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BUD DORMANCY

Denis P. Lavender

Professor. Department of Forest Science, Oregon
State University. Corvallis, OR 97331

ABSTRACT--The classical definition of dormancy is
relevant only to the shoot apical meristems of
perennial, woody, temperate-zone plants and is
weak in that it specifies neither physiology nor
anatomy. Nonetheless, such plants do have a
definite annual growth cycle composed of
distinctly different, but intergrading,
physiological states. Plant physiology must be
in harmony with the environment throughout the
year if vigorous growth is to occur. Dormancy
may also be defined in terms of the mitotic
activity of cells of buds or of resistance to
stress ("hardening off"); the latter. frequently
confused with "classical dormancy," is a
physiological condition common to the entire
plant, not just the shoot apical meristem.
Budbreak speed, which may be a good indicator of
seedling vigor, is currently evaluated by two
general approaches (one relating number of
chilling hours to dormancy release, the other
comparing mortality and budbreak speed), each of
which has its limitations. However, the speed
with which buds resume growth in spring is a
function of the physiological state of the bud
and hence may not mirror whole-plant vigor.
Budbreak speed may reflect seedling vigor less
when stock has been weakened by natural stresses
or mishandling, but more when the seedling's
normal physiological sequence during dormancy has
been disrupted. So far, other measures of
seedling vigor, including the oscilloscope
technique, dry-weight fraction, and hormone
analysis, have been found unsatisfactory for
describing probable differences in seedling
physiology during dormancy or for predicting
seedling vigor.

2.1 INTRODUCTION

The annual life cycle of most temperate-zone perennial plants includes two major phases: a period of shoot elongation, usually relatively brief, during which the plant axes are extended and new foliage is exposed, and a period of dormancy, generally much longer, during which there is no visible shoot elongation but when active lateral cambial growth as well as differentiation and growth of initials may occur.

Although seedling morphology during dormancy remains relatively constant. seedling physiology changes dramatically from the time of budset in midsummer until budbreak the following spring. Because understanding the sequence of physiological states during this period is essential if nursery managers and foresters are to produce and maintain the most vigorous seedlings possible. this chapter discusses the current knowledge in this area. Data cited generally are drawn from studies of Douglasfir [Pseudotsuga menziesii (Mirb.) Franco] seedlings, primarily because most pertinent experiments have been conducted with this species. Very probably, however. its associates will react in a similar manner.

2.2 PRINCIPLES

2.2.1 Classical Dormancy Defined

The classical definition of dormancy (Doorenbos 1953. p. 1) is "any case in which a tissue predisposed to elongate does not do so." A perennial plant is generally said to be dormant when buds have formed on the terminals of the shoots.

2.2.2 Entering and Breaking Dormancy

Dormancy may be induced either by the external environment or by internal plant physiology.

A dormant bud is said to be quiescent when dormancy is imposed by the environment, e.g., drought stress, low temperatures. In Oregon, the quiescent period for Douglas-fir commonly extends from midsummer until late September and from mid-February until buds begin to expand. usually in early April. "Summer dormancy" is a synonym for quiescence.

A dormant bud is said to be in rest when dormancy is maintained by agents within the bud itself (Romberger 1963). A resting bud cannot elongate under even very favorable environments. "Winter dormancy" is a synonym for rest.

Dormancy may be broken by a range of treatments (Romberger 1963). but under natural conditions a bud in rest gradually becomes quiescent in response to exposure to temperatures of approximately 5°C (Lavender 1981). The length of time a bud must be exposed to the chilling temperatures necessary to satisfy the transition from rest to quiescence varies

with species, and possibly with ecotype (Lavender 1981). For Douglas-fir, this chilling requirement appears to be about 12 weeks (van den Driessche 1975, Lavender and Stafford 1984); no data so far suggest that this requirement varies with ecotype.

2.2.3 Locus of Dormancy

Some workers (Perry 1971. Zimmermann and Brown 1971, Nooden and Weber 1978. Bachelard 1980. Hanover 1980) believe dormancy to be a property of the apical meristems of shoots [although Zimmermann and Brown (1971) do suggest that phloem may be dormant when it produces callose]. But very few discuss data defining the locus of dormancy in perennial woody plants, and I am aware of only four such papers which report responses of coniferous species.

Worrall (1971) and Lavender et al. (1970) both present evidence demonstrating that the lateral cambia in the shoots of Douglas-fir seedlings do not enter rest. In contrast, Little and Bonga (1973) and Lavender and Hermann (1970) show that the lateral shoot meristems of balsam fir [Abies balsamea (L.) Mill.] and Douglas-fir, respectively, do enter rest. However, the experimental design, especially for the last study, does not permit separating the effects of chilling from those of the passage of time per se; therefore, the data, at least for Douglas-fir. may reflect an endogenous rhythm rather than a chilling requirement. The same comment applies to a report by Gouwentak (1941). who noted an apparent chilling requirement for the lateral cambia of flowering ash (Fraxinus ornus L.).

