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Responses of loblolly pine, sweetgum and crab grass roots to localized increases in nitrogen in two watering regimes

K. H. LUDOVICI[1] and L. A. MORRIS[2]

[1] *USDA Forest Service, 3041 Cornwallis Road, Research Triangle Park, NC 27709, USA*

[2] *Daniel B. Warnell School of Forest Resources, University of Georgia, Athens, GA 30602, USA*

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Summary Root responses to differences in availability of nitrogen and soil water were studied in loblolly pine (*Pinus taeda* L.) seedlings grown in monoculture and in competition with sweetgum (*Liquidambar styraciflua* L.) or crab grass (*Digitaria* spp.). Rhizotron cells were maintained at high soil water availability (approximately −0.1 MPa) or subjected to three dry-down cycles to low soil water availability (approximately −1.0 MPa), over two growing seasons. Localized increases in nitrogen availability were created by adding nitrogen in solution to root ingress cores placed in each rhizotron cell. Presence of competitors reduced loblolly pine root growth regardless of the nitrogen or soil water treatment. On average, both total root length density and root surface area were reduced 60% when loblolly pine seedlings were grown with crab grass and 31% when grown with sweetgum. Low water availability reduced loblolly pine root length density and root surface area by 25 and 28%, respectively, compared with well-watered seedlings. Sweetgum root surface area was reduced 18% by the low water availability treatment, whereas crab grass root surface area was unaffected by this treatment. At all soil depths, loblolly pine root surface area and root length density were increased in localized areas of increased nitrogen availability. Sweetgum and crab grass root surface areas were also greater in areas of increased nitrogen availability. In the high soil water availability treatment, loblolly pine root surface area increased 128% in localized areas of increased nitrogen in all competition treatments. In the low soil water availability treatment, loblolly pine roots responded to increased nitrogen only in the absence of competitors. In general, loblolly pine and sweetgum roots responded to increases in resource availability similarly, whereas crab grass roots were relatively less affected.

Keywords: Digitaria spp., Liquidambar styraciflua, nitrogen availability, Pinus taeda, roots, water availability.

Introduction

Several researchers (Lyr and Hoffman 1967, Rogers and Head 1969, Coutts 1983) have suggested that roots locate soil resources entirely by chance. However, evidence from split-root experiments (Coutts 1983) indicates that roots supplied with water or nutrients grow faster than roots deprived of these resources, suggesting that the distribution of nutrients and water within the soil probably impacts the distribution of roots. Most fine roots of loblolly pine (*Pinus taeda* L.) occur in the upper 0.15 m of a forest soil (Pritchett 1979, Vogt et al. 1983, Van Rees and Comerford 1986), where soil properties including water and nutrient availability, aeration, soil strength and temperature are most favorable for root growth. Proliferation of roots in the surface horizon is expected because this soil layer is rich in organic compounds and serves a primary role in water entry from precipitation and water storage (Damman 1971, Kimmins and Hawkes 1978, Davis et al. 1983, St. John 1983, Eissenstat 1991, Stone and Kalisz 1991). The gradual decline in root density with soil depth likely reflects the absence of abrupt soil horizon boundaries and the gradual decrease with depth in concentrations of organic matter and available nutrients.

Nitrogen is one of the nutrients most limiting to plant growth in forest soils. Competition for nitrogen may be intense (Caldwell and Richards 1986, Wilson and Newman 1987) and can lead to an overall decrease in root development when neighboring plants take up nitrogen and reduce its availability (Hodgkins and Nichols 1977). Reduced foliar nitrogen concentrations occur in tree seedlings grown in mixed plant communities. Morris et al. (1993) found that nitrogen deficiencies occurred in loblolly pine seedlings grown in intense grass competition and that, in general, foliar nitrogen concentrations were affected more by competition than were other macronutrients. Reduced nitrogen concentrations were associated with decreased water availability and reduced root length.

Competitive success depends on the ability both to deplete soil resources accessible to existing roots, and to make accessible additional resources through positive root growth responses (Goldberg 1990). Root competition among species involves general and localized responses to water and nutrient availabilities. Root proliferation (as measured by surface area or length density) in areas of high nutrient availability can lead to a competitive advantage. Successful competitors will likely tolerate zones of limited resources and have relatively large responses to zones of increased soil resources.

