

# Root length and biomass in mixtures of broomsedge with loblolly pine or sweetgum

Bruce R. Zutter, Robert J. Mitchell, Glenn R. Glover, and Dean H. Gjerstad

**Abstract:** Root length density (RLD) and root biomass density (RBD) of fine roots (<2 mm) were examined in a factorial combination of loblolly pine (*Pinus taeda* L.) and broomsedge (*Andropogon virginicus* L.) and a factorial combination of sweetgum (*Liquidambar styraciflua* L.) and broomsedge to determine the extent to which competition may influence belowground plant response. Broomsedge and sweetgum seedlings were planted, grown for 1 year, and cut before planting of pine seedlings. Sampling occurred 1 year after planting of pine. Broomsedge had a significant negative effect ( $p < 0.10$ ) on RBD and RLD of sweetgum and loblolly pine in the upper 30 and 45 cm of soil, respectively. RLD and RBD of broomsedge increased with increasing broomsedge density ( $p < 0.10$ ) and decreased with addition of either tree species, with sweetgum having a greater effect. Patterns in the effects of competitors on RBD and RLD were similar to those noted for aboveground biomass. Specific root length (SRL) of broomsedge was three and five times greater than that of sweetgum or loblolly pine, respectively ( $p < 0.05$ ). The addition of interspecific competitors reduced the percentage of total RLD of pine and sweetgum and RBD of broomsedge in the 0- to 15-cm soil depth with a corresponding increase in the 15- to 30-cm depth.

**Résumé :** La densité linéaire et la densité de biomasse des racines fines (< 2 mm) ont été étudiées dans un dispositif factoriel de pin à encens (*Pinus taeda* L.) et de carex à balais (*Andropogon virginicus* L.) et dans un dispositif factoriel de liquidambar (*Liquidambar styraciflua* L.) et de carex à balais pour déterminer dans quelle mesure la compétition influence la réponse souterraine des plantes. Les semis de carex à balais et de liquidambar furent plantés, cultivés pendant 1 an et coupés avant de planter les semis de pin. L'échantillonnage a été effectué 1 an après avoir planté les semis de pin. Le carex à balais a eu un effet négatif et significatif ( $p < 0,10$ ) sur la densité linéaire et de biomasse des racines du liquidambar et du pin à encens dans les premiers 30 et 45 cm de sol, respectivement. La densité linéaire et la densité de biomasse des racines du carex à balais ont augmenté avec la densité de cette plante ( $p < 0,10$ ) et ont diminué après l'ajout de l'une ou l'autre des espèces d'arbre, le liquidambar ayant l'effet le plus important. Les effets des plantes compétitives rapportés à l'hectare sur la densité linéaire et de biomasse des racines ressemblaient à ceux qu'on observe pour la biomasse aérienne. La longueur spécifique des racines du carex à balais était respectivement trois à cinq fois plus grande que celle du liquidambar et du pin à encens, ( $p < 0,05$ ). L'addition de compétiteurs interspécifiques a réduit le pourcentage de la densité linéaire totale des racines du pin et du liquidambar et celui de la densité de biomasse totale des racines du carex à balais dans les 15 premiers centimètres de sol en provoquant une augmentation correspondante entre 15 et 30 cm de profondeur.

[Traduit par la Rédaction]

## Introduction

Competition for soil resources is important in structuring early successional forest communities of the southeastern United States (Mitchell et al. 1993, 1999; Morris et al. 1993; Perry et al. 1993, 1994; Mou et al. 1995; Ludovici and Morris 1996; Burch et al. 1997). Although considerable work has been recently published that investigates the relationships among resource interactions and aboveground plant performance in these regeneration situations (see Mitchell et al. 1999), less is known about the belowground structure in communities that vary in composition and density (Burch et al. 1997).

Root system structure and differences in belowground traits among species have important influences on plant competition (Tilman 1988; Grime et al. 1991; Casper and Jackson 1997); the cycling of water, nutrients, and energy (Feldman 1988); and the productivity of stands (Hendricks et al. 1993). However, few studies have quantified how fine roots vary among different competitive scenarios. Understanding competitive effects and responses belowground is important in that the quantity and distribution of roots within the soil will affect the nutrient pool and water available to a plant and its competitors. Part of the problem in these investigations is the difficulty in distinguishing roots among species. This has led to root studies in which functional groupings of plants are removed from communities (Burch et al. 1997); however, this approach does not allow for an array of competitive environments to be studied.

Loblolly pine (*Pinus taeda* L.), sweetgum (*Liquidambar styraciflua* L.), and broomsedge (*Andropogon virginicus* L.) are common associates during early succession on upland cutover sites planted to loblolly pine in the Upper Coastal Plain of the southeastern United States (Miller et al. 1995).

Received August 23, 1998. Accepted March 11, 1999.

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Field studies of competition among these species have primarily focused on aboveground responses and most often of loblolly pine alone (Morris et al. 1993; Perry et al. 1993; Mitchell et al. 1999). In this study, factorial arrangements of loblolly pine and broomsedge and sweetgum and broomsedge were used to determine the extent to which competition may influence belowground plant response. Based on previous work with sweetgum and loblolly pine in pots or rhizotrons it was hypothesized that addition of interspecific competitors would reduce fine root length and biomass (Jifon et al. 1995; Ludovici and Morris 1996). Since fine roots are most abundant in the upper surface layers of the soil (Eissenstat and Van Rees 1994; Fredericksen and Zedaker 1995), the reduction might be expected to be proportionately greater in the surface layers such that root distributions would shift to deeper layers of the soil.

