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Article *in* Tree Physiology · October 1989

DOI: 10.1093/treephys/5.3.379 · Source: PubMed

David South
Auburn University

Tree Physiology 5, 379–385

Seasonal changes in intensity of bud dormancy in loblolly pine seedlings[1]

JAMES N. BOYER and DAVID B. SOUTH

School of Forestry and Alabama Agricultural Experiment Station, Auburn University, AL 36849-5418, USA

Received November 5, 1987

Summary

The terminal buds of six-month-old loblolly pine (*Pinus taeda* L.) seedlings remained closed for approximately six months, although bud dormancy, as measured by rate of bud break in a standard greenhouse environment, was only exhibited for about one month. The peak of bud dormancy was in December for seedlings grown near Auburn, Alabama. However, the timing and intensity varied with seed source and may have been affected by the warm fall temperatures. Seedlings from the more northern provenances entered dormancy first and reached a deeper state of dormancy than seedlings from southern provenances. The rate of shoot elongation was not consistently related to the rate of bud break.

Introduction

A perennial plant is generally said to be dormant when buds have formed on the terminals of the shoots (Lavender 1985). However, in young loblolly pine seedlings, the terminal bud, which may remain closed for approximately six months (usually October through March), may be in a truly dormant state (as measured by rate of bud break in an environment which is conducive to growth) for only a relatively small portion of the time between bud-set and subsequent flushing in the spring. When loblolly pine seedlings are raised from seed sown in February or March and fertilized and irrigated adequately, they may set buds in midsummer, flush after a short time, set another bud, and perhaps flush again. Thus, the presence of a bud does not necessarily indicate that the bud is dormant.

In this paper, dormancy or rest (Doorenbos 1953, Romberger 1963) is defined as a condition in which, under favorable greenhouse conditions, bud break is inhibited. The point of maximum rest (Fuchigami et al. 1982) is defined as the date at which buds require the longest chilling to resume growth. It is believed that this condition is maintained by agents within the bud itself (Romberger 1963, Lavender 1985). Quiescence (imposed dormancy) refers to inhibition of growth because of an unfavorable environment.

Loblolly pine buds pass through a cycle of pre-dormancy (also termed preliminary rest or paradormancy), deep dormancy (mid-rest or possibly endodormancy), and post-dormancy (after-rest or ecodormancy) when the bud is once again quiescent

[1] *Alabama Agricultural Experiment Station Journal Series Number 9-871371P.*

(Samish 1954, Vegis 1964, Lang et al. 1987). The depth of bud dormancy changes continuously, however, not in discrete steps.

With exposure to near-freezing temperatures, the bud dormancy cycle of northern conifers progresses from deep dormancy to quiescence (Berry 1965, Nienstaedt 1967, Lyr et al. 1970, Steinhoff and Hoff 1972, Campbell and Sugano 1975, van den Driessche 1975, Nelson and Lavender 1979, Wells 1979, Lavender 1981). This "chilling requirement" is adaptive because it prevents shoot growth during brief warm periods in the fall when new growth would be damaged by subsequent low temperatures (Nienstaedt 1967, Lavender 1981).

The dormancy cycle of loblolly pine seedlings has not been as intensively studied as that of more northern conifers. Little is known about the initiation of bud dormancy following bud-set, the timing of "maximum rest" (Fuchigami et al. 1982), or how long the buds remain in a relatively "dormant" state.

The objectives of this study were to determine the date of maximum rest for loblolly pine seedlings grown in central Alabama, and to determine the duration of the relatively dormant condition.

Materials and methods

In both 1985 and 1986, loblolly pine seedlings with set buds were sampled during the fall and winter to determine relative bud dormancy status. Relative bud dormancy was determined by using either (1) mean days to bud break or (2) the percent of buds active after four weeks in the greenhouse. A bud was considered broken or active when the bud scales had opened sufficiently to reveal green tissue of the enclosed primordial shoot (Carlson 1985). All seedlings were grown outdoors and were less than one year old at sampling.

