Geotropic Lateral Roots *of Container-grown* Longleaf Pine Seedlings

David B South, Jason Shelton, and Scott A Enebak

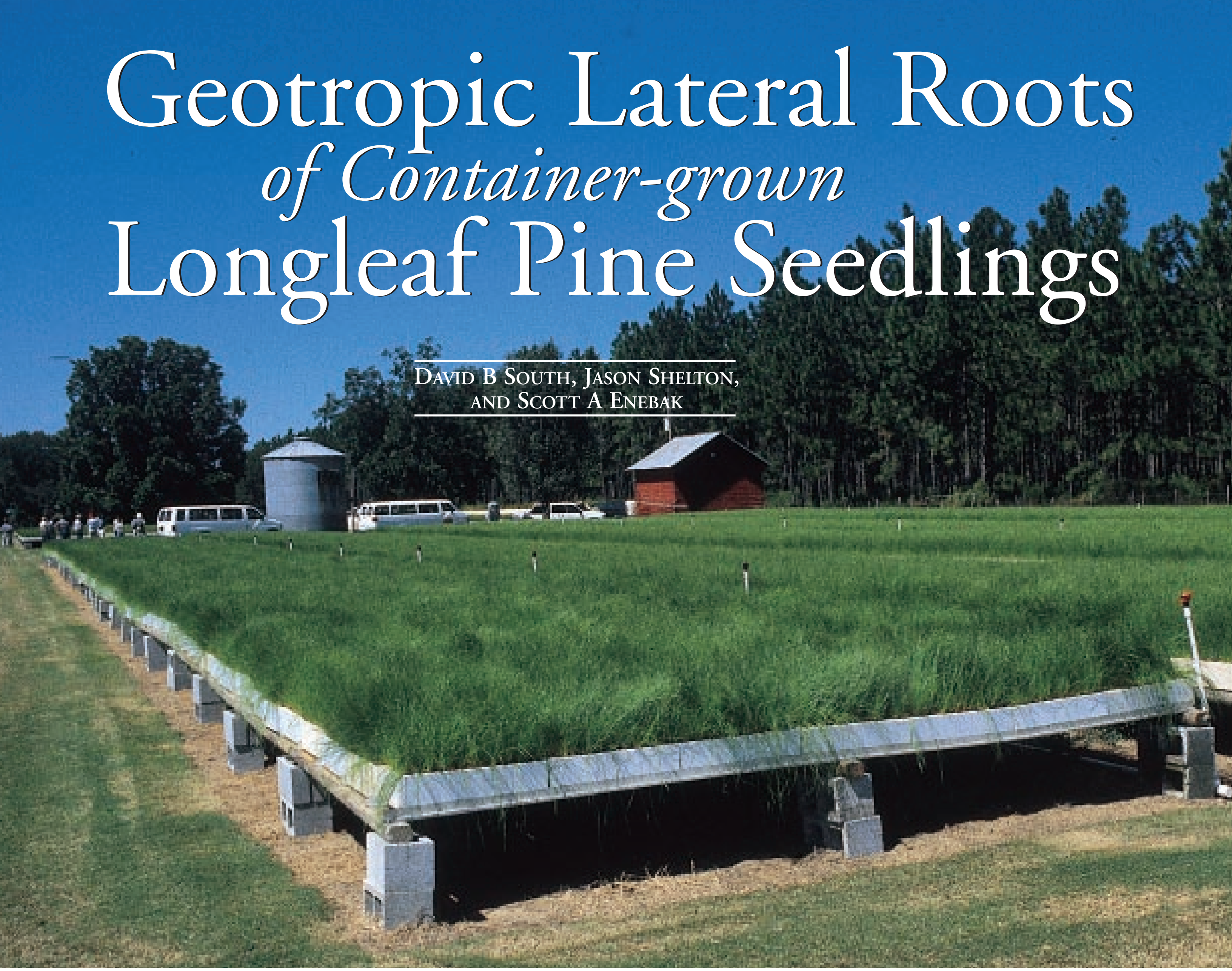

Photo by Kas Dumroese

Longleaf pine growing in containers in an open compound in Georgia.

