phase, and between these two major point events the other GS values were assigned). A computer model (Table 1) for assigning GSs during endodormancy and ecodormancy was developed, based on the curves generated. We have used this model to assign GS to plants based on the timing of bud set, maximum rest (top of bell-shaped curve) and end-of-rest (at the base of the bell-shaped curve when time of bud burst is relatively constant). The times of bud set, maximum rest, end-of-rest, and the shape and height of the bell-shaped curve will depend on environment and genotype interactions.

Several mathematical models have been developed for the ecodormancy phase (315° to 360°GS), when the chilling requirement is complete and buds are at full growth competence (Hanninen, 1995). During this phase, the rate of development increases with increasing temperature (Kobayashi and Fuchigami, 1983b). The model developed by Kobayashi and Fuchigami (1983b) for the ecodormancy phase was also based on rates of bud development in response to temperature. As with the other stages discussed above, the rate of development was stage- and temperature-dependent; the rate was slowest at early ecodormancy (e.g., 315°GS) and at later stages increased again, typical of biological growth processes. Also during this phase, the temperature range for promoting growth competence widens with progressively later growth stages from 315° to 360°GS, supporting the early findings of Vegis (1964). As in previous models, GSs were assigned between 315° to 360°GS, based on the degree of growth competence (Kobayashi and Fuchigami, 1983b). Conceptually, GSs can be assigned to stages between 315° to 360°GS if the end-of-rest and the time of bud burst are known.

Determination of GSs during endodormancy

We use the following protocol for assigning GSs during endodormancy when either testing a new genotype or conducting experiments during the endodormant period. If clonal materials are used, five plants are taken weekly from the test environment, beginning before bud set and ending at bud burst (or in late winter and early spring when chilling requirement is suspected to be satisfied) and placed in a greenhouse at 25 °C day/20 °C night, and a 12-h photoperiod (or naturally short photoperiod). The number of days required for terminal and axillary budburst are determined and plotted against the date the plants were placed in the greenhouse. In most deciduous plants, including plants not sensitive to photoperiod, a bell-shaped curve is generated. Assign the following GS: 1) 180°GS = bud set (before the rise in the curve at the left of the bell-shaped curve); 2) 270°GS = maximum rest (at the peak of the bell-shaped curve); and 3) 315°GS = end-of-endodormancy (at the point when the right side of the bell-shaped curve reaches the base when no change in time of bud burst is observed). The data are then entered into the computer program (Table 1) to determine the other GSs. The GSs can then be related to calendar date, e.g., when plants were placed in the greenhouse. Assigning GS in all our dormancy studies has improved communication and interpretation of results. Others have also used this conceptual model to relate physiological or operational practices to GSs (Burr 1990; Richie and Tanaka, 1990).

Why dormancy models fail

There have been many reports of models failing to predict timing of bud burst under differing environmental conditions (Hanninen, 1995; Kramer, 1994a, 1994b). Hanninen's recent work shows that some models predict end points quite accurately in spite of using non-causal variables (e.g., photoperiod). These models often fail, however, when certain environmental variables are used, e.g., the warm condi-

Table 1. BASIC program for calculating degree growth stage.

```

50      PRINT "          GROWTH STATE MODEL          "
      PRINT : PRINT
      INPUT "Please enter name of plant: "; plant$
      PRINT
      PRINT "Enter the days of budbreak of " ; plant$
      INPUT "at 180 GS (Dvm) : ", dvm
      PRINT "Enter the days of budbreak of " ; plant$
      INPUT "at 270 GS (Dvm) : ", dmr
      CLS
100     PRINT "          " ; Plant$; " GROWTH STAGE MODEL"
      PRINT : PRINT
      PRINT "1. Growth stage between 180 GS to 270 GS"
      PRINT "2. Growth stage between 270 GS to 315 GS"
      PRINT "3. Growth stage between 315 GS to 360 GS"
      PRINT
      INPUT "Please enter selection (1, 2, or 3)", nu%
      ON nu% GOSUB 300, 250, 400
      PRINT TAB(17); "Degree of GS :"; g
      PRINT : PRINT : PRINT
      PRINT "1. To continue analyzing"; plant$
      PRINT "2. To analyze another plant"
      PRINT "3. To quit"
      PRINT
250     INPUT "Please enter selection (1, 2, or 3)", nu%
      IF nu% > 3 THEN GOTO 250
      CLS
      ON nu% GOTO 100, 50
      GOTO 450
300     PRINT : PRINT "Days of budbreak (" ; dvm ; "-" ; dvm;
      g = 90 * (d - dvm) / (dmr - dvm) + 180
      g = INT (g + .5)
      RETURN
350     PRINT : PRINT "Days of budbreak (" ; dmr ; "-" ; dvm;
      g = 45 * (d - dmr) / (dvm - dmr) + 270
      g = INT (g + .5)
      RETURN
400     PRINT : PRINT "Days of budbreak (" ; dvm ; "-" ;
      INPUT "0) : ", d
      g = 45 * (dvm - d) / dvm + 315
      g = INT (g + .5)
      RETURN
450     SYSTEM

