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Nursery response of container *Pinus palustris* seedlings to nitrogen supply and subsequent effects on outplanting performance

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ABSTRACT

Container longleaf pine (*Pinus palustris*) seedlings often survive and grow better after outplanting than bareroot seedlings. Because of this, most longleaf pine are now produced in containers. Little is known about nursery fertilization effects on the quality of container longleaf pine seedlings and how that influences outplanting performance. We compared various fertilization rates (0.5, 1, 2, 3, or 4 mg nitrogen (N) per week for 20 weeks) for two crops (2004 and 2005) of container longleaf pine, grown inside a fully-controlled greenhouse (2004 and 2005) or in an outdoor compound (2005). Seedlings grew larger in the nursery with increasing amounts of N. After 20 weeks of fertilizer treatment, seedlings received two additional fertigations at the same treatment rate to promote hardening, N concentrations declined sharply, and seedlings shifted biomass production toward roots. Overall, shoots showed more plasticity to N rate than did roots. Survival of either crop after outplanting was unaffected by nursery N rate. For both crops, no seedlings emerged from the grass stage during the first year after outplanting, and during the second year, more seedlings exited the grass stage and were taller as N rate increased up to 3 mg per week. By the third field season, nearly all seedlings in the 2004 crop had exited the grass stage, whereas 44% of 2005 crop grown at 1 mg N had yet to initiate height growth, either because of differences in seed source between the two crop years or because of droughty conditions. Our data suggests that an application rate of about 3 mg N per week for 20 weeks plus two additional applications during hardening yields satisfactory nursery growth as well as field response for the container type we used. The potential for improving field performance by using more robust fall fertilization during nursery production should be investigated.

1. Introduction

The longleaf pine (*Pinus palustris* Mill.) ecosystem once dominated the southeastern United States, occupying more than 36 million hectares. Longleaf pine features a stemless grass stage to ensure its seedlings survive the frequent, low-intensity surface fires characteristic of their fire-adapted ecosystem (Barnett, 1999). For decades, foresters discriminated against planting longleaf pine. Low seedling survival due to poor seedling quality, grass stage persistence for several years, and faster initial growth from other southern conifer species led to the reluctance to plant longleaf pine (Croker, 1990; Barnett, 2002). In addition, intense harvesting during the past century reduced this forest type by nearly 98% and caused many other terrestrial species to become threatened and endangered (Noss et al., 1995; Outcalt, 2000; Barnett, 2002; Jose et al., 2006).

Two recent shifts in focus have brought attention to the production of longleaf pine for restoration and reforestation. First, federal incentive programs have encouraged restoration of longleaf pine ecosystems (Hainds, 2002), and second, land managers are moving from pulpwood to sawtimber production because of higher economic returns (Kush et al., 2004). To meet this demand, use of container longleaf pine has increased dramatically because survival and growth often exceeds bareroot stock (Boyer, 1989; Barnett and McGilvary, 1997; South et al., 2005). In 2008, 84% of the 76 million longleaf seedlings produced were grown in containers (Dumroese et al., 2009). Despite high demand for container longleaf pine seedlings, detailed research is lacking concerning its production and an absence of standards has caused subsequent variation in stock quality (Hainds, 2004). Based on the limited research, Barnett et al. (2002a,b) published interim guidelines for producing container longleaf pine, and these standards were recently updated (Dumroese et al., 2009). Although a target seedling is described, no fertilizer regimes to obtain that target are provided.

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Proper fertilization is critical during production of reforestation stock; fertilization influences the quality and quantity of plant growth within the container (Landis, 1989). Proper seedling nutrient levels can be linked to improved drought tolerance, cold hardiness, survival, competitive advantage, and growth, and reduced transplant shock (van den Driessche, 1991; Grossnickle, 2000). Excessive fertilizer during nursery production, however, can reduce growth because of salt accumulation (Jacobs and Timmer, 2005) as well as cause seedlings to grow too large for their containers and consequently perform poorly after outplanting, as exemplified by longleaf pine (South and Mitchell, 2006). Thus, finding an optimum fertility target for reforestation stock is fundamental (Salifu and Jacobs, 2006). Although this optimum fertility and subsequent stock quality can be described in the nursery, seedling performance after outplanting is paramount (Landis and Dumroese, 2006). Unfortunately, the field response of longleaf pine seedlings has yet to be related to specific nutrient rates, especially nitrogen (N), used in container nurseries (Dumroese, 2003; Jackson, 2006).

Therefore, our null hypothesis was that nursery N rate used to produce container longleaf pine would have no effect on outplanting survival, growth, and/or time spent in the grass stage. To test the hypothesis, we grew two crops in subsequent years under a variety of nursery N treatments and outplanted them to monitor survival and growth of individual seedlings for three field seasons.

2. Materials and methods

2.1. Nursery

Longleaf pine seedlings were grown at the USDA Forest Service, Southern Research Station facility in Pineville, Louisiana (latitude 31.3, longitude −92.4) inside a double polycarbonate-coved, fully-controlled greenhouse (2004 and 2005), and in a nearby (within 20 m) outdoor compound (2005) where seedlings were exposed to ambient conditions. We filled Ropak® Multi-Pot containers, commonly used to grow longleaf, with a 1:1 (v:v) Sphagnum peat moss:vermiculite medium. Each plastic Multi-Pot (61 cm long × 36 cm wide) consisted of 96 cavities (441 cavities m^{-2}) having 98 ml volume (3.8 cm diameter × 12 cm deep). Seeds were sown in early April and each year we used a different Florida seed source that was appropriate for outplanting in Louisiana. Three weeks after sowing, we thinned cavities having two seedlings by gentle pulling the extra seedling out. Frequency of irrigation or fertigation (irrigation with soluble fertilizer added) was determined gravimetrically; after irrigating containers to field capacity and allowing them to drain for 1 h, we measured the field capacity mass of the containers. When container mass reached 75% of field capacity, seedlings were fertigated or irrigated as required.

Nursery N treatments began 4 weeks after sowing (early May) and continued once per week for 19 weeks (mid-September; 20 applications total). In 2004, greenhouse seedlings received one of five nursery N treatments: 0.5, 1.0, 2.0, 3.0, or 4.0 mg N seedling^{-1} week^{-1} (hereafter simply mg N). Based on 2004 observations, greenhouse and outdoor grown seedlings in 2005 received one of three nursery N treatments: 1.0, 2.0, or 3.0 mg N. In both years, during the hardening phase, seedlings received two additional applications, at the same treatment rates, 3 and 6 weeks after weekly fertigation ceased (mid-October and mid-November, respectively). Therefore, seedlings in the 0.5, 1.0, 2.0, 3.0, or 4.0 mg N seedling^{-1} week^{-1} treatments received 11, 22, 44, 66, and 88 mg N total. We mixed the appropriate amount of fertilizer (Peters Professional® 20-19-18 [20N:19P_2O_5:18K_2O; The Scotts Company, Marysville, OH, USA]) into the volume of water required to return each replicate within each nursery N treatment to field capacity, and seedlings were hand-fertigated. Given the average field capacity mass (7.6 kg) and a target irrigation mass of 75% field capacity mass (i.e., 5.7 kg), each container received approximately 1.9 L per irrigation, or 20 ml per seedling. Thus, our weekly fertigation solutions for the 0.5, 1, 2, 3, and 4 mg N rates were approximately 25, 50, 100, 150, and 200 ppm N, respectively; the proportion of nutrients was constant: 100N (27NO_3^-; 20NH_4^+; 54urea): 42P: 75K: 0.75Mg: 0.1B: 0.05Cu: 0.05Fe: 0.28Mn: 0.05Mo: 0.08Zn. The applied ppm of N (25–200), P (10–80), and K (20–158) were similar to those reported by Landis (1989) for general seedling production.

Each nursery N rate included three Ropak® Multi-Pot containers that served as replicates. In 2004, we had 288 seedlings per nursery N treatment (1440 total). In 2005, we grew 288 seedlings per nursery N treatment per growing area (1728 total).

