Root System Architecture: the Invisible Trait in Container Longleaf Pine Seedlings

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Abstract: Longleaf pine (*Pinus palustris* Mill.) seedlings cultured in four cavity volumes (60 to 336 ml [3.7 to 20.5 cubic inches]), two root pruning treatments (with or without copper coating), and 3 nitrogen levels (low to high) were grown for 29 weeks before they were outplanted into an open area in central Louisiana. Twenty-two months after outplanting, 3 seedlings were excavated from each of the 24 treatment combinations to evaluate effects of nursery cultural treatments on seedling growth and root system architecture. This paper reports some preliminary observations from that sample. Seedlings cultured in copper coated cavities had more lateral roots egressing into the top 10 cm (3.9 in) of soil whereas those cultured without copper root pruning had most of their lateral roots egressing into deeper (> 10cm [> 3.9 in]) soil layers. Regardless of nursery treatments, adventitious roots that originated near the air-pruned taproot end in some seedlings grew horizontally instead of vertically downward as in most container seedlings. Relationships between root system architecture and longleaf growth and mechanical stability are discussed.

Keywords: artificial regeneration, first-order lateral roots, horizontal root anchorage, mechanical stability, *Pinus palustris*, taproot, vertical root anchorage

Introduction

The longleaf pine ecosystem is one of the most biologically diversified ecosystems. During the last two decades, public and private land managers and owners have actively committed to restore this ecosystem, of which 97% has been lost since the turn of the 20th century (Landers and others 1995; Outcalt 2000). One of the 15-year goals in the Range-Wide Conservation Plan for Longleaf Pine calls for increasing the area of longleaf forests from the current 1.4 million hectares (3.5 million acres) to 3.2 million hectares (7.9 million acres; America's Longleaf 2009). Natural regeneration is only feasible on a small portion of the existing longleaf forests and it depends on bumper seed crops that take place every 5 to 7 years. Therefore, establishment of most new longleaf forests will rely on artificial regeneration with bareroot or container stock.

Improvements made in seedling container technology and nursery cultural practices in the last few decades resulted in the preference of container to bareroot stock for longleaf pine regeneration (Brissette and others 1990; Barnett and McGilvray 2000; Barnett and others 2002; Dumroese and others 2009). Percentages of container stock in longleaf seedlings grown in the southern U.S. increased from 70% in 2005 (McNabb and Enebak 2008) to 84% in 2008 (Dumroese and others 2009). Greater first year field survival and early stem growth of container longleaf seedlings compared with that of bareroot seedlings is one reason for this preference (Barnett and McGilvray 2000; South and others 2005). Another advantage is that the outplanting window can be extended from the 10 days or so with bareroot stock to 1-3 months (in cold storage for several weeks after extracting from the containers) with container stock (Barnett and McGilvray 2000; Pickens 2012). Research showed that field performance of container longleaf pine seedlings increases with increasing container cavity volume (South and others 2005; Sword Sayer and others 2009, 2011; Sung and others 2010), nitrogen fertilization level in the nursery (Jackson and others 2012), and copper root pruning treatments (Haywood and others 2012).

The stand establishment benefits gained from planting container stock, however, may not be fully realized without considering root system. For example, 11 years after outplanting, container lodgepole pine (*P. contorta* var. *contorta* Dougl.) saplings grew less and had different root system architecture than naturally regenerated trees (Halter and others 1993). The container lodgepole pine trees had less structural lateral root symmetry, a concentration of lateral roots 10 cm (3.9 in) below the soil surface, and a greater number of constricted, kinked, or coiled roots compared to their natural counterparts (Halter and others 1993). Naturally regenerated longleaf pine seedlings have straight taproots extending deep into the soil profile from which most first-order lateral roots originate and then extend in a horizontal plane at a uniform depth throughout their entire length (Heyward 1933). Hodgkins and Nichols (1977) found that most lateral roots of natural longleaf trees are within the top 10 cm (3.9 in) of soil. As expected, root system architecture of container longleaf pine differs from that of naturally grown trees in at least two aspects. First, taproots are air pruned when they reach the container drainage holes. Once outplanted, adventitious roots originate near the site of air pruning and usually grow downward (South and others 2001). Second, lateral roots of longleaf pine seedlings, similar to the roots of all container seedlings, are deflected when they contact cavity walls. Although vertical ribs mitigate root circling common in early types of containers (Burdett 1979; Barnett and Brissette 1986), the downward extending lateral roots result in a cage-like appearance of the root plug (Burdett 1978; Barnett and McGilvray 2002). Numerous studies have shown that growing tree seedlings in cavities having their interior surface coated with copper compounds can stop lateral root extension and prevent formation of the cage-like appearance (Ruehle 1985; see Dumroese and others forthcoming). As with other conifers grown in copper-treated containers (for example, Wenny and others 1988), egress of lateral roots of longleaf pine seedlings after outplanting was uniform along the length of root plugs, contrasting with most lateral roots egressing from the bottom of the root plug when cultured in non-root pruning cavities (Sword Sayer and others 2009; Sung and others 2009, 2012).

