

Cavity Size and Copper Root Pruning Affect Production and Establishment of Container-Grown Longleaf Pine Seedlings

Mary Anne Sword Sayer, James D. Haywood, and Shi-Jean Susana Sung

Abstract: With six container types, we tested the effects of cavity size (i.e., 60, 93, and 170 ml) and copper root pruning on the root system development of longleaf pine (*Pinus palustris* Mill.) seedlings grown in a greenhouse. We then evaluated root egress during a root growth potential test and assessed seedling morphology and root system development 1 year after planting in central Louisiana, USA. Seedling size was increased by copper root pruning in small cavities but was unaffected by this treatment in larger cavities. Before planting, copper root pruning increased taproot and secondary lateral root dry weights at the expense of primary lateral root dry weight and increased root growth potential in the top 5 cm of the root plug. Across treatments, survival was 97%, and all seedlings were in the grass stage. Of the lateral root dry weight that elongated during the first year after planting, 33% more occurred in the upper 5 cm of soil when seedlings were treated with copper. Within each cavity size, copper root pruning did not affect the general morphology of 1-year-old seedlings. However, relationships between root collar diameter and root egress by depth indicated that this treatment has the potential to increase the range of cavity sizes used for seedling production. FOR. SCI. 55(5):377–389.

Keywords: copperblock, copper oxychloride, *Pinus palustris* Mill., Superblock, taproot

FOREST REGENERATION in the southern United States benefits from container seedling technology in several ways. For example, with a reduction in the natural extent of longleaf pine from 37.5 million ha in the late 1800s to less than 2 million ha at present (Landers et al. 1995, Outcalt and Sheffield 1996, Outcalt 2000), a major application of container seedlings has been the reestablishment of longleaf pine ecosystems (Johnson and Gjerstad 2006). Container production is also being evaluated for the artificial regeneration of shortleaf pine (Barnett and Brissette 2004) and is providing the forest industry with an effective system for the culture of genetically improved seedlings (Menzies et al. 2001).

Past research has demonstrated that an important benefit of container seedlings is retention of a dense network of fibrous roots within the plug as seedlings are transferred from the nursery to the field (Goodwin 1976, Barnett and Brissette 1986). The root plug protects delicate fine roots from damage during planting, which reduces the likelihood of water deficit and severe planting shock (Becker et al. 1987, Barnett 2002).

The natural root system of *Pinus* species is characterized by a network of fibrous roots extending from large primary lateral roots that reach horizontally through the soil from a taproot. Together, the taproot and several large primary lateral roots provide anchorage as seedlings mature into trees (Coutts 1987). Furthermore, the absorption of water and mineral nutrients by fibrous roots is optimized when large primary lateral roots are healthy and uniformly distributed around the circumference of the taproot.

Container seedling cultural conditions have the potential to alter root system morphology in the nursery. For example, inadequate cavity size relative to the length of the cultural period may limit root system development as seedlings grow and root competition for growing space increases (Romero et al. 1986, South et al. 2005, South and Mitchell 2006). Early evaluations showed that depending on container type, root strangulation and spiraling and an absence of root egress were possible (Barnett and Brissette 1986, Brissette et al. 1991, Romero et al. 1986). In response, container cavities were improved with ribs that train primary lateral roots to grow vertically rather than horizontally (Barnett and Brissette 1986). Modifications also include coatings that chemically prune lateral roots, thereby stimulating new root proliferation at the root plug-soil interface after planting (McDonald et al. 1984, Ruehle 1985, Barnett and McGilvray 2002, South et al. 2005).

Improvements in seedling establishment attributed to the containerization of nursery stock dictate that container-grown southern pine seedlings will continue to be in high demand. Additional gains may be possible with container seedling technology that simulates natural root system morphology after planting. By using root system morphology after seedling production and 1 year after planting and first-year field performance, our objectives were to evaluate the effect of copper root pruning and cavity size on the first-year establishment of longleaf pine.

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Materials and Methods

Greenhouse Study

Seedling Culture

Longleaf pine seeds of mixed seedlots from Florida were sown in six container types in April 2004. Treatments were container types that differed by cavity size and application of Root Trim (US Environmental Protection Agency Registration No. 81293-2, containing copper oxychloride) to the cavity wall. Cavity sizes were small (60 ml), medium (93 ml), and large (170 ml). Root pruning was accomplished with Copperblock containers; otherwise, Superblock containers were used (Beaver Plastics, Ltd., Acheson, AB, Canada). Approximately 700 longleaf pine seedlings were grown in each of the six container types using standard cultural practices (Barnett and Brissette 1986).

In summary, the growing medium was a 1:2 mixture of commercial peat moss and vermiculite. Sown containers were randomly placed on greenhouse benches. The growing medium contained Osmocote 19-6-12 slow release fertilizer (The Scotts Miracle-Gro Company, Marysville, OH) at a rate of 3.6 kg/m³. Between early June and the end of September 2004, a 0.05–0.06% solution of Peter's Professional 20-20-20 water-soluble fertilizer (J.R. Peters, Inc., Allentown, PA) was applied weekly to root plug saturation. Between July and mid-October 2004, a 3% solution of benomyl fungicide was applied twice monthly to root plug saturation. Between fertilizer and fungicide applications, seedlings were watered to root plug saturation as needed to maintain vigor. Seedlings were grown for 27 weeks under ambient light in a greenhouse in which air temperature was maintained at 20–25°C. Six weeks before planting, fertilization was stopped, and watering was reduced to encourage bud set.

Root System Development

Seedlings were sampled 10, 17, and 27 weeks after sowing to evaluate root system development. At each sampling period, 25 seedlings were randomly selected by container type. The growing medium was washed from root systems, primary lateral roots ≥ 0.5 cm long were excised from the taproot, and secondary lateral roots were stripped or cut from excised primary lateral roots. The shoot was severed from the root system at the rootcollar. Dry weights of the shoot, taproot, primary lateral roots, and secondary lateral roots were determined after drying to equilibrium at 70°C. The sum of taproot and primary and secondary lateral root dry weights was calculated.

Root Growth Potential (RGP)

One day before planting, 25 seedlings were randomly selected from each container type. Root plugs remained intact, and seedlings were planted in pots containing masonry sand and placed in a greenhouse using a randomized complete block layout with five blocks. Blocks were the location in the greenhouse. Each block contained five potted seedlings from each container type. Seedlings were watered

twice weekly and were maintained for 28 days under ambient light and air temperature.

After 28 days, the seedling root systems were washed. A root plug template of each cavity size was drawn and separated into three depths (top, middle, and bottom). Two depths were similar among all cavity sizes: 0–5 and 5–10 cm. The third depth was 10–13.3 cm for the small cavities and 10–14.9 and 10–15.2 cm for the medium and large cavities, respectively. Root plugs were visually partitioned by depth, and egressed roots (≥ 0.5 cm long) were excised from the outer face of each depth. Growing medium was washed from the residual root plug, and the shoot was severed at the rootcollar. Dry weights of the residual root plug and egressed roots from each root plug depth were measured after drying to equilibrium at 70°C. Dried egressed roots were ground (1 mm² mesh) and combusted (450°C, 8 h), and their ash weights were determined. Egressed root dry weight was expressed on an ash-free basis, and total root system dry weight was calculated.