Beginning 9 weeks after sowing (5 weeks after initiation of nursery N treatments; early June) and continuing at 5-week intervals for 25 weeks (mid-November), we randomly measured 10 seedlings per replicate (30 per treatment; 6 sample times total). The fourth sample occurred 1 week after the weekly fertigation ceased and the final (sixth) sample occurred 1 week after the final fertigation (just prior to outplanting). Root-collar diameter (RCD) was measured twice at perpendicular angles at ground-line and the mean recorded. We measured the longest needle (either primary or secondary), and determined biomass after carefully washing the roots, segregating seedlings into shoots (needles, buds) and roots (basipetal from the cotyledon scar), and oven-drying at 60 °C to constant mass. Shoots and roots were subsequently ground and analyzed for N concentration using a LECO-2000 (LECO Corp., St. Joseph, MI, USA).

2.2. Outplanting

Immediately prior to outplanting, we removed seedlings from either the greenhouse or outdoor compound, extracted them from their containers by nursery N treatment, pooled them by replication and subsequently randomly re-allocated them into 4 replications (2005 seedlings remained segregated by growing location), left needles unclipped, and outplanted them (mid-November) on a mowed site within the Palustris Experimental Forest (latitude 31.0, longitude −92.6) near McNary, Rapides Parish, Louisiana. The area is gently sloping (1–3%) with a moderately drained and slowly permeable Beauregard silt-loam (fine-silty, thermic Plinthaquic Paleudult); this soil develops a perched water table during prolonged wet periods during winter and can be droughty during summer (Kerr et al., 1980). In 2004, 25 seedlings from each nursery N treatment were dibble-planted within a row at 60-cm spacing. Each row was 1 m apart. Each treatment was randomly assigned within each of 4 replicates (400 seedlings total). In 2005, 16 seedlings from each nursery N × nursery type (greenhouse or outdoor compound) combination were dibble-planted in a similar manner (384 seedlings total). Seedlings were outplanted with their buds at ground level and care was taken to ensure treatments were not confounded by planter technique.

At outplanting, we measured RCD of each seedling as described above. For three consecutive growing seasons, we re-measured seedling survival, RCD, and height (ground-line to tip of terminal bud). Seedlings were deemed to exit the grass stage when RCD $\geqslant$ 25 mm and height $\geqslant$ 10 cm (Wahlenberg, 1946). Accord™ herbicide (glyphosate *N*-(phosphonomethyl) glycine, isopropylamine salt; Dow AgroSciences, Indianapolis, IN, USA) was applied at 1.25 kg ai ha^{-1}on May 2005 to reduce weed competition. A wildfire burned the plots on 21 March 2007.

Rapides Parish weather data (Southern Regional Climate Center; http://www.srcc.lsu.edu/) proximate to the outplanting site was recorded at Oakdale (latitude 30.8, longitude −92.7; precipitation) and the Louisiana State University Dean Lee Research Station (latitude

31.2, longitude −92.4; temperature). We used Palmer Drought Severity Index (PDSI; Palmer, 1965) values for central Louisiana (Division 5) to quantify prolonged periods of abnormally dry or wet weather (National Climatic Data Center; http://ncdc.noaa.gov).

2.3. Statistical analyses

We used SAS (version 9.2; SAS, Inc., Cary, NC, USA) for all analyses. Differences in morphological variables and N concentrations across treatment levels were identified using PROC GLIMMIX assuming a Gaussian response distribution and an identity link function. Raw data were averaged within replicate. Separate models were created for each year for the nursery and outplanting data because of methodological differences in treatment application across years. In both 2004 and 2005 models, replicate was included as a random effect. Binary survival and "exit the grass stage" data were also analyzed using PROC GLIMMIX assuming a binomial response distribution and a logit link function for survival; the binary response (yes or no) for "exit" was based on seedlings having both RCD $\geqslant$ 25 mm and height $\geqslant$ 10 cm. Again, replicate was included as a random effect. Type III tests of fixed effects were used to examine interactions and main effects. Differences of least squares means were adjusted for multiple comparisons using the Tukey–Kramer method. Because most of the dependent variables for seedling morphology indicated different response functions between extremes of their distributions conditional on N rate, we used quantile regression (PROC QUANTREG; $\tau = 0.05, 0.50, 0.95$) rather than using the least squares approach that examines an average, single effect (Koenker and Hallock, 2001; Cade and Noon, 2003) to compare treatments at the final nursery sample date. For all N rates combined at the final nursery sample date, we calculated the non-parametric Kendall rank correlation coefficients (PROC CORR) for shoot and root biomass and for shoot and root N content.

3. Results

3.1. Nursery

For the 2004 crop, nursery N rate, sampling date, and their interaction caused significant effects on every morphological characteristic measured (Table 1). All seedlings grew larger as the growing season progressed, but increasing amounts of N generally yielded greater growth (Fig. 1). The general pattern for tissue N concentration was the same for the first four sample dates (5 weeks after fertigation began to 1 week after weekly fertigation ceased): all N rates yielded significantly different concentrations (Fig. 2A and B). Despite weekly fertigation, tissue concentrations declined; except for sample date 1, in general, shoot N concentrations were lower than root concentrations when N rate was $\leqslant$2 mg N. Concomitant with the decreasing concentrations were increases in content, although shoot N content for seedlings receiving $\leqslant$1 mg N appeared static or decreasing (Fig. 2C and D). Although seedlings received two more fertigations 3 and 6 weeks after weekly fertigation ceased, tissue N concentration continued to decline (sample date 5 and 6). All root N concentrations were significantly different at the last sample date, immediately before outplanting; the 4 mg N having the highest concentration. For shoots, N concentration decreased as N rate decreased, with all N rates except 0.5 and 1 mg being significantly different. During this same time, root N content increased for all fertilization rates, but shoot N content decreased, especially in the two highest N rates (3 and 4 mg). During the hardening phase (sample dates 4 through 6), we observed a pronounced allometric shift toward root biomass production (Figs. 1 and 3). At the lowest rate (0.5 mg), all additional growth from cessation of the weekly fertigations until outplanting was in the root system, whereas rates $\geqslant$1 also showed modest shoot biomass gains (7–35%), although this was not a function of increased needle length (Fig. 1).

At the final sample date, the Kendall rank correlation coefficient was 0.5911, indicating a significant ($P < 0.0001$) positive correlation between root biomass and shoot biomass across varying N rates (Fig. 4). Seedlings receiving higher N rates showed greater variation in biomass and N content (Fig. 4). Final RCDs of seedlings receiving $\geqslant$2 mg N were not significantly different, but were approximately 54% greater than seedlings receiving the lowest rate (0.5 mg N). At the lower quantiles ($\tau \leqslant 0.50$), RCD showed a significant, negative, quadratic response to N application rate, with maximum RCD at the 3 mg rate (Table 2; Fig. 5). Seedlings in the 95% quantile, however, had a significant, positive, linear response to increasing N rate. Seedlings given $\leqslant$2 mg N had similar final needle length; needle lengths were about 30% longer when fertilizer rate increased to 3 mg N, and 54% longer at 4 mg N. Final root biomass was relatively unaffected by N rate; all N rates yielded similar root biomass except for the lowest rate, which had about 60% that of the other treatments. At the lower quantiles ($\tau \leqslant 0.50$), root biomass showed a significant, negative, quadratic response to N application rate, with maximum biomass occurring with the 2 mg rate (Table 2; Fig. 5). Final shoot biomass was more plastic in response to N rate, with nearly every increase in N causing a significant increase in biomass (Fig. 1). For the lower quantiles ($\tau \leqslant 0.50$), this significant response was positive and linear (Table 2; Fig. 5). The Kendall rank correlation coefficient was 0.6378, indicating a significant ($P < 0.0001$) positive correlation between root N content and shoot N content across varying N rates; that is, N content in both tissues increased with increasing N application rate (Fig. 4).

Table 1
Analysis of variance table and *P* values for seedling morphological characteristics during nursery production.