In this study, we evaluated the responses of loblolly pine seedlings and two commonly occurring competing plant species, sweetgum (*Liquidambar styraciflua* L.) and crab grass (*Digitaria* spp.) to differences in soil water and nitrogen availability. Inclusion of sweetgum, a competitor species with less root proliferation than crab grass, provided an intermediate level of competition and resource removal. The inclusion of two watering regimes within the competition treatments, enabled a quantitative assessment of the impact of soil water availability on loblolly pine root growth rate. The specific objectives of this study were: (i) to determine whether differences in root response to localized increases in soil nitrogen availability exist among these three competing species; and (ii) to evaluate the extent to which depth distribution of competing loblolly pine, crab grass and sweetgum roots can be altered by water and nitrogen availability.

Materials and methods

Experiment design

The influences of water and nitrogen availability on loblolly pine seedlings grown with herbaceous and woody competitors were evaluated under controlled rhizotron conditions during the summers of 1993 and 1994. The work was conducted in the University of Georgia, Whitehall Experimental Forest rhizotron described by Torreano (1992). The experimental design was a 3 × 2 factorial combination of three competition treatments (loblolly pine alone, loblolly pine grown with crab grass and loblolly pine grown with sweetgum) and two soil water availability treatments (high or low) replicated in three incomplete blocks. To evaluate effects of localized nitrogen on root distribution, each main plot treatment cell was split into three soil depths (0–0.3, 0.3–0.6 and 0.9–1.2 m) with two nitrogen treatments (with and without additional ^{15}N-labeled nitrogen applied to root ingress cores) within each depth increment.

The rhizotron consisted of 16 individual 1 × 1 × 2 m (length × width × depth) cells with a tempered glass plate installed at a 7° angle as the inner wall. Rhizotron cells were filled with a 5/1 (v/v) mixture of washed sand (No. 10 fine masonry sand and fritted clay (Terra Green Soil Conditioner, Southern Turf Co., Norcross, GA). (The use of all trade or firm names in this publication is for reader information only and does not imply endorsement by the USDA of any product or service.) The mixture had a sandy-loam texture and provided minimal structural impedance (maximum cone resistance of < 0.5 MPa), excellent aeration and uniform nutrient and water distribution throughout the cell depth. Nutrient holding capacity was relatively low allowing manipulation of labile nutrient concentrations. Soil nutrient analyses were performed by A&L Analytical Laboratory, Inc. (Memphis, TN) using a double-acid extraction (0.05 M HCl plus 0.025 M H_2SO_4). Initial concentrations of NH_4-N, P, K, Ca and Mg were 5, 13, 116, 220 and 65 mg kg^{-1}, respectively, with a measured acidity of pH 5.1 (1/1 soil/water mixture). These conditions were within the range of acidic, nutrient-poor conditions found in many southern forest soils (Pritchett and Fisher 1987). Methyl bromide was used to sterilize the soil medium before transplanting.

Root ingress cores were made from stainless steel screen with a 300-micron aperture (80 mesh) (Tylinter Industrial Wire Cloth Co., Mentor, OH). Each core measured 0.08 m in diameter and 0.45 m in length and was open at the top and bottom. Three cores were placed at each of the three depths (0–0.3, 0.3–0.6 and 0.9–1.2 m) as the rhizotron cells were filled, and positioned so that the middle 0.3 m of each core encompassed the appropriate depth. The cores were randomly located along an arc of radius 0.15 m, centered at one of the seedlings placed 0.53 m from the window.