```

tions predicted for climatic warming models. Dormancy models often have high accuracy (under some conditions) and low realism (low accuracy under real situations where environments may vary outside the realm of the model). Hanninen (1995) warns that models need to be tested under a wider range of environmental extremes and predictors need to be related to physiological processes to be realistic.

We have reported that the breaking of endodormancy can occur abruptly at any stage of endodormancy (between 180° to 315°GS) by exposing buds to sublethal stress (Fuchigami and Nee, 1987; Nee, 1987; Shirazi and Fuchigami, 1993, 1995; Siller et al., 1992; Wisniewski et al., 1994, 1996). The effective level of stress is growth stage-dependent and may be related to the perturbation and loss of membrane integrity as determined by electrolyte leakage (Fuchigami and Nee, 1987; Nee, 1986; Shirazi and Fuchigami, 1995; Wisniewski, 1994, 1996). The breaking of endodormancy following exposure to near-lethal stress is quite rapid (Shirazi and Fuchigami, 1995). The ability to break endodormancy with near-lethal stress is temperature- and time-dependent. The effects of near-lethal stress also differs under controlled and natural fluctuating conditions (Shirazi and Fuchigami, 1995). Following near-lethal stress, bud burst occurs quite rapidly under controlled warm conditions. In contrast, under fluctuating conditions in natural environments, exposing buds to near-lethal stress from 180° to 290°GS did not promote earlier bud burst, whereas exposure after this stage did (Shirazi and Fuchigami, 1995). Recovery and/or repair of tissues injured by near-lethal stress under the fluctuating conditions may nullify the effects of near-lethal stress at the early stages of endodormancy. At late stages, however, near-lethal stress of buds may have a pronounced effect on timing of bud burst. This situation may, under some environments, explain some of the discrep-

ancies reported by scientists testing models to predict the timing of bud burst. The dramatic effect of near-lethal stress of endodormancy suggests that models to predict bud burst timing should account for near-lethal stresses. Failure to do so may cause erroneous predictions of bud burst. We have found that many forms of stresses, if used at the near-lethal dosage level, can have the same effect (Fuchigami and Nee, 1987; Shirazi, 1995).

Farmers and scientists have known for many years that cultural practices may also influence the timing of endodormancy, as indicated by changes in timing of leaf coloration and/or defoliation, bud set and cold hardiness. As a result of these observations and assumptions growers have learned to adjust cultural practices to influence the timing of plant development. Two practices used often to induce earlier bud set are withholding of water and nitrogen fertilization. We have observed that timing and concentration of nitrogen fertilization can have a dramatic effect on timing of bud set, endodormancy development and bud burst of 1-year-old grafted apple nursery stock. Plants with a heavy nitrogen application late in the season (e.g., after September) set buds later, entered endodormancy later and broke bud dormancy earlier than plants treated with low nitrogen in late July. As with the above finding, failure to account for cultural practices by commerce may cause erroneous predictions of bud burst.

CONCLUSIONS

The adoption of the standard dormancy terminology the Dormancy Working Group and ASHS has improved communication and reduced confusion among scientists reporting dormancy research. The standardized terminology is useful in describing the three major forms of bud dormancy in woody temperate plants. However, the terminology does not describe ontogenetic, physiological events occurring during the annual cycle of woody plants.

Failure to report dormancy research in reference to these phenological events has inhibited our understanding of the physiological, anatomical and biochemical processes occurring during the annual development of plants. This problem can be illustrated by using the analogy of a road map. Assume that this map has three cities (analogous to point events), in an area the size of Texas. Between each city there are numerous towns. Unfortunately, this map contains only a general outline of the area (e.g., Texas) and a rough indication of where these cities are located; no information is supplied on roads, distance, etc. If you were asked to find one of the towns between two of the major cities, and then asked to relate this to someone, would this be a problem? This is similar to where we are in our understanding of the ontogenetic development of plants. Woody temperate plants develop three major forms of dormancy within a year. There are numerous other transitional stages between each form of dormancy but the "map" lacks "roads" and "distances." Thus, locating a specific point event and relating this to someone are problems.