Container-grown seedlings

In 1985, four seedlots (S.E. Virginia, N. Georgia, S.E. Georgia, and N. Florida) were chosen to represent a range of provenances by latitude. Each seedlot, which was a bulk open-pollinated collection from a first-generation seed orchard, was stratified for 60 days at 2–4 °C. On April 14, 1985 the stratified seeds were sown in 164-cm^3 containers (Leach-cells, Ray Leach Nursery, Canby, Oregon) filled with a commercial mix comprising equal parts by volume of peat, perlite, vermiculite and pine bark. The seedlings were grown outdoors at Auburn, Alabama (32°30′ N latitude, 85°30′ W longitude, and 200 m elevation). There were four replications for each seed source. Twelve seedlings from each replication were sampled on five occasions from mid-November 1985, to late January 1986. Chilling hours (0–8 °C) were monitored throughout the sampling period. Sampled seedlings were removed from the containers, potted in coarse sand, and placed in a heated (16–35 °C) greenhouse providing a 15-h photoperiod (300 W incandescent lights). The activity of terminal buds was checked every other day and the mean number of days until bud break was calculated for each sample date. Initial height and height after 8 weeks were measured for each seedling. Seed source and sampling date effects were determined by ANOVA.

Bare-root seedlings

Loblolly pine seed from a single open-pollinated family (originating in eastern North Carolina) was stratified for 42 days at 2–4 °C. On April 3, 1985, four replications of seed were sown in plots (1.2 m × 1.2 m × 1.0 m deep) containing coarse sand at Auburn. Five seedlings from each replication were lifted every two weeks during the fall and winter of 1985–1986. The lifted plants were hydroponically cultured in a heated (16–36 °C) greenhouse in which the daily photoperiod was extended to 15-h with incandescent lamps. The percentage of buds that had broken was recorded after 28 days. This measure of relative dormancy is inversely related to mean number of days to bud break.

In 1986 a similar study was conducted with seedlings grown at a nursery approximately 80 km south of Auburn. Seeds from an open-pollinated family from Alabama, which had been stratified at 2–4 °C for 60 days, were sown on April 13, 1986. Every two weeks from the following September until March, 15 seedlings were lifted from a single nursery bed and the relative dormancy of their buds assessed as described above.

Results

In both years of study, the relative state of bud dormancy increased rapidly from mid-November to mid-December and the date of maximum rest occurred in mid-December. Buds remained in this relatively dormant condition until early January when dormancy was released rapidly. The timing of maximum rest and the pattern of deepening and breaking dormancy were similar for both bare-root (Figure 1) and

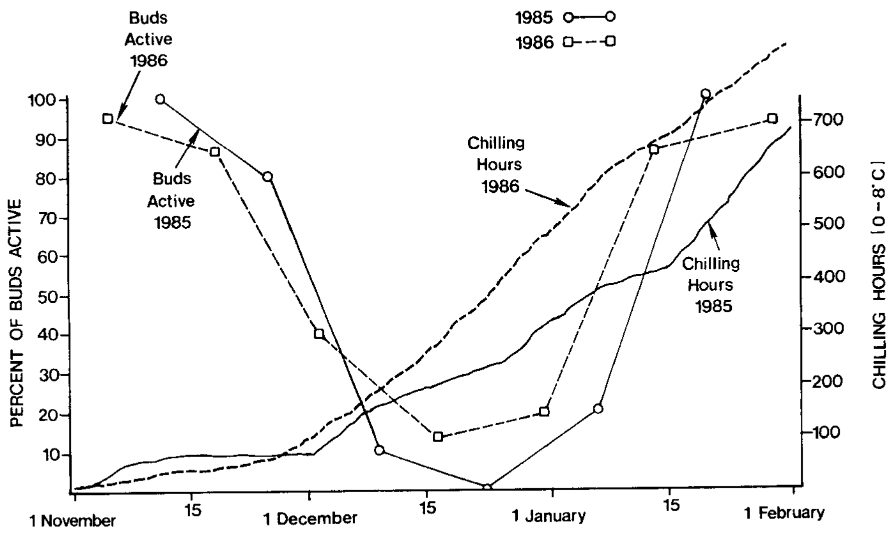

Figure 1. Accumulated chilling hours (0–8 °C) and the percentage of buds active after 28 days for bare-root seedlings grown outdoors and sampled from November to January. Each point represents 20 seedlings.

container-grown (Figure 2) seedlings.

The container-grown seedlings showed a significant ($P > F < 0.0001$) seed source by sample date interaction because seedlings of the northern seed sources became dormant first (i.e., December 11), and began the cycle toward quiescence before seedlings of the southern sources had reached their deepest rest (Figure 2). Seedlings of southern sources did not reach maximum rest until two weeks after the seedlings of the northern provenances. Until early January, seedlings of northern sources required more time to break bud and exhibited less shoot elongation than seedlings of southern sources. After that time, shoot elongation was similar, regardless of seed source (Figure 3).