## Materials and methods

### Study area

The study utilized approximately 2 ha of an old field located at Auburn University's E.V. Smith Research Center near Shorter, Ala. Prior to study establishment the area had been in row crop production for more than 20 years with the last crop, soybeans (*Glycine max* (L.) Merrill), being harvested in 1987. The study area was chisel-plowed in early October 1988 to breakup any plowpan created as a result of repeated tillage. To minimize the influence of other plant species, the entire area was sprayed with glyphosate (4.4 kg/ha) in early September, disked in mid-October, and then fumigated with 98% methyl bromide and 2% chloropicrin. The soils are of the Compass series (coarse-loamy, siliceous, thermic Plinthic Paleudults) consisting of a 25–30 cm loamy sand surface layer overlying a sandy loam from about 30–80 cm, and then a sandy clay loam layer to approximately 140 cm. These soils are representative of upland loblolly pine sites located in the Upper Coastal Plain of the southeastern United States.

### Study establishment

The study design consisted of a factorial combination of loblolly pine and sweetgum each planted at densities of 0, 1, 2, and 4 plants/m<sup>2</sup> and broomsedge at 0, 4, and 16 plants/m<sup>2</sup>.

Treatment plots were 490 × 898 cm. Plant layout was accomplished by dividing the treatment plot into 44 subplots measuring 82 × 122 cm, an area of 1 m<sup>2</sup>. Within each subplot there were 24 potential planting locations, 4 rows of 6 locations each, at a 20.4-cm spacing between locations. The location of the appropriate number of plants of each species was randomly assigned within each subplot. At the greatest density (i.e., *Pinus*, 4/m<sup>2</sup>; *Liquidambar*, 4/m<sup>2</sup>; *Andropogon*, 16/m<sup>2</sup>), all planting positions were occupied. Treatments were replicated four times in a randomized complete block design.

Commercially grown 1–0 bareroot sweetgum seedlings were planted in December 1988. Broomsedge were established as rooted tillers excavated from a site near the study area in February and March of 1989. These species were allowed to grow together during the 1989 growing season and then severed near the groundline in December 1989. This procedure was used to establish these two species as sweetgum primarily occurs as sprouts and broomsedge often is established before loblolly pines are planted on, or invade, cutover sites. Commercially grown 1–0 bareroot loblolly pine seedlings were planted in February 1990. The three species were allowed to grow together during the 1990 growing season. Additional details with regard to study design and establishment can be found in Perry et al. (1993) and Mitchell et al. (1999).

### Plant sampling and processing

A subset of treatments (species × density combinations) was selected for sampling of roots because of the extensive amount of time and labor required in sampling and processing roots. The treatments represented a factorial combination of loblolly pine planted at densities of 0 and 2 plants/m<sup>2</sup> and broomsedge planted at 0, 4, and 16 plants/m<sup>2</sup>, and a second factorial combination consisting of sweetgum planted at densities of 0 and 2 plants/m<sup>2</sup> and broomsedge planted at 0, 4, and 16 plants/m<sup>2</sup>.

Soil cores were collected by block from three of the four experimental blocks in the fall of 1990. Soil cores measuring 90 cm in length were extracted using a tractor-mounted Giddings probe (Giddings Machine Co., Fort Collins, Colo.) with a plastic sleeve fitted inside the probe. From five to ten 3.8 cm diameter cores were collected from a 1-m<sup>2</sup> area within each plot. Upon returning to the laboratory, each core was briefly refrigerated at 4°C until it was cut using a band saw into 15-cm segments corresponding to soil depths of 0–15, 15–30, 30–45, 45–60, 60–75, and 75–90 cm. Soil was carefully washed from the roots and roots sorted by species and living versus dead. Roots were separated by species and living versus dead based on their general appearance and morphology (Vogt and Persson 1991). Roots that were dark brown to black in color were classified as dead. Loblolly pine roots were brown in color and often had ectomycorrhizal associations, while sweetgum were lighter in color with denser branching. Broomsedge roots were typically thinner and very light in color. Roots were stored in 20% methanol at 4°C until length and biomass measurements were made. Total length of living fine roots (<2.0 mm) was determined on each sample using a root-length scanner (Comair Root Length Scanner, HDH Systems Intl., Port Melbourne, Victoria, Aust.) capable of detecting roots 0.1 mm and greater in diameter. Once root length was determined, samples were oven-dried at 65°C for 48 h and weighed. Fine root length was expressed as root length density (cm of root/cm<sup>3</sup> of soil) and biomass as root biomass density (mg of root/cm<sup>3</sup> of soil).

Aboveground biomass per hectare was also determined for purposes of comparison of effects of competition with those noted for fine root length and biomass density. Plant dimensional measurements and survival counts were made on eight interior subplots in each treatment plot during early September 1990. Eight plants of each species, one randomly selected from eight interior subplots, were chosen for collection of dimensional measurements. All species were measured for height and crown diameter. In addition, basal diameter of broomsedge clumps and loblolly pine stems were recorded to provide better estimates of plant biomass from nondestructive measurements. Three individuals of each species were randomly selected from designated subplots within each treatment plot, measured, harvested, and dried at 65°C to a constant mass. Destructive samples allowed for development of species and treatment specific biomass equations ( $n = 12$ ) based on nondestructive dimensional attributes. These equations were used to estimate individual plant biomass of the eight nondestructively sampled plants. These individual plant biomass estimates were used combined with plant density assessments to compute aboveground biomass per hectare for each species on all treatment plots.

### Data analysis

Root length and biomass of each species were analyzed considering soil depth as a repeated factor (Moser et al. 1990; Littell et al. 1991). A multivariate repeated measures ANOVA and a univariate split-plot ANOVA (soil depth as the subplot factor) were conducted. Often tests of the error variance structure were non-significant and (or) results from the two approaches were consistent with each other so results from the univariate split-plot ANOVA are presented. In most instances there was a significant interaction between soil depth and density of either one or both species. Thus, a univariate ANOVA appropriate for a randomized

**Table 1.** Analysis of variance of loblolly pine, sweetgum, and broomsedge fine root length and biomass density as influenced by plant density and soil depth.