Although roots may enter quiescence as a result of either unfavorable soil moisture or temperature, I am aware of no published reports which unequivocably demonstrate that roots enter rest (Romberger 1963. Lavender et al. 1970, Zimmermann and Brown 1971).

The consensus, then, of the relatively limited literature is that rest occurs, almost without exception, in the apical meristems. In contrast. "cold hardiness," a marked change in plant physiology which frequently develops during rest (Weiser 1970) and which may represent a more general resistance to the stresses of harvest, storage, and outplanting, occurs, at least to some degree, throughout the entire plant.

2.2.4 Changes in Seedling Physiology during Dormancy

Smith and Kefford (1964), Vegis (1964), Sarvas (1974). and Fuchigami et al. (1982) all favor the concept of an annual cycle of discrete phases for perennial plants. In contrast. Campbell (1978) prefers the idea of a continually and gradually changing seedling physiology through dormancy, noting no evidence for discrete divisions of this period for Douglasfir: Lavender and Hermann (1970) also do not

support a sharply compartmentalized concept. Nonetheless. Douglas-fir seedlings clearly do respond to a series of environmental signals throughout their annual cycle; for seedlings to have maximum vigor, their annual cycle must be in phase with the natural environment (Lavender 1981).

2.2.4.1 Environmental cues

Moisture.--Wareing (1969). discussing only photoperiod, felt that the shortening photoperiods of late summer and early fall provide a reliable cue to boreal species and those indigenous to climates with rainy summers that winter is coming. But, as Lavender (1981) notes, species in the western United States, which is characterized by warm to hot, dry summers, initiate quiescence by mid-July. Not only is this date characterized by long photoperiods, it precedes any significant shortening of the daily photoperiod by at least a month. In such environments, increasing moisture stress probably initiates quiescence (Blake et al. 1979), a hypothesis compatible with Vegis' (1964) belief that quiescence is cued by weather patterns that precede periods of environmental stress.

Photoperiod.--Although moisture stress seems to be a major factor inducing and maintaining quiescence during warm summer weather, quiescent and resting Douglas-fir seedlings are definitely sensitive to photoperiod (Lavender and Wareing 1972, McCreary et al. 1978. Lavender and Stafford 1984). In addition. unpublished data (Lavender 1970) demonstrate that Douglas-fir seedlings exposed to a 16-hour photoperiod for 6 weeks in September and early October and then maintained under natural outdoor conditions into spring broke bud about 3 weeks later than seedlings maintained under a natural photoperiod in fall but which were otherwise treated the same. The mechanism of this response is not known. It may be that the extended photoperiod in fall delays the onset of rest and retards the subsequent physiological sequence during dormancy. Lavender and Stafford (1984) note that, during rest, Douglas-fir seedlings require a period of short days (a 9-hour daily photoperiod) and mild temperatures (ca. 20°C) to prepare for the following "chilling period."

The sensitivity of Douglas-fir seedlings to photoperiod continues during rest. A long photoperiod (greater than 14 hours daily) may stimulate more rapid budbreak in seedlings whose chilling requirements have not been fully satisfied (Lavender and Hermann 1970. Campbell 1978). And although a long (16-hour) daily photoperiod during the first weeks of late fall chilling inhibits budbreak (Lavender 1978b. unpubl. data), the same photoperiod in midwinter stimulates budbreak even at temperatures as low as 4°C (Lavender 1978a).

Temperature.--Sensitivity to photoperiod aside, the prime environmental factor regu-

lating seedling physiology during winter is temperature. Like many other perennial temperate-zone plants (Perry 1971). species such as Douglas-fir and western hemlock [Tsuga heterophylla (Raf.) Sarg.] have definite requirements for exposure to temperatures of about 5°C to prepare for vigorous shoot elongation in spring (van den Driessche 1975, Nelson and Lavender 1979). Consequently, the speed and vigor of budbreak in these species are largely a function of the number of hours of chilling temperatures the seedlings have received (Lavender and Hermann 1970, Nelson and Lavender 1979) (Fig. 1). To complicate matters, however, chilling occurring early in winter may be more effective than that occurring later for both Douglas-fir (Campbell 1978) and sweetgum (Liquidambar styraciflua L.; Farmer 1968). After the chilling requirements have been met, buds become active in spring primarily in response to rising temperatures (Perry 1971).
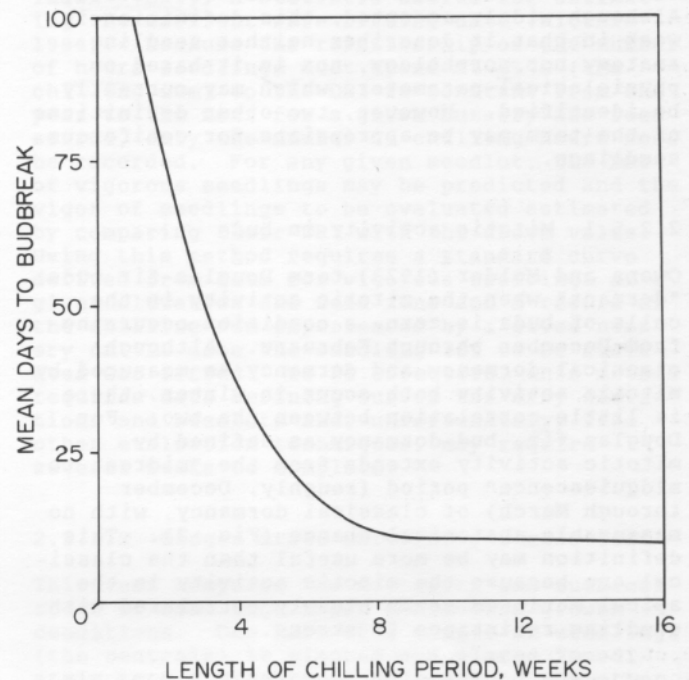

