

Longleaf Pine Root System Development and Seedling Quality in Response to Copper Root Pruning and Cavity Size

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

ABSTRACT

Cultural practices that modify root system structure in the plug of container-grown seedlings have the potential to improve root system function after planting. Our objective was to assess how copper root pruning affects the quality and root system development of longleaf pine seedlings grown in three cavity sizes in a greenhouse. Copper root pruning increased seedling size, the allocation of root system dry weight to the taproot, and the fraction of fibrous root mass allocated to secondary lateral roots compared with primary lateral roots. It decreased the allocation of root system dry weight to primary lateral roots and led to a distribution of root growth potential that more closely resembled the root growth of naturally sown seedlings. These effects of copper root pruning may benefit longleaf pine establishment. However, because copper root pruning increased competition for cavity growing space among the taproot and fibrous roots, we suggest that recommendations regarding cavity size and seedling quality parameters be tailored for copper-coated cavities.

Keywords: copper oxychloride, *Pinus palustris* Mill., root growth potential, taproot, toppling

The establishment of longleaf pine (*Pinus palustris* Mill.) by artificial regeneration is successful across the natural range of this species with the renewed use of repeated fire, which helps to control competing vegetation (Stanturf et al. 2004), and the development of technology to produce planting stock in containers (Barnett and McGilvray 1997). Planting container-grown longleaf pine seedlings normally yields well-stocked stands. In some circumstances, however, young longleaf pine planted as container-grown seedlings become unstable in high winds. This instability, referred to as toppling, is characterized by poor stem form, ranging from an increase in stem sinuosity to windthrow (Burdett 1979, South et al. 2001). In some cases, toppling has been linked to site preparation, regeneration, and thinning methods that adversely affect root system structure and in turn reduce tree stability (Burdett 1979, Fredericksen et al. 1993, Zwolinski et al. 1993).

The root system of naturally regenerated seedlings is characterized by the horizontal elongation of primary lateral roots from around the circumference and along the length of the taproot. Conversely, cavity shape and size restrict the taproot and primary lateral roots of container-grown seedlings. In most situations, container-grown seedlings adapt to these limitations. For example, in response to air-pruning of the taproot at the bottom of the cavity, one or more adventitious roots expressing positive geotropism develop proximal to the tip of the taproot (Esau 1977, South et al. 2001). Alternatively, one or more existing primary lateral roots grow vertically and replace the arrested taproot (South et al. 2001).

Other root system irregularities are the vertical growth of primary lateral roots along the cavity wall to the drain hole where air-pruning takes place and the horizontal growth of these major roots, which leads to root spiraling (Barnett and Brissette 1986, Romero et al. 1986, Brissette et al. 1991). Although these roots elongate into mineral soil after planting, vertical tree stability may be compromised by unnatural primary lateral root form (Burdett et al. 1986, Fredericksen et al. 1993, Zwolinski et al. 1993). Furthermore, if spiraling leads to root strangulation, tree vigor and stability will be jeopardized (Burdett 1979).

The application of a copper-containing compound to the wall of container cavities affects root system development in several ways. For example, the tips of elongating primary roots are chemically pruned, which arrests their elongation (McDonald et al. 1984, Ruehle 1985, South et al. 2005). In the absence of the root apical meristem, the normal balance of plant growth regulators is disrupted, and root primordia distal to the root tip elongate (Aloni et al. 2006). This phenomenon prevents the vertical and horizontal elongation of major roots along the cavity wall and increases the proliferation of fibrous roots inside the root plug (Burdett et al. 1986, Tsakalimi and Ganatsas 2006). Copper root pruning may also lead to a distribution of root growth potential (RGP) that more closely mimics that of naturally regenerated pine (Burdett et al. 1986).

Because root collar and taproot size are closely correlated in container-grown longleaf pine seedlings, modification of root system development by container type may interfere with interpretation of

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This article uses metric units; the applicable conversion factors are: millimeter (mm): 1 mm = 0.039 in.; centimeters (cm): 1 cm = 0.39 in.; cubic centimeters (cm³): 1 cm³ = 0.155 in.³; cubic meters (m³): 1 m³ = 35.3 ft³; kilograms (kg): 1 kg = 2.2 lb; liter (l): 1 l = 61.02 in.², = 0.908 quart (dry), = 1.057 quart (liquid).