Field Experiment

Study Site

The study site is on the Palustris Experimental Forest, Rapides Parish, Louisiana, USA (31°10'N, 92°41'W). The soils are a Beauregard silt loam (fine-silty, siliceous, superactive, thermic Plinthaquic Paleudults) and a Malbis fine sandy loam (fine-loamy, siliceous, subactive, thermic Plinthic Paleudults) that are moderately well-drained with a very gentle to gentle slope (Kerr et al. 1980). Dominant vegetation before study establishment consisted of grasses and forbs. Vegetation was burned and rotary mowed in spring 2004. Large brush was felled by hand.

Experimental Design

The experiment was established using a 3 $\times$ 2 factorial randomized complete block design with four blocks. In July 2004, 24 0.13-ha treatment plots, 36 $\times$ 36 m each, were delineated. Treatment plots were blocked based on soil series and apparent soil drainage using depth to mottles with a chroma of 2 or less as a drainage indicator. The six container types were randomly assigned to six plots per block.

In early November 2004, 27-week-old longleaf pine seedlings were carefully extracted from containers and planted at 2 $\times$ 2 m with customized planting punches. More care was required to ensure the integrity of Copperblock root plugs compared with Superblock root plugs, suggesting that the operational use of copper root pruning will depend on research to remedy this problem. Treatment plots are 12 rows of 12 trees each and measurement plots contain the interior eight rows of eight trees each.

In fall 2005, survival was evaluated and six randomly selected seedlings per measurement plot were excavated. Using shovels, the residual root plug and lateral roots within a 25-cm radius of the stem and to a 30-cm depth were excavated. Soil was removed from roots with a garden trowel, and seedlings were bagged and transported to the laboratory.

Measurements

A root plug template of each cavity size was drawn and delineated into three depths as previously done for RGP measurements. In addition, a fourth root plug depth (base) extended vertically 20 cm from the base of the root plug. Root collar diameters (RCDs) were measured, and root systems were untangled and allowed to emulate their field conformation. Root plugs were aligned with the appropriate root plug template, and lateral roots extending from the outer edge of the template were excised at the apparent root plug-soil interface for each of the four root plug depths. First-order lateral roots originating from the taproot and having a diameter ≥ 1.5 mm were counted. The residual root plug was washed and separated into taproot and lateral roots. Roots excised from the base depth of the root plug were separated into taproot and lateral roots. The shoot was severed at the root collar, and fascicles were separated from the stem. Dry weights of the excised roots at each root plug depth, residual root plug components, foliage, and stem were determined after drying to equilibrium (70°C). Taproot and lateral root dry weights were calculated. To remove the influence of seedling size from evaluation of how cavity size affects root egress after planting, the fraction of root dry weight extending from the root plug in each of the four root plug depths was calculated.

Statistical Analyses

Before all analyses of variance, experimental errors were evaluated for normality by the Shapiro-Wilk statistic (SAS Institute, Inc. 1991). Normality tests and main and interaction effects were considered significant at an α level of 0.05. To establish normality, data were transformed to square root or natural logarithm values. As warranted, means were compared by the Tukey-Kramer procedure and considered significantly different at an α level of 0.05.

Root System Development

Seedling tissue dry weights at the end of the cultural period and taproot and primary and secondary lateral root dry weights at each measurement date were evaluated by analysis of variance (ANOVA) using a completely random design with two main effects: cavity size (small, medium, or large) and copper root pruning (Superblock or Copperblock).

RGP

Dry weights of the residual root plug, egressed roots, and total root system were analyzed by ANOVA using a randomized complete block design with five blocks. Cavity size (small, medium, or large) and copper root pruning (Superblock or Copperblock) were the main effects. Dry weights of egressed roots from the three root plug depths were evaluated by ANOVA using a randomized complete block split plot in space design with five blocks (Steel and Torrie 1980). Whole plot effects were cavity size and copper root pruning treatments, and the subplot effect was root plug depth (top, middle, or bottom).

Field Experiment

ANOVA of seedling morphological variables (RCD, number of first-order lateral roots, and dry weights of shoot, taproot, lateral roots, and total root system) was conducted using a randomized complete block design with four blocks. Cavity size (small, medium, or large) and copper root pruning (Superblock or Copperblock) were the main effects. Number and dry weight of egressed lateral roots by root plug depth were evaluated by ANOVA using a randomized complete block split plot in space design with four blocks (Steel and Torrie 1980). Whole plot effects were cavity size and copper root pruning, and the subplot effect was root plug depth (top, middle, bottom, or base).

For each copper root pruning treatment, the relationship between RCD and six independent seedling variables 1 year after planting was evaluated by ordinary least-squares regression. The independent variables were number of first-order lateral roots, taproot dry weight, and dry weights of the egressed roots by root plug depth. Subsequently, simple linear relationships between RCD and root dry weights corresponding to either the top, middle, bottom, or base among the three Superblock and Copperblock cavity sizes were evaluated by ordinary least squares regression. Residuals were assessed by the Shapiro-Wilk statistic (SAS Institute, Inc. 1991), and RCD was transformed as needed to natural logarithm values to ensure that residuals were normally distributed. Mean square errors (s^2) of pairs of regression lines were assessed by Levene's test of homogeneity of variance (Snedecor and Cochran 1980). The slope and y-intercept of appropriate pairs of regression lines with constant s^2 were evaluated by the general linear test approach and the F statistic (Neter and Wasserman 1974). Coefficients of determination and F statistics were considered significant at an α level of 0.05.

Results

Root System Development

Seedling size was significantly affected by cavity size and copper root pruning (Table 1). Throughout the cultural period, large cavities consistently led to greater shoot and root system dry weights than did medium and small cavities (Figure 1a and b). At 17 and 27 weeks postsowing, shoot and root system dry weights were greater in the medium cavities than in the small cavities. At 10-weeks postsowing, shoot dry weight was significantly larger in Copperblock cavities than in Superblock cavities, but root system dry weight was unaffected by copper root pruning. By 17 weeks postsowing, the interaction between copper root pruning and cavity size indicated that this effect was restricted to the small cavities. Specifically, the shoot and root system dry weights of seedlings grown in small Superblock cavities were 34 and 31% less than those of seedlings grown in small Copperblock cavities. Copper root pruning also interacted with cavity size at the end of the cultural period to reduce the shoot dry weight of seedlings grown in small Superblock cavities (30%) compared with those grown in small Copperblock cavities. At this time, a similar, nearly

Table 1. Probabilities of a greater *F* value for longleaf pine seedling shoot and root system dry weights and the dry weights of three root system components in response to copper root pruning (Superblock or Copperblock) and cavity size (small, medium, or large), at 10- and 17-weeks postsowing, and after the 27-week cultural period in the greenhouse

Source of variation	df	Shoot dry weight ^a	Root system dry weight ^b	Taproot dry weight ^c	Primary lateral root dry weight ^d	Secondary lateral root dry weight ^b
10 weeks postsowing						
P	1	0.0231	0.2484	0.0001	0.0001	0.3995
S	2	0.0002	0.0001	0.1465	0.0001	0.0001
P × S	2	0.2432	0.4151	0.7461	0.8158	0.0643
17 weeks postsowing						
P	1	0.0092	0.3577	0.0001	0.0001	0.6383
S	2	0.0001	0.0001	0.0001	0.0001	0.0001
P × S	2	0.0167	0.0010	0.0019	0.0026	0.0007
27 weeks postsowing						
P	1	0.0001	0.0002	0.0001	0.0001	0.0216
S	2	0.0001	0.0001	0.0001	0.0001	0.0001
P × S	2	0.0008	0.0682	0.0049	0.2146	0.5803

P, copper root pruning; S, cavity size.

