NEEDLELESS SHOOTS AND LOSS OF APICAL DOMINANCE IN GREENHOUSE-GROWN LOBLOLLY PINE

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Abstract.--When loblolly pine (Pinus taeda) is winter planted in the greenhouse and outplanted in May, abnormal growth in the form of multiple apical and needleless shoots has been observed. Results indicate that the tendency to produce abnormal morphology is related to preplanting hardening off. Further, preplanting shortened days and subsequent chilling influenced seedling dormancy and reduced the frequency and severity of abnormal growth.

Keywords: Pinus taeda L., apical dominance, tubelings, abnormal growth

INTRODUCTION

Control crossed loblolly pine (Pinus taeda) tubelings planted in the greenhouse in January and outplanted in May have been observed to produce growth abnormalities after outplanting. Growth abnormalities developed over the course of the summer, and became evident in August. Abnormalities included a loss of apical dominance, the production of needleless shoots, the development of shoots with primary needles, and the production of shoots with sterile scales only (failure of secondary needles to develop). Needleless shoots included both the leader and lateral branches. Symptoms combined to form a needleless basket whorl. Basket whorls often contained a stunted or absent terminal, with long, needleless branches surrounding the terminal. After overwintering, seedlings that expressed the growth abnormalities were observed to resume normal growth. However, several competing leaders were observed on many trees in year two.

Seedlings exhibiting this abnormal growth are of dubious use in the evaluation of progeny tests, and the use of this material could result in erroneous or invalid conclusions about individual tree or family performance. By determining the causes of the observed abnormal growth, procedural changes may be developed to reduce the possibility of invalid conclusions in progeny test evaluation.

Lammas growth, or late season extension of primordia that often produce needleless shoots, was characterized by Rudolph (1964). Hinesley (1982) observed that attempts to bypass the normal chilling requirements of Abies fraseri resulted in stunting, loss of apical dominance, terminal bud abortion, lack of symmetry and other morphological abnormalities. Slee et al. (1976) described needleless shoots, loss of apical dominance, dieback, stem forks, and basket whorls on Pinus caribaea grown in lowland areas of Malaysia. Slee (1977) attributed the presence of the deformities to relatively constant daylength and temperatures near the equator. Out-of-phase dormancy (OPD) influences long shoot growth behavior (Greenwood 1981). Loblolly pine subjected to OPD first cease growth for several months, and later may exhibit needleless shoots, loss of apical dominance, and slow growth.

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Loblolly pine exhibits a mixture of fixed and free growth, producing several flushes during the growing season (Lanner 1976). True dormancy is induced by declining photoperiod and continues until the chilling requirement is satisfied. Boyer and South (1989) found loblolly pine is released from dormancy in early January, following 600 hours of chilling. Garber (1983) found that when buds become dormant before the onset of chilling the chilling requirement may be as little as 400 hours.

To characterize and determine influences on the abnormal growth, two experiments were conducted. The first examined loblolly pine growth response differences from seedling production by two Virginia State agencies. The second experiment examined the effects of preplanting imposed dormancy treatments and the effect of postplanting supplemental water on loblolly pine seedling growth and morphology.

METHODS

Experiment 1: Greenhouse Effects

Fifty seedlings each of five full-sib families (all were Virginia provenances) were raised in either the Virginia Department of Forestry greenhouse in New Kent, Virginia, or the VPI&SU Reynolds Homestead Research Center greenhouse in Critz, Virginia, and later outplanted on the Appomattox-Buckingham State Forest near Appomattox, Virginia.

Germinants were planted into Leach® tubes in a mixture of 1:1 peat moss and vermiculite and were fertilized with Osmocoat® nine-month slow release fertilizer consisting of 18:6:12 N:P:K at a rate of 3 grams of fertilizer per liter of soil. Micronutrients were applied as Micromax® micronutrients at a rate of 1.1 grams per liter. Banrot® was used to prevent damping off. Lighting was set to mimic daylength over the course of the summer, starting at 13:42 hours, increasing to 14:45 hours on February 19, then decreasing to 13:27 hours by April 23. Seedlings were kept well watered.

New Kent seedlings were placed outside in a seed orchard on April 12, after 14 weeks of growth. Reynolds Homestead seedlings were placed in a lathe house on April 24, after 16 weeks of growth. Seedlings were kept well watered.

On May 18, seedlings were planted on the Appomattox-Buckingham State Forest, on a site that had been clearcut, chopped and burned the previous September. To control competing vegetation, a mixture of Oust® (0.224 kg/ha ai) and Roundup® (0.456 kg/ha ai) was applied before planting. Seedlings were planted into ten blocks, with factorial combinations of two greenhouses and five families. The experimental unit was the mean value of three seedlings.

Seedlings were examined twice monthly, with root collar diameter (RCD) recorded to the nearest .01 mm, flush height and sterile region height to the nearest mm. The number of sterile scales and the number of needles were counted on each flush. The number and height of lateral branches were recorded. Total final height, the ratio of branch height to total height, and the number of secondary needles per total stem units were calculated. A ratio of branch to apical height of greater than one indicated a loss of dominance. Analysis was conducted using a general linear models procedure (SAS Inst. 1988).