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Table 1. Container types varying in copper root pruning treatment and cavity size used to produce longleaf pine seedlings.

| Container type | Cavity size treatment | Copper root pruning treatment | Cavities per unit/cavities per m ² | Cavity volume (ml) | Cavity depth(cm)..... | Cavity top diameter |
|---------------------|-----------------------|-------------------------------|---|--------------------|--------------------------------|---------------------|
| Superblock 198/60 | Small | None | 198/936 | 60 | 13.3 | 2.8 |
| Superblock 112/105 | Medium | None | 112/530 | 108 | 15.0 | 3.6 |
| Superblock 77/170 | Large | None | 77/364 | 170 | 15.2 | 4.2 |
| Copperblock 198/60 | Small | Root Trim ^a | 198/936 | 60 | 13.3 | 2.8 |
| Copperblock 112/105 | Medium | Root Trim | 112/530 | 108 | 15.0 | 3.6 |
| Copperblock 77/170 | Large | Root Trim | 77/364 | 170 | 15.2 | 4.2 |

^a Roots pruned with copper oxychloride applied to cavity wall.

rootcollar diameter as the standard, nondestructive measure of seedling quality. Other nondestructive measures of seedling quality would be valuable. One option, root-bound index (RBI), reflects the ratio of rootcollar and cavity diameters (South et al. 2005, South and Mitchell 2006). This variable is an indirect, nondestructive measure of how well the cavity accommodates both the taproot and fibrous roots. With the determination of acceptable ranges of values, rootcollar diameter and RBI could be used together to indicate seedling size, the progression of fibrous root growth, and the potential for root binding.

It is hypothesized that cavity size and copper root pruning affect root system development and, subsequently, standard measures of seedling quality for longleaf pine. We further hypothesize that copper root pruning affects the vertical distribution of RGP along the length of the root plug. Our objectives were to assess how cavity size and copper root pruning affect longleaf pine root system development during production, seedling quality at the end of the cultural period, and RGP before planting. Root system development was assessed by the fraction of root dry weight as taproot and primary and secondary lateral roots. Seedling quality was evaluated by the standard, nondestructive measure of rootcollar diameter, an alternative nondestructive measure, RBI, and two other destructive variables: number of primary lateral roots and shoot-root ratio.

Materials and Methods

Greenhouse Experiment

Longleaf pine seeds of mixed seedlots from Florida were sown in six container types in April 2004. Treatments were Superblock and Copperblock containers (Beaver Plastics Ltd., Acheson, Alberta, Canada) that differed by three cavity sizes (Table 1). Superblock and Copperblock containers were distinguished by the application of Root Trim (US Environmental Protection Agency Reg. No. 81293-2, containing copper oxychloride) to the cavity wall of Copperblock cavities.

Using standard cultural practices (Barnett and Brissette 1986), longleaf pine seedlings were grown in four, seven, and nine Superblock and Copperblock containers having small, medium, and large cavities, respectively. In April, seeds were sown in container cavities containing a commercial peat moss and vermiculite mixture and Osmocote 19-6-12 slow-release fertilizer (Scotts Miracle Grow Co., Marysville, OH) at a rate of 3.6 kg/m³. Containers were placed in random locations on greenhouse benches, and seedlings were fertilized weekly by broadcast application of a 0.05–0.06% solution of water-soluble fertilizer (i.e., 20-20-20) to saturation. Seedlings were fertilized between early June and the end of September 2004. Seedlings were grown for 27 weeks under ambient light in a greenhouse where air temperature was maintained at 20–25°C.

At 10, 17, and 27 weeks after sowing, 25 seedlings were randomly selected from each container type. The growing medium was washed from the root system, rootcollar diameter (RCD) was measured, and the stem was severed from the root system. Primary lateral roots ≥ 0.5 cm in length were counted. Primary lateral roots were excised from the taproot, and all secondary lateral roots were stripped or cut from the primary lateral roots. Dry weights of the shoot, taproot, primary lateral roots, and secondary lateral roots were determined after drying to a constant weight at 70°C. Shoot-root ratios and fractions of root system dry weight as taproot and as primary and secondary lateral roots were calculated. RBI was calculated by dividing RCD by cavity diameter and expressing this value as a percentage (i.e., 0–100%) (South et al. 2005, South and Mitchell 2006).

RGP Experiment

At the end of the 27-week cultural period, 25 seedlings were randomly selected from each container type. Root plugs remained intact, and seedlings were planted in pots (1.5 l volume) of masonry sand. Potted seedlings were placed on benches in a greenhouse using a randomized complete block layout with five blocks representing location in the greenhouse. Each block contained five potted seedlings from each of the six container types. Seedlings were well watered and maintained for 28 days under ambient light and air temperature ranging between 20 and 25°C.