FIGURE 1. GENERAL RELATIONSHIP BETWEEN LENGTH OF THE CHILLING PERIOD EXPERIENCED BY A PLANT AND MEAN NUMBER OF DAYS UNTIL BUDBREAK IN A GROWTH-PROMOTING ENVIRONMENT.

For Douglas-fir. Campbell (1978) suggests that temperature may function both to satisfy physiological requirements for chilling and growth and, as a source of information, to guide Douglas-fir from various provenances in using the growing season to maximum advantage. Lavender et al. (1973) suggest a scenario wherein air and soil temperatures and photoperiod all interact to permit the earliest possible bud activity compatible with the risk of frost for any given year.

2.2.4.2 Genetic variation

Sweet (1965) notes that bud activity of seedling laterals precedes that of the terminal and that this delay in terminal bud activity is inversely related to the incidence of late frosts in the area of the seed source. This adaptation allows the species to maximize exposure of lateral foliage during spring, when weather is generally very favorable for photosynthesis, while reserving terminal growth until frost danger is past. Hermann and Lavender (1968, unpubl. data) note not only the same relationship but also that lateral buds on lateral shoots began growing after less chilling than similar buds on the terminal shoot.

2.2.5 Other Definitions of Dormancy

Thus far, this discussion has focused on the classical definition of dormancy (see 2.2.1). Although widely accepted, this definition is weak in that it describes neither seedling anatomy nor morphology, nor is it based on physiological parameters which may currently be identified. However, two other definitions of the term may be appropriate for coniferous seedlings.

2.2.5.1 Mitotic activity in buds

Owens and Molder (1973) term Douglas-fir buds "dormant" when the mitotic activity in the cells of buds is zero. a condition occurring from December through February. Although classical dormancy and dormancy as measured by mitotic activity both occur in winter, there is little correlation between the two. For Douglas-fir. bud dormancy as defined by mitotic activity extends from the "midrest to midquiescence" period (roughly. December through March) of classical dormancy, with no measurable anatomical change (Fig. 2). This definition may be more useful than the classical one because the mitotic activity in the apical meristem seems closely correlated with seedling resistance to stress.

FIGURE 2. RELATIONSHIP BETWEEN CLASSICAL DORMANCY
(A) AND DORMANCY AS DEFINED BY THE
MITOTIC ACTIVITY OF CELLS (B).

2.2.5.2 Resistance to stress, or "hardening off"

The second alternative definition of dormancy is maximal resistance to stress, which many nursery managers and foresters call "hardening off." Though classical dormancy and dormancy as measured by mitotic activity apply primarily to tissues within the apical bud. "hardening off" refers to the entire seedling. Many forest workers use this term to describe frost resistance, yet cold is only one of several stresses to which seedlings are maximally resistant during winter. In this sense, dormancy may be analogous to the concept of "vegetative maturity" used by horticulturists (Fuchigami et al. 1977).

