LONGLEAF PINE BUD DEVELOPMENT: INFLUENCE OF SEEDLING NUTRITION

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Abstract—A subset of seedlings from a larger study (Jackson and others 2006, 2007) were selected and evaluated for two growing seasons to relate bud development, and root-collar diameter (RCD), and height growth with three nursery fertilization rates. We chose seedlings in the 0.5 (lowest), 2.0 (mid-range), and 4.0 (highest) mg of nitrogen per seedling treatments. Buds moved through three developmental phases and we confirmed that when RCD reached 25 mm (1 inch), seedlings were usually ≥ 10 cm (4 inches), had elongated buds, and were exiting the grass stage. After two growing seasons, heights greater than 10 cm (4 inches) were reached on 20, 60, and 65 percent of the 0.5, 2.0, and 4.0-N seedlings, respectively. On average, higher N rates yielded seedlings with larger RCDs, taller heights, and more seedlings exiting the grass stage. On an individual seedling basis, however, we detected a reduction in RCD increment growth with increasing RCD at outplanting across all fertilizer treatments. This phenomenon may be related to root binding, but we have insufficient data to confirm the nature of this response. Further studies are needed to resolve this issue.

INTRODUCTION

The longleaf pine (*Pinus palustris* P. Mill.) grassland forest of the southern Coastal Plain is among the most endangered ecosystems in North America (Noss and others 1995). Its native range once stretched from southern VA to east TX, covering almost 90 million acres. Now, the species occupies only about 2.2 million acres spread across the southern landscape in isolated patches (Shibu and others 2006). The thoroughness of the harvest and unique characteristics of the species have made regeneration difficult (Wahlenberg 1946).

The grass-stage nature of the species, a unique silvical characteristic, is poorly understood. Lack of seedling shoot elongation for a number of years after outplanting has contributed to longleaf pine's infrequent regeneration success. This, combined with application of management practices designed for loblolly (*Pinus taeda* L.) and slash (*Pinus elliottii* Engelm.) pines, resulted in frequent regeneration failures. As a result, attempts to regenerate longleaf pines have been largely avoided for many years in favor of other species.

In this paper, we will review the status of knowledge of bud development of longleaf pine, relate bud condition to initiation of seedling height growth, and report the response of seedling buds to application of varying nutrient regimes in the nursery.

BOTANICAL CHARACTERISTICS

Longleaf pine is a long-lived, native, evergreen conifer with scaly bark. Needles are in bundles of 3; they are slender, dark green, and 20 to 46 cm (8 to 18 inches) long. Cones are 15 to 25 cm (6 to 10 inches) long. Generally, seeds/kg (pound) equals 10,800 (4,900). The wintering buds are typically large with silvery-white scales. Compared to other southern pines, many of its characteristics are very distinctive (Boyer 1990). Survival and growth are closely related to longleaf pine's unique, silvical characteristics: its lack of seed dormancy that results in fall germination, its well-known grass stage and delayed height growth, and its high resistance to fire damage (Croker and Boyer 1975).

While in the grass stage, seedlings develop extensive root systems. Development can be followed by observing increases in RCD. When it approaches 2.5 cm (1 in), active height growth is imminent. Grass-stage seedlings, once they reach 0.8 cm (0.3 in) in root-collar diameter, are highly resistant to fire, even during the growing season. Seedlings in early height growth, up to a height of about 0.6 to 0.9 m (2 to 3 ft), become susceptible to damage by fire. Once beyond this stage, longleaf pines are again fire resistant depending on fire intensity (Bruce 1951, 1954).

Longleaf pine is intolerant of competition and considered a fire sub-climax species because fire is necessary to reduce hardwood overstories that readily overtop this species while in the grass stage (Croker and Boyer 1975, Wakeley and Muntz 1947, Wells and Shunk 1938). The species will grow best in the complete absence of competition, including that from other members of the species. Longleaf seedlings will usually survive for years under an overstory of parent pines. Growth, however, is very slow. Seedlings respond promptly with an increased rate of growth when released from overstory competition (Boyer 1990).