^a Data at 27 weeks postsowing were transformed to their natural logarithm values to establish normally distributed experimental errors.

^b Data at 10, 17, and 27 weeks postsowing were transformed to their square root values to establish normally distributed experimental errors.

^c Data at 10 weeks postsowing were transformed to their square root values, and data at 17 and 27 weeks postsowing were transformed to their natural logarithm values to establish normally distributed experimental errors.

^d Data at 10 and 17 weeks postsowing were transformed to their square root values, and data at 27 weeks postsowing were transformed to their natural logarithm values to establish normally distributed experimental errors.

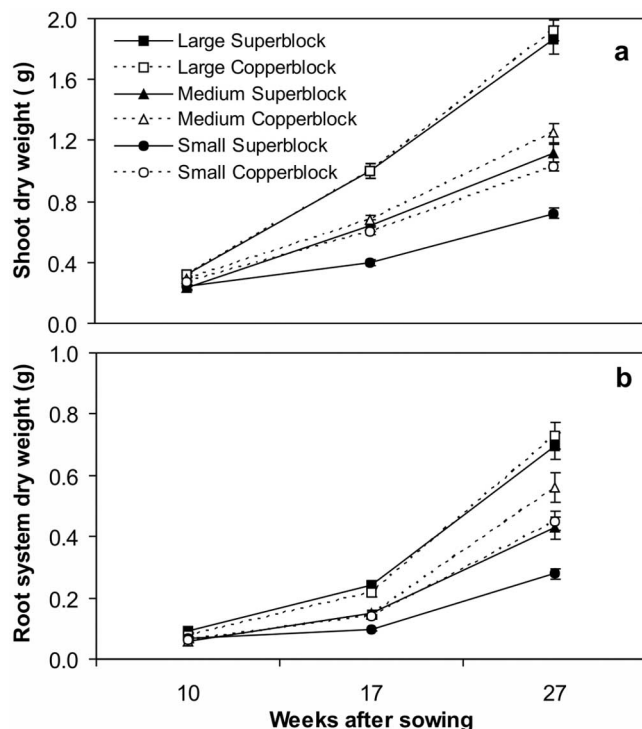


Figure 1. Container-grown longleaf pine seedling shoot dry weight (a) and total root system dry weight (b) in response to copper root pruning (Superblock and Copperblock), and cavity size (large, medium, and small) at 10- and 17-weeks postsowing and after the 27-week cultural period in the greenhouse. Error bars represent 1 SEM.

significant effect on root system dry weight was observed when seedlings were grown in small cavities.

Dry weights of the taproot and primary and secondary lateral roots were significantly affected by cavity size (Table 1). At 17 and 27 weeks postsowing, taproot dry weight was greater in large cavities than in medium and small cavities (data not shown). Similar responses were observed

10, 17, and 27 weeks postsowing for primary and secondary lateral root dry weights. Furthermore, as the cultural period progressed, primary lateral root dry weight at 17 weeks postsowing and secondary lateral root dry weight at 17 and 27 weeks postsowing were significantly greater in the medium cavities than in the small cavities.

Throughout the cultural period, dry weights of the taproot and primary lateral roots were significantly affected by copper root pruning (Table 1). Averaged among cavity sizes, taproot dry weights were larger and primary lateral root dry weights were smaller when seedlings were grown in Copperblock containers than in Superblock containers (Figure 2). By 27 weeks postsowing, copper root pruning led to a 21% increase in secondary lateral root dry weight.

Seventeen weeks after sowing (i.e., approximately two-thirds through the cultural period), copper root pruning interacted with cavity size to significantly affect primary and secondary lateral root dry weights (Table 1). At this time, primary lateral root dry weight in large and medium cavities was reduced 42 and 43% by copper root pruning, but there was no effect when seedlings were grown in small cavities (Copperblock large: 45 ± 3 mg; Copperblock medium: 31 ± 2 mg; Copperblock small: 26 ± 1 mg; Superblock large: 77 ± 4 mg; Superblock medium: 54 ± 5 mg; and Superblock small: 32 ± 2 mg). As cavity size decreased from large to medium and from medium to small, secondary lateral root dry weight decreased significantly when seedlings were produced in Superblock containers (Superblock large: 93 ± 6 mg; Superblock medium: 46 ± 4 mg; and Superblock small: 27 ± 3 mg). For Copperblock containers, this decrease was less with significant differences found only between large and small cavities (Copperblock large: 70 ± 7 mg; Copperblock medium: 54 ± 6 mg; and Copperblock small: 41 ± 3 mg). As cavity size decreased from large to medium, secondary lateral root dry weight decreased 51 and 23% with Superblock and

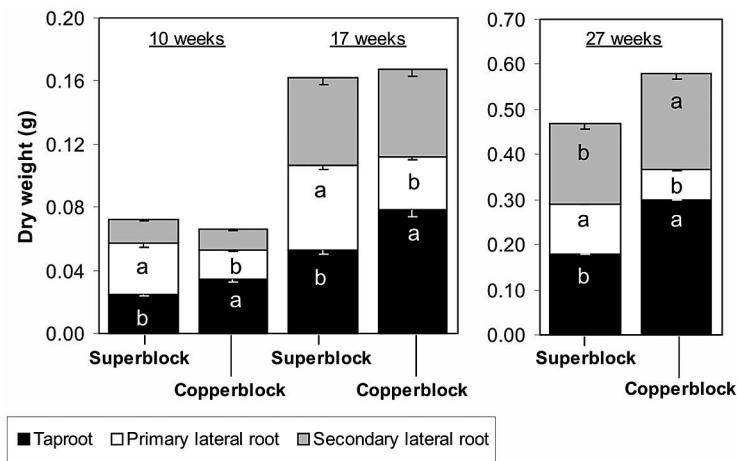


Figure 2. Dry weights of the taproot and primary and secondary lateral roots of container-grown longleaf pine seedlings in response to copper root pruning (Superblock or Copperblock), 10, 17, and 27 weeks after sowing. Error bars represent 1 SEM. Within a measurement period and root category, means associated with a different letter are significantly different at an α level of 0.05 by the Tukey-Kramer procedure. For clarity, the y-axis scales for 10 and 17 weeks postsowing and 27 weeks postsowing are different.