Competition treatment

Union Camp Corporation provided the loblolly pine seeds (Family 0225-10-0005-AA). The seeds were germinated and then planted in Ray Leach® tubes filled with the rhizotron soil. Eight-week-old loblolly pine seedlings were transplanted to the rhizotron and grown for two growing seasons in monoculture or in mixed cultures with crab grass or sweetgum. Four seedlings were planted in each cell so that the root systems of two seedlings could be monitored at each rhizotron window. Seedlings were planted 0.38 m apart at distances of 0.15 and 0.53 m from the rhizotron window. Vegetative inoculum of the ectomycorrhizal fungus *Pisolithus tinctorius* Coker and Couch (Pt) was provided by Mycorr Tech,® Inc. (Pittsburgh, PA). A 100-ml aliquot of commercially prepared vegetative inoculum was added to a core of rhizotron soil as each seedling was transplanted.

Sweetgum seed was provided by the Georgia Forestry Commission (Family 678). One week after the loblolly pine seedlings were transplanted to the rhizotron, stratified sweetgum seeds were sown directly into the sweetgum competition cells. Twenty-five seeds were sown at each of 16 predetermined locations where each loblolly pine seedling would be proximal to eight sweetgum seedlings. Sweetgum seedlings were thinned to one per location over a period of six weeks. Crab grass seed was purchased from Azline Weed Seed Co. (Leland, MS). One week after the loblolly pine seedlings were transplanted to the rhizotron, the crab grass seeds were sown at a rate of 4.2 g m^{-2}, or approximately 7,300 large crab grass seeds per grass competition treatment cell.

Water availability treatment

Rhizotron cells were watered daily for seven weeks until loblolly pine, sweetgum and crab grass plants were well established. For the duration of the 1993 experiment, natural rainfall was excluded by placing rainfall shields over the rhizotron cells before precipitation events began. Seedlings were maintained at high soil water availability (approximately −0.1 MPa) or subjected to two dry-down cycles during 1993 (Weeks 8 and 9 and Weeks 18–21 of the experiment) by withholding water. All rhizotron cells were wetted to field capacity when soil water potentials approached −1.5 MPa at 0.3-m depth in the driest rhizotron cell or measured predawn xylem pressure potential was less than −0.3 MPa. All rhizotron cells were kept at field capacity during the fall and subjected to ambient rainfall after leaf senescence and through the spring. In summer 1994, ambient rainfall was again excluded, and all seedlings were watered to field capacity daily, except during the drying cycle (Weeks 60 and 61 of the experiment). Rhizotron cells were watered with a complete nutrient mix (N,P,K 20,20,20) seven times during 1993 and three times in 1994. Total additions of elemental N, P and K to each treatment cell were 113.5, 48.4 and 93.5 g, respectively.

Soil water content was monitored by time domain reflectometry (TDR) (Topp et al. 1982), by means of pairs of stainless steel probes that were placed horizontally at depths of 0.05, 0.15, 0.3, 0.6, 0.9 and 1.5 m as the rhizotron cells were filled. Coaxial cable was connected to each pair of rods and permanently affixed through cell bottom drain ports to allow easy access with no future disturbance. A Tektronix® cable tester (Tektronix model 1502B TDR Cable Tester, Beaverton, OR) was used to measure the reflected signal. Readings were registered in millivolts and related to steel probe length, with a resulting k value used to calculate soil water content (MC) based on the equation of Topp et al. (1982). Soil water content was evaluated twice weekly throughout both growing seasons. Soil water retention curves developed from intact cores using Tempe cells were used to convert water content to water potential.

Nitrogen split-split plot treatment

In addition to base fertilization, additional nitrogen was added twice during the 1993 growing season and three times during 1994 to appropriate ingress cores in the form of ammonium sulfate solution tagged with ^{15}N. One core at each depth received additional nitrogen, and the other two cores received no additional nitrogen. Tygon® tubing was used to connect cores placed at depths of 0.3–0.6 and 0.9–1.2 m to the soil surface to facilitate addition of $^{15}NH_4SO_4$ solution. At each addition, 0.5 g of N containing 0.05 g of ^{15}N was applied, for a total nitrogen treatment addition of 2.5 g of N to each supplemented core.

Measurements and analyses

Seedling heights and diameters were measured weekly. Total aboveground biomass was collected from each cell at the end of the experiment and dried at 70 °C to constant weight.