Source of variation <sup>a</sup>	df	Root length			Root biomass density		
		MS	F	P > F	MS	F	P > F
<b>Loblolly pine</b>							
Blk	2	0.0322	0.17	0.8524	0.0158	0.27	0.7775
Brm	2	5.0934	26.26	0.0050	1.0771	18.25	0.0098
Linear	1	6.3823	32.89	0.0046	1.3758	23.31	0.0085
Quadratic	1	3.8072	19.62	0.0114	0.7784	13.19	0.0221
Error(Brm)	4	0.1940			0.0590		
Dp	5	4.1531	38.81	0.0001	2.6080	61.23	0.0001
Dp × Blk	10	0.0509	0.48	0.7506	0.0754	1.77	0.2480
Dp × Brm	10	0.3381	3.16	0.0320	0.3153	7.40	0.0167
Error(Dp)	20	0.1070					
<b>Sweetgum</b>							
Blk	2	0.1760	0.15	0.8614	0.0220	0.48	0.6498
Brm	2	18.5320	16.31	0.0119	0.2694	5.88	0.0644
Linear	1	22.3618	19.69	0.0114	0.3355	7.33	0.0537
Quadratic	1	14.7023	12.94	0.0228	0.2033	4.44	0.1028
Error(Brm)	4	1.1359			0.0458		
Dp	5	12.1614	47.57	0.0001	0.2071	24.45	0.0019
Dp × Blk	10	0.1429	0.56	0.6795	0.0118	1.40	0.3325
Dp × Brm	10	6.9264	27.10	0.0003	0.0669	7.90	0.0177
Error(Dp)	20	0.2557			0.0085		
<b>Broomsedge</b>							
Blk	2	2.0945	0.39	0.6857	0.2467	0.46	0.6449
Brm	1	2.3590	0.44	0.5215	1.0967	2.04	0.1839
IC	1	0.9752	0.18	0.6783	0.1631	0.30	0.5941
L vs. S	1	1.8891	0.35	0.5654	0.8789	1.63	0.2301
Brm × IC	1	1.6111	0.30	0.5950	0.1642	0.31	0.5928
Brm × L × S	1	7.4447	1.39	0.2652	0.7566	1.41	0.2631
Error(Trt)	10	5.3448					
Dp	5	21.8969	88.60	0.0001	6.6581	102.87	0.0001
Dp × Blk	10	0.2626	1.06	0.4047	0.0577	0.89	0.4749
Dp × Brm	5	0.9987	4.04	0.0037	0.3699	5.72	0.0165
Dp × IC	5	0.2041	0.83	0.4756	0.2427	3.75	0.0520
Dp × L × S	5	0.0758	0.31	0.7901	0.0489	0.76	0.4619
Dp × Brm × IC	5	0.0519	0.21	0.8614	0.0511	0.79	0.4486
Dp × Brm × L × S	5	0.4859	1.97	0.1510	0.0793	1.23	0.3112
Error(Dp)	50	0.2471			0.0647		

<sup>a</sup>Blk, block; Brm, broomsedge density (competition level); linear, linear effect of broomsedge density; quadratic, quadratic effect of broomsedge density; IC, interspecific competition effects (addition of sweetgum or loblolly pine competition); L vs. S, loblolly competition vs. sweetgum competition; Dp, soil depth.

complete block design was conducted at each soil depth. Response variables for loblolly pine and sweetgum were analyzed with broomsedge density (treatment) and block as factors. Response variables for broomsedge were analyzed considering block and treatment as factors with treatment partitioned into five orthogonal contrasts. Contrasts examined (i) the effect of broomsedge density, (ii) the effect of the addition of interspecific competitors (loblolly pine or sweetgum), (iii) effect of the type of interspecific competitor (loblolly pine vs. sweetgum), (iv) interaction of (i) and (ii), and (v) the interaction of (i) and (iii).

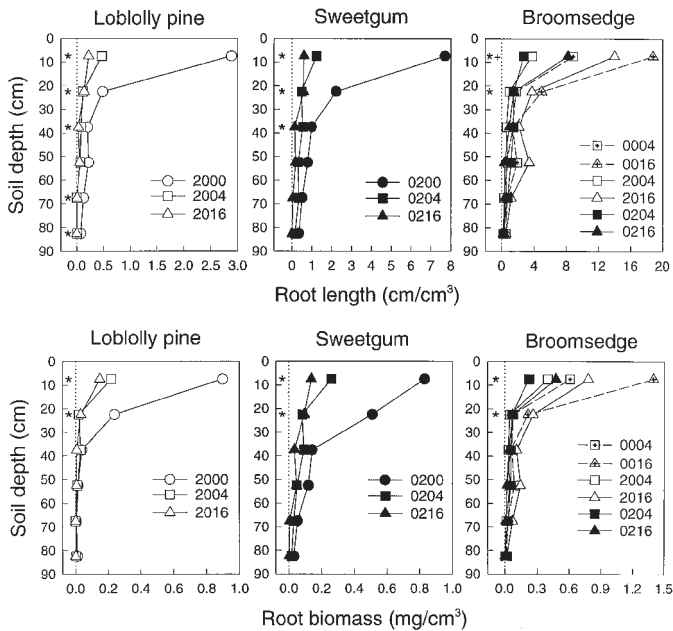
## Results

Root length density of all three species declined with increasing soil depth (Table 1, Fig. 1). In addition, loblolly pine and sweetgum root length density averaged across all

depths each decreased with the addition of broomsedge ( $p < 0.0001$ ; Table 1). Effects of broomsedge on root length density of both loblolly pine and sweetgum varied with soil depth (Fig. 1). Significant negative effects of broomsedge on root length density of both species were observed in each of the upper three 15-cm layers in the upper 45 cm of the soil ( $p < 0.10$ ; Table 2). Significant effects of broomsedge on root length of loblolly pine were also noted at 60–75 cm and 75–90 cm depths. Effects of broomsedge density were typically curvilinear in nature (significant linear and quadratic effects; Tables 1 and 2), with little to no effect from 4 to 16 plants/m<sup>2</sup> (Fig. 1).