A root plug template of each cavity size was drawn and delineated into three root plug depths (top, middle, bottom). Two root plug depths were similar among all container types: 0–5 and 5–10 cm. For the small container types, the third root plug depth was 10–13.3 cm, and the depths for the medium and large container types were 10–14.9 and 10–15.2 cm, respectively. After 28 days, the masonry sand was washed from seedling root systems. Root plugs were laid over the appropriate template and visually partitioned into the three root plug depths. Then, egressed roots, ≥ 0.5 cm in length, were excised from the outer face of each root plug depth and counted.

Statistical Analyses

All data were transformed to square root or natural logarithm values as needed to establish normally distributed experimental errors. Ten, 17, and 27 weeks after seedlings were sown in the greenhouse study, seedling variables (RCD, number of primary lateral roots, shoot-root ratio, RBI) were evaluated by analysis of variance (ANOVA) using a completely random 2 × 3 factorial design with two main effect treatments: copper root pruning (no copper root pruning: Superblock; copper root pruning: Copperblock), and cavity size (small, medium, large). Fractions of total root system dry weight as taproot and as primary and secondary lateral root dry

Table 2. Mean squares and probabilities of a greater *F* value for root collar diameter, number of primary lateral roots, shoot-root ratio, and root-bound index (RBI) of longleaf pine seedlings in response to copper root pruning and cavity size at three times during the cultural period (i.e., 10, 17, and 27 weeks postsowing).

| Source of variation | df ^a | Root collar diameter | | Number of primary lateral roots ^b | | Shoot-root ratio ^c | | RBI ^c | |
|-----------------------|-----------------|----------------------|---------------|--|---------------|-------------------------------|---------------|------------------|---------------|
| | | MS | Pr > <i>F</i> | MS | Pr > <i>F</i> | MS | Pr > <i>F</i> | MS | Pr > <i>F</i> |
| 10 weeks after sowing | | | | | | | | | |
| P ^d | 1 | 1.3067 | 0.0001 | 0.1457 | 0.7221 | 1.5233 | 0.0001 | 0.3687 | 0.0002 |
| S ^d | 2 | 0.4065 | 0.0088 | 9.8466 | 0.0003 | 0.3739 | 0.0049 | 0.1154 | 0.0115 |
| P × S | 2 | 0.0361 | 0.6486 | 4.3280 | 0.0253 | 0.0217 | 0.7258 | 0.0042 | 0.8462 |
| Residual | 144 | 0.0831 | | 1.1471 | | 0.0677 | | 0.0251 | |
| 17 weeks after sowing | | | | | | | | | |
| P | 1 | 2.1361 | 0.0002 | 0.1344 | 0.6413 | 0.3410 | 0.0347 | 0.3963 | 0.0001 |
| S | 2 | 9.6605 | 0.0001 | 5.4820 | 0.0002 | 0.0425 | 0.5691 | 1.3802 | 0.0001 |
| P × S | 2 | 0.6633 | 0.0129 | 0.0516 | 0.9197 | 0.0368 | 0.6138 | 0.1410 | 0.0011 |
| Residual | 144 | 0.1480 | | 0.6166 | | 0.0751 | | 0.0198 | |
| 27 weeks after sowing | | | | | | | | | |
| P | 1 | 18.5856 | 0.0001 | 0.2116 | 0.6605 | 0.2290 | 0.1613 | 1.1445 | 0.0001 |
| S | 2 | 32.2622 | 0.0001 | 3.1363 | 0.0630 | 0.0893 | 0.4634 | 1.6325 | 0.0001 |
| P × S | 2 | 2.7042 | 0.0202 | 0.5153 | 0.6303 | 0.0617 | 0.5872 | 0.2211 | 0.0019 |
| Residual | 144 | 0.6747 | | 1.1129 | | 0.1155 | | 0.0339 | |

^a df, degrees of freedom; MS, mean square; Pr > *F*, probability of a greater *F* value; P, copper root pruning treatment; S, cavity size treatment.

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

^c Data were transformed to their natural logarithm values to establish normally distributed experimental errors.

weights were evaluated by ANOVA using a completely random 2 × 3 factorial split plot in time design. The whole-plot effects were copper root pruning and cavity size, and the subplot effect was cultural period (10, 17, and 27 weeks after sowing). Cultural period and its interactions with copper root pruning and cavity size were tested to evaluate developmental responses in root system morphology over the 27-week cultural period.