Brown-spot needle blight [*Mycosphaerella dearnessii* M.E. Barr; syn. *Scirrhia acicola* (Dearn.) Siggers 1932] can have great impact on the rate of seedling development and extend duration of the grass stage. During several decades following the massive harvest of longleaf pine, many seedlings remained in the forest floor infected with brown-spot needle blight. These provided a source of the fungus that infected newly planted seedlings and reduced seedling survival, vigor, and initiation of height growth. Prescribed fire was frequently used to destroy foliage infected by the disease (Grelen 1978, Pessin 1944, Siggers 1932). During more recent years, the source of inoculum has been greatly reduced and the disease is not a major problem if seedlings enter height growth within 2 or 3 years.

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While seedlings are in the grass stage, no distinct annual rings are evident in either the root or stem. Spring and summer wood are distinguished only after true terminal buds are formed (Pessin 1934). There is no way to determine how long seedlings may have remained in the grass stage.

BUD DEVELOPMENT AND INITIATION OF HEIGHT GROWTH

Development of buds during the grass stage is slow and can take several years. Pessin (1939) and Wahlenberg (1946) report that terminal buds go through several developmental stages. They classified the buds in three stages. The first stage is "*pincushion*"—a term suggested by Wakeley (1954). The fascicular meristem lies in a horizontal plane forming a flat surface or slightly convex masses of small, unopened needle sheaths or exposed, upward-pointing needle tips. Few or no discernable bud scales are present. Second, "*round*"—a slight convex curvature develops in this fascicle-bearing surface and a semblance of a bud appears. Few if any are longer than thick, covered with either hard and white or soft, felt-like brown scales. Third, "*elongated*"— buds cylindrical, longer than thick with pointed, conical tips, and covered with white scales. These buds develop into the main axis from which the fascicles arise laterally (Wakeley 1954). After the elongated bud develops, elongation of the main axis is rapid (Pessin 1939).

Wahlenberg (1946), based on many observations, defined that seedlings had exited the grass stage when they were ≥ 10 cm (4 inches) in height, and that this height growth was achieved when RCD reached 25 mm (1 inch). Pessin (1939), Wakeley (1954), and others who have done extensive research with longleaf pine seedling establishment have confirmed these relationships.

PHYSIOLOGICAL STUDIES OF GRASS-STAGE SEEDLINGS

Longleaf pine seedlings lack epicotyl elongation and do not exhibit shoot growth until two or more years after outplanting. Allen (1960, 1964) and Brown (1958, 1964) have conducted the most thorough evaluations of the physiology of bud development in grass-stage seedlings. Their research shows that growth promoting and inhibiting substances change as longleaf seedling buds enter their elongation phase. Their studies could not identify any biochemical or physiological rationale for seedlings remaining in the grass-stage condition, or of any product which, when applied, would effectively shorten the grass stage if applied to buds. Kossuth (1981) and Kraus and Johansen (1959) applied plant growth regulators to longleaf buds in the pincushion stage with no or limited growth response. Hare (1984) applied cytokinnin-like substances to grass-stage seedlings and obtained a stimulatory effect. After seven decades of research, however, the longleaf pine grass stage remains an enigma.

Because longleaf pine seedlings are adapted to fire regimes, they resprout needles quickly if defoliated by fire while in the grass stage. The terminal bud is protected by the surrounding dense needle cluster. In addition, underground root reserves enable longleaf seedlings to bolt from the grass stage when the carbohydrate-rich taproot becomes sufficiently large to propel the terminal bud above flame lengths (Platt and others 1988).

RESPONSE TO NUTRIENT APPLICATIONS

Early Observations

The relation between seedling RCD and emergence from the grass stage has been known for many years (Allen 1953, Hinesley and Maki 1983, Lauer 1987, White 1981). For bareroot seedlings, tree height after outplanting increases with increasing seedling RCD, however, best height performance occurs when seedlings are outplanted with RCDs greater than 10 mm (0.4 inch) (Lauer 1987, White 1981). Survival is not as consistently related to seedling RCD at planting; if RCD exceeds 10 mm, both the smallest and largest seedlings tend to have acceptable rates of mortality.

Although relationships between RCD and emergence from the grass stage are known, little emphasis has been given to nursery nutrient regimes needed to achieve consistent seedling sizes. It may be possible to shorten the grass stage by increasing seedling quality, which does not necessarily correspond to seedling size (Wakeley 1954). Hinesley and Maki (1983) reported that fall fertilization in the bareroot nursery resulted in substantial overwintering dry weight gains and increases in nutrient content and concentrations in one year old longleaf pine. In the field, the rate of emergence from the grass stage and subsequent height growth were improved by this fall fertilization treatment.