Changes in lateral root architecture of container seedlings have been attributed to physical instability after outplanting (Burdett 1978, 1979; Burdett and others 1986). Most of the regenerated longleaf pine forests are within 240 km of the Atlantic and Gulf States coasts, which have experienced increasing frequency and intensity of tropical wind storms, including hurricanes, in recent years. Although stems of longleaf pine trees suffered less wind damage by hurricanes than loblolly pine (Gresham and others 1991; Johnsen and others 2009), concern remains that longleaf pine stands originated from container stock may be more prone to juvenile stem instability, such as toppling and leaning. Therefore, studies elucidating the association between sapling stem instability and root system architecture in container longleaf pine saplings are ongoing (Sung and others 2009, 2012).

This paper reports preliminary results of root system architecture in outplanted longleaf pine seedlings cultured in combinations of four cavity volumes, two root pruning treatments, and three relative nitrogen rates.

Materials and Methods

Greenhouse Study

The first phase of this study was conducted in a USDA Forest Service, Rocky Mountain Research Station's greenhouse located in Moscow, Idaho USA (46.72,-117.00) and was described in detail by Dumroese and others (forthcoming). Briefly, longleaf pine seeds of mixed seedlots from Louisiana were sown into cavities filled with a 1:1 (v:v) Sphagnum peat moss:vermiculite medium on 15 May. The study was a randomized complete block design with 4 cavity volumes x 2 copper root pruning treatments (copper coating of the cavity or no copper coating) x 3 nitrogen (N) rates x 3 replications. Styroblock™ containers (no copper) and their equivalent-sized Copperblock™ containers (interior portions of each cavity except the ribs coated with copper oxychloride) were used. Specifications for the containers are in Table 1.

We calculated our N rates relative to those used in Jackson and others (2012). Therefore, we used the low (0.5 mg N [1 mg = 0.00004 oz] per seedling per week for 20 weeks [hereafter simply mg N]), medium (2 mg N), and high (4 mg N) rates of Jackson and others (2012) but calculated the exact amount of N based on container volume relative to the Ropak #3-96 used by Jackson and others (2012). See Dumroese and others (forthcoming) for a complete description. Fertigations (irrigation with soluble fertilizer added) began 4 weeks after sowing and continued once per week for 19 weeks (20 applications total). Frequency of irrigation or fertigation was determined gravimetrically. Every time container mass reached 75% of the field capacity mass, we irrigated or fertigated seedlings. Once each week, we calculated the amount of fertilizer to add to a sufficient amount of irrigation water in order to apply the appropriate nutrient regime and return the containers to field capacity. We custom blended fertilizers. Our stock fertilization solution was 110, 77, 63, 28, and 20 mg per l P, K, S, Ca, and Mg, respectively, plus micronutrients (Peters Professional® S.T.E.M.™, The Scotts Company, Marysville, Ohio USA) applied at 15 mg per l (1mg per liter = 0.0001 oz per gallon) and Sprint 330 (chelated Fe; 10% Fe; Becker Underwood, Inc., Ames, Iowa USA) added at 20 mg per l. To that we added ammonium nitrate to achieve the desired N amount per seedling per container size and N rate. Fertigation solutions were carefully applied by hand to ensure an even distribution of nutrients and minimize leaching. From the end of the fertigation period (22 October) until harvested on 4 December, seedlings were irrigated when container mass reached 75%.

Table 1. Characteristics of Styroblock™ and Copperblock™ containers (Beaver Plastics, Ltd., Acheson, Alberta, Canada).