At the end of the 28-day RGP test, numbers of egressed roots from the root plug depths were evaluated by ANOVA using a randomized complete block 2 × 3 factorial split plot in space design with five blocks. The whole-plot effects were copper root pruning and cavity size, and the subplot effect was root plug depth (top, middle, bottom).

Normality tests and main and interaction effects were considered significant at an α level of 0.05. As warranted, means were compared by the Tukey-Kramer procedure and considered significantly different at an α level of 0.05.

Results

Greenhouse Experiment

Ten weeks after sowing, RCD was significantly affected by copper root pruning and cavity size (Table 2). At this time, RCD was increased by copper root pruning (not root pruned: 1.73 ± 0.03 mm [± standard error]; copper root pruned: 1.90 ± 0.04 mm), and the use of large cavities was compared with small cavities (small: 1.73 ± 0.04 mm, medium: 1.79 ± 0.04 mm; large: 1.90 ± 0.05 mm). Significant treatment interaction resulted in a larger RCD with small cavities at 17 (data not shown) and 27 weeks postsowing (Figure 1a) when cavities were copper-coated. With medium and large cavities, however, copper coating did not significantly affect RCD at 17 and 27 weeks postsowing. At 27 weeks postsowing, RCD was larger when seedlings were grown in large cavities compared with medium and small cavities regardless of copper root pruning treatment. At this time, the RCD in small cavities was significantly less than that in medium cavities in the absence of copper root pruning, but RCD was similar between small and medium cavities with copper root pruning.

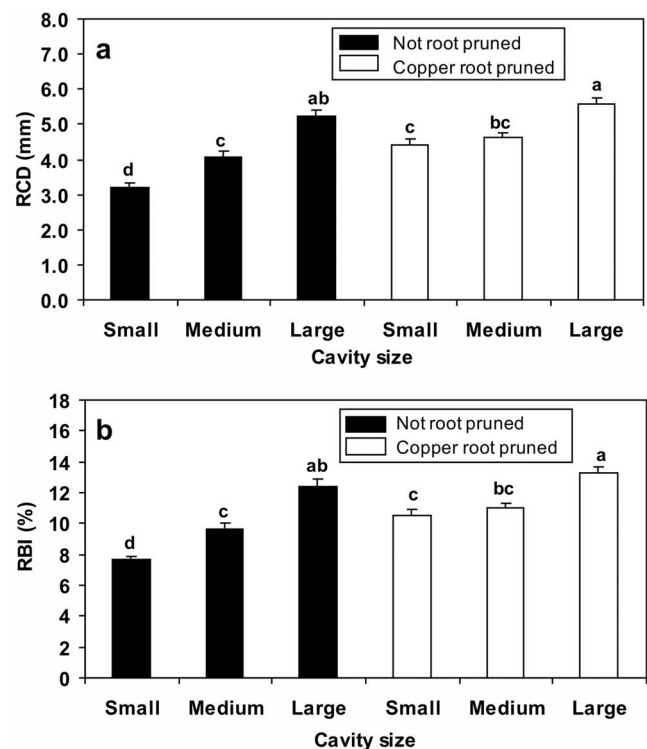


Figure 1. Container-grown longleaf pine seedling RCD (a), and RBI (b) in response to copper root pruning (not root pruned, copper root pruned) and cavity size (small, medium, large) 27 weeks after sowing. Error bars represent 1 SEM.

The number of primary lateral roots at least 0.5 cm long was significantly affected by treatment interaction at 10 weeks postsowing, but treatment effects were not detectable by the end of the 27-week cultural period (Table 2). At 10 weeks postsowing, the number of primary lateral roots was less for copper root-pruned seedlings grown in medium cavities (19.9 ± 1.9) compared with seedlings grown in large cavities regardless of copper root pruning

Table 3. Mean squares and probabilities of a greater *F* value for fraction of longleaf pine seedling root system dry weight as taproot and primary and secondary lateral roots in response to copper root pruning, cavity size, and cultural period (i.e., 10, 17, and 27 weeks postsowing).