Copperblock containers, respectively. As cavity size decreased even more from medium to small, this variable decreased 41 and 24% with Superblock and Copperblock containers, respectively.

At 17 and 27 weeks postsowing, copper root pruning interacted with cavity size to significantly affect taproot dry weight (Table 1). At 17 weeks postsowing, the taproot dry weight of seedlings produced in large cavities was greater for Copperblock containers than for Superblock containers, and the taproot dry weight of seedlings produced in large cavities of both container types was greater than that of seedlings produced in small and medium cavities (Figure 3). By 27 weeks postsowing, the same relationship was apparent for seedlings produced in Superblock containers, but taproot dry weights were equivalent among Copperblock cavity sizes. Also, at this time, taproot dry weights of

seedlings produced in large cavities were statistically similar between the two container types.

RGP

After the 28-day RGP test, copper root pruning significantly affected dry weights of the residual root plug and the total root system (Table 2). Residual root plug dry weight was 13% greater in Copperblock containers than in Superblock containers. A similar effect was observed for total root system dry weight. Cavity size significantly affected residual root plug dry weight and egressed root dry weight by the end of the RGP test with greater values for large cavities and smaller values as cavity size decreased from large to small. Interaction between copper root pruning and cavity size revealed that total root system dry weights were

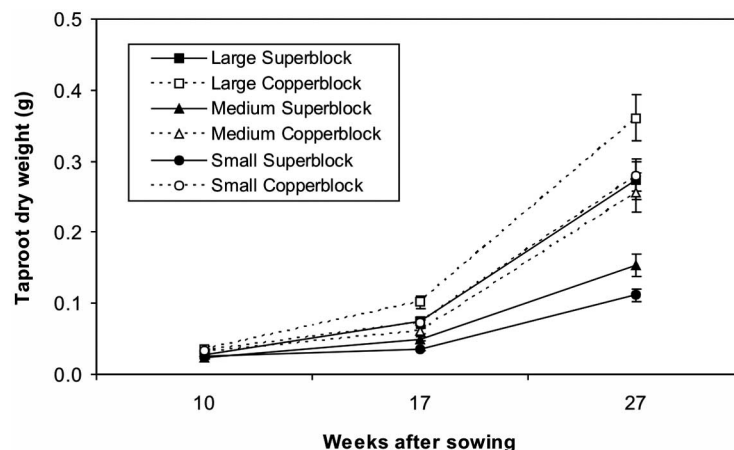


Figure 3. Taproot dry weight of container-grown longleaf pine seedlings in response to copper root pruning (Superblock or Copperblock), and cavity size (large, medium, or small), 10, 17, and 27 weeks after sowing. Error bars represent 1 SEM.

Table 2. Probabilities of a greater *F* value for longleaf pine seedling root system morphological variables and RGP in response to copper root pruning (Superblock or Copperblock) and cavity size (small, medium, or large) after the 27-week cultural period and being maintained in pots in the greenhouse for 28 days

Source of variation	df	Residual root plug dry weight	Total egressed root dry weight	Total root system dry weight	RGP ^a
P	1	0.0349	0.0603	0.0138	0.0002
S	2	0.0001	0.0046	0.0001	0.0548
P × S	2	0.0978	0.1463	0.0414	0.6441
D	2	—	—	—	0.0001
D × P	2	—	—	—	0.0001
D × S	4	—	—	—	0.3457
D × P × S	4	—	—	—	0.0086

P, copper root pruning; S, cavity size; D, root plug depth.

^a RGP represents egressed root dry weight by root plug depth after maintenance in pots of sand in a greenhouse for 28 days. Data were transformed to their square root values to establish normally distributed experimental errors.

similar among the medium cavities (0.93 ± 0.04 g) and among the large cavities (1.30 ± 0.04 g) and were significantly different between the small Copperblock (0.79 ± 0.05 g) and small Superblock cavities (0.56 ± 0.05 g).

The dry weight of egressed roots was significantly affected by copper root pruning and cavity size (Table 2). Three-way interaction between these effects and root plug depth significantly affected the dry weight of egressed roots. As depth increased from the top to the bottom of the root plug of the Superblock containers, the dry weight of egressed roots increased with medium and large cavities (Figure 4). The same trend was found with small Superblock cavities, but the dry weight of egressed roots from the top and middle root plug depths were statistically similar. The dry weight of egressed roots in the top and middle root plug depths of Superblock containers were not significantly affected by cavity size, but in the bottom root plug depth of Superblock containers, these variables were significantly lower for small cavities than for large cavities. For each

cavity size, dry weights of egressed roots from the Copperblock root plugs were similar among root plug depths.

Field Study

Across treatments, 97% of the seedlings survived, and all of these remained in the grass stage (height ≤ 12 cm) after the first growing season. No significant copper root pruning effects were observed on general seedling morphology 1 year after planting (Table 3). All seedling morphological variables were significantly affected by cavity size. RCDs of seedlings grown in medium and large cavities were comparable and significantly greater (32%) than those of seedlings grown in small cavities (Table 4). Significant reductions in foliage, stem, and root dry weights, number of first-order lateral roots, and dry weights of the taproot and lateral roots were also apparent as cavity size decreased from large to medium and from medium to small.

The dry weight of lateral roots egressed from the root

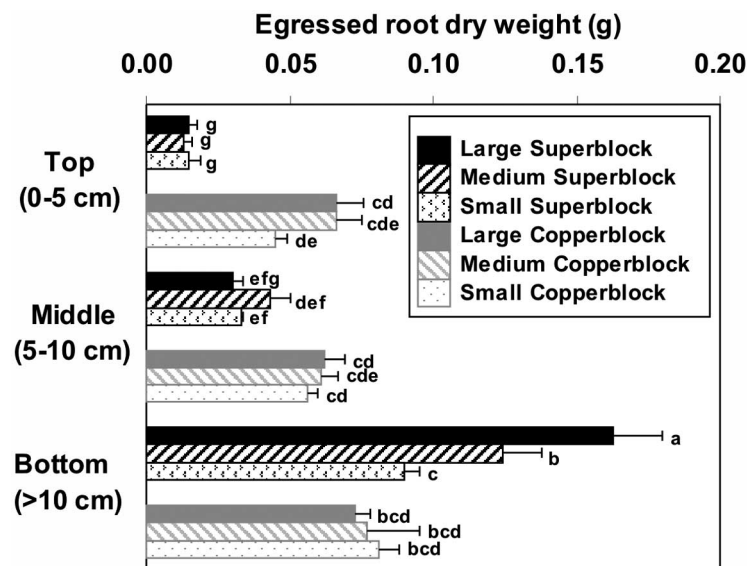


Figure 4. Dry weight of new lateral roots egressed from three root plug depths of container-grown longleaf pine seedlings planted in pots and maintained in a greenhouse for 28 days. Treatments were copper root pruning (Superblock or Copperblock) and cavity size (large, medium, or small), during seedling production. Error bars represent 1 SEM.

