# ENVIRONMENT AND SHOOT GROWTH OF WOODY PLANTS

## D.P. LAVENDER

# FOREST RESEARCH LAB

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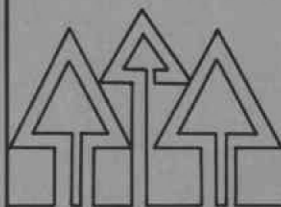
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## The Author

Denis P. Lavender is professor of forest physiology, Department of Forest Science, School of Forestry, Oregon State University.

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## Acknowledgment

# SUMMARY

Perennial woody plants have a complex annual cycle keyed to the environment. Temperate plants have an annual dormant period commonly broken by exposure to low temperatures, although daily photoperiods of 16 hours or longer may partially substitute for the chilling. Shoot growth in the spring is normally stimulated by rising air and soil temperatures, with photoperiod playing a minor role, if any. In temperate regions, duration of shoot elongation is controlled primarily by endogenous factors, although moisture stress may be more limiting than generally recognized. Shortening photoperiods are the major stimulation inducing dormancy in arctic regions and, probably, in temperate areas that seldom experience a summer drought. Many angiosperms and coniferous species are characterized by ecotypes that sharply differ in thermoperiod or photoperiod requirements for optimum growth and in chilling necessary to break dormancy. The dormant period is an intergrading series of physiological states, each of which has an optimum environment.

# INTRODUCTION

This paper was originally prepared as a background contribution to an I.U.F.R.O. symposium, "Control of Shoot Growth in Trees" (Lavender 1980). The assignment was to review effects of the environment upon the annual growth cycle of the apical meristems of woody plants, with reference to variations within a given plant (terminal vs. lateral buds), between plants of a given seed source (plant age and history), between plants of a given species (photoperiodic or thermo-periodic ecotypes), and between species. Because extensive literature reports various aspects of this subject, my review will reference others, such as those discussing dormancy (Doorenbos 1953, Samish 1954, Downs 1962, Romberger 1963, Vegis 1964, Wareing 1969, Perry 1971) and photoperiodism (Wareing 1956, Nitsch 1957). This review is concerned with apical and not lateral meristems of the shoot because another contribution to the symposium addressed the subject of radial growth.

# BUD BREAK

Sarvas (1974, p. 92-93) suggests that the zero point of the annual growth cycle is the beginning of the state he terms "Dormancy 2" [roughly equivalent to the end of rest and after rest (Perry 1971)], because that is when the physiology of a given population varies minimally among individuals. No clearly defined phenological event marks this point, so this paper will begin discussing the annual growth cycle by evaluating how environment affects bud break.

## CHILLING REQUIREMENTS

The role of low temperatures in breaking dormancy was first discovered in 1801 (Doorenbos 1953), but workers did not investigate this phenomenon in woody plants until the early 20th century. Then, although delayed foliation in peaches was reported in Georgia in 1890 (Weinberger 1950), low temperatures generally were not related to breaking of dormancy until 1907, when it was recognized that peaches differed in their rest period (Chandler 1957), and 1920, when Colville reported his chilling studies.

Today "chilling requirement" refers to the temperature (commonly around $5^0C$) and duration of exposure necessary to prepare the apical meristems of temperate perennial plants to resume growth when temperatures become favorable in the spring. Confined largely to plants that are exposed to freezing temperatures during the winter, such a requirement serves to prevent active shoot growth during brief warm spells in winter months, when such growth would be damaged by subsequent low temperatures.

During the past 25 years, many researchers (Olson et al. 1959; Perry and Wang 1960; Berry 1965; Roberts and Main 1965; Nienstaedt 1966, 1967; Jensen and Gatherum 1967; Nagata 1967a; Lyr et al. 1970; Steinhoff and Hoff 1972; van den Driessche 1975; Nelson and Lavender 1979; Wells 1979) have studied the chilling requirements of different forest trees. The requirements reported ranged from 0 weeks for a southern source of red maple to 17 weeks for Douglas-fir (Wells 1979).

In evaluating the chilling requirements of species or ecotypes within species, a major problem is that reported trials generally have not

used standard regimes for either chilling or the growth response subsequent to treatment. Most workers used temperatures below 5°C and assumed that temperatures between 0°C and 5°C were equally effective in breaking dormancy of test plants. But Wommack[1] showed that 5°C is optimum for Douglas—fir and definitely more efficient than either 0°C or 10°C. Studies in both the U.S. and Germany (Olmsted 1951, Lyr et al. 1970) suggest that below—freezing temperatures may be most efficient. Erez and Lavee (1971) demonstrated a range of efficiencies for temperatures between 3°C and 10°C, as well as different optimal temperatures for chilling terminal and lateral buds on the same seedling.

Chilling studies under controlled conditions maintain the desired temperature with, at most, minor fluctuations. But when evaluating how natural over—winter temperatures affect bud release from dormancy, researchers must consider not only the varying efficiencies of lower temperatures to satisfy chilling requirements, but also the effect of higher temperatures (Bennett 1950). Weinberger (1950) suggested that, for peaches in the southeastern United States, cumulative degree—hours below 7.2°C are a good measure of the chilling the trees have received and that at least 750 such hours must be accumulated by February 1 if the buds are to break normally. But Weinberger (1967) was unable to correlate the hours below 7.2°C with the speed of bud break for peaches in California over a 10—year period; instead, bud break strongly correlated with maximum mean temperatures in November and December (i.e., higher maxima in these months delayed bud break the next spring). He did not explain the variance in these data. I suspect that the California climate may have more frequent winter days with temperatures above 20°C.

Earlier, Bennett (1950) had shown that a chilling period interrupted by temperatures above 20°C less efficiently satisfies chilling requirements. In Israel, temperatures as high as 18°C do not negatively affect the chilling sequence; however, temperatures above 18°C apparently reverse the physiological sequence stimulated by low temperatures during the days immediately preceding (Erez and Lovee 1971).

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[1] Wommack, D. E. 1964. Temperature effects on the growth of Douglas—fir seedlings. Ph.D. dissertation, School of Forestry, Oregon State University, Corvallis. 176 p.