Deep dormancy (maximal stress resistance) for Douglas-fir (Hermann 1967) and red-osier dogwood (Cornus sericea L., syn. Cornus stolonifera Michx.; Kobayashi and Fuchigami 1983) generally occurs from December through February, a period corresponding well with dormancy as defined by mitotic activity but poorly with dormancy as classically defined (Fig. 3). The relative dormancy curve for a typical Douglasfir seedling population is defined by the number of days to budbreak once a growth-favoring regime has begun. As previously noted, this curve, at least from mid-September until March. is a function primarily of the number of days of chilling the seedlings have received. The relative stress resistance curve. based on published data (Lavender 1964. Hermann 1967. Alden 1971. Lavender and Wareing 1972) and numerous operational observations. demonstrates that Douglas-fir seedlings are most resistant to the stresses inherent in nursery harvest, storage, and outplanting from December through February. This latter curve may be a more useful definition of dormancy for personnel concerned with reforestation than the classical curve because it describes responses correlated with the success of a plantation. That is, if seedlings are disturbed when relative resistance to stress is low, their potential for survival and growth may be correspondingly low: if, on the other hand, reforestation procedures are conducted when resistance to stress is relatively high. seedling survival potential will be higher.
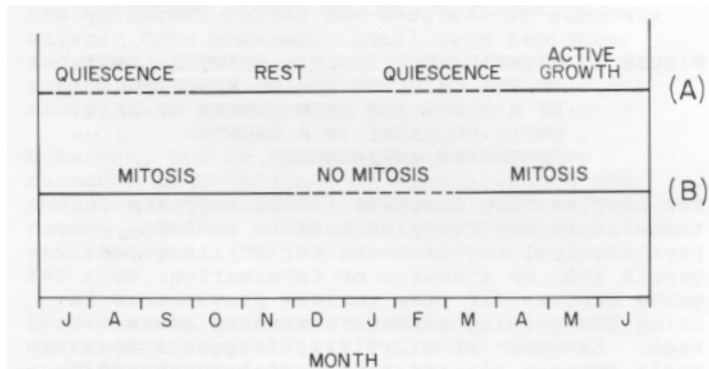
As mentioned earlier, the phenomena of classical dormancy and dormancy release are seated in the apical meristems of a perennial plant. However, the physiological condition of the bud may be correlated with that of the entire seedling. There is evidence that chemical substances exported from an actively expanding terminal bud will stimulate the lateral cambia of Douglas-fir seedlings to initiate cell division, but no evidence that such buds are a prerequisite for root elongation (Lavender and Hermann 1970). In fact, root growth commonly precedes bud growth of Douglas-fir seedlings in spring (Ritchie and Dunlap 1980): however. this study also shows that the root regeneration potential of Douglas-fir seedlings in winter is closely associated with the transition from rest to quiescence. And Alden ,(1971) notes that Douglas-fir trees which
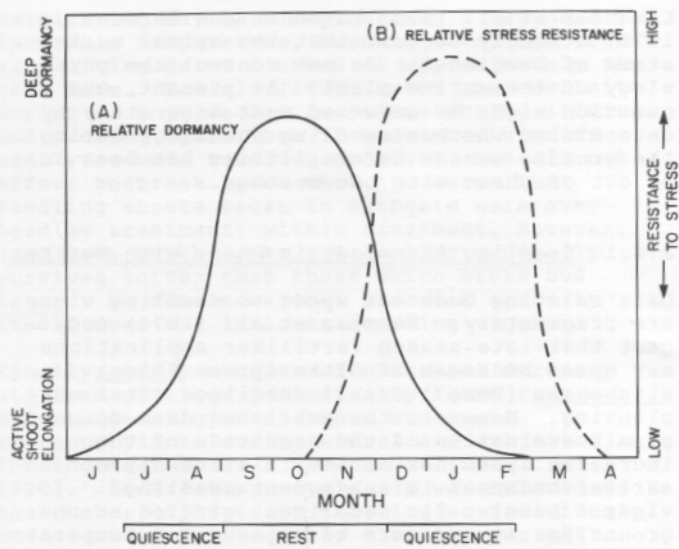
FIGURE 3. RELATIONSHIP BETWEEN CLASSICAL DOR-
MANCY (A) AND DORMANCY AS DEFINED BY
STRESS RESISTANCE ("HARDENING OFF")
(B) IN DOUGLAS-FIR. (THE CURVE
DEFINING STRESS RESISTANCE IS BASED
ON DATA FOR THE PERIOD EARLY OCTO-
BER-EARLY MARCH. VERY PROBABLY,
INCREASED RESISTANCE TO DROUGHT
STRESS PARALLELS DEVELOPMENT OF
QUIESCENCE IN MIDSUMMER, BUT I KNOW
OF NO PUBLISHED DATA WHICH DEFINE A
STRESS-RESISTANCE CURVE FOR THE
SUMMER MONTHS.)

developed cold resistance earliest in fall broke
bud earliest in spring, and that trees which
broke buds latest in spring were also the last
to deharden; but whether these relationships
were causal or merely correlated is unknown.

2.3 PROCEDURES FOR EVALUATING BUD DORMANCY AS AN
    INDICATOR OF SEEDLING VIGOR

2.3.1   Budbreak Speed as a Measure of Vigor

As previously noted, for species with a chilling
requirement, the time generally required to break
bud in a growth-promoting environment is reduced
as the length of the seedling chilling period is
increased (Fig. 1). Under controlled conditions,
however, the exact shape of the curve is affected
by seedling ecotype, seedling treatment before
chilling, temperature maintained during the
chilling period, and temperature and photoperiod
of the growth-stimulating environment (van den
Driessche 1975. Campbell 1978, Lavender 1981,
Kobayashi and Fuchigami 1983, Kobayashi et al.
1983). The same factors are important deter-
minants of the curve under natural conditions,
but the relationship between chilling and growth
response is more complex. Natural temperatures
are continuously fluctuating; warm spells during
the chilling period may reduce the efficiency of
that chilling (Lavender 1981). whereas cool
spells during the bud-

break period will slow the growth response.
Winter shade (Lavender 1981) and rainfall
(Westwood and Bjornstad 1978) also can affect
budbreak speed. Given this wide range of
variables, two general approaches currently are
used for assessing budbreak speed as an
indicator of seedling vigor or growth and
survival potential.