In recent years, nursery production of longleaf pine planting stock has shifted markedly from bareroot to container production. Although container technology has developed rapidly, little research has been done to evaluate container stock quality and field performance. South and others (2004) did find container seedling RCD was related to root growth potential and field survival, and they demonstrated a strong relationship between second year RCD (they call it ground-line diameter) and emergence from the grass stage. Results of this study, however, indicate that seedling quality can decline if seedling size becomes too large for the container.

Dumroese and others (2005) report a wide disparity of recommended fertilizer rates to use in container production of longleaf pine. Unfortunately, we lack good empirical data to suggest appropriate fertility guidelines for producing quality container longleaf seedlings.

Current Studies

Jackson and others (2006, 2007) conducted a study to relate morphology, nutrition, and bud development of longleaf pine seedlings to five different fertilizer application rates: 0.5, 1.0, 2.0, 3.0, and 4.0-mg N (nitrogen) per seedling. Each treatment consisted of 12 containers (each with 96 cavities)—3 replications of 4 containers each. One hundred seedlings randomly selected from each treatment were outplanted in four 25-seedling rows for field evaluations. Seedling RCDs were recorded at the time of outplanting.

Bud Development Study

To evaluate bud development from the Jackson and others (2006) study, a subset of seedlings were selected for additional RCD, height, and bud evaluations in year 2 after outplanting. Five seedlings from each replication were selected in March 2006 from the 0.5, 2.0, and 4.0-N treatments. To reduce variability, seedlings selected for the bud evaluations were within 1 mm of the average RCD for the selected treatments of the main study.

Our study objective was to evaluate bud development of longleaf pine seedlings throughout the second growing season after outplanting and relate performance data (RCD, height) to the three nursery fertilizer application rates.

Measurements—RCDs and heights were measured and photos of buds were taken on six dates during the second year after planting (table 1). These data were combined with measurements and photos taken at the time of outplanting and at the end of the first year in the field.

Results—On average, all seedlings increased RCD growth after outplanting, but the rate of increase was higher for the 2.0-N and 4.0-N fertilizer treatments than 0.5-N (fig. 1). These two treatments had similar slopes, indicating similar accrual of RCD. Moreover, we found that a RCD of 25 mm was the point where most seedlings emerged from the grass stage, that is, achieved heights ≥ 10 cm as established by Wahlenberg (1946) (fig. 2). This was confirmed with the larger Jackson and others (2007) dataset.

Seedlings of the 0.5-N treatments had the smallest RCDs when planted and throughout the study. Even after two full years, average RCD did not reach the point where they were initiating height growth (table 1). Both the 2.0- and 4.0-N treatments were superior to the 0.5-N treatments, but differences between these higher N rates were small (fig. 1, table 1). Both reached 25 mm in RCD during the summer months of the second year in the field, and only about 1 month separated the respective seedlings in reaching this threshold late summer. About 20 percent (n = 4) of the 0.5-N seedlings emerged from the grass stage; the average height of this treatment was 7.7 cm. About 60 percent (n = 11) of the seedlings in the 2.0-N treatment left the grass stage; average height was 11.8 cm. In the 4.0-N treatment, 65 percent (n = 13) of the seedlings were taller than 10 cm; the average height was 13.7 cm.

The development of seedlings from the 0.5-N, 2.0-N, and 4.0-N treatments are illustrated in figure 3. After 2 years, the buds of the 0.5-N treatment remained in the grass stage and were in the "round' stage of development. Although "elongated" buds were present in both the 2.0-N and 4.0-N treatments, the 4.0-N seedlings more in a more advanced stage. The photo record of bud development indicated that they were in the elongated stage with white bud scales when they reached 25 mm in RCD.