# LIGHT

A second complication with field trials is light. In California, Chandler et al. (1937) reported that shaded peach trees broke bud normally, whereas the remainder of the plantation suffered from extremely delayed foliation. They suggested that the difference was primarily an effect of the sun's rays heating the buds above air temperature. Other studies (Erez et al. 1966, 1968) also showed that light during the chilling period inhibits subsequent bud break, but they attributed this inhibition to the light intensity. In contrast, a daily photoperiod during chilling substantially increased the speed of bud break of Douglas-fir (Lavender and Wareing 1972, Lavender 1978).

# PHOTOPERIOD

A third major problem in evaluating requirements is the interaction of light with temperature, not only during the chilling period, but also during subsequent growth. Long photoperiods (exceeding 14 hours) can stimulate bud break and substitute for chilling (Olmsted 1951; Olson et al. 1959; Smith and Kefford 1964; Roberts and Main 1965; Erez et al. 1966; Nienstadt 1966, 1967; Nagata 1967a; Worrall and Mergen 1967; Farmer 1968; Wareing 1969, Lavender and Hermann 1970; van den Driessche 1975). However, the consensus is that--save for exceptional species such as European beech, European birch, European larch, (Wareing 1953, 1969), or species of poplar (Van der Veen 1951), which are stimulated by long photoperiods to break buds even when the seedlings are not chilled--long photoperiods speed bud growth only when the plants already have received a partial chilling.

Certainly, no evidence supports a photoperiodic response in the rapidity of bud growth by fully chilled seedlings. In fact, at Oregon State University, we consider Douglas-fir fully chilled when bud growth is as rapid under short as under long photoperiods.[2] In contrast, however, a study using provenances of Douglas-fir (White et

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[2]Hermann, R. K. and D. P. Lavender. 1964. Unpublished manuscript, Forest Research Laboratory, Oregon State University, Corvallis.

al. 1979) suggested that either temperature or photoperiod may stimulate the spring flush in Douglas-fir saplings. And Campbell and Sugano (1975) suggested that a daily 11.5-hour photoperiod speeds bud break more than a 10-hour photoperiod, even after 100 days of chilling at $4^0C$. The variance in these results may reflect effects of soil temperature and seed source, which differed for all three studies.

Although photoperiodic responses have been shown for experimental populations, photoperiod probably does not control bud break under natural environments for autochthonous plants. Yet, as Pauley and Perry (1954) noted, a minimum photoperiod is required to maintain shoot growth after bud burst.

# TEMPERATURE

## Air Temperature

Initiation of growth in spring correlates with genotype and with spring temperatures (Worrall and Mergen 1967). Studies such as that of van den Driessche (1975) have shown that Douglas-fir from a range of ecotypes break buds after about 1,250 hours of chilling in a growth environment at $24^0C$ and after 2,070 hours at $12.8^0C$. Similarly, Campbell and Sugano (1975) showed that Douglas-fir seedlings grown from seed collected throughout western Oregon and Washington initiated shoot growth more rapidly as the temperature of the growth environment increased from $14^0C$ to $22^0C$. My own work has shown that, given sufficient exposure to $4^0C$ temperature and to a 16-hour daily photoperiod, Douglas-fir seedlings will initiate normal shoot growth at $4^0C$ (Lavender 1978); in contrast, Richardson et al. (1975) found that peach buds failed to initiate growth after several months at $4.5^0C$.

Save for my data, the preceding data confirm many empirical observations that relate initiation of shoot growth in the spring to increasing temperature (Rudolph 1964, Richardson et al. 1975, Kozlowski 1971), but they also complicate evaluation of the relative chilling requirements of populations. Work with Norway spruce (Worrall and Mergen 1967) suggests that the chilling requirement of a species is the number of hours after which another 10 days of chilling reduces time to bud break by less than a single day.

However, Nienstaedt (1967) suggested that relative time to bud break of fully chilled seedlings of different populations reflects not the relative dormancy of those species, but the relative heat requirements for spring bud burst; thus, relative dormancy of several species can be measured by the ratio of days to bud break for unchilled seedlings and fully chilled seedlings.

Obviously, Nienstaedt's suggestion is valid only if each trial uses equivalent, constant photoperiods and temperatures. Even so, it begs the questions (especially in regard to Lavender's data) raised by Sarvas (1972) and Kozlowski (1971, p. 362) about initiation of active growth--i.e., when does the accumulation of chilling units necessary to break dormancy cease, and when does the accumulation of heat units necessary for spring growth begin?

In contrast to work strongly suggesting that air temperatures regulate growth initiation in the spring, Blaue and Fechner (1976) reported surprisingly constant dates of growth initiation for Engelmann spruce over diverse climatic conditions with sharply different air and soil temperatures.

## Soil Temperature

The initiation of spring growth seems significantly controlled by the available heat. Most evidence cites air temperatures as the source; however, a recent review (Thielges and Beck 1976) strongly suggests that soil temperatures control initiation of spring growth. Certainly the soil represents a tremendous heat reservoir, so incremental changes in its temperatures indicate the likelihood of damaging frosts far more than similar changes in mean air temperatures. In a study of sapling Douglas-fir (Emmingham 1977), buds on trees grown from seeds collected near the Oregon coast swelled when soil temperature reached 5°C at a depth of 20 cm, and buds in a mountain plantation swelled after snow melt when the soil temperature rose rapidly from 1°C to 7°C. In a controlled-environment study (regime: 20°C air, 5°C soil), Lavender et al. (1973) noted that bud break of Douglas-fir seedlings was greatly delayed with an 8-hour but not with a 16-hour photoperiod. These data suggest a modulated control system wherein photoperiod may limit bud break during cool springs (when cold soils protect little against late frosts) but not during warm springs (when soil temperatures are higher). That would explain why

a definite photoperiod response in speed of bud break was shown by Douglas—fir seedlings under a controlled $20^0C$—day, $7^0C$—night thermoperiod, but not under a $25^0C$—day, $10^0C$—night thermoperiod with correspondingly higher soil temperatures (Irgens—Moller 1957).

## PLANT CHARACTERISTICS

Generally ecotypes indigenous to the warmer portions of a species' range will have lower chilling requirements and respond more rapidly to increasing spring temperatures than ecotypes from the cooler portions of the range (Olson et al. 1959, Perry and Wang 1960, Kriebel and Wang 1962, Nienstadt 1967, Farmer 1968). In contrast, both Wommack (see footnote 1) and van den Driessche (1975) demonstrated no differential chilling requirements for terminal buds of Douglas—fir seedlings grown from seed collections over diverse climates in western North America. The latter, however, reported a greater chilling requirement for lateral buds of seedlings from an interior source (severe climate) than from a coastal—source (mild climate). A pattern of higher chilling requirements for buds of seedling ecotypes from severe winter climates than for similar seedlings from mild climates differs sharply from stratification requirements for seeds. Low—elevation seed sources of both Douglas—fir (Tanaka 1972) and ponderosa pine[3] require a longer stratification than do seeds collected from colder sites.