Table 3. Probabilities of a greater *F* value for longleaf pine seedling morphological variables 1 year after planting in response to copper root pruning (Superblock or Copperblock) and cavity size (small, medium, or large), during seedling production

Source of variation	df	RCD	FDW	SDW	FOLR	RDW	LRDW	TRDW
P	1	0.8853	0.9259	0.7383	0.2057	0.5127	0.3215	0.7136
S	2	0.0005	0.0001	0.0001	0.0006	0.0002	0.0002	0.0006
P × S	2	0.4862	0.9298	0.9781	0.7536	0.9166	0.8536	0.9551

P, copper root pruning; S, cavity size. RCD, root collar diameter; FDW, foliage dry weight; SDW, stem dry weight; FOLR, number of first-order lateral roots; RDW, total root system dry weight; LRDW, lateral root dry weight; TRDW, taproot dry weight.

Table 4. Mean morphological variables of longleaf pine seedlings 1 year after planting in response to cavity size (small, medium, or large) during seedling production

Seedling morphological variable	Cavity size		
	Small	Medium	Large
Root collar diameter (mm)	11.2 (0.5)b ^a	14.0 (0.6)a	15.6 (0.8)a
Foliage dry weight (g)	6.8 (0.6)c	12.2 (1.1)b	17.0 (1.1)a
Stem dry weight (g)	1.1 (0.1)c	2.0 (0.1)b	2.9 (0.3)a
Number of first-order lateral roots	5.2 (0.6)c	7.2 (0.7)b	9.2 (0.3)a
Total root system dry weight (g)	3.5 (0.3)c	5.8 (0.6)b	8.2 (0.7)a
Lateral root dry weight (g)	1.4 (0.1)c	2.2 (0.3)b	3.3 (0.2)a
Taproot dry weight (g)	2.1 (0.2)c	3.5 (0.3)b	4.9 (0.2)a

Values in parentheses are one standard error of the mean.

^a Variable means associated with a different letter are significantly different at an α level of 0.05 by the Tukey-Kramer procedure.

plug of seedlings 1 year after planting was significantly affected by cavity size (Table 5). The dry weight of egressed lateral roots, averaged among the four root plug depths, dropped from 0.37 to 0.16 g as cavity size decreased from large to small. The number, dry weight, and fraction of dry weight of lateral roots egressed from the root plug of planted seedlings was significantly affected by root plug depth and its interaction with copper root pruning. Although some significant differences were observed, distributions of the number and dry weight of lateral roots among the four root plug depths were relatively uniform when seedlings were grown in Superblock containers (Figure 5a and b). In contrast, these variables decreased significantly with an increase in root plug depth for seedlings grown in Copperblock containers. At the top root plug depth, the number and dry weight of egressed roots were more than twofold greater for seedlings grown in Copperblock containers than for seedlings grown in Superblock containers. The number and dry weight of egressed roots in the middle, bottom, and base root plug depth were similar between container types. One exception to this generalization was observed. In the bottom

root plug depth, the dry weight of egressed lateral roots was significantly less (52%) for seedlings grown in Copperblock containers than for those grown in Superblock containers. Absence of a significant three-way interaction for fraction of egressed root dry weight suggests that seedling size did not influence root egress responses to cavity size and copper root pruning.

Regression Analyses

One year after planting, multiple regression models containing a subset of six root system variables (FOLR, TAP, TOP, MID, BOT, and BAS) explained 77 and 78% of the RCD variability of seedlings grown in Superblock and Copperblock containers, respectively, regardless of cavity size (Table 6). With Superblock containers, partial coefficients of determination for TAP and FOLR were significant. With Copperblock containers, partial coefficients of determination for FOLR, TAP, and TOP were significant. For both Superblock and Copperblock containers, the majority of RCD variation was explained by TAP.

Table 5. Probabilities of a greater *F* value for the number and dry weight of roots egressed from the root plug in each of the four root plug depths (top, middle, bottom, and base), 1 year after planting in response to copper root pruning (Superblock or CopperblockTM) and cavity size (small, medium, or large), during seedling production

Source of variation	df	Number of egressed roots by root plug depth	Egressed root dry weight by root plug depth ^a	Fraction of egressed root dry weight by root plug depth
P	1	0.0291	0.0965	0.9921
S	2	0.1717	0.0003	0.9999
P × S	2	0.6069	0.9805	0.9996
D	2	0.0001	0.0001	0.0001
D × P	2	0.0001	0.0001	0.0001
D × S	4	0.2362	0.2591	0.2605
D × P × S	4	0.2132	0.0892	0.1614

P, copper root pruning; S, cavity size; D, root plug depth.

^a Data were transformed to their square root values to establish normally distributed experimental errors.

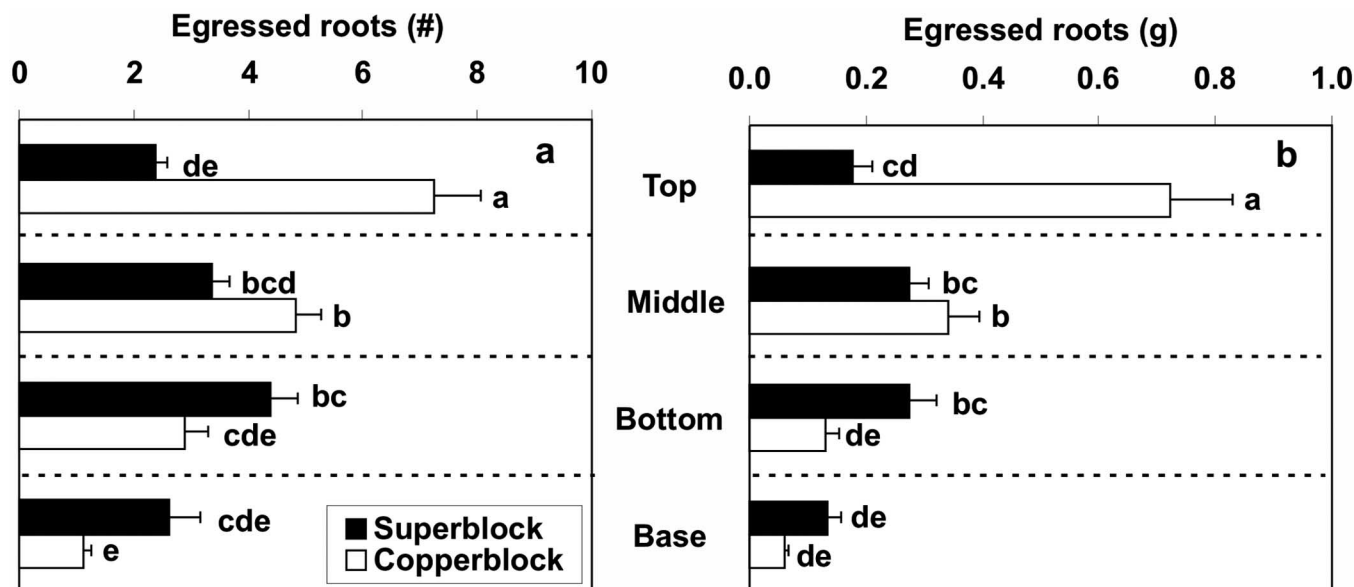


Figure 5. Number (a) and dry weight (b) of lateral roots, averaged among three cavity sizes, extending from longleaf pine seedling root plugs 1 year after planting in central Louisiana. Variables represent lateral roots in four root plug depths (top, middle, bottom, or base) between the root plug silhouette and either a 25-cm radius from the seedling stem (top, middle, or bottom) or a 20-cm depth (base). The treatment was copper root pruning (Superblock or Copperblock) during seedling production. Error bars represent 1 SEM. Means associated with a different letter are significantly different at an α level of 0.05 by the Tukey-Kramer procedure.