2.3.1.1 Dormancy release index and
        chilling sums

This methodology, thoroughly discussed by Ritchie
(1984), involves developing standard curves for
seedling ecotypes of interest which relate number
of chilling hours to dormancy release (Fig. 1).
For example, the number of days required for
budbreak in a fully chilled coastal Douglas-fir
(var. menziesii) seedling is 10; 10 divided by the
average number of days to budbreak yields the
"dormancy release index" (DRI), a statistic useful
for estimating the earliest safe lifting date
(Ritchie 1984). Because the relationship of the
number of hours seedlings must spend at <5°C (the
chilling sum) to the DRI is constant from one
year to the next for a given nursery and seed
source, only the number of chilling hours need be
recorded. For any given seedlot, the DRI of
vigorous seedlings may be predicted and the vigor
of seedlings to be evaluated estimated by
comparing their DRI with the above value. Using
this method requires a standard curve derived from
data for vigorous seedlings at a given elevation
and seed zone and a record of the chilling sum
experienced by a given nursery on the date the
seedling lot to be evaluated was lifted. To be
effective, this method requires data defining
curves for many elevations and seedlots and,
unfortunately, like other evaluation techniques.
may require several weeks to complete.

2.3.1.2 Oregon State University stress test

This test compares the mortality and budbreak
speed of seedlings under controlled growth
conditions. One half of a sample of seedlings
(the controls) is planted and placed immediately
into a greenhouse adjacent to the other half of
that sample, which has been exposed to a standard
stress (e.g., 15 minutes at 30°C and 30% relative
humidity) before being planted; mortality and
budbreak data are recorded for 2 months for each
sample half. The data are then compared on the
assumption that a more vigorous seedlot will
exhibit lower mortality and faster budbreak, and
less difference between these parameters, for the
control and stressed populations than a less
vigorous seedlot (Hermann and Lavender 1979).

This technique requires no standard curve
defining dormancy release nor a record of
chilling sums but depends instead on the dif-
ferences in budbreak speed and mortality of
controls and stressed seedlings to define
seedling vigor. Unfortunately, although the test
does define quite well seedling lots with very
high or *very* low field-survival poten-

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tial, estimates for the great majority in between--which have good field-survival potential--have large standard deviations.

2.3.2 Other Measures of Seedling Vigor

Ritchie (1984) discusses several other techniques for measuring seedling dormancy, among them the oscilloscope, dry-weight fraction. and plant growth regulators (hormone analysis)

The oscilloscope technique, which is based upon the effect of passing a square-wave electrical current through seedling stem tissue, is reviewed by Jaramillo (1981). However. because bud dormancy is seated in the bud, not in stem tissue, unless the bud exports materials which control stem physiology during dormancy. measurements of stem tissue, however accurate, can only produce data at best correlated with bud dormancy.

The same limitation applies to determining dry-weight fraction, which is based primarily upon measurements of seedling stems and foliage, not buds. It is worth noting, however. that one mechanism plants use to lower their sensitivity to frost--reducing their hydration--could produce the curve Ritchie (1984) describes for seedling dry-weight fraction; moreover, that curve approximates the one shown for seedling stress resistance in Figure 3.

Zaerr and Lavender (1980), reviewing qualitative and quantitative measurements of plant growth regulators in seedling shoots at different seasons of the year, conclude that little current data relate such measurements to seedling vigor (see also Zaerr, this volume). Wareing (1969) reviews a large number of papers which demonstrate that dormant buds have high levels of "growth inhibitory substances" and low levels of "growth promoters." However, most of the data discussed suffer from deficient methods or from experimenters assuming that the significant transition from "dormant" to "active" state occurs at the time of budbreak when, in all probability, it occurs sometime between midrest and budbreak.

Until more accurate methods of determining levels of plant growth regulators are developed and until studies utilizing such methods to thoroughly describe the levels of growth regulators throughout dormancy are conducted. observations of these compounds cannot identify probable differences in seedling physiology during dormancy nor yield predictions of seedling vigor.

2.4 PREDICTIVE ABILITY OF BUDBREAK TESTING

The question of whether budbreak speed is a good predictor of whole-seedling vigor probably cannot be answered with precision until we understand the nature of growth coordination between seedling parts. Current data (Lavender and Hermann 1968, unpubl. data;

Lavender et al. 1970, Lavender and Hermann 1970) strongly suggest that the apical meristems of Douglas-fir do not control the physiology of the entire plant. At present, the question might be answered most accurately by determining whether seedling phenology during the growing season before lifting has been in or out of phase with the weather.

2.4.1 Seedling Phenology in Phase with Weather

Data relating budbreak speed to seedling vigor are fragmentary. Benzian et al. (1974) suggest that late-season fertilizer applications may speed budbreak of Sitka spruce (Picea sitchensis (Bong.) Carr.] seedlings after outplanting. However, the published data do not permit evaluation of the magnitude of the increased speed nor of the relationship of earlier budbreak to subsequent seedling vigor. Douglas-fir seedlings, girdled at the groundline by exposure to extreme low temperatures in 1972, broke bud vigorously when placed in a greenhouse, only to die when the roots had exhausted their respiratory substrate (Lavender and Hermann 1972, unpubl. data). Presumably, overall seedling vigor was not affected by the dead stem elements early in this trial; nonetheless, budbreak speed did not accurately predict future seedling growth potential. Heiner and Lavender (1972) demonstrate that seedling survival under drought conditions is strongly correlated with budbreak speed. However, this relationship may reflect a drought-avoidance strategy: i.e., early budbreak and budset, rather than seedling vigor. may allow ecotypes from droughty areas to complete shoot growth before severe drought.