| Source of variation | df ^b | Fraction of root system dry weight | | | | | |
|----------------------------------|-----------------|------------------------------------|---------------|------------------------------------|---------------|-------------------------|---------------|
| | | Taproot ^a | | Primary lateral roots ^a | | Secondary lateral roots | |
| | | MS | Pr > <i>F</i> | MS | Pr > <i>F</i> | MS | Pr > <i>F</i> |
| Copper root pruning (<i>P</i>) | 1 | 1.3240 | 0.0001 | 2.0668 | 0.0001 | 0.0070 | 0.2925 |
| Cavity size (<i>S</i>) | 2 | 0.1066 | 0.0001 | 0.0112 | 0.0609 | 0.2042 | 0.0001 |
| <i>P</i> × <i>S</i> | 2 | 0.0119 | 0.1031 | 0.0435 | 0.0001 | 0.0367 | 0.0035 |
| Error <i>a</i> ^c | 144 | 0.0051 | | 0.0039 | | 0.0062 | |
| Cultural period (<i>T</i>) | 2 | 0.0564 | 0.0001 | 1.1704 | 0.0001 | 1.4139 | 0.0001 |
| <i>T</i> × <i>P</i> | 2 | 0.0037 | 0.5303 | 0.0081 | 0.1368 | 0.0043 | 0.6216 |
| <i>T</i> × <i>S</i> | 4 | 0.0431 | 0.0001 | 0.0218 | 0.0003 | 0.0514 | 0.0002 |
| <i>T</i> × <i>P</i> × <i>S</i> | 4 | 0.0120 | 0.0871 | 0.0096 | 0.0531 | 0.0258 | 0.0229 |
| Error <i>b</i> ^c | 288 | 0.0058 | | 0.0040 | | 0.0089 | |

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

^b df, degrees of freedom; MS, mean square; Pr > *F*, probability of a greater *F* value.

^c Error *a*: df = *P* × *S* × (*n* - 1), where *n* = 25 seedlings. Error *b*: df = *P* × *S* × (*n* - 1) × (*T* - 1).

treatment (not root pruned: 29.4 ± 2.1; copper root pruned: 34.4 ± 2.8). By 17 weeks postsowing, the number of primary lateral roots was not significantly affected by copper root pruning but was significantly affected by cavity size with smaller values when seedlings were grown in medium or small cavities compared with large cavities (small: 27.7 ± 1.1; medium: 30.2 ± 1.5; large: 34.8 ± 1.1). At the end of the 27-week cultural period, seedlings averaged 34 primary lateral roots across all six container types.

Shoot-root ratio was significantly affected by copper root pruning at 10 and 17 weeks postsowing and by cavity size at 10 weeks after sowing, but treatment effects were not detectable by the end of the 27-week cultural period (Table 2). At 10 and 17 weeks postsowing, shoot-root ratios were 24 and 10% larger in response to copper root pruning. At 10 weeks postsowing, seedlings grown in medium cavities had larger shoot-root ratios compared with seedlings grown in small and large cavities (small: 4.1 ± 0.2; medium: 4.9 ± 0.2; large: 4.2 ± 0.2). At the end of the 27-week cultural period, mean shoot-root ratio across all six container types was 2.8.

Ten weeks after sowing, RBI was significantly affected by cavity size (Table 2), with larger RBI values for seedlings grown in large cavities compared with small cavities. Also, at this time, copper root pruning significantly increased RBI regardless of cavity size. At 17 (data not shown) and 27 weeks postsowing (Figure 1b), significant treatment interaction led to larger values of RBI for seedlings produced in small cavities when they were copper root pruned. At 17 and 27 weeks postsowing, the RBI of seedlings produced in medium and large cavities did not differ by copper root pruning treatment.

The fraction of root system dry weight allocated to the taproot and primary lateral roots was significantly affected by copper root pruning (Table 3). Regardless of cavity size, the fraction of taproot dry weight was consistently greater with copper root pruning (Figure 2a). The reverse was observed with fraction of primary lateral root dry weight (Figure 2b). Fraction of taproot dry weight was significantly affected by interaction between cavity size and cultural period, with greater values observed in small cavities compared with large cavities at 10 weeks after sowing and greater values observed in small cavities compared with both medium and large cavities by 17 and 27 weeks after sowing.

Interaction among cultural period, copper root pruning, and cavity size had a significant effect on the fraction of root system dry weight as secondary lateral roots (Table 3). Without root pruning, the fraction of secondary lateral root dry weight was significantly