ABSTRACT

More than 95% of container-grown longleaf pine (*Pinus palustris* P. Mill.) seedlings had roots growing downward vertically (geotropically) when examined 7 to 8 mo after transplanting into sand. Geotropic roots were rarely the original taproot (< 0.5%) but were usually adventitious lateral roots that had formed about the callus tissue. Air-pruning in the nursery results in callus formation at the end of the taproot and typically, 1 or more adventitious roots emerge just above the callus tip. Although many first-order lateral roots were deflected downward by container walls, few exhibited positive geotropic growth after transplanting. Most grew in directions other than straight down. In this study, about 4% of the seedlings lacked geotropic roots. Longleaf pines with a long taproot or sinker roots are less susceptible to toppling at a young age than are trees without vertical roots.

Geotropism is the response of plant organs, in either growth or position, to the pull of gravity (Ford-Robertson 1971). Taproots of naturally regenerated longleaf pine seedlings typically express positive geotropic response (grow vertically downward) while first-order lateral roots typically exhibit no geotropism. Heyward (1933) said that a striking characteristic of laterals "was their tendency to extend in a horizontal plane at a uniform depth throughout their entire length." His observation was later supported by Hodgkins and Nichols (1977) who excavated first-order lateral roots and found all growing in a horizontal plane that ranged from 3.1 cm to 22.8 cm (1.2 to 9.0 in) below the soil surface.

KEY WORDS: *Pinus palustris*, geotropism, taproot, container-grown, root growth, toppling

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In contrast, second-order lateral roots of longleaf pine occasionally do exhibit geotropism. These vertically oriented roots are sometimes called "sinker" roots (Wahlenberg 1946; Sutton and Tinus 1983). A seedling with a normal taproot may have several sinker roots that grow downward (Heyward 1933; Lenhart 1934). Although Pessin (1939) drew lateral roots of 12-y-old longleaf trees that suddenly grew downward, it is not clear if these were first-order or second-order lateral roots that suddenly acquired a positive geotropic growth or if they were adventitious roots that grew downward soon after they emerged from the lateral root.

TABLE 1

Analysis of variance (probability of a greater F-value) for morphological variables of container-grown Pinus palustris *7 to 8 mo after transplanting in sand*

Factor	RCD	Total green weight	Shoot dry weight	Plug dry weight	Egressed root dry weight	Sinker root number		
						Type A	Type B	Total
Block	0.089	0.010	0.273	0.001	0.001	0.529	0.003	0.444
Treatment (T)	0.317	0.797	0.459	0.482	0.320	0.319	0.214	0.787
Seedlot (S)	0.001	0.006	0.001	0.017	0.001	0.057	0.010	0.222
T x S interaction	0.428	0.586	0.537	0.605	0.651	0.080	0.978	0.470

Adventitious roots can result when roots are injured and the original root is replaced by roots arising near the injured surface (Wilcox 1955; Esau 1977; Sutton 1980). Heyward (1933) noted that when the taproot of a longleaf pine seedling was severed at a depth of 86 cm (34 in), a wound callus formed and 3 adventitious roots emerged from the taproot. Pessin (1939) noted that sometimes 1 or 2 roots take over the function of the taproot (as illustrated in his Figure 3-C). Therefore, adventitious roots formed at the end of the taproot can be geotropic.

Root morphology of container-grown seedlings differs from that of seedlings developing after natural regeneration. Natural seedlings have first-order lateral roots that grow horizontally while container-grown seedlings often have lateral roots that are deflected downward (Ruehle 1985a, b). In addition, natural longleaf pine seedlings that are less than 91 cm (36 in) tall typically have 1 geotropic root: the taproot (Heyward 1933). In contrast, little is known about the geotropic nature of taproots and lateral roots of container-grown longleaf pine seedlings. Therefore, roots from over 700 seedlings were excavated and examined to quantify the number and origin of geotropic roots.

MATERIALS AND METHODS

Seeds were collected from 2 forest collections (North and South Carolina), 2 seed production areas (North Carolina and Georgia), and 4 seed orchards (Alabama, Florida, Mississippi, and Texas). On 6 April 1999, each seedlot was separated into 3 groups for treatment prior to sowing. Seeds representing the control group were soaked in distilled water 9 min. The second group was soaked 9 min in a 0.25% (weight of active ingredient per weight of water) active ingredient solution containing benomyl. Seed coats from the third group were coated with mancozeb at a rate of 0.11% (weight of active ingredient per weight of seed). On the next day, seeds were single-sown into HIKO™ V-93 containers (93 cm^3 [6 in^3] volume; 4.1 cm [1.6 in] top diameter; 8.7 cm [3.4 in] deep; 526 cavities/m^2 [49/ft^2]). Operational fertilization and irrigation practices, similar to the guidelines set out by Barnett and McGilvery (1997), were used to grow the seedlings at the International Forest Company Nursery at Odenville, Alabama.