To improve communication and accuracy in describing the ontogenetic development of woody temperate plants we propose the development and adoption of a numerical conceptual model as the next project by the Dormancy Working Group. The °GS model was described in this report as an example of a numerical conceptual model to describe the ontogenetic development of woody temperate plants. The model identifies the major point events numerically and the intervening events are further divided by numerical means. Mathematical models were then used to describe methods of quantifying the various growth stages. In contrast to many phenological models that predict the timing of major point events, the °GS conceptual model lends itself to the development of realistic models that relate to

physiological processes. These realistic models would be accurate regardless of the environment, whereas growth models that are not related to physiological processes (therefore not realistic) will fail under certain environments. A numerical model of the ontogenetic development of woody temperate plants would provide a framework for quantifying developmental processes.

We also discussed the need for incorporating other factors into predictive models. The status of dormancy can be altered by cultural practices and the environment. Failure to understand how these factors influence dormancy and consider them in growth models will reduce the accuracy of these models.

Literature Cited

- Aitkens, S.N., W.T. Adams, N. Schermann, and L.H. Fuchigami. 1995. Genetic variation and genotype-by-environment interaction for fall cold hardiness in coastal Douglas-fir. *For. Ecol. Mgt.* 8:187–195.
- Burr, K. 1990. The target seedling concepts: bud dormancy and cold hardiness, p. 79–90. In: Rose, R., S.J. Campbell, and T.D. Landis (eds.). *Target Seedling Symp.: Proc. Combined Meeting of the Western Forest Nursery Assn. USDA For. Serv. Gen. Tech. Rpt. RM 200.*
- Campbell, R.K. 1978. Regulation of bud-burst timing by temperature and photoregime during dormancy, p. 19–33. In: C.A. Hollis and A.E. Squillace (eds.). *Proc. Fifth North American Forest Biology Workshop. Forestry Dept., Univ. of Florida, Gainesville.*
- Campbell, R.K. and A.I. Sugano. 1975. Phenology of bud burst in Douglas-fir related to provenance, photoperiod, chilling, and flushing temperature. *Bot. Gaz.* 136:290–298.
- Campbell, R.K. and A.I. Sugano. 1979. Genecology of bud-burst phenology in Douglas-fir: Response to flushing temperature and chilling. *Bot. Gaz.* 140:223–231.
- Cannell, M.G.R. and R.I. Smith. 1983. Thermal time, chill days and prediction of budburst in *Picea sitchensis*. *J. Appl. Ecol.* 20:951–963.
- Cannell, M.G.R. 1989. Chilling, thermal time and the date of flowering of trees, p. 99–113. In: C.J. Wright (ed.). *Manipulation of fruiting. Butterworths, London.*
- Cannell, M.G.R. 1990. Modelling the phenology of trees, p. 11–27. In: H. Jozefek (ed.). *Modelling to understand forest functions. Silva Carelica 15.*
- Cannell, M.G.R. and R.I. Smith. 1986. Climatic warming, spring budburst and frost damage on trees. *J. Appl. Ecol.* 23:177–191.
- Dennis, F.G., Jr. 1987. Two methods of studying rest: temperature alternation and genetic analysis. *HortScience* 22:820–824.
- Dennis, F.G., Jr. 1995. Dormancy: Manifestations and causes, p. 437–460. In: M. Pessaraki (ed.). *Handbook of plant and crop physiology. Marcel Dekker, New York.*
- Erez, A. and G.A. Couvillon. 1987. Characterization of the influence of moderate temperatures on rest completion in peach. *J. Amer. Soc. Hort. Sci.* 112:677–680.
- Fishman, S., A. Erez, and G.A. Couvillon. 1987a. The temperature dependence of dormancy breaking in plants: Mathematical analysis of a two-step model involving a cooperative transition. *J. Theor. Biol.* 124:473–483.
- Fishman, S., A. Erez, and G.A. Couvillon. 1987b. The temperature dependence of dormancy breaking in plants: Computer simulation of processes studied under controlled temperatures. *J. Theor. Biol.* 126:309–321.
- Fuchigami, L.H., C.J. Weiser, K.D. Kobayashi, K. Timmis, and L.V. Gusta. 1982. A degree growth state (°GS) model and cold acclimation in temperate woody plants, p. 83–116. In: P.H. Li and A. Sakai (eds.). *Plant cold hardiness and freezing stress. Mechanisms and crop implications. vol. 2. Academic, New York.*
- Fuchigami, L.H. and C.C. Nee. 1987. Degree growth stage model and rest-breaking mechanisms in temperate woody perennials. *HortScience* 22:136–145.
- Hakkinen, R. 1990. Analysis of phenological time series, p. 29–33. In: H. Jozefek (ed.). *Modelling to understand forest functions. Silva Carelica 15.*
- Hakkinen, R. and P. Hari. 1988. The efficiency of time and temperature driven regulation principles in plants at the beginning of the active period. *Silva Fennica* 22:163–170.
- Hanninen, H. 1990. Modelling bud dormancy release in trees from cool and temperate regions. *Acta Forestalia Fennica* 213:1–47.
- Hanninen, H. 1990a. Modelling the annual growth rhythm of trees: Conceptual, experimental, and applied aspects, p. 35–45. In: H. Jozefek (ed.). *Modelling to understand forest functions. Silva Carelica 15.*