Designation (US or Canada)	Cavities (number)	Volume (ml [in^3])	Depth (cm [in])	Diameter (cm [in])	Density (cavities m^{-2} [ft^{-2}])
4A or 313A	198	60 (3.7)	13 (5.1)	2.8 (1.1)	936 (87.0)
6B or 412B	112	95 (5.8)	12 (4.7)	3.6 (1.4)	530 (49.4)
10S or 412A	77	125 (7.6)	12 (4.7)	4.2 (1.7)	364 (34.0)
20 or 615A	45	336 (20.5)	15 (5.9)	5.9 (2.3)	213 (19.8)

Field Study

Seedlings were extracted from containers on December 4, pooled by replication, boxed, shipped, stored at 5 °C (41 °F) for one week, and outplanted on December 11. The study site is in an open area on the Palustris Experimental Forest on the Kisatchie National Forest near McNary, Rapides Parish, Louisiana (Lat./Long.: 31.0, -92.6). The area is gently sloping with Beauregard silt loam (fine-silty, siliceous, thermic Plinthaquic Paleudult) soils that are moderately drained and slowly permeable. The site develops a perched water table during prolonged wet periods in winter and can be droughty in summer (Kerr and others 1980).

The experimental design for the field portion of the experiment was a randomized complete block design with split-plots replicated three times. Whole plots were combinations of container volume, copper root pruning, and relative N rates, and the split plots were soils amended with either 0 (control) or 100 kg P per hectare (89.1 lbs per acre) of diammonium phosphate incorporated using a tractor and disc. Fifteen seedlings from each of the original 24 nursery treatments were outplanted at 0.6 × 0.9 m (2.0 × 3.0 ft) spacing in each of the split-plots.

Seedling root collar diameter (RCD) was measured before outplanting. Seedling height and ground-line diameter was monitored from year 1 through 3. One seedling from each treatment was excavated 22 months after outplanting in October. Seedlings were excavated at 15 cm (5.9 in) radius from the stem with a shovel. After carefully washed residual growth medium and soil off the root system, seedlings were severed at the root collar. Growth parameters, such as height, RCD, and dry weight of needle, stem, taproot, and lateral roots were recorded. Root system architecture was assessed by placing a root system over a root plug template of each cavity size. Zone A was the upper 5 cm (2 cm) of the root plug, zone B included the next 5 cm (2 cm) of root plug basipetal zone A, and zone C included the remainder of the root zone (> 10 cm [3.9 in] below the top of the original root plug). Only those lateral roots that originated within root plug and had at least 3 mm diameter were counted as first-order lateral roots (FOLRs). Assessment methodology and preliminary results of root system architecture from selected seedlings are reported here.

Results and Discussion

Sapling stability is supported by vertical anchorage provided by a taproot or sinker roots (Burdett 1978; Mason 1985; Burdett and others 1986; Coutts and others 1999). Sapling stability may also be supported by symmetrical, horizontal lateral roots (Coutts and others 1999). The upper soil layers in forests usually have a greater amount of organic matter and mineral nutrients. Exploration of the upper soil layers by horizontal lateral roots and their mycorrhizal associations can benefit tree growth (Balisky and others 1999; Sword Sayer and others 2009). Based on the criteria for sapling stability and growth, each seedling was assessed with a set of root system architecture parameters. The following descriptive results from the excavation study are shown in Tables 2 and 3 and in Figures 1-4 (All figures show seedlings that were cultured in a greenhouse in Moscow, Idaho for 29 weeks, harvested in early December and promptly outplanted in central Louisiana, and sampled 22 months later. Each horizontal zone between two lines on the root plug template was 1 cm.)

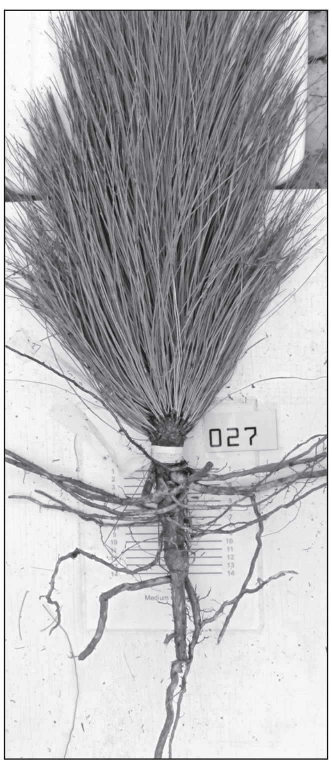

Figure 1. Longleaf pine Seedling #27 was raised in a 95 ml cavity coated with copper and given the medium rate of nitrogen each week for 20 weeks starting 4 weeks after sowing.