							Nitrogen concentration	
	df	Root-collar diameter	Longest needle length	Shoot biomass	Root biomass	Shoot-to-root ratio	Shoot	Root
2004								
Nitrogen rate (*N*)	4	<0.0001	<0.0001	<0.0001	0.0004	0.0025	<0.0001	<0.0001
Sample date (*S*)	5	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
$N \times S$	20	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
2005								
Nursery type (*T*)	1	0.0086	0.1414	<0.0001	0.6662	0.0260	<0.0001	<0.0001
Nitrogen rate (*N*)	2	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
$T \times N$	2	0.0148	0.4537	<0.0001	0.3662	0.0209	0.0109	0.0025
Sample date (*S*)	5	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
$T \times S$	5	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
$N \times S$	10	<0.0001	<0.0001	<0.0001	<0.0001	0.0034	0.0012	<0.0001
$T \times N \times S$	10	0.0017	0.5131	0.0372	0.3539	0.6491	0.5054	0.0407

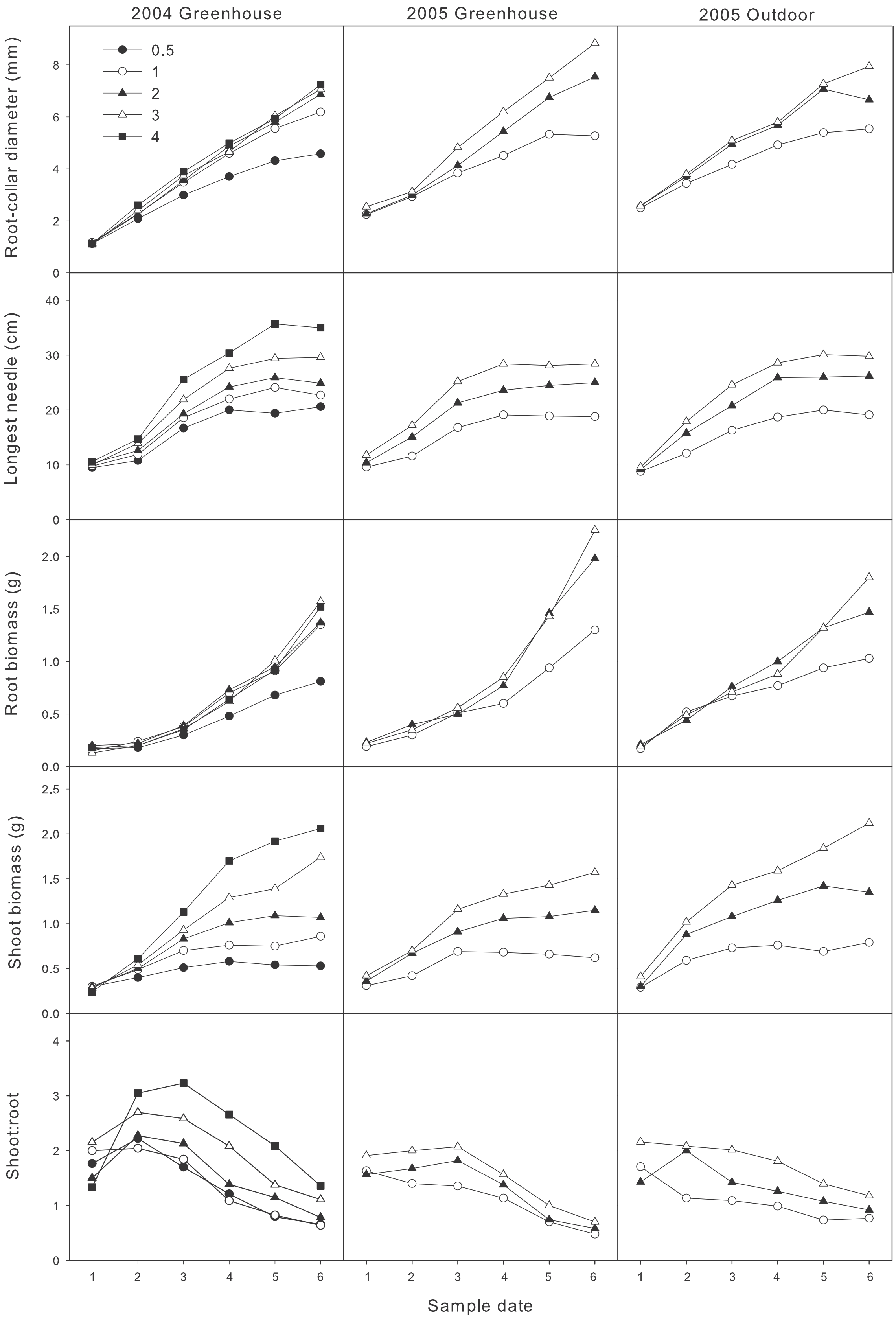

Fig. 1. Morphological variables during nursery production of seedlings receiving 0.5, 1, 2, 3, or 4 mg N week^{-1} for 20 weeks plus two additional applications at the same rate 3 and 6 weeks later. Each data point represents the average value for 30 seedlings. Sample 1 occurred the first week of June, 9 weeks after sowing and 5 weeks after fertigation began. Seedlings were sampled about every 5 weeks through the second week of November (six samples total). Sample 4 occurred during the third week of September, 1 week after the weekly fertigations ceased. Sample 6 occurred mid November, 1 week after the final fertigation.

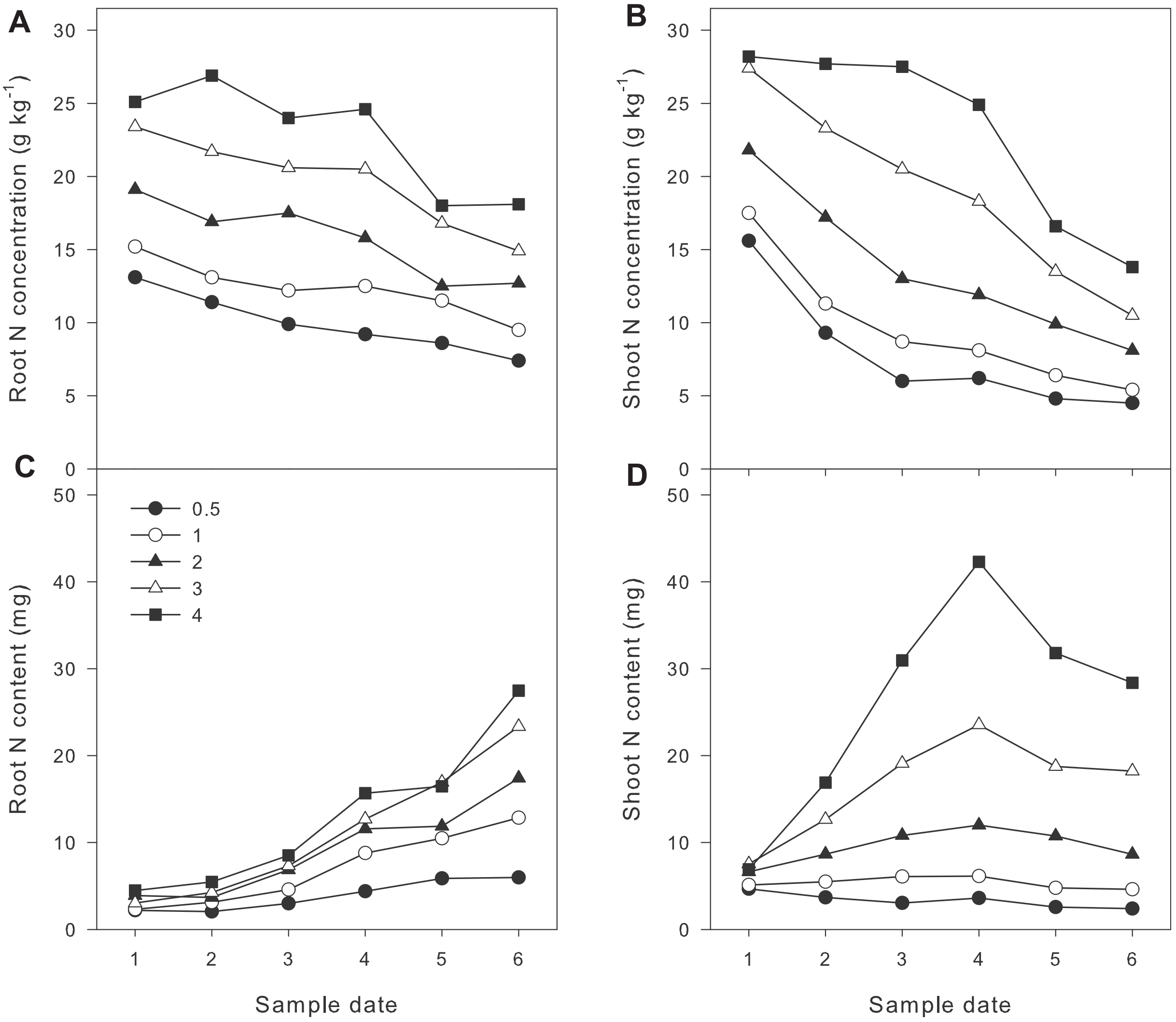

Fig. 2. Concentrations and contents of nitrogen (N) in tissues of 2004 seedlings receiving 0.5, 1, 2, 3, or 4 mg N week^{-1} for 20 weeks plus two additional applications at the same rate 3 and 6 weeks later. Each data point represents the average value for 30 seedlings. Sample 1 occurred the first week of June, 9 weeks after sowing and 5 weeks after fertigation began. Seedlings were sampled about every 5 weeks through the second week of November (six samples total). Sample 4 occurred during the third week of September, 1 week after the weekly fertigations ceased. Sample 6 occurred mid November, 1 week after the final fertigation.