Root ingress cores were excavated from each cell, wrapped in foil and paper bags and stored at 4 °C until processing was complete. A 0.075-m length of soil was discarded from both ends of every core, leaving the middle 0.3 m of soil and root volume as the working sample. This remaining volume of soil was sieved, roots were extracted, and the soil was air-dried.

Extracted roots were separated by species, washed and stored in damp paper towels at 4 °C. Root surface areas were measured for each species with a portable leaf area meter (Model 3000, Li-Cor, Inc., Lincoln, NE). Root samples were photocopied to enable root length measurements from the images with a Lasico linear probe (Model 71A-M, Lasico, Los Angeles, CA). Samples were dried at 70 °C for 24 h and weighed. Root densities were calculated from root length and core soil volume measurements.

The experiment was analyzed as a factorial combination of competitor and watering treatments, with rhizotron depth increment as a split within these main plots and root ingress cores as split-split plots (with and without additional ^{15}N labeled nitrogen). Data on belowground parameters were statistically analyzed using appropriate ANOVA for a split-split plot analysis (SAS Institute 1985, Cary, NC) and reported at the 0.05 level of significance. Duncan's multiple range test was used to separate means at the 0.05 level of significance.

Results

Competition effect

Compared to the stem volume of seedlings grown in monoculture, loblolly pine stem volume was reduced 19% when seedlings were grown in competition with sweetgum, and 65% when grown in competition with crab grass (Table 1). Competition-induced decreases in soil water content were evident two weeks after crab grass emergence and subsequent decreases were significant for all measurements to a depth of 0.9 m during the dry-down cycles (data not shown).

Compared with seedlings grown in monoculture, loblolly pine root surface area and root length density decreased more than 30% when seedling were grown in competition with sweetgum, and more than 60% when seedlings were grown in competition with crab grass (Table 1). Loblolly pine root dry weight decreased 9% when grown with sweetgum, and 60% when grown with crab grass, compared with loblolly pine monoculture (Table 1).

For all species, root surface area, root length density and root weight decreased with increasing depth in the rhizotron, averaged across watering regime, nitrogen supplement and competition treatment. Loblolly pine and sweetgum root surface

Table 1. Characteristics of loblolly pine and competitor species in different competition treatments, at the conclusion of the experiment, averaged across watering regimes, nitrogen supplements and rhizotron depths.

Characteristic	Loblolly pine monoculture	Sweetgum	Crab grass	$P > F$
Stem volume (m^3)				
Loblolly pine	0.121	0.098	0.042	0.001
Sweetgum	–	0.029	–	–
Root surface area ($m^2\ m^{-3}$)				
Loblolly pine	0.150 a[1]	0.099 b	0.057 c	0.0001
Competitor	–	0.083	0.347 c	0.0001
Root length density ($m\ m^{-3}$)				
Loblolly pine	178.67 a	124.00 b	70.67 c	0.0001
Competitor	–	235.33	–	–
Root dry weight ($g\ m^{-3}$)				
Loblolly pine	23.33 a	21.33 a	9.33 b	0.001
Competitor	–	11.33	28.67	0.0001

[1] Means in a row with dissimilar letters are significantly different at the 0.05 level according to Duncan's multiple range test.

areas were similar at 0–0.3-m depth, but crab grass root surface area was nearly six times greater at that depth (Figure 1).

Water effect

Loblolly pine root surface area, root length density and root weight, averaged across competition and nitrogen addition treatments, were 40, 33 and 26% greater, respectively, in the high water availability treatment than in the low water availability treatment (Table 2). Loblolly pine and sweetgum root surface areas were similar in both water availability treatments and both had one-third of the root surface area of crab grass. Sweetgum root length density was greater than that of loblolly pine in both water availability treatments (Table 2). The watering regimes did not significantly impact crab grass root surface area or root weight.

There were more roots of all species in the surface horizon than at other soil depths (Table 3). However, sweetgum and crab grass root surface areas and root weights were not predictably affected by water availability at any depth. The effect of increased water availability on loblolly pine root surface area was not linearly related to soil depth. The high water availability treatment increased loblolly pine root surface area by 20% at 0.3–0.6-m depth and by 250% at 0.9–1.2-m depth compared with values in the low water availability treatment (Table 3). The corresponding increases in loblolly pine root length density were 3% at 0.3–0.6-m depth and 261% at 0.9–1.2-m depth (Table 3).