Nienstaedt (1967) suggested that spruce species indigenous to mild climates have a lower chilling requirement than those from more severe climates. But white spruce, indigenous to a severe climate (Nienstaedt 1966), has a chilling requirement of 4 to 8 weeks, considerably less than the 12 weeks for Douglas—fir (van den Driessche 1975) or 8 weeks for western hemlock (Nelson and Lavender 1979), both from coastal North America. That comparison does not substantiate the pattern for genera suggested by Nienstaedt (1967).

Heslop—Harrison (1964, p. 227) noted "that the most powerful means available to the higher plant for adaptation to regionally varying climates is the ability to adjust the developmental cycle." Douglas—

[3]Jenkinson, J. L. 1979. Personal communication. U. S. Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, California.

fir seedlings grown from seed collected on a droughty slope in southwest Oregon initiated bud break in spring ·more rapidly than similar seedlings grown from seeds collected from a mesic area at the same elevation in Corvallis; early bud break in that area was the only phenological or morphological trait correlated with seedling survival during a subsequent imposed drought (Heiner and Lavender 1972). Perhaps, thus far, unidentified variation in chilling requirements is one major mechanism for drought avoidance in Douglas-fir.

## Plant Age

The chilling requirement of a species may vary with age. Seedlings of white spruce must be chilled 4 to 8 weeks to break bud normally, while grafts taken from 30-year-old trees require only 2 weeks (Nienstaedt 1966).

## Bud Type

The lateral buds of hemlock (Nelson and Lavender 1979), poplar (Witkowska-Zuk 1969), and red maple (Perry and Wang 1960) have lower chilling requirements than the terminal buds of those species. And buds on the lateral shoots of Douglas-fir, whether terminal or lateral, require less chilling than the corresponding buds on the terminal shoots (see footnote 2). In contrast, terminal buds of peach require less chilling than do lateral buds (Erez et al. 1968).

Perhaps the most interesting relationship of relative heat requirements for bud growth is that reported by Sweet (1965) for Douglas-fir. He showed that seedlings indigenous to areas characterized by late spring frosts had a greater delay of terminal bud break after lateral bud break than did plants from locations with less probability of damaging spring frosts. However, time of terminal bud break in New Zealand did not correlate with the climate of the seed source in the United States (Sweet 1965).

## Plant History

Defoliation of red-osier dogwood in mid-fall delays bud break the next spring (Fuchigami et al. 1977). Similar results have been

shown for Douglas-fir, but, interestingly, an apparently much less traumatic treatment--exposure of both Douglas-fir and hemlock seedlings to 16-hour photoperiods under natural conditions in September--delayed bud break as much as 3 weeks the next spring.[4] The photoperiod of the previous season similarly affected speed of bud break of Norway spruce seedlings (Sandvik 1980). Given short (12-hour) photoperiods for 2 weeks in either late July or August, they initiated shoot growth about 3 weeks earlier than the control. Therefore, photoperiodic response cannot be measured by short-term growth patterns alone.

Anatomical and biochemical studies have demonstrated that the initiation of growth in seeds or buds is a complex biological phenomenon. The foregoing discussion clearly shows that the data relating levels of environmental parameters to plant growth are not unequivocal. Unfortunately, no one study accounted for all the variables noted in the remaining trials. Species differences, which reflect both diverse survival strategies and a spectrum of environmental constraints, further obscure potential response patterns which could substantiate cause-and-effect hypotheses. Therefore, the data support only general relationships, i.e., normal bud burst is largely a response to temperature sequence--first low temperatures to satisfy chilling, then moderate temperatures to stimulate growth. Not surprisingly, photoperiod per se is not implicated strongly as a control of growth initiation of autochthonous plants under natural conditions. That is because the utility of photoperiod to control growth lies in its consistency at a given date from one year to the next, whereas the date of environmental stress, such as frost, may vary widely in successive years.

# SHOOT ELONGATION

Research personnel concerned with growth of perennial woody plants have long been puzzled as to the reason shoot elongation of temperate-zone trees is only a very short part (ca 90 days) of the annual growth cycle. The studies reviewed in this section are

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[4]Lavender, D. P. 1973. Unpublished data. School of Forestry, Oregon State University, Corvallis.

concerned primarily with identifying the basic causes for a growth habit that appears very conservative.

## ENDOGENOUS RHYTHM

An early paper describing periodicity of shoot growth of trees indigenous to the northeastern United States (Cook 1941) reviewed previous European work, as well as data for 16 hardwoods and conifers in New York, and concluded that:

> . . . temperature at the beginning of the growing season may hasten or retard the start and early course of growth but thereafter is not of major importance. Nor does current rainfall, except in case of drought, materially affect it. The shape and placement of the growth curves themselves [are] constant and [appear] to be characteristic for each species.

Johnston (1941), Kramer (1943), Kozlowski and Ward (1957a and b), Gaertner (1964), and Blaue and Fechner (1976) agree that shoot growth begins in the spring before the danger of frost is past, but—for many species—ends long before the fall frosts begin.

## LIGHT

In his review of phytotrons, Downs (1980) noted that light intensities, which do not exceed one-fourth of full sunlight in many research laboratories, commonly are criticized as too low. He also noted, however, that plants grown under intensities approaching full sunlight do not achieve sufficient additional growth (over those grown at about 50% of sunlight) to warrant the expense and technology necessary to produce such high irradiance. Warrington et al. (1978) agree, as their data show that intense light produces abnormal growth, resulting in plants typical neither of greenhouse nor field-grown material. A caveat, however, is that these data are true only for those plants which, in nature, are normally not exposed to prolonged periods of full sunlight.

Horticulturists have long recognized that plants moved directly from a greenhouse environment to full sunlight may lose foliage, and container-grown seedlings are allowed to harden off in areas

protected by shade frames.  In natural conditions, however, shoot growth is rarely affected by high radiation unless vegetation management sharply diminishes shade on crop plants, or unless seedlings grown in low—elevation nurseries are planted at extreme elevations and exposures.  The latter situation is discussed in a report describing Engelmann spruce plantations in the Rocky Mountains (Ronco 1975).