For the 2005 crop, N rate, sampling date, and their interaction again caused significant effects on morphology, similar to the 2004 crop (Table 1). In addition, nursery type often interacted to affect results. Overall, RCD of greenhouse seedlings was 7% greater than those grown outdoors. Although total biomass of seedlings was similar regardless of growing area (2.95 g indoors vs. 2.85 g outdoors), shoot biomass was 28% greater for seedlings grown outdoors, whereas root biomass was 29% greater for seedlings grown inside the greenhouse. Needle length was unaffected by growing location. N concentrations followed the same pattern as for 2004 seedlings (data not shown). Even so, seedlings from both nursery types were fairly similar (Fig. 1).

3.2. Outplanting

3.2.1. Precipitation, temperature, and drought

During the year (January to November) preceding the 2004 outplanting, precipitation was 116% of normal (Fig. 6A). After outplanting, precipitation for the remainder of November was good (137 mm), normal for December (159 mm), but only one-third of normal for five of the next 6 months, with October being especially dry (4 mm, 3% of normal), resulting in mild drought conditions for most of the growing season (Fig. 6B). Despite outplanting the second crop under moderate drought conditions, 127 mm of rainfall was recorded within a month. Precipitation in January through March was 69% of normal and rainfall in April was 247 mm, more than double the normal rate (117 mm). Precipitation from May through September was about 81% of average (Fig. 6A). This resulted in moderate drought conditions for most of 2006 until a much wetter than normal October (436 mm vs. 128 mm) relieved the drought (Fig. 6B). Conditions were generally "normal" for most of 2007 and 2008. Total precipitation for 2005, 2006, 2007, and 2008 was 64%, 103%, 85%, and 84% of normal, respectively. Observed average temperatures were similar to historic averages (data not shown).

3.2.2. Seedling response

For the 2004 crop, survival after 3 years was unaffected by nursery N rate ($P \geqslant 0.6115$) (Table 3; Fig. 7). Overall, survival was high: 0.5, 1, 2, 3, and 4 mg N yielded 81%, 88%, 86%, 92%, and 78%, respectively, after three field seasons. N rate affected total RCD every year after outplanting (Table 3). After three field seasons, the two highest N rates (3 and 4 mg) yielded significantly (15%) more RCD than the two lowest rates (0.5 and 1), with the 2 mg rate intermediate

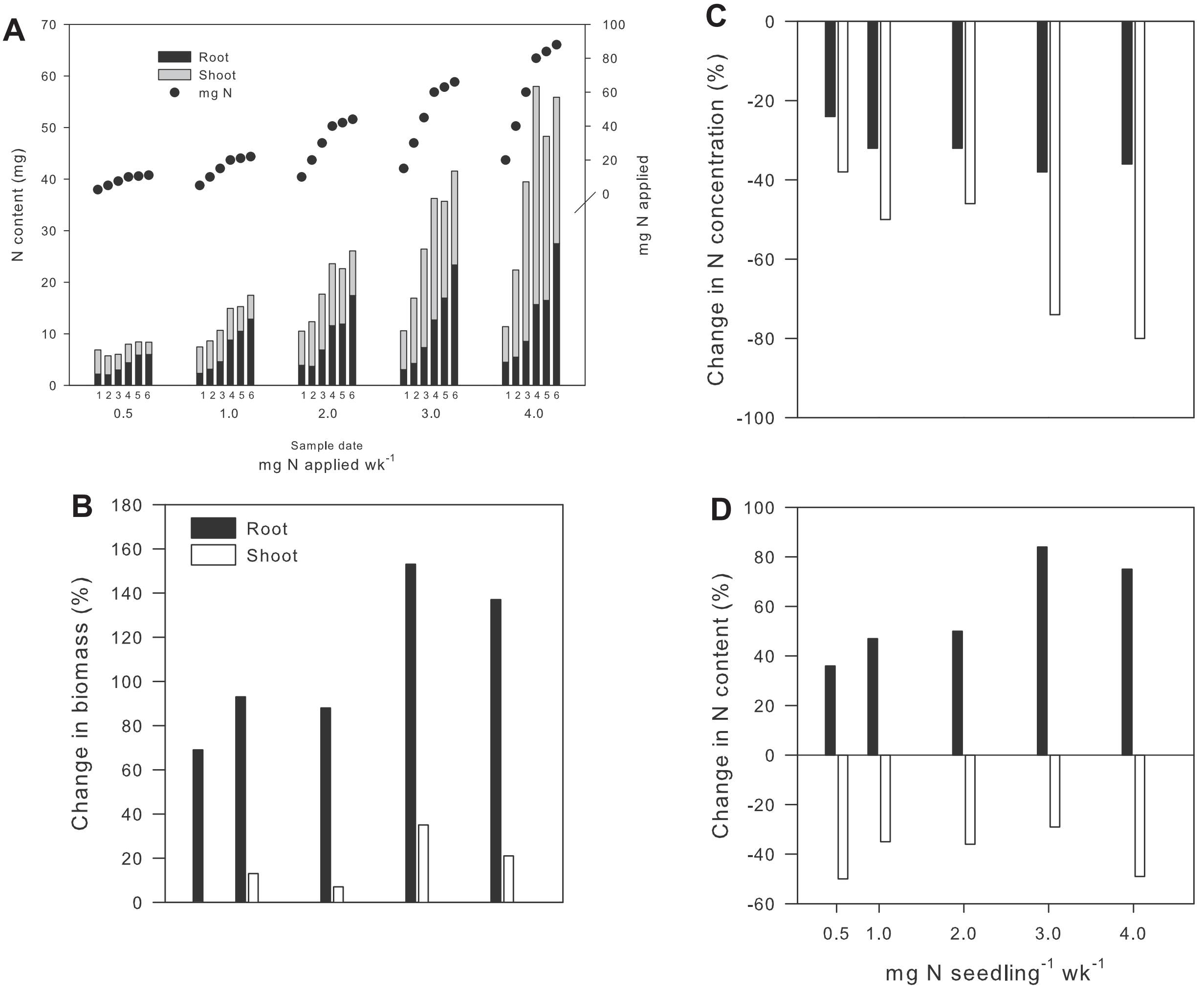

Fig. 3. For the 2004 crop, the (A) N content of roots and shoots of seedlings receiving 0.5, 1, 2, 3, or 4 mg N week^{-1} for 20 weeks plus two additional applications at the same rate 3 and 6 weeks later sampled at six times during the growing season. Each bar represents the average value for 30 seedlings. Sample 1 occurred the first week of June, 9 weeks after sowing and 5 weeks after fertigation began. Seedlings were sampled about every 5 weeks through the second week of November (six samples total). Sample 4 occurred during the third week of September, 1 week after the weekly fertigations ceased. Sample 6 occurred mid November, 1 week after the final fertigation. Full circles represent the cumulative mg N applied per treatment by sample date. Also, the percentage change in (B) biomass, (C) N concentration, and (D) N content for each fertilizer rate from sample 4 through sample 6.