When RCDs at outplanting were regressed to those 2 years after planting for each seedling in each fertilizer treatment, a negative relationship developed with the 4.0-N levels (fig. 4). This was unexpected and prompted further examination of the data. Changes in seedling RCD growth between measurement periods indicated the 4.0-N seedlings grew more than the others during the first year after outplanting (table 2), but during the second year incremental growth was less than that for the 2.0-N treatment and no better than the 0.5-N treatment. So,

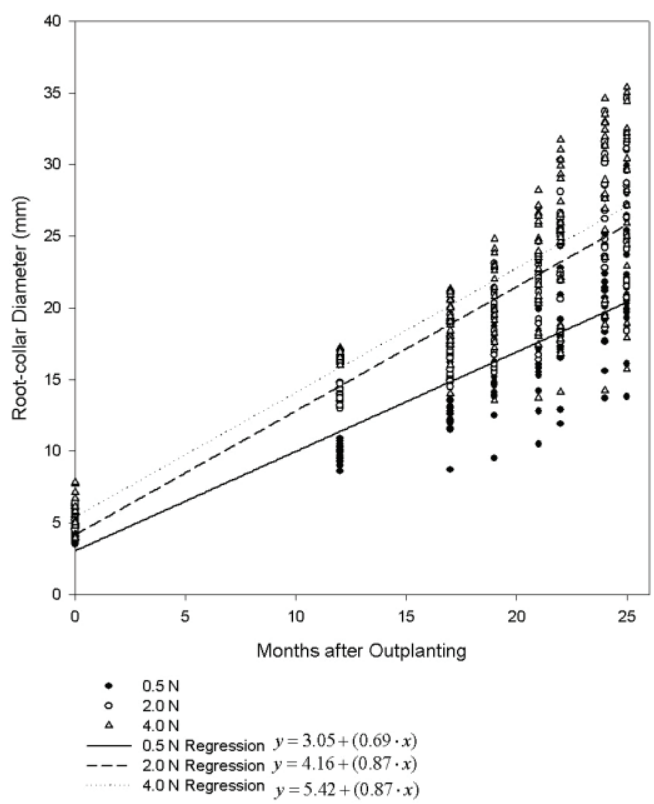

Figure 1—Root-collar diameter growth over a 2-year period of seedlings fertilized in the nursery with 0.5, 2.0, and 4.0 mg of nitrogen per seedling.

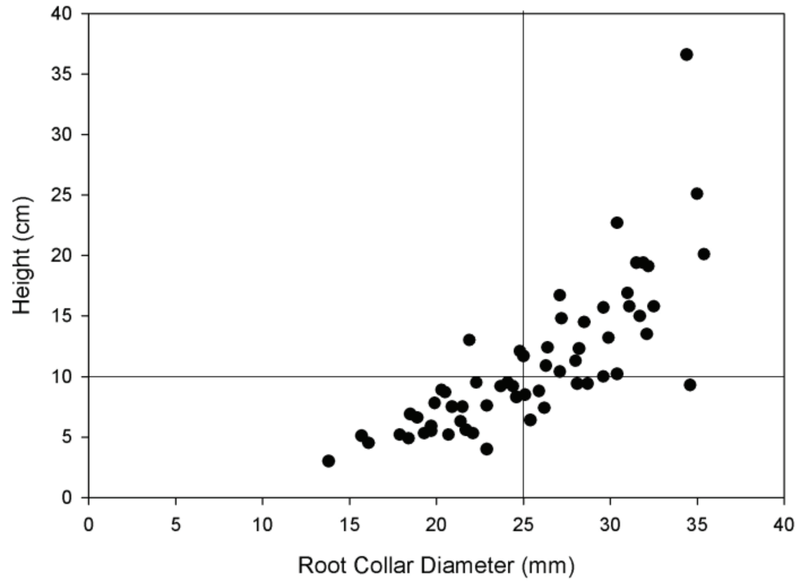

Figure 2—Relationship of longleaf pine seedling height to root-collar diameter. The lines at 10 cm height and 25 mm root-collar diameter indicate emergence from the grass stage into height growth.

Figure 3—Average bud development after 2 years in seedlings representing 0.5 N (left), 2.0 N (center), and 4.0 N (right). Seedlings in the 0.5 N treatment remained in the grass stage and were characterized by a round bud. Seedlings in both the 2.0 N and 4.0 N treatments were in the elongated stage and entering height growth. They exhibited white scaled bud formation.