Perhaps the strongest evidence thus far relating budbreak speed with seedling vigor was demonstrated when Lavender (1984. unpubl. data) studied populations of Douglas-fir seedlings grown from southern Oregon seed sources and then transplanted during the winter following their second growing season. Although the seedlings were transplanted with extreme care, mean budbreak date was about 3 weeks later for the transplants than for similar, undisturbed seedlings. This delayed budbreak was strongly correlated with relative shoot growth, which was only one-third as great for the transplanted seedlings as for the undisturbed. No data so far explain this correlation, but it could reflect disruption of the endogenous physiology of both the buds and the remainder of the plant by the transplanting process.

In contrast. Darbyshire (1983) reports that nursery stress treatments during midwinter harvest of Douglas-fir seedlings affected final seedling size significantly, but not budbreak speed. Further, the date of lifting (Feb. 10, 24) significantly influenced budbreak speed--the later lifted seedlings broke their buds 2 weeks sooner after outplanting than the earlier lifted stock--but seedling vigor (in terms of growth increment) was unaffected. The more rapid budbreak after

outplanting may have represented a response to favorable temperature, because seedlings from all lifting dates flushed at approximately the same date. Daniels (1979) notes that definite drying of Douglas-fir seedlings during lifting and packing operations in midwinter significantly reduced seedling survival, but did not affect budbreak speed when the dates that seedling shoots began to elongate were averaged by treatment; within treatment, however. seedlings which broke bud earlier generally survived better than those which broke bud later. He concludes that budbreak speed by itself does not indicate seedling vigor.

Finally, early studies of classical dormancy utilized cuttings periodically taken from a wide range of gymnospermous and angiospermous plants during winter and subjected to forcing regimes in a greenhouse (Colville 1920). Budbreak speed clearly was related to the number of hours of chilling an individual bud received but, equally clearly, was not related to the vigor of the parent plant during flushing because the bud had been severed from the parent plant at time of budbreak.

2.4.2 Seedling Phenology Out of Phase with Weather

Lavender and Cleary (1974) emphasize that nursery-grown Douglas-fir seedlings may be stimulated to actively elongate their terminal shoots until mid-September or later by frequent irrigations but that the field survival potential of plants so grown is low. As an explanation, Lavender and Stafford (1984) propose that seedlings grown out of phase with the natural environment require a longer chilling period to prepare buds for the spring flush of growth. Put another way: for any given number of hours of chilling (short of the chilling requirement) that seedlings of a given seed source may receive, those that grow for prolonged periods in the seedbed will break bud more slowly in a growth-stimulating environment than will those grown "in phase" in the nursery. If the disruption in the seedling dormancy sequence, which is normally triggered by summer moisture stress, is suffi-ciently great, seedlings will not receive adequate chilling to permit normal budbreak in spring and will die (Hermann and Lavender 1976). And this problem will be exacerbated if recent predictions of rising mean global temperatures prove to be correct (Seidel and Keyes 1983).

Hermann and Lavender (1979) note that the mean budbreak of seedlings with low vigor. i.e., those produced by nursery regimes favoring late summer flushes of shoot growth. may be delayed by 10 or more days when compared with that of more vigorous plants.

In summary, budbreak speed may reflect seedling vigor less when stock has been weakened from the natural stresses or mishandling of harvest, storage, or outplanting, but more when the seedling's normal physiological sequence during dormancy has been disrupted.

2.5 CONCLUSIONS AND RECO!'d4ENDATIONS

Bud dormancy is a property solely of the apical meristems of perennial temperate-zone woody plants. Current data are not sufficiently precise to define physiological changes occurring in buds during the dormant period or to relate such changes to the physiology of the whole plant. Attempts to use growth responses of buds to characterize seedling vigor are based, at best, on correlations unless bud growth potential has been impaired by a disruption of physiology during the dormant period.

Bud activity, then, is but a single tool which may be used to estimate seedling vigor. To be used effectively, it should be supported by a thorough knowledge of the seedlings history both in nursery seedbeds and in the processing and storage facility.

REFERENCES

Alden. J. N. 1971. Freezing resistance of tissues in the twig of Douglas-fir (Pseudo-tsuga menziesii (Mirb.) Franco). Ph.D. Thesis. Oregon State University, Corvallis. 149 p.

Bachelard, E. P. 1980. Control of dormancy. Pages 273-296 in Control of shoot growth in trees (C. H. A. Little, ed.). Canadian Forestry Service, Fredericton, New Brunswick, Canada. 357 p.

Benzian, B., R. M. Brown. and S. C. R. Free-man. 1974. Effect of late-season topdressings of N (and K) applied to conifer transplants in the nursery on their survival and growth on British forest sites. Forestry 47(2):153-184.