Few publications relate light intensity to shoot growth or phenology. A report of a study lasting only 10 weeks (Steinbrenner and Rediske 1964) noted that seedlings of both Douglas—fir and ponderosa pine grown under 16,000 lux had heavier and taller shoots than did similar seedlings grown under 4,000 lux.  In contrast, Gifford (1967) reported that both 6,000 and 20,000 lux had little effect on the shoot growth of quaking aspen cuttings grown under three temperatures.  A series of studies wherein seedlings were grown for 5 years under 13, 25, 45, or 100 percent of full sunlight (Logan 1965, 1966) found that broadleaved trees (such as yellow birch, white birch, sugar maple, and silver maple) generally grew better at lower light intensities than did conifers (red pine, white pine, jack pine, and eastern larch), which grew well only at the two higher intensities.  Similarly, reports describing the growth response of western conifers and Norway spruce (Fairbairn and Neustein 1970, Emmingham and Waring 1973) noted that 2—year—old seedlings all grew most in full light.

Kozlowski (1971) has reviewed other reports generally noting that effects of light intensity upon shoot growth vary widely between species.  One reason for such variation is that in many studies light intensity was controlled by degrees of shade of natural light; there—fore, the proportion of any exposure to "full sunlight" varied according to the climate in which the trials were conducted.

Drew and Ferrell (1977) reviewed effects of light intensity upon plant growth and reported multi—year data for effects of several levels of shade on growth and phenology of Douglas—fir.  When plants were grown under low light, the root/shoot ratio increased with increasing temperature.  Furthermore, 9 percent of full sunlight resulted in early dormancy of Douglas—fir seedlings and a corresponding early bud break the next year.

Wilson and Fischer (1977) reported that light intensity affects both bud formation and stem elongation in striped maple.  Plants grown

under 6 percent of full sunlight developed only. one pair of leaves per bud; primordia for the second pair became bud scales. And Mergen (1963) reports that northern sources of white pine demonstrated greater growth depression than did southern sources when grown under 2,000 ft cd rather than 4,000 ft cd.

In New Zealand, Warrington et al. (1978) evaluated plant growth under high fluxes of radiant energy. Growth habit and accumulated dry weight differed little as light increased from about 50 percent of full mid—summer irradiance to 100 percent, although the shoot length decreased and leaf thickness increased. Warrington et al. (1978) concluded that plants such as soya bean, perennial rye grass, or sorghum do not need more than 50—percent radiation. Nonetheless, their data leave open the possibility of an interaction of light—intensity and treatment, which may at least partially invalidate data from studies conducted in growth facilities providing only 10 percent to 15 percent of full natural irradiance.

Finally, in a review of apical dominance, Phillips (1975) noted that low—light intensities favor both correlative inhibition of lateral buds and hyponasty.

## PHOTOPERIOD

The pioneering work of Garner and Allard (1920) stimulated many studies of how day length (or, more properly, the length of the unbroken daily nyctoperiod) affects the growth and development of woody plants. These trials have been summarized in a number of reviews (Wareing 1949, 1956, 1969; Nitsch, 1957; Rudolph 1964; Kozlowski 1964, 1971; Nooden and Weber 1978), although those published after 1957 emphasize internal control of plant phenology rather than photoperiodic effects per se.

Early workers (Gevorkiantz and Roe 1935; Kramer 1936, 1937; Gustafson 1938; Phillips 1941) found that a daily 14.5—hour photoperiod stimulated shoot growth of many eastern forest species when the seedlings were maintained over winter in a greenhouse, that 9—hour days resulted in early dormancy and increased frost hardiness for diverse angiospermous and coniferous tree seedlings, that long photoperiods could stimulate bud break in unchilled red pine seedlings, and that the effect of illumination supplementing a natural

winter photoperiod depended upon light quality (red light stimulated growth; blue did not).

These data and other investigations enabled Nitsch (1957) to classify a broad range of woody plants according to this scheme:

| Characteristics | Plant class | Example |
|---|---|---|
| • Long days prevent the onset of dormancy | | |
|    Short days cause dormancy | | |
|      Long days cause continuous growth | A | Weigela |
|      Long days cause periodic growth | B | Oak |
|    Short days do not cause dormancy | C | Juniper |
| • Long days do not prevent the onset of dormancy | D | Lilac |

Most of the species Nitsch listed were assigned to Classes A or B; only 5 to 10 percent were in Class C. Nooden and Weber (1978) have revised this tabulation to include the substantial research conducted since 1957.

Downs and Borthwick (1956), Downs and Piringer (1958), and Piringer et al. (1961) extended the early work to many other species and showed that incandescent light surpassed fluorescent light as a source of radiation for extending daylength. This last, of course, really was a comparison between near-red (fluorescent) and far-red (incandescent) radiation.

Fraser (1962), Watt and McGregor (1963), and Bean (1964) used supplemental illumination to extend the growth period of nursery-grown seedlings. Fraser (working with red, white, and black spruce seedlings and a 24-hour photoperiod) and Watt and McGregor (working in Florida and Wisconsin with eastern white and red pines, white and black spruce, and a 20-hour photoperiod) reported that seedlings grew more with an extended photoperiod. However, Bean (working in Tennessee with eastern white pine seedlings under a range of photoperiods, light quality, and treatment periods) reported

that supplemental light stimulated development of secondary foliage but did not increase seedling height.

Japanese scientists (Satoo 1965, Nagata 1967a and b) extended research on photoperiod to Asian coniferous species. Four hours of supplemental light at night (10 p.m. to 2 a.m.) increased the growth of Sakhalin fir two to four times and Sakhalin spruce eight to ten times over growth of a control (Satoo 1965). A study of photoperiods lasting 8 to 24 hours demonstrated that day lengths exceeding 14 hours stimulated much longer internodes in seedlings of Japanese red pine. Light periods of 12 to 14 hours stimulated the maximum production of acicular leaves and duration of growth (Nagata 1967b). In sharp contrast, Hellmers and Pharis (1968) found that coastal redwood requires little periodicity (with one exception—height growth) and that it accumulates dry matter in relation to total radiant energy without regard to cycle.