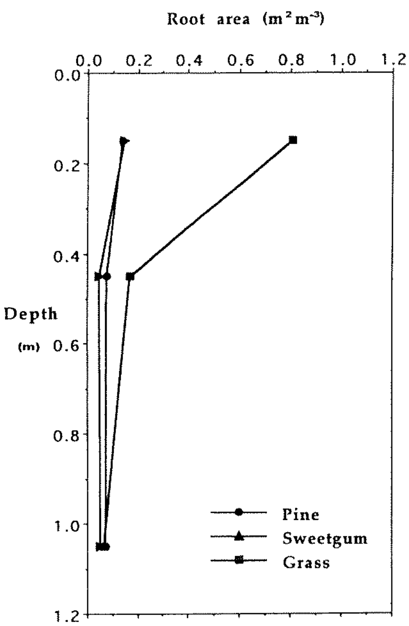

Figure 1. Distribution of within-core root surface areas by depth for loblolly pine and competitor species averaged across watering regimes, nitrogen supplements, and competition treatments.

Table 2. Root responses of loblolly pine and competing species to watering regime and additions of supplemental nitrogen to root ingress cores averaged across three depths in the rhizotron.

Root characteristic	High water availability	Low water availability	^{15}N supplement	No ^{15}N supplement
Surface area (m^2 m^{-3})				
Loblolly pine	0.111a[1]	0.079b	0.141a	0.073b
Sweetgum	0.091	0.075	0.122a	0.063b
Crab grass	0.339	0.355	0.472a	0.285b
Length density (m m^{-3})				
Loblolly pine	134.00a	100.53b	159.13a	97.06b
Sweetgum	223.33	252.67	366.00a	173.33b
Dry weight (g m^{-3})				
Loblolly pine	19.33a	15.33b	23.46a	14.37b
Sweetgum	15.30	10.60	17.77a	8.13b
Crab grass	27.67	31.80	33.73a	25.73b

[1] Means within a main treatment, parameter and species, with dissimilar letters, are significantly different at the 0.05 level according to Duncan's Multiple Range test.

Nitrogen effect

Root surface area, length and dry weight were higher in cores with supplemental nitrogen than without supplementary nitrogen (Table 2). On average, loblolly pine root surface areas increased 93% in cores with supplemental nitrogen, and root length densities of loblolly pine and sweetgum increased by 64 and 111%, respectively. In response to localized areas of increased nitrogen availability, root weights of loblolly pine, sweetgum and crab grass increased 63, 119 and 31%, respectively, averaged across depth in the rhizotron cell.

Increased nitrogen availability increased loblolly pine root surface area and root length density at all depths in the rhizotron. In the cores receiving supplemental N, loblolly pine root surface area increased 107% at the surface, 48% at 0.3–0.6-m depth and 123% at 0.9–1.2-m depth, averaged across watering regimes and competition treatments (Table 4); the corresponding values for root length density were 78, 70 and 42% (Table 4).

Sweetgum root surface area and root length density increased in cores receiving supplemental N at all depths, and the magnitude of the increase was depth dependent. In localized areas of increased N availability, sweetgum root surface area and length density increased 19 and 33%, respectively, in the surface 0–0.3-m cores (Table 4), 296 and 325%, respectively, at 0.3–0.6-m depth and 288 and 239%, respectively, at 0.9–1.2-m depth (Table 4). Crab grass root surface area increased 56% in the surface 0–0.3 m, 88% at 0.3–0.6-m depth and 144% at 0.9–1.2-m depth in the cores receiving supplemental N (Table 4).

Interactions

The effect of supplemental N on loblolly pine root length density differed among the competition treatments when averaged across watering regimes. The magnitude of the response was greatest in loblolly pines grown in monoculture (Figure 2).