Table 6. Coefficients of determination and probabilities of a greater F value for multiple regressions between the RCD of excavated 1-year-old longleaf pine seedlings produced in Superblock or Copperblock containers and six root system variables

Container type	Partial R^{2a} (probability > F)						Model R^{2b}
	FOLR	TAP	TOP	MID	BOT	BAS	
Superblock	0.0157 (0.0352)	0.7498 (0.0001)	0.0053 (0.2143)	0.0011 (0.5290)	0.0006 (0.6736)	0.0005 (0.6975)	0.7655 (0.0001)
Copperblock	0.0361 (0.0015)	0.6190 (0.0001)	0.1211 (0.0001)	0.0060 (0.1776)	0.0009 (0.5765)	0.0010 (0.6005)	0.7761 (0.0001)

Root system variables were the number of first-order lateral roots (FOLR), taproot dry weight (TAP), and egressed root dry weight from the top (TOP), middle (MID), bottom (BOT), and base (BAS) root plug depths of the excavated seedlings. For each equation, the sample size is 72.

^a R^2 , coefficient of determination.

^b The model R^2 was determined with variables that were significant at an α level of 0.05.

Analyses of RCD-TOP relationships required that RCD be transformed to natural logarithm values to achieve normally distributed residuals. For all three cavity sizes, significant coefficients of determination were found for relationships between RCD and BOT in Superblock containers and between log RCD and TOP in Copperblock containers (Table 7). Linear relationships between RCD and either MID or BAS were significant for only one cavity size of each container type and were characterized by smaller coefficients of determination compared with those of the RCD-BOT and log RCD-TOP relationships. Among the RCD-BOT relationships of the three Superblock cavity sizes there were no significant slope differences (Figure 6a). The y-intercept of the RCD-BOT relationship of small Superblock containers, however, was significantly less than that of the medium and large Superblock containers. Similar relationships among Copperblock cavity sizes were absent (Figure 6b). The slope of the log RCD-TOP relationship of small Copperblock cavities was significantly greater than that of the medium Copperblock cavities (Figure 6d). The y-intercept of the log RCD-TOP relationship for small Cop-

perblock cavities was significantly less than that of the medium and large Copperblock cavities. Similar relationships among Superblock cavity sizes were absent (Figure 6c).

Discussion

Root System Development

Dry weight accumulation patterns during the seedling production phase of our study confirm that longleaf pine seedling and cavity sizes are correlated when conventional containers are used (Landis et al. 1990). With copper-coated containers, however, patterns of taproot and primary and secondary lateral root dry weight accumulation shifted and seedlings seemed to benefit when small cavities were used. At the end of the cultural period, for example, taproot dry weights of Copperblock-grown seedlings were similar among the three cavity sizes and were 1.3-fold greater than those of the small and medium Superblock-grown seedlings.

By 17 weeks postsowing, secondary lateral root dry

Table 7. Simple linear relationships (i.e., $y = b_1 + b_2x$), between RCD and the dry weight of egressed roots from either the top, middle, bottom, or base root plug depth of excavated 1-year-old longleaf pine seedlings grown in three cavity sizes of Superblock or Copperblock containers

Independent variable	Cavity size	b_1	b_2	S_{y-x}	Pr > F	R^2
Superblock ^a						
TOP ^b	Small	2.2821	0.5918	0.1853	0.0579	0.1540
TOP	Medium	2.5539	0.5523	0.2026	0.1171	0.1079
TOP	Large	2.6989	0.2138	0.1532	0.0267	0.2040
MID	Small	9.8762	4.4383	2.0504	0.2006	0.0733
MID	Medium	12.7544	4.3541	2.6940	0.0469	0.1678
MID	Large	14.8571	3.7680	2.7993	0.1068	0.1139
BOT	Small	9.7115	4.5366	1.7191	0.0024	0.3486
BOT	Medium	13.1727	4.1052	2.6959	0.0477	0.1665
BOT	Large	14.5362	4.1243	2.6340	0.0223	0.2154
BAS	Small	10.6736	-0.6991	2.1292	0.8964	0.0008
BAS	Medium	13.3345	7.3674	2.8016	0.1323	0.1000
BAS	Large	14.7841	5.594	2.6503	0.0260	0.2057
Copperblock ^a						
TOP ^b	Small	2.2653	0.3865	0.1357	0.0003	0.4498
TOP	Medium	2.4963	0.1689	0.1042	0.0002	0.4757
TOP	Large	2.4922	0.1994	0.1490	0.0003	0.4581
MID	Small	10.7635	6.0894	1.9776	0.0576	0.1543
MID	Medium	12.3927	3.6809	1.8468	0.0705	0.1411
MID	Large	13.2181	3.7856	2.3413	0.0025	0.3460
BOT	Small	11.7596	-0.0165	2.1505	0.9976	0.0000
BOT	Medium	13.2815	2.2151	1.9602	0.4001	0.0324
BOT	Large	14.0288	7.7888	2.6538	0.0529	0.1598
BAS	Small	11.0988	11.2575	2.0433	0.1381	0.0972
BAS	Medium	13.3522	5.4703	1.8975	0.1467	0.0933
BAS	Large	14.3912	12.4658	2.5922	0.0292	0.1984

Values of b_1 and b_2 are y-intercept and slope coefficients, respectively. The dependent variable (y) is RCD and the independent variable (x) is top (TOP), middle (MID), bottom (BOT), or base (BAS) root plug depth. For each equation, the sample size is 24. S_{y-x} , root mean square error; Pr > F, probability of a greater F value; R^2 , coefficient of determination.

^a For all cavity sizes, TOP and MID were 0–5 and 5–10 cm, respectively; and for the small, medium, and large cavities, BOT was 10–13.3, 10–14.9, and 10–15.2 cm, respectively. BAS represented the depth extending 20 cm vertically from the base of the root plug.

^b For regression analyses, values of TOP were transformed to ensure that residuals were normally distributed.

weights declined with a decrease in cavity size. The magnitude of this decline, however, was less for seedlings grown in Copperblock cavities than for those grown in Superblock cavities. As a result, the secondary lateral root dry weight of seedlings grown in small Copperblock cavities was only 24% less than that of seedlings grown in medium Copperblock cavities, but the secondary lateral root dry weight of seedlings grown in small Superblock cavities was 41% less than that of seedlings grown in medium Superblock cavities. At the end of the cultural period, the effect of copper on secondary lateral root dry weight no longer varied by cavity size. At this mid-production time, however, root system differences between small Copperblock- and Superblock-grown seedlings translated into 42% more shoot dry weight when root systems were pruned with copper.