Although natural photoperiods vary continuously throughout the year in temperate regions, with maximal changes at spring and fall equinoxes, constant photoperiods have been used in nearly all the investigations relating photoperiod to woody plant growth. Exceptions are reported by Norwegian and New Zealand workers. Working with Norway spruce and Douglas-fir seedlings, Robak (1962) showed that both species under an artificial photoperiod equivalent to that at 50° N. latitude entered dormancy earlier than similar seedlings under the natural photoperiod of Stend, Norway (60° 15' N.). Magnesen (1969, 1971, 1972), using diverse seed sources of Norway spruce, demonstrated that shortening photoperiods triggered terminal bud formation and that seedlings grown from a northerly seed source had a longer critical photoperiod than those of southerly origin. Investigations with Monterey pine in New Zealand (Jenkins et al. 1977) showed that shoot elongation was generally stimulated more by increasing photoperiods than by long photoperiods per se, results suggesting that changes in day length may regulate growth responses under natural conditions more than laboratory data indicate.

Long photoperiods stimulate increased growth in studies of six Pacific Northwest species (Douglas-fir, western hemlock, mountain hemlock, Pacific silver fir, Engelmann spruce, and white spruce) by Owston and Kozlowski (1976), McCreary et al. (1978) and Arnott (1979). Western hemlock and Douglas-fir seedlings grew better with a variety of light breaks during the dark period than did similar plants grown

under natural day length. The other species increased growth with delayed terminal bud set under a 24-hour photoperiod if the supplemental light was at least 20 to 80 lux.

In contrast to generally positive growth responses to extended photoperiods, studies with species of spruce (Pollard and Logan 1977) and oak (Immel et al. 1978) showed no increased growth. The daily photoperiod must be no longer than 4 hours to reduce needle formation of spruce; varying the day length from 6 to 15 hours had no effect. Extending the day length up to 24 hours did not increase the dry weight of either northern red or chestnut oak seedlings.

Photoperiodic ecotypes have been substantially researched. In a series of trials with Douglas-fir, Irgens-Moller (1957, 1962, 1968), who collected seedlings along an east-west transect from the Pacific Ocean to eastern Oregon and grew them in a cold frame in Corvallis, noted that bud break of seedlings of origins above 100-meter elevation was speeded more by a 16-hour than an 8-hour photoperiod. No such effect was noted for seedlings of origins below 100-meter elevation. Similar work compared the time of bud set for plants grown from Rocky Mountain and coastal seed sources. Seedlings from all sources initiated dormancy earlier under 9-hour than under 19-hour daily photoperiods, but time of bud set between the two photoperiod regimes differed more for seedlings of interior sources. Later work demonstrated that seedlings of Rocky Mountain origin responded much more rapidly to photoperiod changes than seedlings of coastal origin (Irgens-Moller 1968).

Working with a wide range of tree species, Vaartaja (1959, 1962) demonstrated photoperiodic ecotypes in many. Seedlings from seed collected in the northern portion of a tree's range generally responded more to photoperiod treatments and had a longer critical day than did those from seed collected in southern portions of the range. Vaartaja suggested that photoperiodic stimuli may control growth of northerly seed sources, whereas endogenous rhythms may control southerly sources of any given species.

Langlet (1959) presented interesting data that probably reflect this concept. Height measurements of 17-year-old Scots pine saplings in New Hampshire correlated well with length of the first day in which temperatures rose above 6°C at the seed source. Tallest saplings were from seed collected in areas with the shortest day length.

Nienstaedt and Olson (1961) showed that eastern hemlock grown from seed collected in regions with a long frost-free season maintained growth longer under a range of photoperiods than did those grown from seed collected in regions with short growing seasons.

Studies in Norway and Sweden (Robak 1962; Dormling et al. 1968; Magnesen 1969, 1971, 1972; Dormling 1973; Heide 1974a and b) showed that seedlings of Norway spruce provenances from arctic areas have a longer critical photoperiod than those from central Europe.

European larch grown from seeds collected from relatively low-elevation sources in Poland at Blizyn (330 m) and Ipoltica (800 m) grew continuously with a 16-hour day, whereas those grown from seed collected at Pragelato (1,900 m) grew only intermittently (Simak 1970).

Pacific Northwest species (Malcom and Pymar 1975, McCreary et al. 1978) generally followed the pattern for Sitka spruce and Douglas-fir already described--seedlings of a given species grown from northerly or high-elevation seed sources had longer critical photoperiods than seedlings from southerly seed sources.

## TEMPERATURE

As Leopold and Kriedemann (1975) noted, the temperature range in which life can exist ($0°C$ to $50°C$) is an exceedingly small part of the range (0 K to 10,000 K) in which atoms exist. Nonetheless, even small variations within the life zone may dramatically affect shoot growth. High temperatures or high light intensities, which favor rapid growth, stimulate juvenile leaves; whereas low temperatures associated with high light intensities and low growth rates frequently stimulate xeromorphic foliage (Allsopp 1964). But isolating the effects of temperature, as one environmental factor influencing the rate and extent of shoot growth of woody plants, has proven difficult.

A review of early investigations (Tyron et al. 1957) shows that moisture is the limiting factor in dry environments, but that temperature, particularly that of the previous year, correlates well with height growth in the current year. Many workers have reported that shoot growth in year $n$ strongly correlates with size and vigor

of buds formed during the summer and fall of year $n-1$ (van den Berg and Lanner 1971, Owens 1968, Heide 1974b, Cannell et al. 1976, Pollard and Logan 1977). In contrast, a Norwegian study (Mork 1960) related shoot growth of Norway spruce to current-year temperatures and precipitation.

The development of the Clark greenhouse in 1938 and the Earhart Plant Research Laboratory in 1949 (Went 1957) enabled researchers to vary temperature while holding the rest of the environment constant, and thus to evaluate temperature effects upon shoot growth. The rapid proliferation of the growth chamber, pioneered in Pasadena, has permitted trials of woody plants throughout the world. A total list of such work is beyond this paper, but these reports are representative: Kramer 1957; Perry 1962; Hellmers 1963a and b, 1966a and b; Kozlowski 1968; Hellmers et al. 1970; Brix 1967, 1971, 1972; Lavender and Overton 1972; Hellmers and Rook 1973; Cremer 1968, 1972, 1975; Owston and Kozlowski 1976; Bachelard et al. 1978; Tinus and McDonald 1979; Gowin et al. 1980.

As might be expected, response to temperature and photoperiod varied substantially among the species studied, so generalizations are difficult.