- Hanninen, H. 1990b. Modeling dormancy release in trees from cool and temperate regions, p. 159–165. In: R.K. Dixon, R.S. Mehdahl, G.A. Ruark, and W.G. Warren (eds.). *Process modeling of forest growth responses to environmental stress. Timber Press, Portland, Ore.*
- Hanninen, H. 1991. Does climatic warming increase the risk of frost damage in northern trees? *Plant Cell Environ.* 14:449–454.
- Hanninen, H. 1995. Effects of climatic change on trees from cool and temperate regions; an ecophysiological approach to modelling of bud burst phenology. *Can. J. Bot.* 73:183–199.
- Hanninen, H. and R. Backman. 1994. Rest break in Norway spruce seedlings: test of a dynamic temperature response hypothesis. *Can. J. For. Res.* 24:558–563.
- Hari, P. 1968. A growth model for a biological population, applied to a stand of pine. *Communications Instituti Forestalis Fenniae* 66:1–16.
- Hari, P. 1972. Physiological stage of development in biological models of growth and maturation. *Annales Botanici Fennici* 9:107–115.
- Hari, P. and R. Hakkinen. 1991. The utilization of old phenological time series of bud burst to compare models describing annual cycles of plants. *Tree Physiol.* 8:281–287.
- Heide, O.M. 1985. Physiological aspects of climatic adaptation in plants with special reference to high-latitude environments, p. 1–22. In: A. Kaurin, O. Juntilla, and J. Nilsen (eds.). *Plant production in the north. Norwegian Univ. Press, Tromsø.*
- Heide, O.M. 1993a. Daylength and thermal responses of bud burst during dormancy release in some northern deciduous trees. *Physiol. Plant.* 88:531–540.
- Heide, O.M. 1993b. Dormancy release in beech buds (*Fagus sylvatica*) requires both chilling and long days. *Physiol. Plant.* 89:187–191.
- Hunter, A.F. and M.J. Lechowicz. 1992. Predicting the timing of bud burst in temperate trees. *J. Appl. Ecol.* 29:597–604.
- Kobayashi, K.D. and L.H. Fuchigami. 1983a. Modelling temperature effects in breaking rest in red-osier dogwood (*Cornus sericea* L.). *Ann. Bot.* 52:205–215.
- Kobayashi, K.D. and L.H. Fuchigami. 1983b. Modeling bud development during the quiescent phase in red-osier dogwood (*Cornus sericea* L.). *Agr. Meteorol.* 28:75–84.
- Kobayashi, K.D., L.H. Fuchigami, and M.J. English. 1982. Modeling temperature requirements for rest development in *Cornus sericea*. *J. Amer. Soc. Hort. Sci.* 107:914–918.
- Kobayashi, K.D., L.H. Fuchigami, and C.J. Weiser. 1983. Modeling cold hardiness of red-osier dogwood. *J. Amer. Soc. Hort. Sci.* 108:376–381.
- Kramer, K. 1994a. Selecting a model to predict the onset of growth of *Fagus sylvatica*. *J. Appl. Ecol.* 31:172–181.
- Kramer, K. 1994b. A modelling analysis of the effects of climatic warming on the probability of spring frost damage to tree species in The Netherlands and Germany. *Plant Cell Environ.* 17:367–377.
- Landsberg, J.J. 1974. Apple fruit bud development and growth; analysis and an empirical model. *Ann. Bot.* 38:1013–1023.
- Landsberg, J.J. 1977. Effects of weather on plant development, p. 289–307. In: J.J. Landsberg and C.V. Cutting (eds.). *Environmental effects on crop physiology. Academic, London.*
- Lang, G.A., J.D. Early, N.J. Arroyave, R.L. Darnell, G.C. Martin, and G.W. Stuttle. 1985. Dormancy: Toward a reduced, universal terminology. *HortScience* 20:809–812.
- Lang, G.A., J.D. Early, G.C. Martin, and R.L. Darnell. 1987. Endo-, para-, and ecodormancy: Physiological terminology and classification for dormancy research. *HortScience* 22:371–377.
- Lavender, D.P. and S.G. Stafford. 1985. Douglas-fir seedlings: Some factors affecting chilling requirement, bud activity, and new foliage production. *Can. J. For. Res.* 15:309–312.
- Levins, R. 1968. *Evolution in changing environments.* Princeton Univ. Press, Princeton, N.J.
- Levitt, J. 1980. *Response of plants to environmental stresses. vol. 2.* Academic, London.
- Lockhart, J.A. 1983. Optimum growth initiation time for shoot buds of deciduous plants in a temperate climate. *Oecologia* 60:34–37.
- Luomajoki, A. 1986. Timing of microsporogenesis in trees with reference to climatic adaptation. A review. *Acta Forestalia Fennica* 196:1–33.
- Murray, M.B., M.G.R. Cannell, and R.I. Smith. 1989. Date of budburst of fifteen tree species in Britain following climatic warming. *J. Appl. Ecol.* 26:693–700.
- Nee, C.C. 1986. Overcoming bud dormancy with hydrogen cyanamide: timing and mechanism. PhD Diss., Oregon State Univ., Corvallis.
- Nizinski, J.J. and B. Saugier. 1988. A model of leaf budding and development for a mature *Quercus* forest. *J. Appl. Ecol.* 25:643–652.
- Renquist, A.R., R.B. Wensink, L.H. Fuchigami, J.R. Seibel, P.C. Nissila, and E.M. Bates. 1978. Modeling the vegetative maturity of red-osier dogwood. *J. Amer. Soc. Hort. Sci.* 103:742–744.
- Repo, T., A. Makela, and H. Hanninen. 1990. Modelling frost resistance of trees, p. 61–74. In: H. Jozefek (ed.). *Modelling to understand forest functions. Silva Carelica 15.*
- Repo, T. and P. Pelkonen. 1986. Temperature step response of dehardening in *Pinus sylvestris* seedlings. *Scandinavian J. For. Res.* 1:271–284.
- Richardson, E.A., S.D. Seeley, and D.R. Walker. 1974. A model for estimating the completion of rest for 'Redhaven' and 'Elberta' peach trees. *HortScience* 9:331–332.