In general, loblolly pine root surface areas increased at all depths and with all competitors when nitrogen availability was increased; however, the magnitude of the response decreased with increasing competition intensity (Table 5). Sweetgum and crab grass root surface areas also increased in cores with supplemental nitrogen, but, unlike loblolly pine, the magnitude of the response was not necessarily greater under high water availability. Sweetgum root surface area was greater in localized areas of increased nitrogen for all depths (e.g., an 853% increase at 0.9–1.2-m depth) and both water availability regimes, except in surface cores at low water availability where it was decreased by 26% (Table 5). Crab grass root surface area was always greater in localized areas of increased nitrogen

Table 3. Root characteristics of loblolly pine and competitor species within cores by depth and watering regime, averaged across nitrogen supplements and competition treatments.

Root characteristic	Water availability	Depth increment (m)			$P > F$
		0–0.3	0.3–0.6	0.9–1.2	
Surface area ($m^2\ m^{-3}$)					
Loblolly pine	High	0.140	0.083	0.112	0.0008
	Low	0.139	0.069	0.032	
Sweetgum	High	0.158	0.069	0.045	0.57
	Low	0.137	0.030	0.058	
Crab grass	High	0.781	0.175	0.063	0.57
	Low	0.834	0.161	0.069	
Length density ($m\ m^{-3}$)					
Loblolly pine	High	144.73	109.93	147.87	0.0001
	Low	216.13	106.87	41.00	
Sweetgum	High	395.13	228.07	142.00	0.15
	Low	372.6	118.73	169.87	
Dry weight ($g\ m^{-3}$)					
Loblolly pine	High	30.67	18.00	10.67	0.99
	Low	27.33	12.00	6.67	
Sweetgum	High	23.33	7.33	8.00	0.76
	Low	17.33	5.33	7.33	
Crab grass	High	64.67	12.00	4.00	0.76
	Low	71.33	13.33	6.00	

Table 4. Root characteristics of loblolly pine and competitor species within cores by depth and supplemental nitrogen treatment, averaged across watering regimes and competition treatments.

Root characteristic	^{15}N supplement	Depth increment (m)			$P > F$
		0–0.3	0.3–0.6	0.9–1.2	
Surface area ($m^2\ m^{-3}$)					
Loblolly pine	+	0.213	0.098	0.114	0.01
	–	0.103	0.066	0.051	
Sweetgum	+	0.165	0.099	0.101	0.02
	–	0.139	0.025	0.026	
Crab grass	+	1.062	0.244	0.110	0.02
	–	0.680	0.130	0.045	
Length density ($m\ m^{-3}$)					
Loblolly pine	+	214.33	149.47	117.60	0.04
	–	120.60	87.87	82.93	
Sweetgum	+	466.60	353.80	294.40	0.20
	–	350.33	83.20	86.73	
Dry weight ($g\ m^{-3}$)					
Loblolly pine	+	44.00	15.33	11.33	0.007
	–	20.67	14.67	8.00	
Sweetgum	+	28.67	10.00	15.33	0.05
	–	16.00	4.00	4.00	
Crab grass	+	79.33	15.33	6.67	0.05
	–	62.00	10.67	4.00	

availability in both watering regimes. The magnitude of the response ranged from a 36% increase in the 0–0.3-m deep cores to a 443% increase in the 0.9–1.2-m deep cores (Table 5).

The distribution of loblolly pine roots tended to shift downward at high water availability and upward at low water availability, in all competition treatments. Localized increases in nitrogen availability were associated with upward shifts in root distribution for loblolly pine grown in monoculture or with sweetgum, but not for loblolly pine seedlings grown with crab grass.

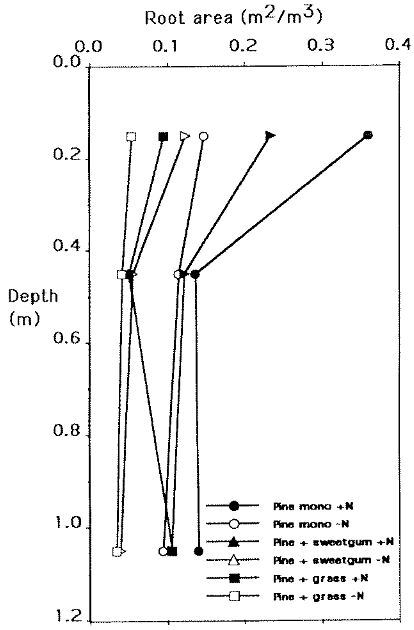

Figure 2. Distribution of root surface areas within cores by depth for loblolly pine seedlings grown with sweetgum or crab grass competition in the presence and absence of a nitrogen supplement, averaged across watering regimes.