Almost without exception, the best growth was between 15°C and 25°C. Kramer (1957) and Kozlowski (1964) suggested that thermoperiod may be important, but Hellmers and Rook (1973) argued that night temperature, not thermoperiod, affects seedling growth. Species response to thermoperiod or night temperature showed little recognizable pattern. As Hellmers et al. (1970) noted, Engelmann spruce--a high-altitude, cold-climate tree--grew best with a 19°C or 23°C day temperature and a 23°C night temperature. Coast redwood--a relatively warm-climate tree--grew best at a night temperature of 15°C.

Another example of variable response for which there is no apparent rationale is the differing growth patterns reported by Callaham (1962) and Lavender and Overton (1972). Callaham found that the optimum temperature and thermoperiod for shoot growth of ponderosa pine varied substantially with the seed source. In contrast, Lavender and Overton (1972) found no such pattern for Douglas-fir; seedlings from eight different seed sources had optimum growth in similar temperatures.

Evaluation of controlled growth-chamber trials of woody plant growth should be qualified. First, almost all experimental populations have been seedlings, yet evidence suggests that optimum temperatures for plant growth decrease with plant age (Cremer 1972). Second, light intensities, especially in older growth facilities, are frequently well below normal solar radiation. Third, reports generally indicate no independent control of root temperatures, but several workers (Adams 1934, Ashby 1960, Hellmers 1963a, Nielsen and Humphries 1966, Chalupa and Fraser 1968, Lavender and Overton 1972, Heninger and White 1974, Rook and Hobbs 1975) have noted substantial effects of root temperature upon shoot and root growth. Fourth, temperature patterns in growth chambers are frequently square curves with abrupt changes from maximum to minimum settings, while natural diurnal temperature patterns approach sine waves. Further, growth chambers are generally engineered to relatively constant temperatures, whereas plants have evolved in environments characterized by fluctuating temperatures that actually stimulate growth.

To obviate the fourth point, population response to temperature has been evaluated by the "heat sum" approach (Hellmers 1963b; Brix 1971, 1972; Hellmers and Rook 1973). The principal weakness of this technique for evaluating growth-chamber studies is that threshold temperatures are not changed with population age, as noted by Wang (1960), who also discusses other deficiencies that affect the use of heat sums in evaluating field-grown populations.

A Finnish paper (Sarvas 1972) described a refinement of the heat-sum principal that uses no threshold temperature, but rather measures effective heat input by comparing time lapse for specific events to time lapse at a standard temperature. The method is painstaking, but it offers promise for better comprehension of environmental effects upon plant growth and development.

## MOISTURE

Unlike most environmental variables, moisture can affect shoot growth by being either deficient or too plentiful.

Gaertner (1964) reviewed many reports of the largely adverse effects of flooding or very wet soils upon tree growth. However, in a study of southern hardwoods (Hosner and Boyce 1962), several species grew better in completely saturated soil than in well-drained

soil on a greenhouse bench. Mueller—Dumbois (1964) and Minore (1970) also reported differences in the capacity of species to tolerate saturated soils, but no populations they studied grew better under saturated conditions.

Although flooding can be a problem, review papers (Zahner 1968; Kozlowski 1958, 1971) have emphasized that moisture deficit, more than any other single environmental factor, limits plant growth. They also emphasize that most estimates of moisture effects on shoot growth have been indirect, as few data relate shoot growth to internal moisture stress.

For example, an analysis of climatic factors influencing growth of ponderosa pine in diverse locations in the western United States (Squillace and Silen 1962) suggested that it grows most rapidly where most of the annual precipitation falls between September and June. Shoot growth of several conifers grown in England from seed sources in the western United States correlated with current—year rainfall (Mitchell 1965).

Early reports (Pearson 1918), as well as those reviewed by Tyron et al. (1957), noted that tree growth on dry sites is limited by moisture, primarily rainfall during spring. Tyron et al. (1957) noted a correlation between spring rainfall and shoot growth of yellow—poplar. However, they also remarked:

> On areas where year—to—year variation in diameter or height has been observed, workers have reported different site factors such as precipitation or temperature most closely related to annual variation in tree increment. This factor may be precipitation, temperature, or length of growing season. Even the same site factor may be more effective in one portion of the year than another. Precipitation in one area may be most effective during the growing season, but in another area the winter, or even last year's precipitation may be most important.

In the Ozarks, Johnston (1941) noted that height growth of several oaks was unaffected by current—year moisture because shoot extension ceased before summer moisture stress (no measurements were made to determine if summer moisture stress affected shoot

growth the next year). In a study of southern species (Wenger 1952), artificial drought limited growth of sweetgum, loblolly pine, and shortleaf pine. A second study of loblolly pine (Zahner 1962) confirmed Wenger's data and showed that drought could reduce seedling growth more than 50 percent.

In Indiana, May–to–November rainfall of the preceding year closely correlated with shoot elongation of eastern white pine, but not of red pine (Motley 1949). In a later study of red pine, shoot growth in 1964 was affected by irrigation in 1963, but not by addition of water in 1964 (Clements 1970).

Using controlled environments, Canadian workers (Glerum and Pierpont 1968) showed that shoot growth of red pine and eastern larch, but not of white spruce, was inhibited by soil tensions of 15 atmospheres. Stransky and Wilson (1964) found that as little as 2.5 atmospheres of soil–moisture tension inhibited height growth of loblolly and shortleaf pine seedlings. The latter trials did not relieve drought stress (seedlings were stressed until dead), whereas the Canadian work used short drought periods.

Under neither regime did any of the plants respond to drought stress by initiating dormancy. Yet growing–season moisture stress may promote early dormancy in Douglas–fir (Emmingham 1977, Griffin and Ching 1977, Blake et al. 1979), white fir (Tappeiner and Helms 1971), and blue spruce (Young and Hanover 1978). Perry (1971) noted:

> Initiation of dormancy is probably the result of interactions between photoperiod, high night temperature, lack of available soil nutrients, and insufficient moisture during July and August. A limiting amount of any of these factors . . . can stop growth and initiate dormancy processes independent of photoperiod.