- Ritchie, G.A. and Y. Tanaka. 1990. Root growth potential and the target seedling, p. 37–51. In: R. Rose, S.J. Campbell, and T.D. Landis (eds.). Target Seedling Symposium: Proc. Combined Meeting of the Western Forest Nursery Assn. USDA For. Serv. Gen. Tech. Rpt. RM-200.
- Sakai, A. and W. Larcher. 1987. Frost survival of plants. Responses and adaptation in freezing stress. Springer-Verlag, Berlin.
- Sarvas, R. 1972. Investigations on the annual cycle of development of forest trees. Active period. *Communicationes Instituti Forestalis Fenniae* 76:1–110.
- Sarvas, R. 1974. Investigations on the annual cycle of development of forest trees. II. Autumn dormancy and winter dormancy. *Communicationes Instituti Forestalis Fenniae* 84:1–101.
- Shirazi, A.M. and L.H. Fuchigami. 1993. Recovery of plants from “near lethal” stress. *Oecologia* 93:429–434.
- Shirazi, A.M. and L.H. Fuchigami. 1995. The relationship of “near-lethal” stress on dormancy and stem cold hardiness in red-osier dogwood. *Tree Physiol.* 15:275–279.
- Siller, J.H., L.H. Fuchigami, and T.H.H. Chen. 1992. Hydrogen cyanamide induced budbreak and phytotoxicity in ‘Redhaven’ peach buds. *HortScience* 27:874–876.
- Vegis, A. 1964. Dormancy in higher plants. *Annu. Rev. Plant Physiol.* 15:185–224.
- Watada, A.E., R.C. Hemer, A.A. Kader, R.J. Romani, and G.L. Staby. 1984. Terminology for the description of developmental stages of horticultural crops. *HortScience* 19:20–21.
- Weiser, C.J. 1970. Cold resistance and injury in woody plants. *Science* 169:1269–1278.
- Wisniewski, M., L.H. Fuchigami, J.J. Sauter, A. Shirazi, and L. Zhen. 1996. Near-lethal stress and bud dormancy in woody plants. In: G. Lang (ed.). Plant dormancy: Physiology, biochemistry and molecular biology. CAB Intl. (In press).
- Wisniewski, M., J. Sauter, V. Stepien, and L.H. Fuchigami. 1994. Effects of sublethal heat stress on endodormancy and ecodormancy of peach and hybrid poplar. *HortScience* 29:511.