Discussion

It has been assumed that deep dormancy of six-month-old loblolly pine seedlings occurs by late October and is released in late December (Garber 1983), after approximately 400 chilling hours (0–8 °C). However, loblolly pine seedlings growing outdoors in Alabama did not become dormant until mid-December, when more than 150 chilling hours had already occurred. Warm temperatures in the fall may have delayed the onset of dormancy in our study because accumulated chilling by December 10 was only 192 h for 1985 and 208 h for 1986 (compared with 338 h for 1983 and 400 h for 1984), whereas Garber reported 317 chilling hours (0–8 °C) by December 2, 1977 in his study. In 1985, temperatures averaged nearly 6 °C above normal during the last two weeks of October and 8 °C above normal the last three weeks of November. November 1986 was also mild, with temperatures averaging over 3 °C above normal. The warm temperature patterns during the fall may have

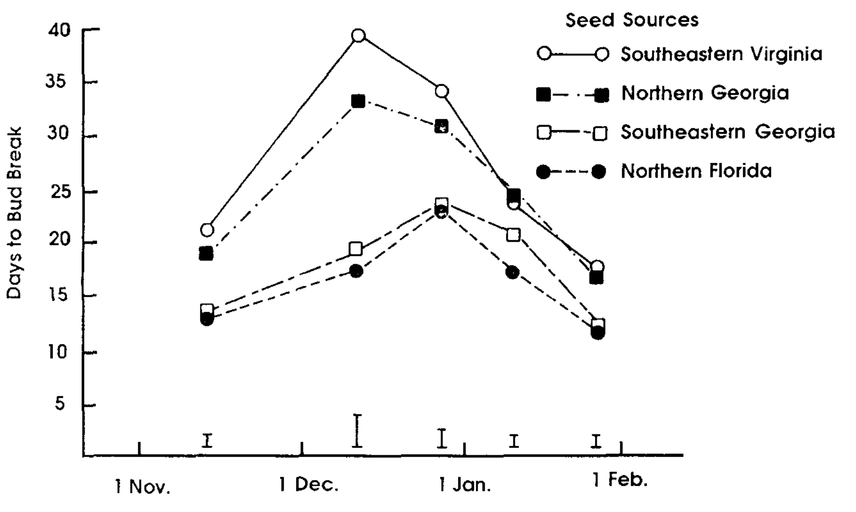

Figure 2. Days to bud break in a 15-h photoperiod of four seed sources grown outdoors in 1985 and sampled from November to January. Each point is the mean of four replications, with 12 seedlings per replication. Bars show standard error of the overall mean for each sample date.

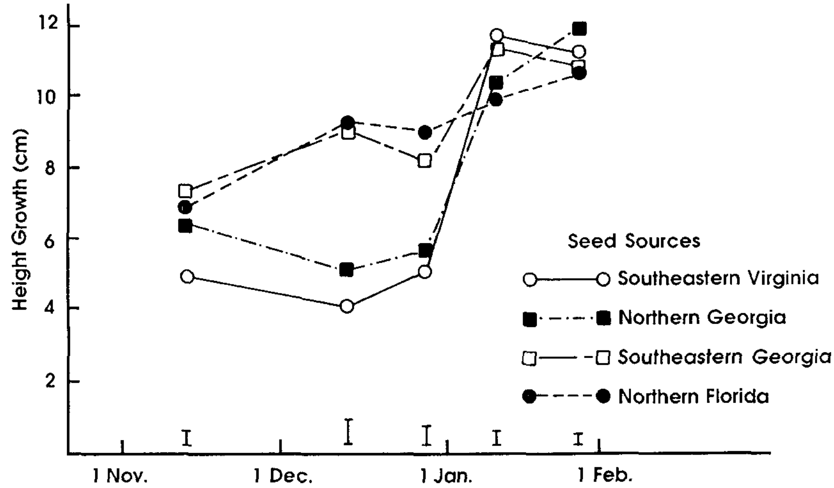

Figure 3. Height growth after 8 weeks in a 15-h photoperiod for four seed sources grown outdoors in 1985 and sampled from November to January. Each point is the mean of four replications, with 12 seedlings per replication. Bars show standard error of the overall mean for each sample date.

influenced timing of the dormancy cycle. Day length was already near the minimum by early December (Figure 4), and changed by only 1–2 min between the time when northern sources and southern sources were most dormant, whereas the minimum daily temperature during the same two week period decreased from 8 to −7 °C. It may be that bud dormancy of seedlings of northern seed sources is more sensitive to day length, whereas bud dormancy of seedlings of southern sources, from regions where photoperiod does not vary as much, is more sensitive to temperature.