Experiment 2: Imposed Dormancy

Each of six families received factorial combinations of preplanting shortened daylength (0, 4, 6 weeks), and preplanting chilling hours (0, 400, 600 hours), as well as postplanting supplemental water supplied as a split plot. Seedlings were planted in four blocks.

Germinants were planted as before, and grown in the VPI&SU greenhouse facilities in Blacksburg, Virginia. Greenhouse care was administered as described in Experiment 1. On April 4, after 12 weeks of growth, dormancy treatments commenced. Seedlings subjected to 6 weeks of shortened daylength were placed under a heavy (100% shadecloth for all but 8 hours per day, while the remaining trees were exposed to natural daylength. Seedlings to be subjected to chilling only were placed in a refrigerator at 3°C (with no supplemental light). Seedlings receiving both treatments were first subjected to shortened days and then subjected to chilling. Seedlings were placed in a lathehouse following the conclusion of treatments.

Because of time constraints and to prevent confounding from storage and additional hardening off, seedlings were planted at the Reynolds Homestead Research Center in two shifts. In the first shift (May 25 and 26), all seedlings that were subjected to daylength only, chilling only, and seedlings that did not receive dormancy treatment (controls) were planted. In the second shift (June 11 and 12), all seedlings subjected to daylength and chilling treatments were planted. The site on which the seedlings were planted was an old field, which had been mowed and chemical treated'with a mixture of Oust (0.224 kg/ha ai) and Roundup (0.456 kg/ha ai).

Watering commenced on July 8, as it was unnecessary before that. Well watered plots received 1 inch (2.54 cm) of water per week from a soakhose. To reduce herbaceous competition, the site was retreated with Roundup on August 4.

Data were collected and analyzed as described in Experiment 1, above. Data were subjected to analysis of variance, with the two planting dates analyzed separately. As a result of this design, interactions between shortened daylength and chilling treatments could not be completely investigated.

RESULTS AND DISCUSSION

Experiment 1: Greenhouse Effects

Seedlings obtained from the New Kent nursery were initially more stout, yellow in appearance, and were more likely to have a terminal bud than seedlings produced at the Reynolds Homestead. The nursery of origin did not, however, produce differences in height growth (Table 1). Differences in seedling appearance may be attributed to the hardening off period. New Kent seedlings were placed outside two weeks earlier than Reynolds seedlings and were exposed to more direct sunlight in the seed orchard.

Symptoms of abnormal growth were first observed in mid-June, during the development of the second flush. By June 30, approximately 20% of the seedlings measured at Appomattox exhibited a loss of apical dominance, and by the end of the growing season, 85% of the seedlings had lost apical dominance. In most cases, the loss of apical dominance occurred in the most recent flush. Nearly all trees in this experiment completed three flushes, with 56% completing four flushes.

Table 1. Initial height, root collar diameter (RCD), and the frequency of a terminal bud at outplanting for five families of tubelings raised in two greenhouses: the Virginia Department of Forestry greenhouse in New Kent, or the VPI & SU Reynolds Homestead Research Center in Critz. Values in a column followed by the same letter are not significantly different at a=.05.

Greenhouse	Height (cm)	RCD (mm)	Bud %
New Kent	23.54 a	3.557 a	80.7 a
Reynolds	23.37 a	3.283 b	40.7 b
Overall Mean	23.45	3.420	60.7

By the end of the first growing season, the greenhouse of origin did not influence height or RCD. However, New Kent seedlings were less likely to lose apical dominance (Table 2). The greenhouse of origin also had an effect on the number of needles per stem unit (Table 2). Again, the New Kent seedlings performed more favorably, expressing more needles per total stem units than the Reynolds seedlings (Table 2). Needle production was influenced by the greenhouse of origin in the second flush, but not in the third. This may be the result of needle formation within the quiescent bud established on the New Kent seedlings before planting.

Differences in greenhouse of origin are interesting because greenhouse treatment and seedling condition were nearly identical. The greatest difference in preplanting treatment of the seedlings was the extended hardening off period for the New Kent seedlings, suggesting that the longer hardening period before planting had a favorable influence on growth.

Table 2. End of growing season growth for tubelings raised in one of two greenhouses (the Virginia Department of Forestry greenhouse in New Kent, or the VPI & SU Reynolds Homestead Research Center greenhouse in Critz) and outplanted on the Appomattox-Buckingham State Forest near Appomattox. Height, root collar diameter (RCD), the number of needles per the total number of stem units for flushes 2 and 3 (N/Unit), and the ratio of branch height to apical height (Final Ratio) are represented. Values within a column followed by the same letter are not significantly different at a=.05.