Blake, J., J. B. Zaerr, and S. Hee. 1979. Controlled moisture stress to improve cold hardiness and morphology of Douglas-fir seed-lings. Forest Science 25(4):576-582.

Campbell, R. K. 1978. Regulation of budburst timing by temperature and photoregime during dormancy. Pages 19-34 in Proceedings of the Fifth North American Forest Biology Workshop (C. A. Hollis and A. E. Squillace, eds.). School of Forest Resources, University of Florida. Gainesville. 429 p.

Colville. F. W. 1920. The influence of cold in stimulating the growth of plants. Journal of Agricultural Research 20:151-160.

Daniels. T. G. 1979. The effects of winter plant moisture stress on survival and growth of 2+0 Douglas-fir seedlings. M.S. Thesis, Oregon State University. Corvallis. 86 p.

Darbyshire, R. L. W. 1983. Impact of nursery processing on the survival, growth, and physiology of 2+0 Douglas-fir seedlings. M.S. Thesis, Oregon State University. Corvallis. 86 p.

Doorenbos, J. 1953. Review of the literature on dormancy in buds of woody plants. Medelingen van de Landbouwhogeschool to Wageningen/Nederland 53:1-24.

Farmer. R. E., Jr. 1968. Sweetgum dormancy release: effects of chilling, photoperiod and genotype. Physiologia Plantarum 21:1241-1248.

Fuchigami. L. H.. M. Hotze, and C. J. Weiser. 1977. The relationship of vegetative maturity to rest development and spring bud-break. Journal of the American Society for Horticultural Science 102(4):450-452.

Fuchigami, L. H., C. J. Weiser, K. Kobayashi, R. Timmis. and L. W. Gusta. 1982. A degree growth stage (°GS) model and cold acclimation in temperate woody plants. Pages 93-116 in Plant cold hardiness and freezing stress (P. H. Li and A. Sakai. eds.). Academic Press. New York.

Gouwentak. C. A. 1941. Cambial activity as dependent on the presence of growth hormone and the nonresting condition of stems. Proceedings of the Koninklijke Nederlandse Akadamie van Wetenschappen 44:654-663.

Hanover, J. W. 1980. Control of tree growth. BioScience 30(11):756-762.

Heiner, T. C., and D. P. Lavender. 1972. Early growth and drought avoidance in Douglasfir seedlings. Oregon State University. Forest Research Laboratory, Corvallis. Research Paper 14. 7 p.

Hermann, R. K. 1967. Seasonal variation in sensitivity of Douglas-fir seedlings to exposure of roots. Forest Science 13:140-149.

Hermann. R. K., and D. P. Lavender. 1968. Unpublished data. Forest Research Laboratory. College of Forestry. Oregon State University. Corvallis.

Hermann. R. K., and D. P. Lavender. 1976. Effect of length of pruned roots upon performance of Douglas-fir planting stock. In Proceedings of the Western Forest Nursery Council and Intermountain Nurserymen's Association meeting, Richmond. B.C.

Hermann. R. K., and D. P. Lavender. 1979. Testing the vigor of coniferous planting stock. Oregon State University. Forest Research Laboratory. Corvallis. Research Note 63. 4 p.

Jaramillo, A. 1981. Review of techniques used to evaluate seedling quality. Pages 84-95 in Proceedings of Intermountain Nurseryman's Association and Western Forest Nursery Association combined meeting. USDA Forest Service Intermountain Forest and Range Experiment Station. Ogden. Utah.

Kobayashi. K. D., and L. H. Fuchigami. 1983. Modeling bud development during the quiescent phase in red-osier dogwood (Cornus sericea L.). Agricultural Meteorology 28:75-84.

Kobayashi. K. D., L. H. Fuchigami, and C. J. Weiser. 1983. Modeling cold hardiness of red-osier dogwood. Journal of the American Society for Horticultural Science 108(3):376381.

Lavender, D. P. 1964. Date of lifting for survival of Douglas-fir seedlings. Oregon State University. Forest Research Laboratory. Corvallis. Research Note 49. 20 p.

Lavender. D. P. 1970. Unpublished data. Forest Research Laboratory. Oregon State University. Corvallis.

Lavender. D. P. 1978a. Bud activity of Douglas-fir seedlings receiving different photoperiods in cold storage. Pages 245-248 in Proceedings of the Fifth North American Forest Biology Workshop (C. A. Hollis and A. E. Squillace, eds.). School of Forest Resources. University of Florida, Gainesville. 429 p.

Lavender. D. P. 1978b. Unpublished data. Forest Research Laboratory. Oregon State University. Corvallis.

Lavender, D. P. 1981. Environment and shoot growth of woody plants. Oregon State University. Forest Research Laboratory. Corvallis. Research Paper 45. 47 p.

Lavender, D. P. 1984. Unpublished data. Forest Research Laboratory. College of Forestry. Oregon State University, Corvallis.

Lavender. D. P., and B. D. Cleary. 1974. Coniferous seedling production techniques to improve seedling establishment. Pages 177-180 in Proceedings of the North American Containerized Forest Tree Seedling Symposium (R. W. Tinus, W. I. Stein, and W. E. Balmer. eds.). Great Plains Agricultural Council Publication 68. U.S. Government Printing Office. Washington. D.C. 458 p.