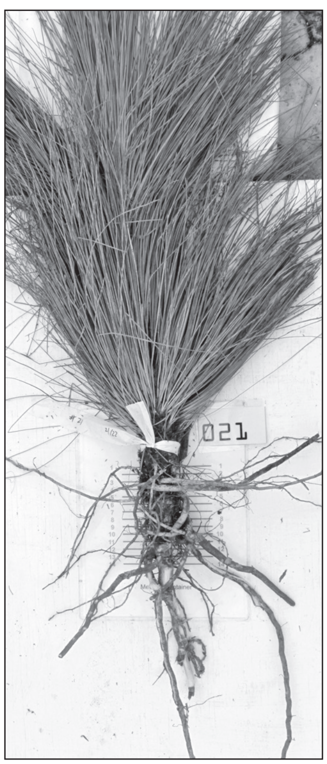

Figure 2. Longleaf pine Seedling #21 was raised in a 95 ml cavity without a copper coating and given the medium rate of nitrogen each week for 20 weeks starting 4 weeks after sowing.

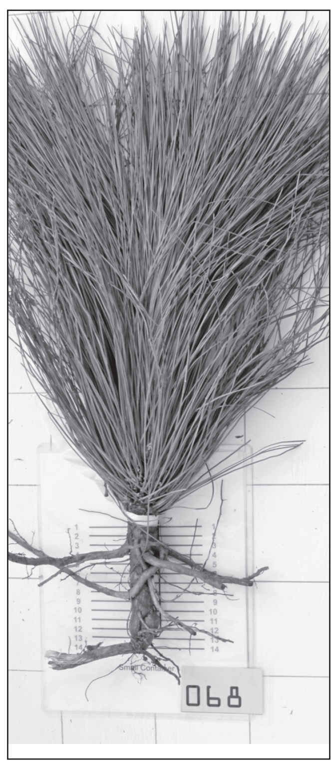

Figure 3. Longleaf pine Seedling #68 was raised in a 60 ml cavity coated with copper and given the medium rate of nitrogen each week for 20 weeks starting 4 weeks after sowing.

Figure 4. Longleaf pine Seedling #29 was raised in a 336 ml cavity without a copper coating and given the high rate of nitrogen each week for 20 weeks starting 4 weeks after sowing.

Table 2. Root collar diameter (RCD) at outplanting and other growth parameters for four longleaf pine seedlings excavated 22 months after outplanting in central Louisiana.

Seedling designation	Cavity volume (ml)[1]	Copper root pruning	Relative N rate[2]	RCD (mm)	Ground line diameter (mm)	Height (cm)	Dry weights (g)			
							Seedling	Needle	Stem	Root
27	95	Yes	Medium	6.85	36.7	40	327	195	55	77
21	95	No	Medium	5.64	42.1	45	348	199	63	86
68	60	Yes	Medium	3.76	28.2	26	173	112	27	34
29	336	No	High	6.94	40.5	58	397	189	85	123

[1] Conversions: 1 in3 = 16.4 ml; 1 in = 25.4 mm = 2.5 cm; 1 oz = 28.3 g)

[2]N application rate was relative to the rates used by Jackson and others (2012) for 90-ml Ropak #3-96 containers. See Dumroese and others (forthcoming) for a complete description of the fertilizer calculations.

Less than 0.1% seedling mortality was observed through year 5. Most of the excavated seedlings had straight taproots that grew the length of the root plug. After seedlings were outplanted, adventitious roots emerged from the callus tissue at the end of the taproot and usually grew downward. South and others (2001) designated such roots as type A sinker roots. An example of this is seen with Seedling #27, which was from the 95-ml container treated with copper, and grown with medium N (Figure 1). This seedling type represented most of the seedlings grown with copper in terms of root system architecture and dry weight allocation. It had a top:root dry weight ratio of 3.2 (Table 2), a straight taproot, two sinker roots extending from the air-pruned end of the taproot, and 12 FOLRs. More than 40% of the FOLRs egressed from the top 5 cm of the root plug (zone A) (Table 3). Only two lateral roots in Seedling #27 showed some spiraling, oblique, or vertical growth within the original root plug.