Effects of broomsedge density on its own root length density also depended upon soil depth (Table 1, Fig. 1). Significantly lower values for root length density were noted with

**Fig. 1.** Fine root length and biomass density of loblolly pine, sweetgum, and broomsedge as a function of planting mixture and soil depth. Numbers alongside of the symbols (*XYZZ*) in each legend are the planting densities of loblolly pine (*X*), sweetgum (*Y*), and broomsedge (*ZZ*) per square metre. A significant effect ( $p = 0.10$ ) of broomsedge density at a given soil depth is noted by an asterisk along the y axis. A significant effect ( $p = 0.10$ ) of adding an interspecific competitor (loblolly or sweetgum) at a given soil depth is noted by a plus sign along the y axis.



decreasing planting density in the both the 0- to 15- and 15- to 30-cm layers of the soil ( $p < 0.10$ ). The addition of loblolly pine or sweetgum significantly reduced the root length density in the upper 15 cm of the soil ( $p < 0.10$ ). Although not statistically significant ( $p = 0.1810$ ), there appeared to be a trend for sweetgum to have a more negative effect than loblolly pine on broomsedge root length density in the 0- to 15-cm soil layer (Fig. 1).

Patterns in fine root biomass density mirrored trends noted for root length density (Tables 1 and 2, Fig. 1). Statistically significant effects of broomsedge density were limited to the upper 30 cm of soil.

Trends in aboveground biomass per hectare were similar to those observed for root length and biomass density. Aboveground biomass of loblolly pine and sweetgum declined with the addition of broomsedge (Table 3, Fig. 2). Broomsedge aboveground biomass increased with increasing broomsedge density regardless of whether it was in monoculture or in mixture with loblolly pine or sweetgum. The addition of sweetgum reduced aboveground biomass of broomsedge (Fig. 2). Interspecific effects on aboveground biomass, root length density, and root biomass density were due to effects on growth as there were no significant effects on plant survival.

In general, root lengths and root biomass of broomsedge were greater than those of either loblolly pine or sweetgum (Fig. 1). For loblolly pine this is partially explained by the 1-year delay in establishment. However, another factor is the difference in root morphology between broomsedge and

the two tree species. The root system of an individual broomsedge plant is much more fibrous with average root diameters of grasses typically being smaller. Specific root length (m/g) of broomsedge was significantly greater than both tree species ( $p < 0.05$ ), approximately three times greater than sweetgum and five times greater than loblolly pine (Table 4). No significant changes in specific root length were noted with increases in the number of competitors, i.e., addition of broomsedge to loblolly pine or sweetgum and broomsedge and the tree species to broomsedge.

There were some differences in the percent distribution of root length and (or) biomass density over the sampled 90-cm soil depth (Fig. 3). The effect of the addition of interspecific competitors was dependent on depth (Table 5). Specifically, interspecific competitors tended to reduce the percentage of roots in the 0- to 15-cm depth and increase the percentage of roots in the 15- to 30-cm depth. This is particularly noticeable in effects on root length density when broomsedge is added to either loblolly pine or sweetgum. The percent distribution of root biomass density was not affected by the addition of broomsedge. The effect on percent distribution of broomsedge roots was only significant for biomass density with the addition of loblolly pine or sweetgum (interspecific competitors).