Lavender. D. P., and R. K. Hermann. 1968. Unpublished data, Forest Research Laboratory. Oregon State University. Corvallis.

Lavender, D. P., and R. K. Hermann. 1970. Regulation of the growth potential of Douglasfir seedlings during dormancy. New Phytologist 69:675-694.

Lavender, D. P.. and R. K. Hermann. 1972. Unpublished data, Forest Research Laboratory. Oregon State University. Corvallis.

Lavender, D. P.. R. K. Hermann, and J. B. Zaerr. 1970. Growth potential of Douglas-fir seedlings during dormancy. Pages 209-222 in Physiology of tree crops (L. C. Luckwill and

C. V. Cutting, eds.). Academic Press. London. 382 p.

Lavender. D. P., and S. Stafford. 1984. Douglas-fir seedlings: Factors affecting chilling requirement, vigor during dormancy. and planting shock. Submitted to Canadian Journal of Forest Research (in review).

Lavender. D. P., G. B. Sweet, J. B. Zaerr, and R. K. Hermann. 1973. Spring shoot growth in Douglas-fir may be initiated by gibberellins exported from the roots. Science 182:838-839.

Lavender, D. P., and P. F. Wareing. 1972. The effects of daylength and chilling on the responses of Douglas-fir (Pseudotauga menziesii (Mirb.) Franco) seedlings to root damage and storage. New Phytologist 71:1055-1067.

Little, C. H. A., and J. M. Bonga.   1973. Rest in the cambium of Abies balsamea. Canadian Journal of Botany 52:1723-1730.

McCreary. D. D.. Y. Tanaka. and D. P. Lavender. 1978. Regulation of Douglas-fir seedling growth and hardiness by controlling photoperiod. Forest Science 24:142-152.

Nelson, E. A.. and D. P. Lavender. 1979. The chilling requirement of western hemlock seedlings. Forest Science 25:485-490.

Nooden, L. D., and J. A. Weber. 1978. Environmental and hormonal control of dormancy in terminal buds of plants. Pages 221-268 in Dormancy and developmental arrest (M. E. Clutter, ed.). Academic Press, New York. 316 p.

Owens. J. N.. and M. Molder. 1973. A study of DNA and mitotic activity in the vegetative apex of Douglas-fir during the annual growth cycle. Canadian Journal of Botany 51:13951409.

Perry. T. 0. 1971. Dormancy of trees in winter. Science 171:29-36.

Ritchie, G. A. 1984. Assessing seedling quality. Pages 243-259 in Forest nursery manual: Production of bareroot seedlings (M. L. Duryea and T. D. Landis. eds.). Martinus Nijhoff/Dr W. Junk Publishers, The Hague/Boston/Lancaster, for Forest Research Laboratory, Oregon State University, Corvallis.

Ritchie, G. A.. and J. R. Dunlap. 1980. Root growth potential: Its development and expression in forest tree seedlings. New Zealand Journal of Forestry Science 10(1):218-248.

Romberger. J. A. 1963. Meristems, growth and development in woody plants. USDA Forest Service Technical   Bulletin   1293.   U.S.   Government Printing Office. Washington. D.C. 214 p.

 Sarvas, R. 1974. Investigations of the annual cycle of development of forest trees. II. Autumn dormancy and winter dormancy. Metsantutkimuslaitksen julkaisuja 84:1. 101 p.

Seidel. S., and D. Keyes. 1983. Can we delay a greenhouse warming? U.S. Environmental Protection Agency. U.S. Government Printing Office, Washington. D.C.

Smith. H., and N. P. Kefford. 1964. The chemical regulation of the dormancy phases of bud development. American Journal of Botany 51:1002-1012.

Sweet, G. B. 1965. Provenance differences in Pacific Coast Douglas-fir. Silvae Genetica 14:46-56.

van den Driessche, R. 1975. Flushing response of Douglas-fir buds to chilling and to different air temperatures after chilling. British Columbia Forest Service Research Division, Victoria. Research Note 71. 22 p.

Vegis. A. 1964. Dormancy in higher plants. Annual Review of Plant Physiology 15:185-224.

Wareing. P. F. 1969. The control of bud dormancy in seed plants. Symposia of the Society for Experimental Biology 23:241-262.

Weiser, C. J. 1970. Cold resistance and injury in woody plants. Science 169:1269-1277.

Westwood. M. N., and H. 0. Bjornstad. 1978. Winter rainfall reduces rest period of apple and pear. Journal of the American Society for Horticultural Science 103(1):142-144.

Worrall, J. 1971. Absence of "rest" in the cambium of Douglas-fir. Canadian Journal of Forest Research 1:84-89.

Zaerr. J. B., and D. P. Lavender. 1980. Analysis of plant growth substances in relation to seedling and plant growth. New Zealand Journal of Forest Science 10(1):186-195.

Zimmermann. M. H., and C. L. Brown. 1971. TREES Structure and Function. SpringerVerlag, New York. 336 p.