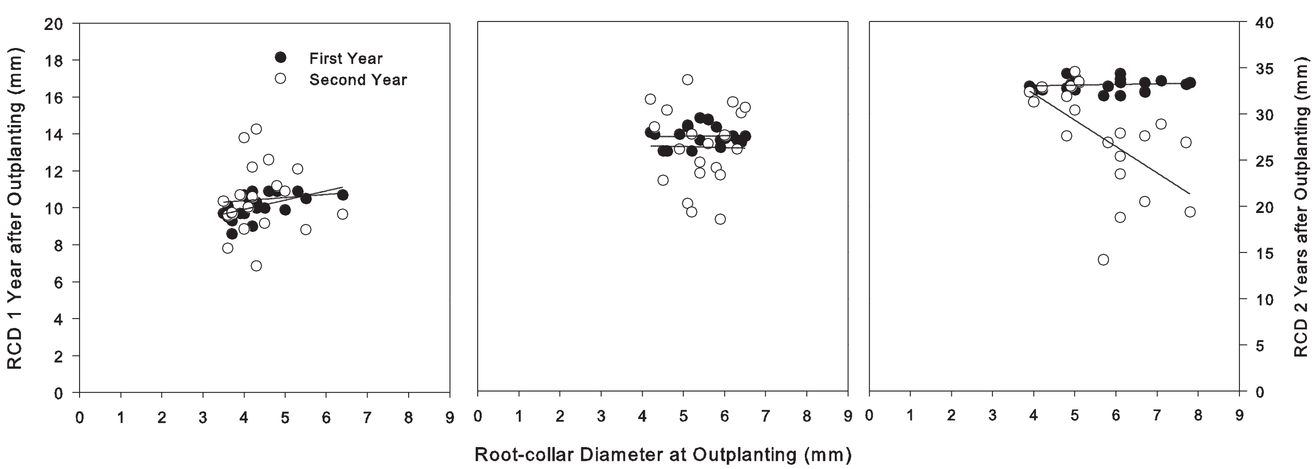

Figure 4—Average RCD increments of 0.5 N (left), 2.0 N (center) and 4.0 N (right) fertilization rates after 1 and 2 years are regressed with RCD at outplanting. The negative slope of incremental growth of the larger seedlings in the 4.0 N treatments during year two was unexpected and merits further experimentation.

Table 1—Average root-collar diameters (mm) of longleaf pine seedlings following planting by date and nutrient treatments

Treatment[a]	11/16/04	11/15/05	4/12/06	6/27/06	8/8/06	9/22/06	10/31/06	12/11/06
0.5 N	4.4	10.1	13.5	15.4	16.9	18.7	20.9	21.7
2.0 N	5.3	13.8	17.1	19.2	21.5	24.1	26.4	25.7
4.0 N	5.7	16.6	19.1	20.9	22.7	24.9	26.7	26.6

[a]Treatments represent applications of mg nitrogen (N) per seedling per week for 20 weeks and at 28 and 32 weeks.

Table 2—Changes in seedling root-collar diameter (mm) growth between measurement periods

Treatment[a]	11/16/04	11/15/05	4/12/06	6/27/06	8/8/06	9/22/06	1/31/06	12/11/06
0.5 N	--	5.7	3.4	1.9	1.5	1.8	2.2	0.8
2.0 N	--	8.5	3.3	2.1	2.3	2.6	2.3	-0.7
4.0 N	--	10.9	2.5	1.8	1.8	2.2	1.8	-0.1

[a]Treatments represent applications of mg nitrogen (N) per seedling per week for 20 weeks and at 28 and 32 weeks.

although early growth of the 4.0-N-treatment seedlings was good, these high, positive rates of incremental growth were not maintained during the second year.

DISCUSSION

For the entire population measured in this study (all treatments combined), we confirmed the relationship between RCDs of 25 mm (1 inch) and heights of 10 cm (4 inches) that Wahlenberg (1946) and others established as the criteria for emergence of longleaf pine seedlings from the grass stage (fig. 1). RCD increased after outplanting, with the largest RCDs found in the two highest fertilization treatments (fig. 1, table 1). Moreover, the two highest fertilizers rates (2.0 and 4.0) allowed 2.5 and 3.25 times more seedlings, respectively, to exit the grass stage than the 0.5-N rate.