Discussion

The competitive ability of plants is closely linked to the ability of their roots to reach and utilize soil water and nutrients. Our findings confirm previous work showing general positive correlations between root growth response and soil water availability (Sands and Nambiar 1987, Wilson and Newman 1987, Torreano 1992, Morris et al. 1993, Ludovici 1996), and nitrogen availability (St. John 1983, Stone and Kalisz 1991). The spatial distribution of these resources and the distribution of absorbing root surface dictate how much of these resources is available for uptake by the plant. The key question remaining, and the one relevant to the manipulation of site resources, concerns the plasticity of root distribution with soil depth.

In general, the competitors, sweetgum and crab grass, responded more to localized increases in nitrogen when water availability was low, whereas loblolly pine roots responded more to increased nitrogen availability when water availability was high. The importance of high water availability for root growth of loblolly pine was indicated by the increases in loblolly pine root area, root length and root dry weight in the high water availability treatment. Although sweetgum root area and root dry weight also increased at high water availability, both crab grass root growth and sweetgum root length were greater at low water availability than at high water availability, possibly indicating the ability of both of these species to shift

Table 5. Root surface areas ($m^2\ m^{-3}$) of loblolly pine and competitor species by watering regime, supplemental nitrogen treatment and depth for each competition treatment.

Competition treatment	Depth (m)	High water availability		Low water availability	
		+ ^{15}N	– ^{15}N	+ ^{15}N	– ^{15}N
Loblolly pine monoculture					
Loblolly pine	0.0–0.3	0.305	0.200	0.415	0.096
	0.3–0.6	0.071	0.218	0.201	0.014
	0.9–1.2	0.270	0.125	0.010	0.062
Loblolly pine + Sweetgum					
Loblolly pine	0.0–0.3	0.303	0.069	0.164	0.176
	0.3–0.6	0.132	0.037	0.111	0.071
	0.9–1.2	0.196	0.044	0.012	0.035
Sweetgum	0.0–0.3	0.220	0.127	0.111	0.151
	0.3–0.6	0.131	0.038	0.066	0.011
	0.9–1.2	0.060	0.037	0.143	0.015
Loblolly pine + Crab grass					
Loblolly pine	0.0–0.3	0.121	0.044	0.069	0.062
	0.3–0.6	0.058	0.032	0.041	0.051
	0.9–1.2	0.181	0.042	0.031	0.026
Crab grass	0.0–0.3	1.112	0.615	1.012	0.745
	0.3–0.6	0.196	0.164	0.292	0.095
	0.9–1.2	0.068	0.061	0.152	0.028

carbon allocation to roots, thus achieving a competitive advantage over young loblolly pine. Based on these findings and our observation of a general lack of response of crab grass roots to increased water availability, we conclude that crab grass is a stronger competitor at low water availability and utilizes more of the available resource more quickly than loblolly pine.

The density of absorbing roots strongly affects initial rates of water and nutrient uptake and competition among plants with roots in the same soil volume (Sands and Nambiar 1984). In our study, sweetgum roots showed the greatest response of the three species to increases in nitrogen availability, with increases in root length density of 600% and increases in root surface areas of 300%. The ability of sweetgum to respond to localized increases in nitrogen and water availability contributes to this species' competitive advantage over loblolly pine on many field sites.

Ludovici (1996) showed that the temporal patterns of loblolly pine root growth and the distribution of loblolly pine roots with depth were similar for seedlings of similar aboveground size when grown in competition with crab grass under two watering regimes. Results from this study indicate that, although the distribution of loblolly pine roots was not changed by reductions in available water, it was altered by the presence of localized zones of increased nitrogen availability.

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