These trends suggest that superior seedling growth was accompanied by greater taproot growth and early establishment of secondary lateral roots when small cavities were treated with copper. With an increase in fine absorbing roots, the uptake of mineral nutrients from the root plug may have been increased so that seedling growth was accelerated. If copper root pruning increases the root absorbing surface area during seedling production, it may provide an opportunity to improve the efficiency of fertilizer application and produce larger seedlings in smaller cavities.

RGP and First-Year Field Performance

One year after planting, growth responses to cavity size were similar to those observed during seedling production with a positive relationship between the size of cavities and seedlings. These results are consistent with the observations of others for longleaf pine, indicating that as long as cavity density during seedling production does not exceed 538 m⁻², seedling sizes before and after planting are correlated (Barnett and Brissette 1986, Brissette et al. 1991).

General seedling morphology was not affected by copper root pruning 1 year after planting. This treatment, however, caused distinct changes in the RGP of planted seedlings and the root system morphology of 1-year-old seedlings. Seedlings produced in Superblock containers averaged 9, 23, and 68% of their RGP in the top, middle, and bottom of the root plug, respectively. One year after planting, the new lateral root growth of these seedlings was relatively uniform in its vertical distribution with an average of 19, 29, 33, and 19% of roots emerging from the top, middle, bottom, and base of root plugs, respectively. Seedlings produced in Copperblock containers were characterized by equivalent amounts of RGP among the top (32%), middle (29%), and bottom (37%) of the root plug, but averaged 52, 28, 14, and 6% of new roots emerging from the top, middle, bottom, and base of root plugs, respectively, 1 year after planting.

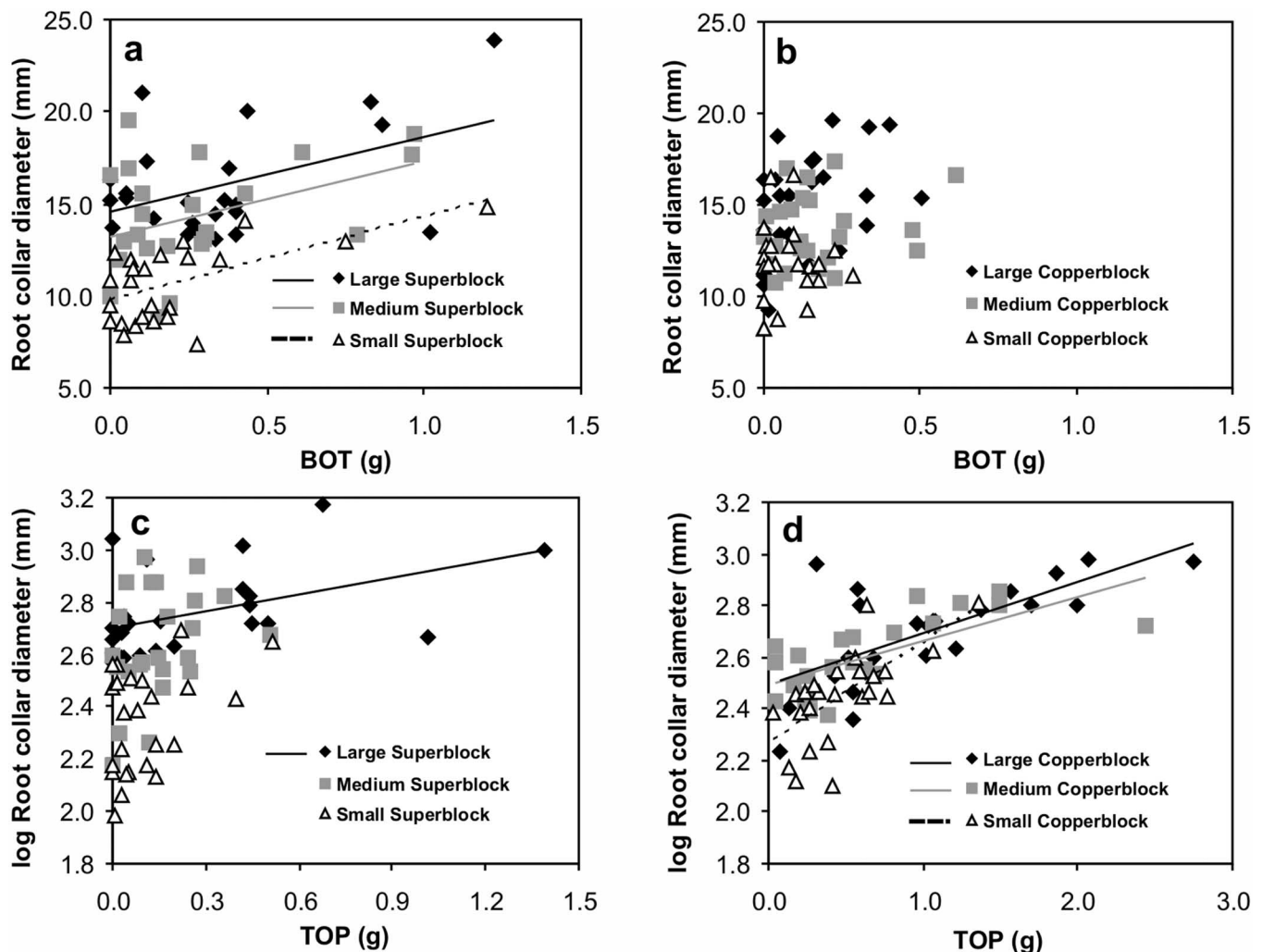


Figure 6. Regression relationships between RCD and the dry weight of roots emerging from the bottom root plug depth (BOT) of small, medium, and large Superblock (a) and Copperblock (b) cavities and regression relationships between the natural logarithm of RCD and the dry weight of roots emerging from the top root plug depth (TOP) of small, medium, and large Superblock (c) and Copperblock (d) cavities. Natural logarithm transformation of TOP was needed to achieve normally distributed residuals. Note the difference in range associated with the x-axis in c and d. Lines represent regressions with significant coefficients of determination (Table 7) for large (solid black), medium (solid gray), and small (dashed black) cavity sizes.

Primary lateral roots near the soil surface become dominant and larger than those deeper in the soil, in part because the pattern of carbon allocation to the root system favors their development (Coutts 1987, Coutts et al. 1999). By changing the distribution of RGP along the depth of the root plug, copper root pruning facilitated root growth near the surface of the soil, which may improve the vertical stability of the stem (Burdett et al. 1986).

In addition to potential benefits of copper root pruning to structural integrity, this treatment may also have improved the ability of our seedlings to acquire soil resources. The fertility of forest soils is frequently dominated by organic matter deposition at the forest floor and the subsequent enrichment of the A horizon by organic matter and mineral nutrients (McColl and Gressel 1995). Similarly, organic matter affects soil water-holding capacity, and both organic matter and soil water content affect mechanical impedance to root elongation (Kramer 1983, Bennie 1996). When seedlings were raised in Superblock containers, only 19% of the roots that grew during the first year after planting were

found in the 0 to 5 cm depth. In contrast, the majority of new root growth occurred at this depth with Copperblock-raised seedlings (52%). If there were steep gradients of fertility with soil depth, the vertical distribution of lateral roots after the first year of establishment may have improved the mineral nutrient uptake of the Copperblock-raised seedlings. Perhaps more important, however, is the potential advantage that this rooting pattern provides to water uptake.