Although chilling is usually considered in terms of releasing dormancy, our data indicate that a significant amount of chilling can occur before the date when buds are most dormant. When terminal buds from southern seed sources were most dormant (the end of December 1985), over 300 chilling hours had accumulated (Figure 1). In 1986, nearly 400 chilling hours had accumulated by the time seedlings were most dormant. For both years, dormancy was apparently not released until late January, after more than 600 chilling hours. Carlson (1985) demonstrated that, for several sources of loblolly pine, the mean days to bud break was not minimized until at least 730 chilling hours (mid-January). However, when the buds become dormant before the onset of chilling, the amount of chilling required to release bud dormancy for some seed sources may be as little as 400 hours (Garber 1983, Boyer and South 1986). These differences suggest that chilling provided before the date buds reach maximum dormancy may not make the same contribution toward releasing dormancy as chilling received after the bud has reached a peak in dormancy. These findings are similar to those of Fuchigami et al. (1982) who report that low temperatures can be associated with the onset of dormancy as well as the release of dormancy.

Bud break was most restricted from early December to early January, whereas height growth, measured after 8 weeks, remained low throughout the fall. Because

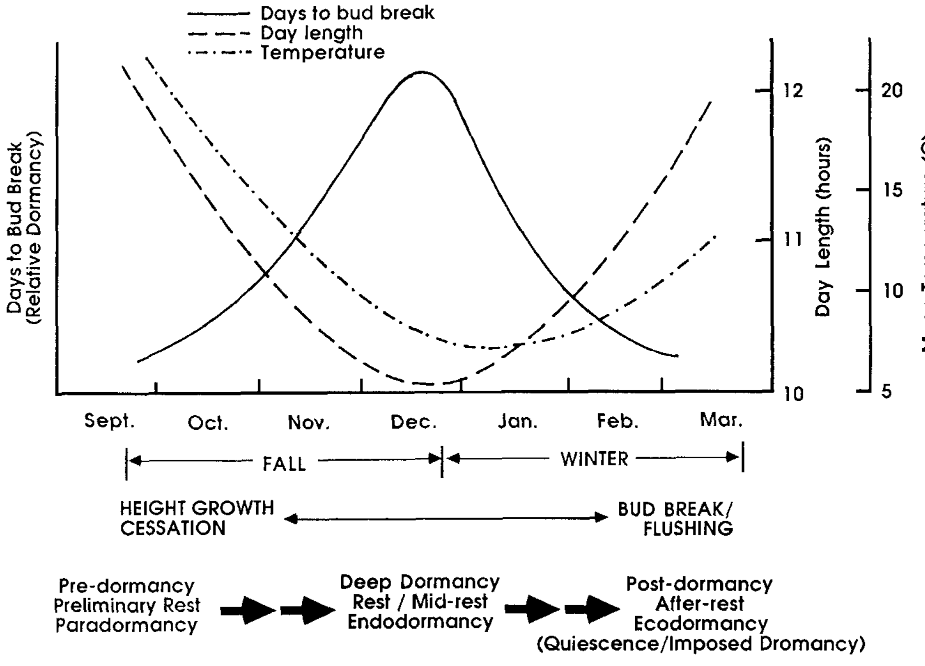

Figure 4. Bud dormancy cycle of loblolly pine in relation to day length and normal average daily temperature at Auburn, AL. Timing and shape of the bud dormancy curve will vary depending on seed source, location and year.

height growth was measured after only eight weeks, it was affected by the timing of bud break to some extent; however, seedlings that broke buds rapidly in mid-November exhibited much less height growth than seedlings with the same time to bud break in January (Figure 3). This indicates that two different processes are occurring: one which controls opening of the bud scales and initiation of growth, and another which regulates the rate of shoot elongation.

Conclusions

In Alabama, the terminal buds of many loblolly pine seedlings remain closed for approximately six months. However, in two different years, the buds of several different seed sources were only in a resting state for about a month. Loblolly pine seed sources differed in timing and intensity of dormancy, with seedlings of northern seed sources reaching the peak of bud dormancy first and becoming more dormant than seedlings of southern provenances. Even though seedlings in pre-dormancy broke bud at the same rate as those in post-dormancy, the latter exhibited much greater shoot growth potential. Bud break and shoot elongation appear to be controlled by different mechanisms, as the two processes do not necessarily follow the same pattern.

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