The three treatments in this evaluation represented the lowest, mid-range, and highest rates of nitrogen application in the Jackson and others (2006, 2007) study. It appears that the 0.5-N rate fails to provide sufficient nutrition to produce seedling quality that performs well (in terms of RCD growth and therefore, emergence from the grass stage) in the field. The 2.0-N application rate resulted in excellent RCD growth, corresponding bud development, and seedlings that exited the grass stage during the second year after outplanting. The 2.0-N treatment was very similar to the 4.0 N treatment in terms of second-year RCD (25.7 vs. 26.6 mm), height (11.8 vs. 13.7 cm), and percentage of seedlings emerging from the grass stage (60 vs. 65 percent), despite the fact that the 4.0-N seedlings received twice as much fertilizer in the nursery. We did observe a negative correlation in the 4.0-N-treatment, but not in original RCD and second-year RCD in the 2.0-N.

Although this is a small data set, it raises the question about the effects of aggressive root growth in small container cavities. Too much root growth can cause binding and may reflect seedlings staying too long in the containers or the application of excessive fertilizers that result in seedlings too large for the container. Lamhamedi and others (1996) suggested that excessive root growth of black spruce (*Picea mariana* [Mill.] B.S.P.) seedlings in the root plug can lead to low root quality and therefore increased susceptibility to water stress in spite of an apparently favorable shoot-to-root ratio. Their results point toward reduced root hydrological function rather than more vigorous shoot growth as the cause. South and others (2004) were able to relate decreases in container longleaf pine seedling survival to root binding in the root plug. They calculated a root bound index (RBI) by dividing seedlings' RCD by cell cavity diameter; a RBI ≥ 30 percent was associated with higher mortality. Using this critical RBI value and our container that had a 38 mm cavity diameter, seedlings having a RCD ≥ 11.4 mm should experience higher mortality rates. It stands to reason that one should probably observe a decrease in overall seedling growth at a level less than that associated with mortality; South and others (1996) did not discuss this. In our study, however, such a relationship is not clear. For instance, in the 4.0-N treatment, seven of the ten seedlings having the largest RCDs at outplanting did not exit the grass stage, but their RBI values ranged from just 15 to 20.5 percent (RCDs ranged from 5.7 to 7.8 mm), values well below the 30 percent value of South and others (2004). The three that did grow out of the grass stage had RBIs of 16 percent (6.1 mm) to 19 percent (7.1 mm). Moreover, in the 2.0-N-treatment, of the eight seedlings with RCDs between 5.7 and 6.5, four of them exited the grass stage (5.8 to 6.0 mm RCD).

During container nursery production, applications of higher rates of N usually promote shoot growth and discourage root growth, whereas low N applications favor root growth. In the Jackson and others (2006) study, root growth between 20 and 30 weeks, when only two fertilizer applications occurred, increased 138 percent for the 4.0 N treatment compared to 69 and 88 percent for the 0.5-N and 2.0-N treatments. Unfortunately, we do not have the data to attempt to correlate root biomass and RCD, but it is quite likely that RBI may be better defined by a covariant analysis of these two variables on outplanting performance, rather than simply RCD.

So, this study is a bit of a conundrum. When looking at the population of seedlings fertilized with 4.0-N, they average the largest RCD, the tallest heights, and the largest number emerging from the grass stage. When looking at individual seedlings within that population, however, it appears that seedlings with the greatest initial RCDs are not performing as well. Although this could be a reflection of "bound roots" it could also be a function of other factors, in particular, genetics. For example, in western white pine (*Pinus monticola* Dougl. ex D. Don), seed dormancy of individual families is highly hereditable, and thought to be an adapted mechanism to extend successful germination of the species across more environmental conditions (Hoff 1987). Perhaps emergence from the grass stage is also highly heritable from a family standpoint, allowing a portion of an individual family to emerge from the grass stage (or remain in the grass stage) as a strategy against untimely environmental conditions. Because our longleaf was a wild-collected source comprised of various families, we cannot discern that. Nor can we confidently state that this is not a measurement artifact that may disappear in subsequent growing seasons as we continue to monitor the seedlings.

We have insufficient data to establish a rational for what appears to be a trend of poor RCD growth of longleaf seedlings during the second year after having been fertilized in the greenhouse at a high 4.0-mg-N/seedling rate. We have an additional study in progress now that may shed some additional insight into this phenomenon. If root binding has a negative effect on growth after establishment, however, many container cultural treatments need to be reevaluated. Over 50 million longleaf pine seedlings are grown annually in containers throughout the South. Further evaluations of this phenomenon of reduced growth during the second year after outplanting are needed to assure that the best quality planting stock is being used in these reforestation practices.

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