Periodic water deficit severe enough to reduce tree vigor is common across the southern pine region during May through September (Barrett 1995, Walker and Oswald 2000). Precipitation events during the later portion of the growing season are often short-lived and accompanied by high rates of evaporation (Barrett 1995, Walker and Oswald 2000). Soil recharge occurs as field capacity is achieved in progressively deeper horizons of the soil (Kramer 1983). By mid-summer, therefore, precipitation events potentially wet the surface soil alone. By increasing root growth near the surface of the soil, copper root pruning has the potential to

improve water-foraging ability. It is likely that any modification of the root system that increases water absorption during late summer and fall stimulates seedling growth and development. Conversely, shallow-rooted seedlings may be more susceptible to water stress than more deeply rooted seedlings during prolonged drought.

Seedlings produced in Superblock containers had equivalent vertical distributions of egressed root dry weight after the RGP test and 1 year postplanting. For seedlings produced in Copperblock containers, however, vertical patterns of egressed root dry weight were different at these two times. During the RGP test, root growth was relatively unconstrained by the planting environment. For Superblock-raised seedlings, consistent root egress patterns suggest that distribution after planting was primarily controlled by RGP. Inconsistency between these two patterns for Copperblock-raised seedlings suggests that the distribution of root egress from the plug was controlled by both RGP and the planting environment. Copper root pruning, therefore, may have led to a pattern of RGP that allowed seedlings to benefit from surface soil resources after planting.

Within each Copperblock and Superblock root plug depth, comparable amounts of new root weight were produced among cavity sizes after the RGP test and 1 year in the field. Specifically, 1 g of new root during the RGP test corresponded to approximately 12, 8, and 3 g of new roots emerging from the top, middle, and bottom plus base of 1-year-old root plugs produced in Superblock containers, respectively and 12, 6, and 2 g of new roots emerging from the top, middle, and bottom plus base of 1-year-old root plugs produced in Copperblock containers, respectively. For both container types, therefore, RGP was a predictor of postplanting root growth within each root plug depth.

To understand the value of placing RGP in the top, middle, or bottom of the root plug, we assessed relationships between first-year field performance and new root development. RCD is often used to gauge field performance (Barnett and Brissette 1986, Johnson and Cline 1991). With RCD as a surrogate for field performance, our regression analyses revealed that to some degree, first-year seedling performance benefited from root egress at all root plug depths regardless of copper root pruning treatment. This relationship, however, was most often seen when seedlings were grown in large cavities. The absorption and conductance of water that is essential to the growth of southern pine seedlings depends on new roots that elongate after planting (Carlson 1986, Hallgren and Tauer 1989, Sword Sayer et al. 2005). Perhaps seedlings produced in the small and medium cavities had not yet reached the size at which their newly developed roots were challenged to meet the demand for water by the developing shoot.

When seedlings were grown in Superblock containers, root growth from the bottom root plug depth had a stronger relationship with first-year RCD than that from the top, middle, or base of the root plug. For these seedlings, significantly different y-intercepts of regressions between first-year RCD and root growth from the bottom root plug depth were found between small cavities and both medium and large cavities. The slopes of these relationships, however, were similar. This finding suggests that regardless of how

much root egress occurs from the bottom root plug depth, seedlings produced in small Superblock cavities will retain their small stature during the first year after planting.

With seedlings raised in Copperblock containers, root growth from the top rather than the bottom root plug depth had the greatest effect on first-year RCD. Similarity between the y-intercept and slope coefficients associated with medium and large Copperblock cavities indicated that the rate at which first-year RCD grew in response to root egress from the top 5 cm of the root plug was equivalent for seedlings produced in either of these two cavity sizes. For seedlings produced in small cavities, the regression between first-year RCD and root growth from the top root plug depth was characterized by a significantly smaller y-intercept than that of seedlings produced in either medium or large cavities. Also, the slope of this regression was significantly greater than that for seedlings grown in medium cavities. Thus, the amount of first-year root collar growth per unit of root egress from the top 5 cm of the root plug was greater using small than medium Copperblock cavities. A similar but nonsignificant trend was observed with seedlings produced in small and large Copperblock cavities. These results indicate that among the seedlings produced in small Copperblock cavities, those producing the largest amount of root growth from the top of the root plug may approach seedlings produced in larger cavities with respect to RCD size. This behavior demonstrates the potential benefit of root growth near the soil surface when planted seedlings are smaller than the size recommended for optimum field performance. Together with the relationship we observed between secondary lateral root growth and shoot size during seedling production, these results suggest that copper root pruning could be used to compensate, in part, for disadvantages of using small cavities if space and cost limitations during seedling culture dictated their use.

Multiple regressions between RCD and six root system variables advocate that first-year seedling performance is improved by number of first-order lateral roots and taproot dry weight. Past research has established the value of these variables when seedling quality is assessed (Johnson and Cline 1991, Kormanik et al. 1998). None of the variables describing root egress by root plug depth contributed significantly to the model of first-year RCD when seedlings were grown in Superblock containers. In contrast, first-year root growth from the top of the root plug explained 12% of the variation associated with the RCD of seedlings produced in Copperblock containers. Based on these results, we propose that surface root growth above that observed in the absence of copper root pruning works together with physiological and environmental factors to stimulate container-grown longleaf pine seedling growth. Ramsey et al. (2003) attributed positive relationships between the development of longleaf pine seedlings and chemical control of local vegetation to a reduction in belowground competition for soil resources. At this early stage of their development, we did not detect an effect of copper root pruning on the general morphology of these seedlings. As they mature from the grass stage to the hardy growing stage (Wahlenberg 1946), and subsequently, become saplings, we will continue to assess early vertical root distribution and its possible effect

on belowground competition as a strategy by which longleaf pine seedlings become more competitive with adjacent vegetation and achieve improved field performance.

Summary

Our results introduce the concept that root system morphology is linked to field performance. Copper root pruning modified longleaf pine seedling root systems by increasing taproot size and secondary lateral root growth, reducing primary lateral root growth, and shifting RGP from the bottom of the root plug to its top. These copper-induced changes led to the production of larger seedlings when small cavities were used. One year after planting, adjustments to root system morphology correlated with an increase in root growth near the surface of the soil. For copper-treated seedlings, first-year field performance, measured as RCD, was a function of root egress from the top of the root plug. Furthermore, root egress from the top of the root plug was more beneficial to first-year field performance for seedlings grown in small Copperblock cavities compared with medium and large Copperblock cavities. Favorable effects of copper root pruning on seedlings grown in small cavities affords an opportunity to produce larger seedlings in smaller cavities, and enhanced root growth in the surface soil has the potential to increase soil resource acquisition and vertical stability. Research will continue to assess whether the early effects of copper root pruning are beneficial as planted longleaf pine mature.

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