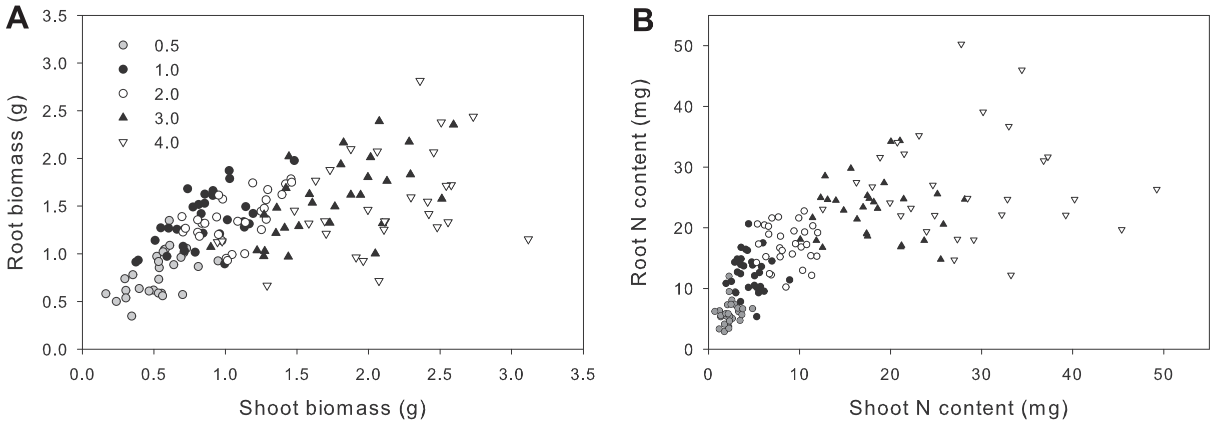

Fig. 4. The correlation between (A) root biomass and shoot biomass and (B) root nitrogen (N) content and shoot N content at the final sample date for the 2004 crop grown with five rates of N. The Kendall rank correlation coefficients (0.6378 and 0.5911, content and biomass, respectively) were significant ($P < 0.0001$), indicating positive correlations among root and shoot attributes across varying N rates ($n = 150$).

Table 2
Parameter estimates and 95% confidence limits for dependent variables for the 2004 crop obtained using quantile regression at $\tau = 0.05, 0.50$, and 0.95. The linear response was a function of nitrogen (N) application rate, whereas the quadratic response was N application rate squared.

		5% Quantile			50% Quantile			95% Quantile		
Variable	Parameter	Estimate	95% Confidence limits		Estimate	95% Confidence limits		Estimate	95% Confidence limits	
Root-collar diameter	Intercept	2.5657	2.1133	2.9857	3.8286	2.7545	4.9804	5.5400	4.3815	8.2899
	Linear	1.8200	1.0482	2.2562	2.3286	1.3517	3.5645	2.0667	0.278	3.6959
	Quadratic	−0.3029	−0.4567	−0.0746	−0.3714	−0.6517	−0.1828	−0.2933	−0.5868	0.2247
Root biomass	Intercept	0.2627	−0.0402	0.3128	0.6274	0.3854	0.8358	1.0570	0.7972	2.5480
	Linear	0.6084	0.4478	0.8363	0.6387	0.3724	0.8875	0.6915	−0.5824	1.5245
	Quadratic	−0.1238	−0.1436	−0.0667	−0.1150	−0.1670	−0.0609	−0.0865	−0.2499	0.2153
Root N content	Intercept	−1.0111	−15.8219	−0.2900	0.5005	−0.8736	2.4289	10.1948	2.0731	28.3296
	Linear	9.2989	5.5064	10.7566	12.0529	8.8642	13.8185	5.115	−6.1400	17.6349
	Quadratic	−1.3413	−1.9682	−0.2674	−1.5002	−1.9185	−0.6480	0.9604	−2.2208	3.1625
Shoot biomass	Intercept	0.0253	−2.3086	0.1454	0.3909	0.2732	0.5132	0.4780	0.1668	1.3615
	Linear	0.4498	0.1190	0.7396	0.3344	0.1208	0.5591	0.7295	−0.2499	1.3622
	Quadratic	−0.0530	−0.1057	0.0362	0.0237	−0.0276	0.0637	−0.0415	−0.1872	0.2657
Shoot N content	Intercept	0.4454	−8.1178	0.8056	1.1291	0.6363	1.9136	5.4584	2.4379	16.1218
	Linear	1.1154	−0.0566	2.8213	1.6811	−0.5842	2.7470	−2.8145	−9.9389	5.2124
	Quadratic	0.7087	0.0174	1.0717	1.2445	0.7997	1.8082	3.1990	1.2329	4.5247

(data not shown). N rate affected RCD increment growth the first year after outplanting (Table 3); seedlings given the highest rates of N (3 and 4 mg) had almost twice as much RCD growth as those given 0.5 mg (data not shown). Subsequent RCD increments were unaffected, averaging about 10 mm per year.

At the end of the second field season, N rates of 0.5, 1, 2, 3, and 4 mg allowed 15%, 24%, 44%, 62%, and 67%, respectively, of surviving seedlings to exit the grass stage (RCD $\geqslant$ 25 and height $\geqslant$ 10 cm). Multiple comparisons revealed that 0.5 mg = 1 mg ($P = 0.9686$) < 2 mg ($P = 0.0752$) < 3 mg ($P = 0.0059$) = 4 mg ($P = 0.9993$). By the end of the third season, 85%, 85%, 92%, 91%, and 92% had exited the grass stage; none of the N rates were significant ($P = 0.4934$). N rate significantly affected height growth increment and total height during the third field season. N rates of 0.5, 1, 2, 3, and 4 mg yielded 22.2, 22.6, 26.3, 32.9, and 34.4 cm of new height growth, respectively, with total height equal to 29.7, 30.5, 37.0, 46.6, and 48.6 cm, respectively (Fig. 8). For increment and total height, the two highest N rates (3 and 4 mg) yielded significantly greater values than the two lowest rates (0.5 and 1), with the 2 mg rate intermediate (data not shown). Overall, much variation was apparent in seedling size with nursery N rate every year after outplanting (Fig. 9).

For the 2005 crop, survival exceeded 96% and was unaffected by N rate, nursery type, or the interaction (Table 2). Growth (total and incremental RCD and height) was unaffected by the interaction of N rate and nursery type (Table 3). Although nursery type significantly affected total RCD at the end of the first field season, this affect dissipated by the end of the second season; nursery type had no effect on RCD increment. N rate significantly affected total and incremental RCD each year after outplanting. For total RCD, each N rate was significantly different each year. The 3 mg N seedlings had 41%, 32%, and 24% more RCD than their 1 mg N cohorts the first, second, and third year after outplanting, and 12%, 11%, and 7% more than those receiving 2 mg N. From the second to third growing season, seedlings given 2 or 3 mg N showed 12% more RCD growth than their 1 mg N cohorts (14.3 vs. 12.8 cm).

At the end of the second growing season, N rate affected the number of seedlings exiting the grass stage ($P < 0.0001$), but nursery type ($P = 0.2708$) and the interaction ($P = 0.6970$) did not. For the greenhouse seedlings, multiple comparisons of grass stage data indicated that 1 mg = 2 mg ($P = 0.1239$) < 3 mg ($P = 0.0019$), whereas all N rates were significantly different for seedlings grown outdoors ($P \leqslant 0.0480$). N rates of 1, 2, and 3 mg allowed 6%, 18%, and 42%, respectively, of surviving seedlings to exit the grass stage. After the third growing season, only N rate affected seedling exit from the grass stage ($P < 0.0001$), and regardless of nursery type, each N rate was significantly different, allowing 56%, 84%, and 94% of the seedlings given 1, 2, and 3 mg, respectively, to exit the grass stage. N rate significantly affected total height and height increment 2 and 3 years after outplanting. Increasing weekly rates of N from 1 to 2 mg and from 1 to 3 mg resulted in 100% (15.6 vs. 31.3 cm) and 159% (15.6 vs. 40.5 cm) more height growth, respectively, after three field seasons (Fig. 8).