Kozlowski (1971) concluded that late–season moisture stress, common in many forested areas, has little effect on trees that initiate dormancy early, but may affect species whose growth extends to fall. The prevalent growth habit of Douglas–fir certainly places it in the first group. However, with adequate late–season moisture, this species is capable of lammas shoots and significant increment. Given such a response, late–season drought may affect the potential growth even of species that initiate dormancy early. However, no data

relate growth in the year after lammas production to growth in the year after a single summer growth flush. The reduced time available for bud growth after lammas production reduces growth potential the next year. Another possibility, which Kozlowski's 1971 review discussed, is that late—season moisture stress may affect trees which initiate dormancy early by reducing formation of needle primordia in the developing bud. Similarly, other papers (Clements 1970, Garrett and Zahner 1973, Pollard and Logan 1977) conclude that moisture stress during the growing season results in small buds on pine and greatly reduces the formation of needle primordia in both red pine and black spruce.

In Australia, moisture seems the limiting factor in growth of Monterey pine, with fall droughts particularly reducing height increment (Cremer 1972). Reports from New Zealand (Rook and Hobbs 1975, Jackson et al. 1976) have also noted that moisture stress severely limits leader growth in this species.


## NUTRIENTS

Although mineral nutrients are essential in a plant's environment, this paper is focused on how shoot growth is affected by factors that may vary during the annual growth cycle. Generally, nutrient supply—high, moderate, or low—remains relatively constant. The many publications discussing nutrition, even when narrowed to those about woody plants, are too many for review within the confines of this paper. However, one generalization that can be made is that moderate deficiencies of nutrients, especially nitrogen, increase apical dominance (Gregory and Veale 1957) and stimulate dormancy.

The interested reader should see a recent text (Mengel and Kirkby 1978) that thoroughly discusses the roles of the many essential elements in plant growth.


## GROWTH PATTERN

Reports consistently show that photoperiod limits active shoot elongation by plants from northerly or high—altitude seed sources; however, many temperate species begin growth early in the spring before danger of frost is past, then terminate shoot elongation

during favorable thermoperiods and photoperiods (Hanover 1980). As Cannell et al. (1976, p. 183) suggest:

> Speaking teleologically, shoot elongation need not occur throughout the available growing season, because it occurs merely to display the needles to best advantage at the right time, whereas apical growth needs to occur throughout the year in order to generate as many new needles as possible.

As Lanner (1976, p. 235) suggests, such a pattern allows time for a resting bud to develop sufficiently to produce maximum shoot growth the next spring. Alternatively, Lavender and Cleary (1974) showed that irrigation in the western United States may extend the active shoot growth of Douglas–fir and ponderosa pine seedlings well into the period of short days. However, seedlings that make such growth in late summer invariably initiate growth later in the next spring than plants that entered dormancy in midsummer.

As noted in the section on moisture and shoot growth, few references relate internal moisture stress during shoot elongation with incidence of dormancy. The pressure bomb system (Scholander et al. 1965) was unavailable from 1930 to 1960 when interest in environmental limitation of shoot growth was high. Borchert (1973, 1975, 1976) makes a theoretical case for the limitation of shoot growth by moisture stress. However, in a recent study,[5] seedlings grew actively while saplings initiated dormancy, although the two groups of plants had the same internal moisture stress. These data suggest a complex interaction of moisture stress with intiation of dormancy in the shoot.

With Douglas–fir from diverse provenances and a range of controlled environments, Lavender and Overton (1972) demonstrated that seedlings from a southern Rocky Mountain seed source grew intermittently when maintained under a long photoperiod, favorable temperatures, and adequate soil moisture. Such a growth pattern evolved in response to the intermittent heavy rains characteristic of the growing season in the southwestern United States. Under identical conditions, seedlings from seeds collected in moist or mesic regions of the Pacific Northwest, where growth is commonly limited

[5]Borchert, R. 1980. Personal communication. Department of Physiology and Cell Biology, University of Kansas, Lawrence.

by a summer-long drought, grew continuously. Studies using controlled genetic material and the pressure bomb might indicate that moisture stress limits shoot elongation more than current publications suggest, especially of plant species indigenous to climates with dry summers.

# DORMANCY

Because of the several reviews of dormancy, this section will refer both to such sources and to individual reports germane to particular aspects. Although whole plants are termed dormant, only apical meristems of temperate plants are generally considered to be dormant during the annual growth cycle. The lateral cambia of Douglas-fir have no dormancy (Lavender et al. 1970, Worrall 1971), although those of balsam fir do (Little and Bonga 1973). Conflicting evidence for the incidence of dormancy in roots has been reviewed by Hermann (1977). Although dormancy prohibits elongation, it does not mean absence of active growth. Owens (1968), Owens and Molder (1976), and Bachelard (1980) all noted initiation of leaf primordia within buds judged "dormant" by external morphology.

The classic definition of dormancy (Doorenbos 1953, p. 1) is that it is "any case in which a tissue predisposed to elongate does not do so." A woody plant is generally said to be "dormant," in common usage, when buds have formed on the terminals of shoots. The dormant period of many temperate plants may extend from midsummer until the next spring, a period sometimes occupying more than 75 percent of the annual growth cycle. Although the external morphology of the plant changes little during this time, the growth physiology undergoes significant changes that govern the plant's response to the environment.

Sarvas (1974) suggested at least two stages, Dormancy I (the "chilling period") and Dormancy II, separated by definite cytological events. He considered Dormancy I a mechanism setting plant physiology to the zero point of Dormancy II; i.e., a mechanism bringing all plants to an equal state of readiness for utilizing heat or initiating spring growth. Sarvas has suggested that Dormancy I and II differ distinctly, but that the dividing line is difficult to define. Campbell (1980, p. 30) has suggested that, for Douglas-fir

at least, dormancy is a period of transition "with potential developmental rates changing continuously in response to cool-season environmental stimuli."

Studies already discussed here have introduced the concepts of "summer dormancy" or quiescence, "winter dormancy" or rest (Romberger 1963), and "post dormancy" or quiescence, all based on plant response (usually short term) to favorable environments such as warm temperature or long photoperiods. However, between bud set and bud burst there remains an amorphous period for which few published data detail either plant physiology or the environment most favorable for development--other than the low-temperature environment postulated by Campbell (1980).