Greenhouse	Height (cm)	RCD (mm)	N/Unit Flush 2	N/Unit Flush 3	Final Ratio
New Kent	40.42 a	12.77 a	0.634 a	0.492 a	1.048 b
Reynolds	39.34 a	13.24 a	0.518 b	0.489 a	1.134 a
Overall Mean	39.88	13.00	0.574	0.491	1.091

Experiment 2: Im^p^osed Dormancy and Supplemental Watering

At the time of outplanting, control seedlings (no dormancy treatments) resembled seedlings raised at Reynolds, as described in Experiment 1. They were slender, generally lacked a bud, and were light green in appearance. This experiment was established at the Reynolds Homestead, where development was generally much slower than at Appomattox. Most seedlings planted at the Reynolds Homestead completed two flushes, with few seedlings completing a third flush. Because growth at the Reynolds Homestead was much slower, expression of growth abnormalities was not as obvious as on the Appomattox site. The summer (especially after planting) was extremely wet; therefore, watering had little effect on the growth of the seedlings.

Shortened days

When outplanted, seedlings subjected to shortened daylengths were smaller and were more likely to have set a terminal bud than the controls. By the end of the growing season, seedlings subjected to four weeks of shortened days did not significantly differ from controls in final height, although they were smaller in diameter. Seedlings subjected to treatment for 6 weeks were both more slender and shorter than control seedlings (Table 3).

Shortened daylength treatments had an influence on needle production in the second flush. Seedlings subjected to shortened days before planting exhibited more needles per total stem units, with the proportion increasing with 4 weeks and again with 6 weeks (Table 3). Shortened days had little influence on the strength of apical control, as reflected in the final ratio of branch to apical height of the seedlings (Table 3).

Table 3. Effect of shortened days before outplanting. End of growing season root collar diameter (RCD), height, needles per total stem units for flush 2 (N/Unit) and the ratio of branch height to apical meristem height (Final ratio). Data represents tubelings exposed to 0, 4, or 6 weeks of 8 hour days before outplanting at the VPI & SU Reynolds Homestead Research Center in Critz. Values within a column followed by the same letter are not significantly different at a=.05.

Short Days	RCD	Height	N/Unit Flush 2	Final Ratio
0 Weeks	8.06 a	28.53 a	0.495 c	0.899 a
4 Weeks	7.37 b	27.28 ab	0.680 b	0.809 a
6 Weeks	7.28 b	26.12 b	0.758 a	0.845 a
Overall Mean	7.57	27.31	0.644	0.851

Chilling

Upon outplanting, seedlings subjected to chilling only were shorter than controls and lacked a bud. By the end of the growing season, 400 hours of chilling resulted in a significant reduction of diameter growth, and 600 hours of chilling resulted in a significant reduction of height and diameter growth. Chilling had little effect on needle production, as is indicated by the number of needles per total stem units (Table 4). Although 600 hours significantly reduced seedling growth, the resulting shoots produced a lower branch height to apical height ratio (Table 4), indicating an increase in apical control.

Table 4. Effect of chilling hours before outplanting. End of growing season root collar diameter (RCD), height, needles per total stem units for flush 2 (N/Unit) and the ratio of branch height to apical meristem height (Final Ratio). Data represents tubelings exposed to 0, 400, or 600 hours of 3°C before outplanting at the VPI & SU Reynolds Homestead Research Center in Critz. Values within a column followed by the same letter are not significantly different at a=.05.

Chilling Hrs	RCD	Height	N/Unit Flush 2	Final Ratio
0 Hours	8.06 a	28.53 a	0.495 a	0.899 a
400 Hours	7.06 b	27.66 a	0.521 a	0.844 a
600 Hours	6.38 c	24.52 b	0.477 a	0.684 b
Overall Mean	7.16	26.90	0.499	0.809

The influence of chilling (decreasing final ratio) and daylength (increasing needles per total stem units) treatments implies that the seedlings lost apical dominance and produced shoots with fewer needles because of an interruption in the normal dormancy cycle of loblolly pine. Although loblolly pine is a recurrent flusher that exhibits free growth, seedlings are influenced by a yearly dormancy cycle.

It is hypothesized that seedlings exhibiting abnormal growth are responding to shortening daylength, with the apex approaching a relatively more dormant state. However, growing conditions were still favorable, allowing lateral branches to continue growth. Further, Martin (1987) indicates that high light, nutrients, and water decrease apical control. The application of shortened days to establish a bud and subsequent chilling may have "reset" the seedlings, or brought them back into phase prior to outplanting.

CONCLUSIONS

Growth abnormalities in winter planted loblolly pine seedlings may influence tree form as several terminals may compete for dominance, resulting in low forking. The development of abnormalities varied with planting site and, although not discussed, by family. The development of abnormalities is likely the result of an interruption in the normal dormancy cycle of loblolly pine. Treatments that increased the dormancy status of the seedlings prior to planting, including more severe hardening off, shortened days and subsequent chilling favorably influenced the number of needles per stem unit and the expression of apical control. These results indicate that 6 weeks of shortened days and 600 hours of chilling before outplanting, as well as a more severe hardening off period, favorably influence seedling form.

As growth differences and the expression of needleless shoots and apical dominance varied between the Appomattox and Reynolds Homestead planting sites, an additional topic that might be investigated is seedling response to dormancy treatments and subsequent outplanting on the Appomattox - Buckingham State Forest.

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