4. Discussion

As expected, our results show that increasing the rate of applied N increased seedling size in the nursery (Landis,1989; Dumroese et al., 2011). This increase in size coupled with a constant rate of fertilizer resulted in declining N concentrations because of growth dilution (Timmer, 1991). Seedling allometry followed the accepted paradigm: reducing N rates favored allocation to roots (Landis, 1989), as was shown specifically for longleaf pine (Entry et al., 1998; Jose et al., 2003). Quantile regression indicated that different portions of the seedling population responded differently to changes in applied N. Root biomass and RCD peaked at 3 mg N for nearly all of the population ($\tau \leqslant 0.75$; Fig. 5) while continuing to increase for the upper segment of the population ($\tau = 0.95$), whereas shoot biomass was just the opposite. In addition, as N rate increased, seedlings became more variable in size (Fig. 4). These differences among seedlings may be explained by Boyer (1990), who concluded that genetic variability is higher within individual longleaf pine seedlings than among stands or sources. During both years, as N rate increased from 1 to 3 mg, root biomass increased about 30%, compared with the 230% increase in shoot biomass; root biomass appears less plastic in response than shoot biomass. Therefore, S:R decreased with decreasing N rate for both crop years (Fig. 1). For the 2004 crop, our S:R, averaged across treatments, was 0.9, about the same as that for the 2005 crop, but much lower than another study we have in progress (S:R = 2.5), and that reported by Sword Sayer et al. (2011) (S:R = 2.8). Given the similarity of nursery fertilization in our studies, the observed phenotypic differences probably reflect genetics; Sword Sayer et al. (2005) noted differences in root development among seed origin. N content of roots and shoots followed a similar pattern. Quantile regression indicated that shoot N content continued to increase exponentially across all segments of the population as N rate increased, whereas for roots, N content for the median and lower quantiles peaked at about 3 mg N (Fig. 5). Given that N content and biomass are correlated (Dumroese et al., 2005), these results are expected.

This threshold for root growth is intriguing, particularly in terms of the Root Bound Index (RBI; ratio of RCD to container

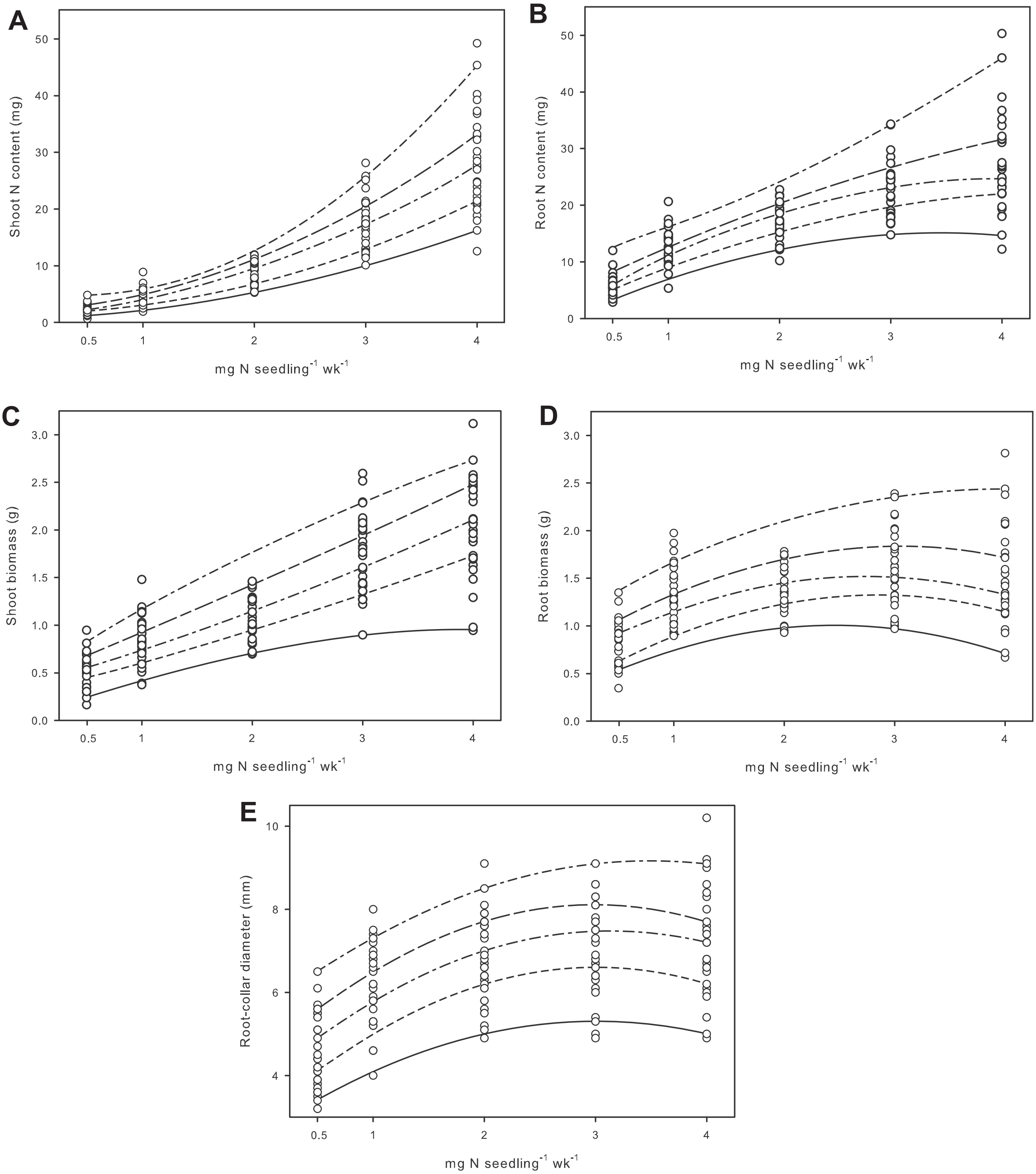

Fig. 5. Quantile regressions for the 2004 crop where τ = 0.05, 0.50, and 0.95 for (A) shoot nitrogen (N) content, (B) root N content, (C) shoot biomass, (D) root biomass, and (E) root-collar diameter vs. N rate.

diameter) defined by South and Mitchell (2006). Although RCD is often considered the most important seedling attribute (South et al., 1993, 2005), too much RCD and subsequent roots can be problematic. For our container type, seedlings would need an RCD of 10.3 mm to reach the critical RBI of 27% as defined by South and Mitchell (2006) where seedling performance is impaired. Despite our use of a typical growing season duration and large doses of N, we were unable to produce seedlings with RCD approaching that critical level. Our data suggests that for our seed sources, moving from 3 to 4 mg N afforded no advantage toward producing more RCD or root biomass for this container type, so it is unclear what additional nursery practice during a typical growing season could be employed to approach that danger threshold. It is possible, however, that extending the growing season beyond typical (i.e., holding the stock over for part or all of another year) may allow seedlings to surpass that threshold, as noted for other conifer species (Balisky et al., 1995; Salonius et al., 2002).

Seedling mortality for both outplanting years was low, unrelated to nursery N application rate, and scattered across a wide range of initial RCDs (Fig. 7). The interim guidelines for producing container longleaf pine seedlings (Dumroese et al., 2009) suggest a minimum RCD of 4.75 mm (for the same container we used in this study) because seedlings below that threshold survived poorly. Most (64%) of the seedlings grown at 0.5 mg N failed to meet that