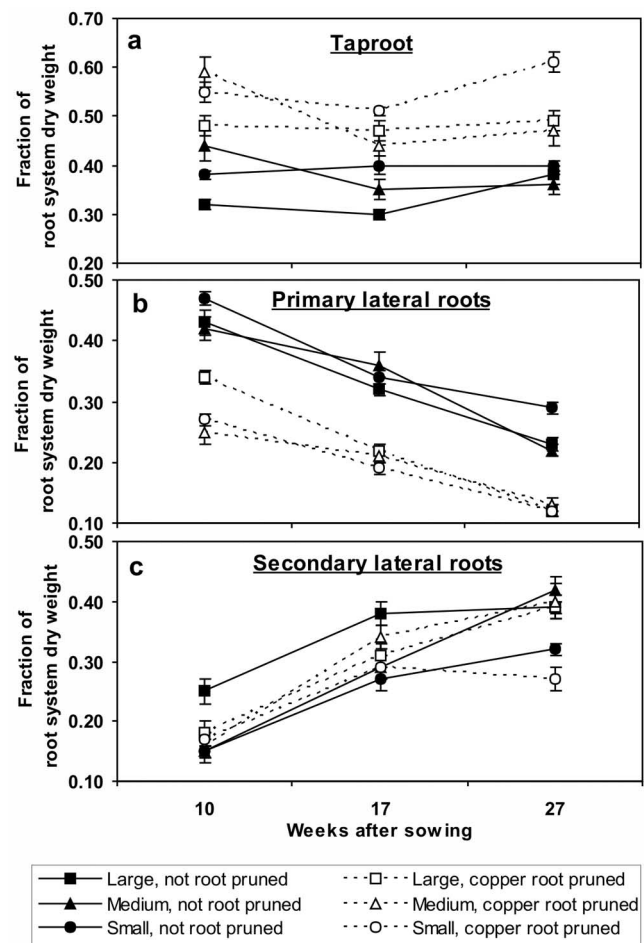


Figure 2. Fraction of container-grown longleaf pine seedling total root system dry weight as taproot (a), primary lateral roots (b), and secondary lateral roots (c) in response to copper root pruning (not root pruned, copper root pruned) and cavity size (small, medium, large) at 10, 17, and 27 weeks after sowing. Error bars represent 1 SEM.

affected by cavity size at 10, 17, and 27 weeks postsowing. For the root-pruned seedlings, the fraction of secondary lateral root dry weight was significantly affected by cavity size at 27 weeks postsowing (Figure 2c). In all cases, small cavities resulted in a lower fraction

Table 4. Mean squares and probabilities of a greater *F* value for number of egressed roots from the root plug of longleaf pine seedlings in response to copper root pruning and cavity size at three root plug depths during seedling production and a 28-day root growth potential test in the greenhouse.

| Source of variation | df ^a | Number of egressed roots ^b | |
|---|-----------------|---------------------------------------|--------|
| | | MS | Pr > F |
| Block (<i>B</i>) | 4 | 0.1685 | 0.6887 |
| Copper root pruning (<i>P</i>) | 1 | 0.0581 | 0.6627 |
| Cavity size (<i>S</i>) | 2 | 4.9174 | 0.0001 |
| <i>P</i> × <i>S</i> | 2 | 0.0415 | 0.8701 |
| Error <i>a</i> ^c | 20 | 0.2966 | |
| Root plug depth (<i>D</i>) ^d | 2 | 21.6695 | 0.0001 |
| <i>D</i> × <i>P</i> | 2 | 21.7910 | 0.0001 |
| <i>D</i> × <i>S</i> | 4 | 0.1569 | 0.4805 |
| <i>D</i> × <i>P</i> × <i>S</i> | 4 | 0.4997 | 0.0353 |
| Error <i>b</i> ^c | 48 | 0.1774 | |

^a df, degrees of freedom; MS, mean square; Pr > *F*, probability of a greater *F* value.

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

^c Error *a*: df = (*P* × *S* - 1) × (*B* - 1). Error *b*: df = *P* × *S* × (*B* - 1) × (*D* - 1).

^d The three root plug depths were 0–5 and 5–10 cm for all three cavity sizes and 10–10.3, 10–14.9, and 10–15.2 cm for the small, medium, and large cavities, respectively.

of secondary lateral root dry weight than one or both of the other cavity sizes.

RGP Experiment

The number of roots egressed from the root plug after the 28-day RGP test was significantly affected by three-way interaction among root plug depth, cavity size, and copper root pruning (Table 4). In the absence of root pruning, the number of egressed roots of seedlings grown in small, medium, and large cavities increased significantly from the top to the middle and from the middle to the bottom of the root plug (Table 5). The number of egressed roots from the root plug of the copper root-pruned seedlings was similar among cavity sizes and root plug depths.

