

Root system development of single and mixed plant functional type communities following harvest in a pine–hardwood forest

Walter H. Burch, Robert H. Jones, Pu Mou, and Robert J. Mitchell

Abstract: To determine how plant functional types influence belowground processes, pure and mixed communities of loblolly pine (*Pinus taeda* L.), broad-leaved (hardwood) woody species, and herbaceous species were established after clear-cutting a pine–hardwood forest. Roots from the pure and mixed communities were observed using minirhizotron tubes, and soil moisture, temperature, and inorganic nitrogen were sampled at various depths over three growing seasons after harvest. Herbs had the greatest standing crop and productivity of roots except when all three functional types were combined. Hardwoods and herbs concentrated root growth in the upper 40 cm of soil, while pine exhibited disproportionately deeper rooting. When pine was mixed with herbaceous vegetation, root density was high in both upper and lower soil horizons. The same additivity was not observed for the pine–hardwood mixture. Hardwood vegetation significantly depressed soil moisture in lower horizons. Pine-only plots had slightly warmer surface soil temperatures during growing season months, and greater soil water nitrate concentrations during the first growing season. Root densities were correlated with nitrate but not with ammonium or water. Overall, community composition following disturbance had strong impacts on spatial and temporal distribution of roots as well as soil resources.

Résumé : Après avoir coupé à blanc une forêt de pin et de feuillus, des communautés pures et mélangées de pin à encens (*Pinus taeda* L.), d'espèces ligneuses à feuilles caduques (feuillus) et d'espèces herbacées furent établies afin de déterminer de quelle façon les types fonctionnels de plantes influencent les processus au niveau du système racinaire. Les racines des communautés pures et mélangées ont été observées à l'aide de minirhizotrons en forme de tube et l'humidité du sol, la température et l'azote inorganique ont été mesurés à différentes profondeurs au cours des trois saisons de croissance qui ont suivi la récolte. Les herbacées avaient la plus forte production et la meilleure productivité racinaire excepté lorsque les trois types fonctionnels étaient combinés. Les feuillus et les herbacées concentraient leur croissance racinaire dans les premiers 40 cm de sol tandis que le pin avait un enracinement disproportionnellement plus profond. Lorsque le pin était mélangé à la végétation herbacée, la densité des racines était élevée dans les horizons supérieurs et inférieurs. La même additivité n'a pas été observée dans le cas du mélange pin et feuillus. La végétation feuillue diminuait significativement l'humidité du sol dans les horizons inférieurs. Dans les parcelles établies seulement avec le pin, la température à la surface du sol était légèrement plus chaude pendant les mois correspondant à la saison de croissance et la concentration de nitrate dans l'eau du sol était plus élevée pendant la première saison de croissance. La densité des racines était corrélée avec les nitrates mais non avec l'ammonium ou l'humidité. Dans l'ensemble, la composition d'une communauté suite à une perturbation avait d'importantes répercussions sur la distribution spatiale et temporelle des racines aussi bien que sur les ressources du sol.

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Introduction

Root system structure and demography, and differences among species in these traits, have important influences on

plant competition (Caldwell 1987; Tilman 1988; Grime et al. 1991), water use and nutrient cycling (Mackie-Dawson and Atkinson 1991; R.J. Mitchell et al. 1997³), and primary productivity (McClougherty et al. 1982). Considering the recent emphasis on ecosystem management (Christensen et al. 1996), land managers would benefit if they knew how alterations of vegetation affected these belowground processes. Because of logistical difficulties, however, few researchers have attempted to study root growth patterns for different species within the same community, especially in forests where the number of species is large.