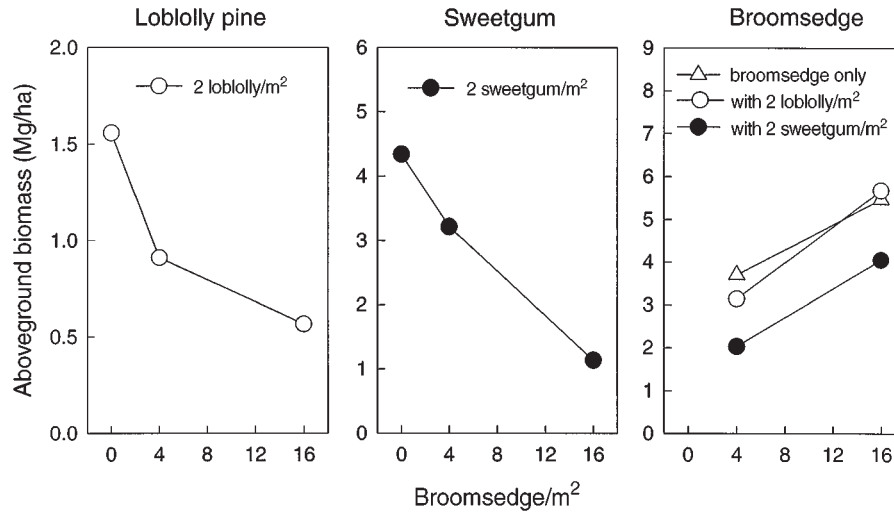
## Discussion

Values for root density were of similar magnitude to those noted in comparable studies. Loblolly pine root length density in this study compared with that Ludovici and Morris (1997) was 0.67 versus 0.50  $\text{cm/cm}^3$  for pine growing alone and 0.12  $\text{cm/cm}^3$  (4 broomsedge/ $\text{m}^2$ ) and 0.07  $\text{cm/cm}^3$  (16 broomsedge/ $\text{m}^2$ ) versus 0.05  $\text{cm/cm}^3$  for pine growing with crabgrass after one growing season over a 120-cm depth. Root length density of crabgrass growing with pine, 2.30  $\text{cm/cm}^3$ , noted by Ludovici and Morris (1997) was similar in magnitude to that for broomsedge in this study: 1.10  $\text{cm/cm}^3$  at 4 broomsedge/ $\text{m}^2$  and 4.20  $\text{cm/cm}^3$  at 16 broomsedge/ $\text{m}^2$ . Tabular data of Torreano and Morris (1998) shows an average root length density of 0.30  $\text{cm/cm}^3$  (0–90 cm depth) for loblolly pine grown alone under several watering regimes and sampled in early August. Eissenstat and Van Rees (1994) noted southern pine root length density in the surface soil (0–10 cm) to range from 0.1 to 2.4  $\text{cm/cm}^3$ .

Estimates of fine root biomass in the upper 30 cm of soil for monoculture loblolly pine averaged 1.28 Mg/ha in this study compared with 0.86 Mg/ha noted by Fredericksen and Zedaker (1995), for a 3-year-old stand planted at a wider spacing (1 × 1 m). Gholz et al. (1986) observed values of similar magnitude in a sapling slash pine (*Pinus elliottii* Englem.) stand.

In contrast to this study, Ludovici and Morris (1997) observed a lower proportion of loblolly pine root length density in the upper 15 cm of soil when grown alone versus when grown in monoculture. This may be related to differences in the soils between the two studies. In the absence of competitors in this study, loblolly pine fine roots might have been expected to proliferate in the more nutrient-rich upper 15 cm soil layer, whereas in the study of Ludovici and Morris (1997), fine roots might have been expected to be more

**Fig. 2.** Aboveground biomass of loblolly pine, sweetgum, and broomsedge as a function of planting density.

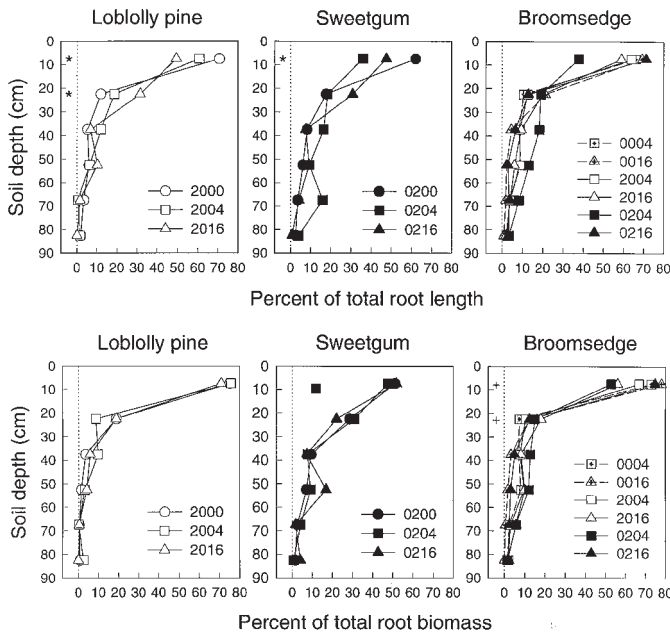


**Table 2.** Summary of statistical significance (probability of greater *F* statistic) of effects of broomsedge density (competition level) on fine root length and biomass density of loblolly pine and sweetgum, and effects of broomsedge density, interspecific competition, and their interactions on fine root length and biomass density of broomsedge from analyses of variance for each soil depth.

Effect <sup>a</sup>	Soil depth (cm)					
	0-15	15-30	30-45	45-60	60-75	75-90
<b>Loblolly pine, root length density</b>						
Brm	0.0052	0.0038	0.0720	0.3337	0.0767	0.0342
Linear	0.0038	0.0062	0.0379	0.2666	0.1012	0.0335
Quadratic	0.0179	0.0045	0.2771	0.3244	0.0713	0.0519
<b>Loblolly pine, root biomass density</b>						
Brm	0.0048	0.0287	0.6643	0.8135	0.4346	0.3424
Linear	0.0040	0.0498	0.3969	0.5491	0.3872	0.2025
Quadratic	0.0129	0.0261	0.9276	0.9344	0.3481	0.5120
<b>Sweetgum, root length density</b>						
Brm	0.0037	0.0339	0.0908	0.1621	0.4941	0.4174
Linear	0.0042	0.0510	0.0442	0.1116	0.2687	0.2378
Quadratic	0.0064	0.0334	0.4036	0.2513	0.8445	0.6317
<b>Sweetgum, root biomass density</b>						
Brm	0.0287	0.0802	0.2513	0.3812	0.4567	0.5878
Linear	0.0237	0.0985	0.1246	0.3248	0.2512	0.3447
Quadratic	0.0578	0.0785	0.6625	0.3313	0.7442	0.8029
<b>Broomsedge, root length density</b>						
Brm	0.0518	0.0964	0.8098	0.6846	0.9414	0.9047
IC	0.0904	0.7583	0.8694	0.8454	0.7950	0.9452
L vs. S	0.1810	0.5100	0.7047	0.5619	0.7696	0.8341
Brm × IC	0.3916	0.8087	0.7143	0.4498	0.7384	0.6492
Brm × L vs. S	0.8033	0.2085	0.1638	0.1935	0.2340	0.5286
<b>Broomsedge, root biomass density</b>						
Brm	0.0628	0.0181	0.6390	0.8432	0.6911	0.9695
IC	0.1195	0.5238	0.9695	0.6810	0.4785	0.8228
L vs. S	0.3335	0.2023	0.4635	0.1267	0.3326	0.5627
Brm × IC	0.8380	0.8697	0.5129	0.1839	0.3252	0.1358
Brm × L vs. S	0.9849	0.0939	0.1928	0.1141	0.1119	0.8578

<sup>a</sup>Brm, broomsedge density; linear, linear effect of broomsedge density; quadratic, quadratic effect of broomsedge density; IC, interspecific competition effects (addition of sweetgum or loblolly pine competition); L vs. S, loblolly pine vs. sweetgum competition.