Seedlings were transported to Auburn, Alabama, and planted into an outdoor sand pit at close spacings (~15 cm [6 in]) on 20 October 1999. The root-collar diameter (RCD) was recorded for approximately 70 seedlings per treatment-seedlot combination. During the following month, seedlings were irrigated once per week to reduce stress. After that period, irrigation ceased.

Eighty seedlings per treatment from the first block were excavated on 1 May 2000. A second block was excavated on 17 to 18 May and the third block was excavated on 12 to 15 June. A total of 720 seedlings were examined. During excavation, each seedling was examined for the presence of a taproot that was short (< 15 cm [6 in]) with signs of air-pruning or was long (> 15 cm [6 in]) with no signs of air-pruning. Lateral roots exhibiting geotropism were called "sinker" roots (Sutton and Tinus 1985). Geotropic, adventitious first-order lateral roots within 2 cm (0.8 in) of the tip of the air-pruned taproot were classified as Type A sinkers (Figure 1). Geotropic, lateral roots more than 2 cm (0.8 in) from the end of the taproot were classified as Type B sinkers (Figure 2). Sinker roots were easy to identify due to their vertical orientation and depth in the soil (> 30 cm [12 in] below the groundline).

The RCD of each seedling was measured. The green weights of 10 seedlings per treatment-seedlot row were recorded and then each seedling was cut at the root collar. Roots which had emerged from the

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Figure 1 • Seedling with 2 vertical Type A roots that emerge just above the callus tissue.

Photo by David South

Figure 2 • The arrow points to a Type B vertical root. The larger sinker root is an adventitious root classified as a Type A vertical root.

original container plug (egressed roots) were cut at the surface of the plug. Shoots, roots within the original plug (plug roots), and roots outside of the original plug (egressed roots) were dried to a constant weight.

Analyses were conducted using a General Linear Model procedure in a SAS-PC program (SAS Institute Inc 1989). The experimental design was a randomized complete block design with 3 replications. Each analysis contained 72 experimental units. Error terms with 46 degrees of freedom (df) were used to test for significance in the block (2 df), treatment (2 df), seedlot (7 df), and treatment by seedlot interaction (14 df) factors. When overall treatment effects were significant ($\alpha = 0.05$), means were compared using Duncan's multiple-range test.

RESULTS

Root measurements were similar among seed treatments and interactions were absent (Table 1). In contrast, significant seedlot effects existed for all variables except the number of Type A sinker roots (which average 1.4 per seedling). Seedlings from seedlot #3 (seed collected in 1981 from a seed orchard in Texas) were larger in the nursery than seedlings from other seedlots, and therefore, were also larger after 7 mo of additional growth (Table 2).

Of 720 seedlings excavated, 3 had a single, long taproot with no sign of air-pruning (Table 3). No lateral roots on these 3 seedlings were growing vertically. All the remaining seedlings had taproots shorter than 15 cm (6 in).

For 717 seedlings, there were 1146 sinker roots for an average of 1.6 per seedling. After these roots emerged from taproots, they grew downward as opposed to perpendicular to the taproot. About 91% of the seedlings had Type A sinker roots (Table 3). Approximately 48% of the seedlings formed a single Type A sinker root and another 21% had 2 Type A sinker roots. Only a few seedlings had 5 or 6 Type A sinker roots.

TABLE 2

The root collar diameter of Pinus palustris *before planting and morphological characteristics 7 to 8 mo after transplanting in sand*

Seedlot	Root collar diameter		Total green weight	Shoot dry weight	Egressed root dry weight	Plug root dry weight	Sinker roots	
	Initial	Final					Type A	Type B
	(mm)		(g)				(number)	
1	6.8 bc	9.9 b	23.1 b	5.1 ab	1.3 b	2.8 b	1.18	0.30 ab
2	6.9 bc	9.8 b	20.6 b	4.6 bc	1.2 b	2.6 b	1.24	0.30 ab
3	7.5 a	11.6 a	27.9 a	5.9 a	1.7 a	3.4 a	1.42	0.43 a
4	7.2 ab	9.9 b	21.8 b	4.7 bc	1.1 b	2.7 b	1.34	0.16 b
5	7.0 bc	10.2 b	23.4 b	5.1 ab	1.3 b	3.0 ab	1.47	0.17 b
6	7.1 bc	10.0 b	21.8 b	5.0 b	1.1 b	2.7 b	1.38	0.16 b
7	7.2 ab	10.9 b	23.7 b	5.3 ab	1.2 b	2.9 b	1.52	0.14 b
8	6.7 c	10.4 b	21.0 b	4.0 c	1.1 b	2.8 b	1.36	0.17 b
LSD	0.4	0.6	3.6	0.8	0.3	0.4	0.22	0.17

Figure 3 • Toppling of a 10-y-old progeny test of longleaf pine after Hurricane Floyd. This container type is not currently used in operational longleaf pine nurseries.