Several unpublished and published studies of Douglas-fir seedlings (Lavender and Wareing 1972) suggest strongly that photoperiod response, in that species at least, may be more subtle than bud set. Two-year-old seedlings were grown in pots in natural conditions during spring and summer until resting buds were well developed in late August. Then the seedlings were exposed to 3 weeks or 6 weeks of 9-hour days with mild temperatures followed by 4, 8, or 12 weeks of 9-hour days at $5^{o}C$, or they were exposed directly to 9-hour days at $5^{o}C$. After chilling, the seedlings were maintained with 12-hour photoperiods at $20^{o}C$ until bud break. Results showed clearly that the short-day treatment before chilling was essential for vigorous growth after chilling. In similar trials, the sequence of long days and chilling resulted in 13 percent mortality, as opposed to no mortality for seedlings treated with short days before chilling.

Sandvik (1980), in trials of other species, showed that short-day treatment in the summer speeded bud break the next spring. In Japan, Nagata (1968) showed that the most vigorous shoot growth of Japanese red pine followed the sequence short, mild days, then short days at low temperature, then long days. At Oregon State University, Fuchigami et al. (1977) demonstrated a series of clearly differing physiological states for red-osier dogwood. White spruce seedlings in Wisconsin chilled in late July required 6 to 8 weeks of low temperatures to achieve satisfactory bud break, whereas similar plants chilled in late September required only 4 to 6 weeks of low temperature (Nienstaedt 1966). Norway spruce seedlings chilled after a long-day regime grew less the next year than did seedlings chilled after exposure to shorter days (Heide 1974b).

These studies strongly suggest that seedlings which have been induced to initiate dormancy by shortened photoperiods or moisture stress require exposure to short, mild days before chilling if early, vigorous shoot growth is to be produced the next spring. Such a requirement may be keyed either to a sequence of relative levels of plant-growth regulatory compounds, which may be fostered by mild, short days, or to continued bud development in the fall (Owens 1968).

Vegis (1953), Dormling et al. (1968), Magnesen (1969), Perry (1971), and Lavender and Overton (1972) have shown that a combination of short days and low temperatures induces dormancy less rapidly than warm, short days. Growth regimes that maintain active growth in seedlings until late summer or early fall may well cause buds to form slowly and thus to miss the necessary exposure to mild, short days before frosts.

# CONCLUSIONS

The annual growth cycle of most temperate-zone plants appears regulated by endogenous rhythms that may be overridden by environmental factors (moisture, nutrients, heat, quality, intensity, or duration of light) whenever these factors, either collectively or individually, strongly limit or stimulate active growth. Because the details of endogenous growth or of response to environmental stresses or stimulation vary widely among plant species indigenous to the temperate zones, botanists, horticulturists, and foresters should be thoroughly familiar with the physiology of their plant populations and the environmental sequences necessary to produce plants of uniformly high vigor. Cultivation of plants according to such guidelines is essential to produce material with maximum survival and growth potential or with sufficiently uniform vigor to permit meaningful scientific trials.

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# CHECKLIST OF PLANTS

| Scientific Name | Common Name |
|---|---|
| *Abies amabilis* (Dougl.) Forbes | Pacific silver fir |
| *Abies balsamea* (L.) Mill. | Balsam fir |
| *Abies sachalinensis* | Sakhalin fir |
| *Acer pennsylvanicum* L. | Striped maple |
| *Acer rubrum* L. | Red maple |
| *Acer saccharinum* L. | Silver maple |
| *Acer saccharum* Marsh | Sugar maple |
| *Betula lutea* Michx. | Yellow birch |
| *Betula papyrifera* Marsh | White birch |
| *Betula pubescens* L. | European birch |
| *Cornus sericea* or *Cornus stolonifera* Michx. | Red-osier dogwood |
| *Fagus sylvatica* L. | European beech |
| *Glycine max.* L. | Soya bean |
| *Juniperus* L. | Juniper |
| *Larix decidua* L. | European larch |
| *Larix laricina* (Du Roi) K. Koch. | Eastern larch |
| *Liriodendron tulipifera* L. | Yellow-poplar |
| *Liquidambar styraciflua* L. | Sweetgum |
| *Lolium perenne* L. | Perennial rye grass |
| *Picea abies* (L.) Karst. | Norway spruce |
| *Picea engelmannii* (Parry) Engelm. | Engelmann spruce |
| *Picea glauca* (Moench.) Voss | White spruce |
| *Picea glehnii* | Sakhalin spruce |
| *Picea mariana* (Mill.) B.S.P. | Black spruce |
| *Picea pungens* Engelm. | Blue spruce |
| *Picea rubens* Sarg. | Red spruce |
| *Picea sitchensis* (Bong.) Carr. | Sitka spruce |
| *Pinus banksiana* Lamb. | Jack pine |
| *Pinus densiflora* Sieb. et Zucc. | Japanese red pine |
| *Pinus echinata* Mill. | Shortleaf pine |
| *Pinus ponderosa* Dougl. | Ponderosa pine |
| *Pinus radiata* D. Don. | Monterey Pine |
| *Pinus resinosa* Ait. | Red pine |
| *Pinus sylvestris* L. | Scots pine |
| *Pinus strobus* L. | Eastern white pine |
| *Pinus taeda* L. | Loblolly pine |
| *Populus tremuloides* Michx. | Quaking aspen |
| *Prunus persica* Batsch | Peach |
| *Pseudotsuga menziesii* (Mirb.) Franco | Douglas-fir |
| *Quercus borealis* Michx. | Northern red oak |
| *Quercus montana* Willd. | Chestnut oak |
| *Sequoia sempervirens* (Lamb) Endl. | Coast redwood |
| *Sorghum bicolor* L. Moench *Syringa* | Lilac |
| *Tsuga canadensis* (L.) Carr. | Eastern hemlock |
| *Tsuga heterophylla* (Raf.) Sarg. | Western hemlock |
| *Tsuga mertensiana* (Bong.) Carr. | Mountain hemlock |
| Weigela | Weigela |

Lavender, D. P. 1981. ENVIRONMENT AND SHOOT GROWTH OF WOODY PLANTS. Forest Research Laboratory, Oregon State University, Corvallis. Research Paper 45. 47 p.

The author reviews literature discussing the effects of the environment, i.e. light, photoperiod, temperature, and moisture, upon the annual growth cycle of perennial, temperate woody plants. The review is limited to a discussion of apical meristems.

KEYWORDS: Dormancy, bud break, photoperiod, shoot elongation, chilling, moisture stress, temperature.

**FOREST RESEARCH LABORATORY**
**SCHOOL OF FORESTRY**
**OREGON STATE UNIVERSITY**
**CORVALLIS, OR 97331-5704**

**ADDRESS CORRECTION REQUESTED**