**Fig. 3.** Percent distribution of fine root length and biomass density of loblolly pine, sweetgum, and broomsedge as a function of planting mixture and soil depth. Numbers alongside of the symbols (XYZZ) in each legend are the planting densities of loblolly pine (X), sweetgum (Y), and broomsedge (ZZ) per square metre. A significant effect ( $p = 0.10$ ) of broomsedge density at a given soil depth is noted by an asterisk along the y axis. A significant effect ( $p = 0.10$ ) of adding an interspecific competitor (loblolly or sweetgum) at a given soil depth is noted by a plus sign along the y axis.



uniformly distributed with soil depth since the artificial soil medium would have provided a more uniform water and nutrient-holding capacity throughout the profile.

Few data are available to compare root length density of pine, sweetgum, and broomsedge in early successional pine stands. Jifon et al. (1995), in a competition study of loblolly pine and sweetgum in pots, suggest that the deeper rooted nature and a greater root length density should give sweetgum an advantage in both nutrient and water uptake. Similar to the study by Jifon et al. (1995), it was observed here that sweetgum had greater root length density. The increase in sweetgum standing crop of root length was not found in terms of root biomass where pine and sweetgum were approximately the same. The greater specific root length of sweetgum roots suggests that they may be smaller in diameter. The small diameter of broomsedge roots are shown by the greater than sixfold increase in length in the surface 15 cm, while only exhibiting less than twice the mass when no competitors are present. Finer roots may allow for greater exploration of soil with less carbon cost. Mou et al. (1995, 1997) found sweetgum roots to more greatly proliferate in P-enriched areas than pine.

Root density (both length and mass) varied with species, depth, competition treatment, and the interaction of these factors. Root length density of woody species in the surface 15 cm was particularly sensitive to competitive interactions. As few as 4 broomsedge plants/m<sup>2</sup> (as compared with pure plots of each tree species) resulted in declines in root length

**Table 3.** Analysis of variance of loblolly pine, sweetgum, and broomsedge aboveground biomass (Mg/ha) as influenced by plant density.

Source of variation <sup>a</sup>	df	MS	F	P > F
<b>Loblolly pine</b>				
Blk	3	0.3654	5.90	0.0319
Brm	2	1.0138	16.37	0.0037
Linear	1	1.6344	26.38	0.0021
Quadratic	1	0.3931	6.35	0.0453
Error(Brm)	6	0.0619		
<b>Sweetgum</b>				
Blk	3	1.289	0.94	0.4798
Brm	2	10.5818	7.68	0.0222
Linear	1	20.9044	15.16	0.0080
Quadratic	1	0.2592	0.19	0.6797
Error(Brm)	6	1.3786		
<b>Broomsedge</b>				
Blk	3	1.8624	0.75	0.5422
Brm	1	18.7425	7.53	0.0167
IC	1	9.0517	3.64	0.0788
L vs. S	1	7.2203	2.90	0.1122
Brm × IC	1	2.0022	0.80	0.3859
Brm × L × S	1	0.3269	0.13	0.7228
Error(Trt)	15	2.4874		

<sup>a</sup>Blk, block; Brm, broomsedge density (competition level); linear, linear effect of broomsedge density; quadratic, quadratic effect of broomsedge density; IC, interspecific competition effects (addition of sweetgum or loblolly pine competition); L vs. S, loblolly competition vs. sweetgum competition.

**Table 4.** Specific root length (m/g) of loblolly pine (LP), sweetgum (SG), and broomsedge (BR) by species mixture.

Species mixture (No./m <sup>2</sup> )			Specific root length (m/g)		
LP	SG	BR	Loblolly pine	Sweetgum	Broomsedge
2	0	0	33.3	—	—
0	2	0	—	65.1	—
0	0	4	—	—	204.7
2	0	4	25.8	—	154.1*
0	2	4	—	53.0	181.7*
0	0	16	—	—	155.2
2	0	16	35.5	—	183.7*
0	2	16	—	54.9	185.5*

\*Significant difference ( $p = 0.05$ ) between values for broomsedge and loblolly pine or between values of broomsedge and sweetgum.

density of nearly six- and eight-fold for pine and sweetgum, respectively. This differs from the report by Burch et al. (1997) in which pine root length density did not vary through the 0- to 30-cm depth in the first year and was not particularly sensitive to vegetation treatments. This may be explained in part by differences in the ways roots were measured in the two studies. Minirhizotron tubes may disrupt the environment, particularly in the surface 10–15 cm through increasing light or decreasing soil moisture (Upchurch and Richie 1983; Vos and Groenwold 1987; Levan et al. 1987;

**Table 5.** Analysis of variance of percent distribution of loblolly pine, sweetgum, and broomsedge fine root length and biomass density as influenced by plant density and soil depth.