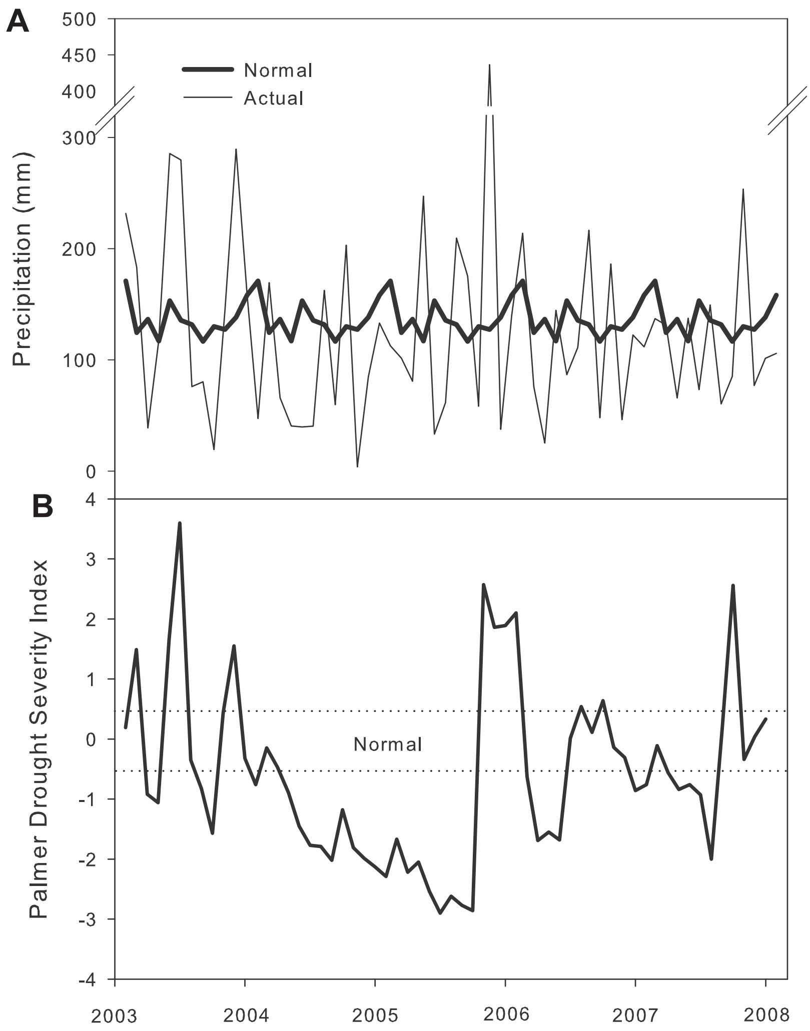

Fig. 6. (A) Rapides Parish weather data and (B) the Palmer Drought Severity Index (PDSI; Palmer, 1965) beginning the year prior to the 2004 outplanting and continuing 3 years after the 2005 outplanting. PDSI categories: Wet: 0.5–2, slightly; 2–3, moderately; 3–4, very. Drought: −0.5 to −1, incipient; −1 to −2, mild; −2 to −3, moderate; −3 to −4, severe.

Table 3
Analysis of variance table and *P* values for seedling morphological characteristics after outplanting.

		Survival			Root-collar diameter			Root-collar diameter increment			Height		Height increment
	df	Year 1	Year 2	Year 3	Year 1	Year 2	Year 3	Initial–Year 1	Year 1–2	Year 2–3	Year 2	Year 3	Year 2–3
2004													
Nitrogen rate (*N*)	4	0.6187	0.9757	0.6115	<0.0001	<0.0001	0.0005	<0.0001	0.7968	0.2497	<0.0001	0.0011	0.0029
2005													
Nursery type (*T*)	1	0.4859	0.2983	0.7437	0.0141	0.0714	0.1249	0.3811	0.4123	0.3442	0.4033	0.4834	0.4356
Nitrogen rate (*N*)	2	0.8645	0.3982	0.4019	<0.0001	<0.0001	<0.0001	<0.0001	0.0005	0.0249	<0.0001	<0.0001	<0.0001
T × *N*	2	0.7637	0.3749	0.7195	0.3206	0.2033	0.3806	0.2497	0.3604	0.2981	0.5683	0.5009	0.4876

threshold, and half of those died after outplanting (Fig. 7). For all other N rates, most (85%) of the seedlings exceeded that threshold, and of those that did not, mortality was 18% (Fig. 7), indicating that low RCD values may be acceptable if N concentrations and contents are sufficient. The benefit of additional N was to shift more seedlings into having favorable RCD. As with RCD growth during nursery production, additional N tended to shift populations toward exit from the grass stage (Fig. 9). Although we observed a similar pattern among rates for initial RCD and first year RCD, additional N moved the population closer to Wahlenberg's (1946) critical RCD thresholds. Similarly, in year 3, seedlings in each treatment had a similar and broad distribution pattern similar to those presented by Ramsey et al. (2003), but increasing N shifted more of each population toward greater RCD and total height values (Fig. 9).

At our highest N application rate (4 mg) we were unable during nursery production to approach the critical RBI identified by South and Mitchell (2006); although we saw a trend toward reduced survival with this rate; this observation may be a function of the increased variation in seedling shoot biomass, relative to root

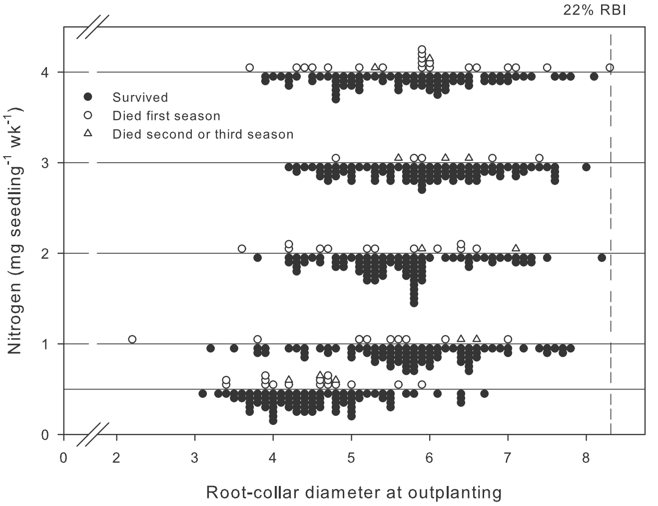

Fig. 7. Survival and mortality of the 2004 crop by nursery nitrogen rate and root-collar diameter at outplanting ($n = 400$). The root bound index (South and Mitchell, 2006) for the seedling with the largest diameter (represented by the vertical dashed line) was 22%, about 80% of the critical value (27%).

biomass (Fig. 4) and/or continued shoot biomass increase at all quantiles relative to declining root biomass, particularly at quantiles $\leqslant 0.50$ (Fig. 5). Thus, poorer S:R may be causal. Barnett (1984) reported that container seedlings, clipped once to 25 cm immediately before outplanting under severe moisture stress conditions, survived better than control seedlings. Similarly, South (1998) noted that clipping needles of bareroot seedlings improved survival after outplanting. In addition to reducing S:R, clipping presumably reduced transpiration.

We observed differences in field performance between outplanting years. Overall, growth was better with the 2004 than the 2005 crop (Fig. 8). Although this difference could be a function of seed source, the 2004 crop was outplanted into soil with much better initial soil moisture than the 2005 crop as reflected by the PDSI data. Using Haywood's (2005, 2007) application of Palmer's (1965) PDSI yields, in our opinion, a better qualification of site moisture than mere observations of precipitation; use of the PDSI technique could allow for better comparisons across studies, especially those that also span multiple years. Field performance may also have been influenced by the March 2007 wildfire. The older 2004 seedlings may have had more belowground resources to allocate to re-growth after the fire (Guo et al., 2004) despite the fact that March wildfires (which this experiment experienced) are more detrimental than those in May (Grelen, 1975).

Outplanted longleaf pine seedlings are fairly resilient in terms of survival regardless of site preparation (Haywood, 2000, 2005; Ramsey et al., 2003; Ramsey and Jose, 2004; Knapp et al., 2006). Therefore, research focuses on reducing residence time in the grass stage by applying weed control, including mulching, herbicides, controlled burning, and fertilization. Herbaceous competition has long been known to lengthen the grass stage (Pessin and Chapman, 1944), so its control aids in reducing residence time (Ramsey et al., 2003; Haywood, 2005). Conversely, fertilization with N and/or phosphorus has been neutral or detrimental in effect, usually attributed to enhanced growth of the competition (Derr, 1957; Bengston, 1976; Ramsey et al., 2003). The goal of these silvicultural treatments is to provide the seedling improved opportunity for resource allocation; greater resource use leads to RCD that is required for eventual initiation of height growth.