About 18% of the seedlings had one or more Type B sinker roots. Single Type B sinkers were the most common and occurred on 108 seedlings while 2, 3, and 4 Type B roots occurred on 20, 4, and 1 seedlings, respectively. Sometimes seedlings with Type A sinker roots also had Type B sinker roots (Table 3). Only rarely did Type B lateral roots take over the sole function of geotropism.

About 4% of the seedlings (30 seedlings) had no sinker root or long taproot. Although these seedlings had lateral roots, none were demonstrating geotropism 7 to 8 mo after transplanting.

DISCUSSION

Air-pruning of the taproot is common among container-grown longleaf pine seedlings. Typically, callus formation occurs after air-pruning. One or two adventitious roots typically emerge just above the callus and these roots are usually geotropic. For some seedlings, 3 or more adventitious roots may branch at the end of the taproot and all can express positive geotropism. In a few cases, no adventitious roots are formed and the seedling lacks a long taproot or sinker root. Seedlings without any taproot or sinker roots are likely more susceptible to toppling by strong winds (Chaveasse 1978; Mason 1985; Burdett and others 1986). Toppling of planted longleaf pine is usually not a problem but high winds associated with hurricanes have toppled some container-grown longleaf pines in Alabama and North Carolina (Figure 3).

After emergence from the taproots, most first-order lateral roots grow horizontally until they are deflected by the container wall (Ruehle 1985b). When there is no copper compound on the cavity wall, the root turns and grows up, down, or horizontally along the cavity wall. When such roots grow down, this does not appear to be true geotropism since the downward growth is not maintained after transplanting. After the seedling is transplanted, most first-order lateral roots grow in a horizontal direction. Few express true geotropism and become sinker roots. In this study, less than 1 in 5 seedlings had a non-adventitious lateral root that was truly geotropic. Most seedlings had several first-order lateral roots that initially grew down the cavity wall and toward the drainage hole. In some cases, 76% of the first-order lateral roots will be air-pruned within 5 mo of sowing (Ruehle 1985b).

It is generally believed the site of georeaction is located in the rootcap (Barlow 1974; Esau 1977; Sutton 1980). Although it is assumed that all roots contain a rootcap, only a few pine roots have positive

TABLE 3

Frequency of container-grown Pinus palustris *seedlings with different types of vertical roots. No seedling had more than 6 vertical roots*

Vertical root	Number of vertical roots per seedling							
	0	1	2	3	4	5	6	Total
Type A only	-	346	154	38	11	4	1	554
Type A and B	-	-	58	29	15	1	1	104
Type B only	-	24	5	0	0	0	0	29
Short taproot only	30	-	-	-	-	-	-	30
Long taproot only	-	3	0	0	0	0	0	3
Total	30	373	217	67	26	5	2	720

geotropic growth. After the taproot's tip is destroyed by air-pruning, new adventitious roots and sometimes old lateral roots can become geotropic. It is not known how the geotropic "switch" is turned on in root tips that were initially not geotropic. One author suggests that inhibitors are involved in determining the geotropic response (Barlow 1974).

CONCLUSIONS

When air-pruning causes the taproot of longleaf pine to form a callus, elongation of the taproot stops. Typically, callus tissue is formed at the tip of the taproot and new adventitious roots emerge just above this callus. These adventitious roots are positively geotropic. In some seedlings, 1 or more lateral roots may also become positively geotropic. Although the root system of container-grown longleaf pine differs from that of natural seedlings, it is not known if this difference has any practical implications.

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AUTHOR INFORMATION

David B South Professor
southdb@auburn.edu

Jason Shelton
Graduate Student

Scott A Enebak
Associate Professor
enebasa@auburn.edu

School of Forestry and Wildlife Sciences
and Alabama Agricultural Experiment Station

Auburn University, AL 36849-5418