In contrast, Seedling #21 was from 95-ml container not treated with copper and grown with medium N (Figure 2). This seedling had a shoot-to-root ratio (S:R) of 3.0 (Table 2) and its taproot did not show any sign of being air-pruned, extending to a depth of at least 32.5 cm (12.8 in) in soil (taproot end broke off during excavation). This lack of visible air-pruning on the taproot was also observed in some of the copper-pruned seedlings, and was also observed by South and others (2001). Unlike copper-pruned seedlings, Seedling #21 had more than 40% of its FOLRs egressing from zone C (> 10 cm [>3.9 in]) of its root plug (Table 3). This was typical for longleaf pine seedlings grown without lateral root pruning treatment (Sword Sayer and others 2009; Sung and others 2009, 2012).

Not all adventitious roots extending from the air-pruned end of taproots are type A sinker roots because some adventitious roots extend horizontally. Formation of these horizontal, thus non-sinker, adventitious roots maybe due to root plug end being in contact with either a hardpan or a rock or compaction of fine-textured soils by the dibble used for outplanting (Landis and others 2010). An example is Seedling #68 grown in the 60-ml container treated with copper and given medium N (Figure 3). It had a S:R dry weight ratio of 4.1 (Table 2), a straight but short taproot, 2 adventitious roots extending horizontally from the air-pruned end of the taproot, and 8 FOLRs. Non-sinker, adventitious root formation was also observed in some of the excavated seedlings not treated with copper. A sapling with vertical anchorage provided only by the taproot may be at greater risk to topple when exposed to strong winds. Sung and others (2009, 2012) found young longleaf pine saplings with stem instability had very short taproots and/or without sinker roots.

Our final example is Seedling #29, grown in the 336-ml container not treated with copper and given the highest rate of N (Figure 4). It had a S:R dry weight ratio of 2.2 (Table 2), a straight taproot, 3

Table 3. Parameters in root system architecture of the four longleaf pine seedlings excavated 22 months after outplanting and previously described in Table 2.

Seedling designation	Taproot		Sinker root		First order lateral root (number)				
	Length (cm)[1]	Dry wt (g)	Longest (cm)	Total dry wt (g)	Total	Egressed			Deformed in root plug [2]
						Zone A (0 to 5 cm)	Zone B (5 to 10 cm)	Zone C (> 10 cm)	
27	11.5	24.6	28.0	19.2	12	5	6	1	2
21	32.5	43.0	-	-	12	3	4	5	6
68	10.0	13.8	-	7.7[3]	8	4	2	2	6
29	13.5	34.8	40.0	21.9	18	0	2	16	15

[1]Conversions: 1 in3 = 16.4 ml; 1 in = 2.5 cm; 1 oz = 28.3 g)

[2]Deformed first-order lateral roots had their segments of roots within root plug spiraling or extending obliquely or vertically.

[3]Adventitious roots extended horizontally from the taproot end and were not sinker roots.

sinker roots, and 18 FOLRs. This seedling retained a cage-like appearance for its FOLRs 22 months after outplanting. All of its FOLRs egressed from the bottom of the root plug except for 2 FOLRs in zone B (Figure 4). Although this seedling lacked root exploration in the uppermost portions of the soil profile, which is more nutrient rich than soil below, the robust growth of this seedling was most likely influenced by luxury consumption of nutrients during nursery production that were stored in stem or roots and subsequently exploited after outplanting, as was the case with black spruce (*Picea mariana*) in Canada (Malik and Timmer 1996).

Summary

Effects of nursery cultural treatments were found to persist in longleaf pine seedlings for 22 months (almost 2 years) after outplanting. For example, we observed that seedlings grown without copper root pruning had most of their lateral roots egressing into deeper soil layers compared to those grown in cavities with copper coating. Root system of some non-root pruning seedling still maintained the cage appearance resulted from the vertical downward extension of the lateral roots within root plug. Formation of sinker roots from taproot end did not seem to be affected by cultural treatments.

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