Source of variation <sup>a</sup>	df	Root length density			Root biomass density		
		MS	F	P > F	MS	F	P > F
<b>Loblolly pine</b>							
Dp	5	4557.65	70.58	0.0001	7344.54	139.23	0.0001
Dp × Blk	10	44.12	0.68	0.8036	150.85	2.86	0.1432
Dp × Brm	10	140.09	2.17	0.0495	32.72	0.62	0.6097
Error(Dp)	20	64.58			52.75		
<b>Sweetgum</b>							
Dp	5	2585.72	44.79	0.0001	2884.50	41.72	0.0001
Dp × Blk	10	125.80	2.18	0.0663	233.91	3.38	0.0098
Dp × Brm	10	184.18	3.19	0.0131	50.69	0.73	0.5847
Error(Dp)	20	57.73			69.13		
<b>Broomsedge</b>							
Dp	5	8969.92	132.54	0.0001	11453.4	341.51	0.0001
Dp × Blk	10	26.98	0.40	0.9411	27.07	0.81	0.4949
Dp × Brm	5	184.43	2.73	0.1228	85.59	2.55	0.1300
Dp × IC	5	99.06	1.46	0.2563	213.80	6.38	0.0202
Dp × L × S	5	38.80	0.57	0.4887	7.60	0.23	0.7004
Dp × Brm × IC	5	44.58	0.66	0.4554	5.33	0.16	0.7568
Dp × Brm × L × S	5	288.29	2.40	0.1576	204.22	6.09	0.0228
Error(Dp)	50	67.68			33.54		

<sup>a</sup>Blk, block; Brm, broomsedge density; IC, interspecific competition effects (addition of sweetgum or loblolly pine competition); L vs. S, loblolly competition vs. sweetgum competition; Dp, soil depth.

Burch et al. 1997). The core sampling technique used in this study did not suffer from these limitations.

Competitive responses belowground may reflect complex competitive relationships. In a previous report (Mitchell et al. 1999) showed that aboveground response of loblolly pine was primarily to soil water and light, with a secondary response to nitrogen (N). Sweetgum was much more responsive to competition for N, relative to pine; while broomsedge competitive response was primarily to light (Mitchell et al. 1999). Both sweetgum and broomsedge had greater root length density at all depths, and deeper roots of pines were significantly reduced by competition. Collectively, that would result in greater root overlap between pine and other species in competing for moisture and a reduced ability of deeper pine roots to access deeper, more stable, water sources during drought when surface soil is dry (Mitchell et al. 1993). Sweetgum roots near the surface were reduced by competition. Since N mineralization is predominately found in the surface soil, competition for N may have been more strongly impacted than that for moisture by sweetgum root response (less roots at 0–30 cm, no significant differences deeper in the solum). Also, since N uptake can be diffusion limited, the greater root length density of broomsedge may have given it a competitive advantage in N uptake (Casper and Jackson 1997).

The impact of sweetgum on broomsedge root standing crop may be due to the strong competitive effects of sweetgum on light and strong response of broomsedge to light (Mitchell et al. 1999). Reduced root growth is among the first physiological responses to reductions in light (Logan and Krotkov 1968; Hart 1988). In addition to plant response to reduction in light quantity, light quality may also affect

morphological development in plants. Phytochrome mediated responses to alteration in light quality affect plant form, such as height to diameter growth (Ballaré et al. 1990), or biochemical response such as nitrogen assimilation (Horsley 1993). The extent that light quality changes are associated with root response to light requires further work.

Burch et al. (1997) suggest that niche differentiation occurs between pines and herbaceous plants by year 3. When the ratio of standing crop aboveground to belowground was multiplied by the aboveground standing crop of herbs and pines in mixed communities, greater root density was observed than that predicted in their study. They found that herbs were more shallow rooted and pines more deep rooted, and the niche differentiation associated with soil rooting depth was suggested as a mechanism to avoid competition in natural communities. In the first year, we found no niche differentiation using soil coring techniques. This may explain the large competitive effects seen in the first year of competition and a general decline in competitive responses, particularly to herbaceous plants, with time since pine planting (Green et al. 1991).

In summary, the addition of interspecific competitors decreased fine root length and biomass density of all three species in the upper 30–45 cm of the soil. The effect was most pronounced in the upper 15 cm. Effect of broomsedge on loblolly pine root length density was noted through 90 cm. Effects of competition on root length and biomass density were similar to those noted for aboveground biomass. For each species, the proportion of fine root length or biomass density of in the upper 15 cm decreased, and that in the 15- to 30-cm depth increased, with the addition of intraspecific competitors.

## Acknowledgements

Funds for this research were provided by the Alabama Agricultural Experiment Station, U.S. Department of Agriculture – Cooperative State Research Service Grants Program in Forest Biology and Weed Science, the National Council on Stream and Air Improvement, and gifts from Rayonier Inc., Union Camp Corporation, and Westvaco Corporation.