Bud Dormancy in Perennial Fruit Trees: Physiological Basis for Dormancy Induction, Maintenance, and Release

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Dormancy in temperate-zone deciduous fruit trees is a phase of development that allows the trees to survive unfavorable conditions during the winter. The subject has been reviewed several times (see Saure, 1985). The hallmark of winter dormancy is that it is released by a quantitative accumulation of a certain amount of cold and only part of this cold requirement can be substituted by other means. The interest in understanding the mechanism of dormancy imposition and release has been intensified during the last 30 years. Producers desire to grow temperate-zone fruit trees in warm climates where the cold requirements cannot be satisfied, and are interested in manipulating the dormant period to increase budbreak and obtain even flowering. Producers of the temperate zone also desire regulate dormancy but they want to delay bud break to avoid spring frosts that damage blooms. Based on the last 10 years of research, a theory is emerging that indicates multifaceted control of dormancy. Analyzing the control of dormancy, four major biological factors that change the intensity of dormancy can be identified. They are 1) hormone balance in the bud or in the tree, 2) state of water within the bud, 3) structure of membranes affecting cold resistance and governing resumption of growth, and 4) anabolic potential of buds. Without understanding the interaction of these factors, it is difficult to comprehend dormancy and search for the dormancy-release mechanism.

Lang et al. (1987) classified various stages of dormant buds as para-, endo-, or ecodormant. They equated paradormancy with correlative inhibition or apical dominance, endodormancy with winter or deep dormancy when the dormancy causing factor resides within the bud, and ecodormancy, usually occurring during late winter and spring,

when dormancy is imposed by temperatures unfavorable for growth. Saure's (1985) terms of pre-, true-, and imposed-dormancy are terms which essentially correspond to those proposed by Lang et al. (1987). Fuchigami and Nee (1987) provided evidence that the depth of dormancy changes during the dormant period.

Erez et al. (1979a, 1979b) stated that cold accumulation is reversible by intermittent higher temperatures, but only if given in short cycles. There is a point in cold accumulation, however, where the process becomes irreversible, indicating a fixation of the effect. This state is expressed by a “dynamic model” developed by Fishman et al. (1987a, 1987b). There are additional factors. Low-chilling-requiring cultivars need only a fraction of the amount of chilling other cultivars need (Saure, 1985), but why they need less chilling is not clear. Rootstocks may also influence chilling requirement of the scion (Couvillon et al, 1984; Westwood and Chestnut, 1964) and buds on strong-growing shoots that keep their leaves late into autumn require more chilling than buds on weak shoots (Chandler and Tufts, 1933). The above considerations indicate that dormancy is a process affected by various integrated elements and that their interaction(s) determine the point of time when release of dormancy occurs. Here, we summarize the relevant evidence and reflect on the possible mechanisms involved in imposition and release of dormancy.

INVOLVEMENT OF HORMONES

Auxins, cytokinins, and abscisic acid (ABA) have been suspected to be involved in imposing or breaking dormancy for a long time. Crabbe (1994) concluded that the classical theory of hormonal control of dormancy, meaning that ABA imposes and cytokinins release dormancy, has failed, yet under certain circumstances hormones still play a role in dormancy. During the summer and fall when buds are under correlative inhibition, removal of the terminal bud releases the

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