Discussion

The emergence of new roots from the upper 10 cm of longleaf pine root plugs was nearly 2-fold more with copper root pruning in our RGP test. At the same time, an average of 14 roots emerged from the bottom root plug depth of the copper root-pruned seedlings. This, however, was nearly 2-fold less than that emerging from the bottom root plug depth of seedlings that were not root-pruned with copper. If the role of roots emerging from the bottom root plug depth can be met by fewer roots, copper root pruning may afford some advantages to newly established longleaf pine seedlings. For example, because copper root pruning suspends primary lateral root elongation on contact (McDonald et al. 1984, Ruehle 1985), these roots do not spiral around the cavity wall (Barnett and Brissette 1986, Burdett et al. 1986). On the contrary, the conformation of primary lateral roots positions roots emerging from the root plug so that the developing root system more closely resembles that of a naturally sown seedling (Burdett et al. 1986). Once height growth is under way, horizontal lateral roots bear the pivotal movement transferred from the stem to the taproot during extreme wind events (Burdett et al. 1986, Stokes 1999) and therefore may reduce the risk of toppling.

We also found that copper root pruning led to larger taproot dry weights compared with primary and secondary lateral root dry weights. The root system serves as a reservoir of energy for seedling

growth when photosynthesis is depressed by disturbance immediately after planting (Johnson and Cline 1991). One source of reserve energy to planted longleaf pine is starch stored in root parenchyma cells (Esau 1977, Walkinshaw and Otrrosina 2002). Larger taproots produced in copper-coated cavities may contain more stored starch for immediate energy after planting.

Because RCD is a function of taproot size (Wahlenberg 1946), these distinct effects of copper root pruning on root system development indicate that standard measures of seedling quality, such as RCD, and their interpretation may differ when copper root pruning is used. At the time of planting, RCD is commonly used as a predictor of seedling quality (Johnson and Cline 1991). For container-grown longleaf pine, it is generally accepted that optimum field performance is achieved when RCD is not smaller than 5.0 mm and preferably, exceeds 6.4 mm (Barnett et al. 2002, Larson 2002, South et al. 2005).

RBI also serves as an indicator of seedling quality (South et al. 2005, South and Mitchell 2006). For RBI values between 12 and 37%, South et al. (2005) found that survival declined dramatically beyond 27%. In another study in which performance was measured as root system hydraulic conductivity, the longleaf pine seed source with an average RCD of 6.8 mm outperformed one with an average RCD of 7.3 mm (Sword Sayer et al. 2005). It was suggested that beyond a superoptimal RCD, root growth limitations that developed during seedling production may have superseded seedling size as an indication of seedling quality.

The RCD of seedlings produced in small and medium cavities was suboptimal, averaging less than 5.0 mm at the end of our study. Root-bound indices for all cavity sizes, however, were less than 14%, signifying that root growth was not constrained at the time of planting. These observations and the first-year survival rate of more than 97% after outplanting in the field (data not shown) indicate that in the absence of root binding, longleaf pine seedlings with a RCD smaller than normally desired may be suitable for some, albeit not all, regeneration situations.

The best indicator of longleaf pine seedling quality may change from RCD to RBI depending on cavity type. A cavity volume of 90 cm³ or larger is recommended for the production of longleaf pine seedlings (Barnett and McGilvray 1997, Barnett et al. 2002). However, the diameter of these cavities, and therefore the RBI of seedlings produced in these cavities, varies by dimension. In addition, because RCD increases linearly throughout the cultural period, delays in planting are accompanied by increases in RCD. To avoid RBI values indicative of root binding and produce longleaf pine seedlings with optimal RCD, we propose that target values of RCD for container-grown longleaf pine seedlings be customized by cavity type. Furthermore, the consequences of superoptimal values of RCD that arise from delayed planting should be understood on a cavity-type basis.

An indicator of seedling quality other than RCD would be helpful for assessing seedlings with RCD values falling below the target (i.e., less than 5.0 mm). This is especially true, for example, after a catastrophic event (e.g., major hurricane), when the demand for high-quality seedlings is great and the nursery space needed to produce large container-grown seedlings is limited. Because lateral roots inside the root plug are the foundation from which new roots egress after planting (Barnett and Brissette 1986), their development is critical to establishment. Root plug fibrosity, which is composed of primary, secondary, and higher order lateral roots, therefore, may be a valuable sign of container-grown seedling quality.