The best post-planting treatments can reduce residence time in the grass stage to a single year (e.g. Haywood 2005), that is, seedlings begin stem elongation during their second season in the field. Rarely, however, is seedling quality considered in post-planting treatment application or data interpretation. Nearly all longleaf pine seedling studies, both *in situ* and *ex situ*, fail to provide sufficient detail about container fertilization to allow comparison across studies (e.g. applying fertilizer on an area basis without disclosing the areal dimensions of the container (e.g. Entry et al., 1998; Jose et al., 2003) or applying a liquid fertilizer of known concentration without providing the volume applied (e.g. Rodríguez-Trejo et al., 2003; Sword Sayer et al., 2009). Thus, the inability to calculate the quantity of N applied is a missed opportunity for comparing nursery practices and subsequent seedling performance. Our data show that nursery managers can easily manipulate seedling morphology and nutrient status, and that our best N rate (3 mg N) for this particular set of nursery cultural practices was effective in reducing residence time in the grass stage, comparable with the best site preparation treatments. Combining high quality seedlings with the best silvicultural treatments could amplify the benefits of both. To maximize the benefit, nursery researchers will need to better document their outplanting sites in terms of competition and site preparation treatments, and silvicultural researchers will need to describe more seedling attributes than just RCD; quality outplanting studies require significant effort to avoid confounding (Pinto et al., 2011).

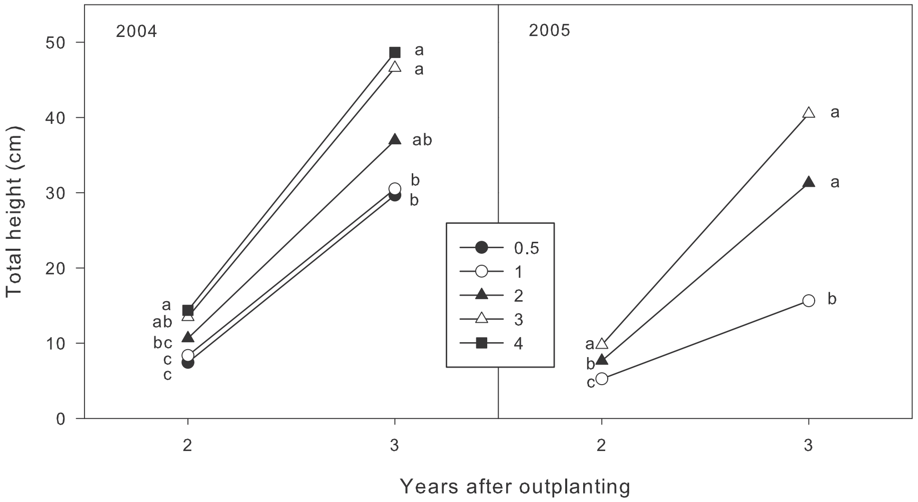

Fig. 8. Total heights for seedlings, by nursery nitrogen rate, outplanted in 2004 and 2005 after 2 and 3 years in the field.

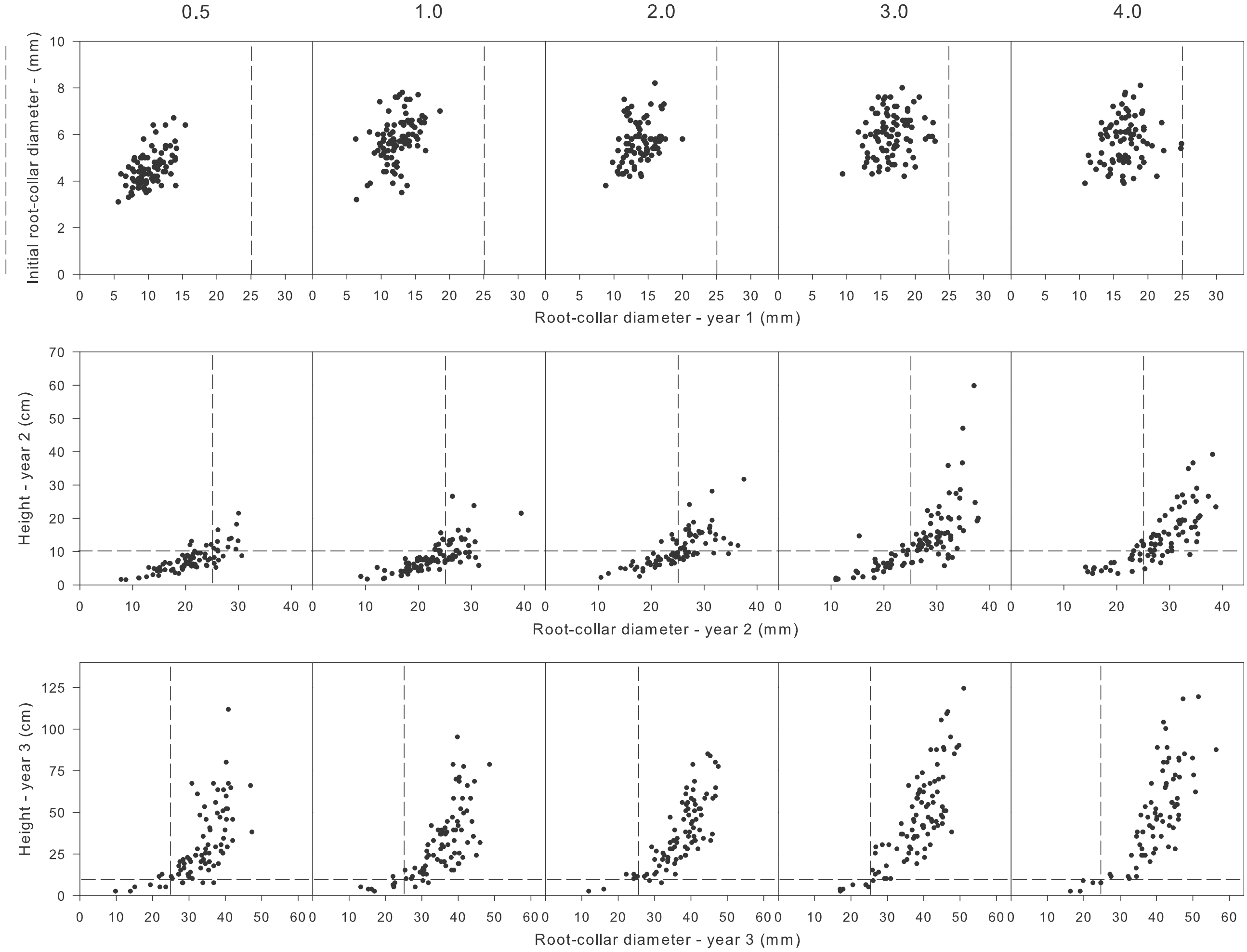

Fig. 9. Distribution of root-collar diameters (RCD) and heights for seedlings grown in each nursery nitrogen rate measured for 3 years after outplanting the 2004 crop. Initial RCD was measured immediately after outplanting (November 2004) with years 1, 2, and 3, measured in December 2005, 2006, and 2007, respectively. The vertical and horizontal dashed lines represent Wahlenberg's (1946) 25 mm RCD and 10 cm height criteria for seedlings to have exited the grass stage. During the first year, no seedlings had heights ⩾ 10 cm.

Finally, although fall fertilization was shown to improve the quality of bareroot longleaf pine (Hinesley and Maki, 1980), more research is needed to assess fall fertilization of container longleaf pine. Rodríguez-Trejo et al. (2003) report applying fall fertilization and noted no improvement in seedling performance, but the rates appear minimal and the actual amount of N applied is unclear. In an earlier study (Dumroese et al., 2005) and this study we observed precipitous declines in foliar and root N concentrations after cessation of weekly fertilization during the fall. Moreover, we noted a greater decline in shoot N content accompanied by little increase in biomass versus a smaller decline in root N content accompanied by a larger increase in biomass, suggesting that in addition to normal N dilution caused by growth, longleaf pine seedlings may be shifting nutrient reserves to their roots. Given longleaf pine's inherent strategy toward root development (Pessin, 1939) and observations that root N content increases as root sink increases (Guo et al., 2004), it may be possible to apply appreciable fall fertilization to maintain or enhance seedling N concentration without undue additional needle biomass (length), especially since we observed negligible needle length extension between weeks 20 and 30 (Fig. 1). Moreover, Davis et al. (in press) found that longleaf pine seedlings given more fertilizer (2 or 4 mg N per week) were more cold hardy than those given a low rate (0.5 mg N). Thus, the aforementioned problems associated with field fertilization, as it pertains to improving plantation establishment and growth, may be mitigated by enhancing seedling nutrient reserves at the nursery.

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