## References

- Ballaré, C.L., Scopel, A.L., and Sanchez, R.A. 1990. Far-red radiation reflected from adjacent leaves: an early signal of competition in plant canopies. *Science* (Washington, D.C.), **247**: 329–332.
- Burch, W.H., Jones, R.H., Mou, P., and Mitchell, R.J. 1997. Root system development of single and mixed plant functional type communities following harvest in a pine–hardwood forest. *Can. J. For. Res.* **27**: 1753–1764.
- Casper, B.B., and Jackson, R.B. 1997. Plant competition underground. *Annu. Rev. Ecol. Syst.* **28**: 545–570.
- Eissenstat, D.M., and Van Rees, K.C.J. 1994. The growth and function of pine roots. *Ecol. Bull.* **43**: 76–91.
- Feldman, L.J. 1988. The habits of roots. *BioScience*, **38**: 612–618.
- Fredericksen, T.S., and Zedaker, S.M. 1995. Fine root biomass, distribution, and production. I. Young pine–hardwood stands. *New For.* **10**: 99–110.
- Gholz, H.L., Hendry, L.C., and Cropper, W.P., Jr. 1986. Organic matter dynamics of fine roots in plantations of slash pine (*Pinus elliottii*) in north Florida. *Can. J. For. Res.* **23**: 529–605.
- Green, T.H., Mitchell, R.J., Paliwal, K.C., Pathre, U.V., Zutter, B.R., and Gjerstad, D.H. 1991. Effects of herbaceous weeds on fourth year water relations and gas exchange of loblolly pine. *Weed Technol.* **5**: 753–758.
- Grime, J.P., Campbell, B.D., Mackey, J.M.L., and Crick, J.P. 1991. Root plasticity, nitrogen capture and competitive ability. *In* Plant root growth: an ecological perspective. *Edited by* D. Atkinson. Blackwell Scientific, London. *Br. Ecol. Soc. Spec. Publ. No. 10*. pp. 131–146.
- Hart, J.W. 1988. Light and plant growth. Unwin Hyman, London.
- Hendricks, J.J., Nadelhoffer, K.J., and Aber, J.D. 1993. Assessing the role of fine roots in carbon and nutrient cycling. *Trends Ecol. Evol.* **8**: 174–178.
- Horsley, S.B. 1993. Mechanisms of interference between hay-scented fern and black cherry. *Can. J. For. Res.* **23**: 2059–2069.
- Jifon, J.L., Friend, A.L., and Berrang, P.C. 1995. Species mixture and soil-resource availability affect the root growth response of tree seedlings to elevated atmospheric CO<sub>2</sub>. *Can. J. For. Res.* **25**: 824–832.
- Levan, M.A., Yeas, J.W., and Hummel, J.W. 1987. Light leak effects on near-surface soybean rooting densities. *In* Minirhizotron observation tubes: methods and applications for measuring rhizosphere dynamics. *Edited by* H.M. Taylor. *Am. Soc. Agron. Spec. Publ. No. 50*. pp. 89–98.
- Littell, R.C., Freund, R.J., and Spector, P.C. 1991. SAS system for linear models. SAS Institute Inc., Cary, N.C.
- Logan, K.T., and Krotkov, G. 1968. Adaptations of the photosynthetic mechanism of sugar maple (*Acer saccharum*) seedlings grown in various light intensities. *Physiol. Plant.* **22**: 104–116.
- Ludovici, K.H., and Morris, L.A. 1996. Responses of loblolly pine, sweetgum and crab grass roots to localized increases in nitrogen in two watering regimes. *Tree Physiol.* **16**: 933–939.
- Ludovici, K.H., and Morris, L.A. 1997. Competition-induced reductions in soil water availability reduce pine root extension rates. *Soil Sci. Soc. Am. J.* **61**: 1196–1202.
- Miller, J.H., Zutter, B.R., Zedaker, S.M., Edwards, M.B., and Newbold, R.A. 1995. Early plant succession in *Pinus* plantations as affected by vegetation management. *South. J. Appl. For.* **19**: 1–18.
- Mitchell, R.J., Zutter, B.R., Green, T.H., Perry, M.A., Gjerstad, D.H., and Glover, G.R. 1993. Spatial and temporal variation in competitive effects on soil moisture and pine response. *Ecol. Appl.* **3**: 167–174.
- Mitchell, R.J., Zutter, B.R., Gjerstad, D.H., Glover, G.R., and Wood, C.W. 1999. Competition among three common associates in secondary successional pine communities: a field study of effects and responses. *Ecology*, **80**(3): 857–872.
- Morris, L.A., Moss, S.A., and Garbett, W.S. 1993. Competitive interference between selected herbaceous and woody plants and *Pinus taeda* L. during two growing seasons following planting. *For. Sci.* **39**: 166–187.
- Moser, E.B., Saxton, A.M., and Pezeshki, S.R. 1990. Repeated measure analysis of variance application to tree research. *Can. J. For. Res.* **20**: 524–535.
- Mou, P., Jones, R.H., Mitchell, R.J., and Zutter, B. 1995. Spatial distribution of roots in sweetgum and loblolly pine monocultures and relations with above-ground biomass and soil nutrients. *Funct. Ecol.* **9**: 689–699.
- Mou, P., Mitchell, R.J., and Jones, R.H. 1997. Root distribution of two tree species under a heterogeneous nutrient environment. *J. Appl. Ecol.* **34**: 645–656.
- Perry, M.A., Mitchell, R.J., Zutter, B.R., Glover, G.R., and Gjerstad, D.H. 1993. Competitive responses of loblolly pine to gradients in loblolly pine, sweetgum, and broomsedge densities. *Can. J. For. Res.* **23**: 2049–2058.
- Perry, M.A., Mitchell, R.J., Zutter, B.R., Glover, G.R., and Gjerstad, D.H. 1994. Seasonal variation in competitive effect on water stress and pine responses. *Can. J. For. Res.* **24**: 1440–1449.
- Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, N.J.
- Torreano, S.J., and Morris, L.A. 1998. Loblolly pine root growth and distribution under water stress. *Soil Sci. Soc. Am. J.* **62**: 818–827.
- Upchurch, D.R., and Ritchie, J.T. 1983. Root observations using a video recording system and mini-rhizotrons. *Agron. J.* **75**: 1009–1015.
- Vogt, K.A., and Persson, H. 1991. Measuring growth and development of roots. *In* Techniques and approaches in forest tree ecophysiology. *Edited by* J.P. Lassoie and T.M. Hinckley. CRC Press, Boca Raton, Fla. pp. 477–501.
- Vos, J., and Groenwold, J. 1987. The relation between root growth along observation tubes and in bulk soil. *In* Minirhizotron observation tubes: methods and applications for measuring rhizosphere dynamics. *Edited by* H.M. Taylor. *Am. Soc. Agron. Spec. Publ. No. 50*. pp. 39–49.