Table 5. Number of new lateral roots egressed from three root plug depths of container-grown longleaf pine seedlings planted in pots and maintained in a greenhouse during a 28-day root growth potential test. Treatments were copper root pruning (not root pruned, copper root pruned) and cavity size (small, medium, large) during seedling production.

| Root plug depth ^a | Root pruning treatment and cavity size | | | | | |
|------------------------------|--|----------------|-----------------|--------------------|-----------------|-----------------|
| | Not root pruned | | | Copper root pruned | | |
| | Small | Medium | Large | Small | Medium | Large |
| Top | 3.48 (0.50) e ^b | 3.84 (0.67) e | 5.00 (0.65) de | 9.80 (1.28) cd | 15.96 (1.46) bc | 16.76 (0.79) bc |
| Middle | 10.20 (0.70) cd | 12.20 (2.13) c | 14.52 (1.80) bc | 10.00 (1.00) cd | 13.08 (1.58) bc | 16.04 (1.76) bc |
| Bottom | 20.68 (1.91) b | 32.52 (4.21) a | 35.80 (1.91) c | 11.40 (0.58) c | 15.32 (2.19) bc | 15.20 (1.43) bc |

Numbers in parentheses are 1 SEM.

^a The three root plug depths were 0–5 cm and 5–10 cm for all three cavity sizes and 10–10.3, 10–14.9, and 10–15.2 cm for the small, medium, and large cavities, respectively.

^b Means associated with the same letter are not significantly different at an α level of 0.05 by the Tukey-Kramer procedure.

In our study, there were two main factors controlling the amount of root plug fibrosity. First, the taproot competed with other roots for growing space, and as the cavity became more occupied, primary lateral roots competed with secondary lateral roots for growing space. We observed the consequences of competition for growing space among root system components at 27 weeks after sowing, when the fraction of root system dry weight allocated to secondary lateral roots was 26% lower in small cavities compared with large and medium cavities regardless of root pruning treatment. In addition, competition for secondary lateral root growing space in small cavities may have been manifested as reduced RGP in the bottom root plug depth without copper root pruning. This response, however, cannot solely be attributed to root competition, because the surface area of the bottom root plug depth differed among cavity sizes. RBI is a function of RCD (South et al. 2005), and as previously mentioned, RCD is a function of taproot size (Wahlenberg 1946). Therefore, RBI is correlated with taproot size. When the taproot dominates cavity growing space so that secondary lateral root growth is hindered, RBI may not only reflect root-binding but also the potential for secondary lateral root growth in the root plug and RGP at the time of planting.

Second, we found that the amount and character of fibrous roots (i.e., primary plus secondary lateral roots) were affected by copper root pruning. By the end of the cultural period, the fraction of root system dry weight as fibrous roots was 24, 14, and 18% less for seedlings grown in small, medium, and large cavities, respectively, in response to copper root pruning. However, a larger fraction of fibrous root mass was composed of secondary lateral roots compared with primary lateral roots when seedlings were root pruned with copper. For longleaf pine, copper root pruning seems to increase taproot growth at the expense of fibrous root growth. However, concurrent changes in the quality of longleaf pine fibrous roots may compensate for this decrease in fine root production. Further research is needed to determine the value of altering the fractions of fibrous root dry weight that occur as primary and secondary lateral roots.

It is important to note that these distinct effects of copper root pruning on root system development were reflected in RCD but not shoot-root ratio. Although copper root pruning led to a decrease in shoot-root ratio 10 weeks after sowing, at 17 and 27 weeks postsowing, carbon allocation to the shoot and root system became similar between the two root pruning treatments. Comparable results from other studies indicate that copper root pruning increases the overall size of seedlings but not their allocation of carbon between the shoot and root system (McDonald et al. 1984, Barnett and McGilvray 2002, Tsakalidimi and Ganatsas 2006). Cavity size and seedling

quality specifications unique to copper-coated cavities are justified by expectations of larger seedlings and greater competition between the taproot and fibrous roots when root systems are pruned with copper.

Summary

Copper root pruning during seedling production changes the morphology of container-grown longleaf pine root systems by increasing the fraction of root system dry weight allocated to the taproot relative to fibrous roots, the ratio of root system dry weight allocated to secondary versus primary lateral roots, and the potential for roots to emerge from the upper 10 cm of the root plug. These changes could benefit newly established longleaf pine by increasing the amount of stored starch available for energy immediately after planting and improving root system morphology as roots egress from the root plug. Specifically, more RGP in the top of the root plug could improve the stability of seedlings once they begin height growth and the acquisition of water and mineral nutrients from the surface soil. These potential benefits, however, are contingent on the production of high quality seedlings. Because seedling quality indicators such as RCD and RBI vary by cavity size and copper root pruning treatment, target values of RCD and RBI should be defined by cavity type.

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