In lieu of studying root system architecture and function for individual species, investigators can target plant functional types, an approach that has been successful in grasslands and deserts (Weaver and Kramer 1932; Caldwell et al. 1991a; Rundel and Nobel 1991; Lee and Lauenroth 1994; Jackson et al. 1996). Such studies have shown that annuals have shallower root systems than perennial herbs and woody plants (Clements et al. 1929; Weaver and Clements 1929; Caldwell et al. 1991a). Also, short-lived, early-successional species

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tend to invest heavily in aboveground carbon accumulation as juveniles and mature early, while long-lived, late-successional species invest heavily in root development as juveniles and mature later (Monk 1966; Strauss and Ledig 1985; Platt et al. 1988; Gleeson and Tillman 1990, 1994). With few exceptions, communities dominated by perennial herbaceous vegetation have greater root to shoot biomass ratios and greater proportions of total ecosystem productivity below ground (Caldwell 1987). From these general trends, it appears that some mixture of plant functional types or species may be more likely to have strong belowground competitive interactions than others (Parrish and Bazzaz 1976; Grime et al. 1991). Nevertheless, few studies have tested this idea in natural communities, particularly outside of deserts and grasslands. Forests are particularly rich in plant functional types and may be useful for studying rooting patterns of different plant functional types. Trees, herbaceous plants, and nonarborescent woody plants typically occur. Additionally, humans often control functional type distribution in forests to meet management goals.

The system that we have studied, an upland pine–oak forest in the southeastern United States, is an important commercial forest type subject to a large variety of silvicultural practices. Typically, trees are harvested and then planted with loblolly pine (*Pinus taeda* L.) seedlings to provide a future timber crop. Since hardwood and herbaceous plants strongly compete with the pine (Miller et al. 1991; Morris et al. 1993), harvest is often followed by mechanical or chemical treatments to reduce abundance of unwanted species (Miller et al. 1991). Such alterations have desirable impacts on growth rate of crop species (Miller et al. 1991); however, the influences of these changes on belowground net primary productivity, soil water quantity, and nutrient dynamics are less clear.

The primary objective of this research was to determine whether functional types that typically occupy upland pine–oak forest in the southeastern United States after clear-cutting differ in their root system structure, productivity, and impacts on soil properties. Ultimately, this research should help scientists and managers evaluate trade-offs between belowground functions (e.g., soil water use and nitrogen retention) and desired aboveground functions (e.g., timber and wildlife forage production) when functional types are used individually or in combination.

Methods

Study site and vegetation treatments

This study was conducted adjacent to the main campus of Auburn University in the upper coastal plain of east-central Alabama. Soils are fine-loamy, siliceous, thermic, plinthic Kandiodults with 40 cm of loamy sand and sandy loams over a thick (>2 m) layer of sandy clay loams. The plinthite layer is uniformly positioned at approximately 1 m depth. Soil pH is low (range 4.7–4.9 in the A and B horizons; unbuffered 1:1 soil–water method) as are organic matter content (2% in Ap horizon and <0.5% in the B horizons; combustion method), plant-available nitrogen (NH_4^+ -N <0.01 $\mu\text{g/g}$ and NO_3^- -N $\leq 2 \mu\text{g/g}$; Kjeldahl method), and other plant-available nutrients (Ca $\leq 70 \mu\text{g/g}$, K $\leq 21 \mu\text{g/g}$, P $\leq 2 \mu\text{g/g}$; Mehlich 1 extraction; see Soil and Plant Analysis Council (1992) for soil analysis procedures). Annual rainfall in Auburn, Alabama, averages 1434 mm, but was 1549 mm during the first year of the study (1992, a wet year), 1127 mm in 1993 (a dry year), and 768 mm during the first 6 months of 1994 (normal year).

Prior to harvest, the site was a slash pine (*Pinus elliotii* Engelm.)

plantation on previously cultivated soil, with a hardwood subcanopy of sweetgum (*Liquidambar styraciflua* L.) and water oak (*Quercus nigra* L.), and a sparse herbaceous layer. In December 1991, the site was harvested (stem only), roller-drum chopped, and burned.

Following harvest, 21 contiguous 7 × 7 m plots were established within a 21 × 49 m area. The periphery of each plot was trenched to a depth of 1.5 m and lined with thick plastic to minimize root growth between plots. Three replicates of seven vegetation composition treatments were randomly assigned to the plots following harvest. The treatments were pure loblolly pine planted at 1 m spacing; naturally regenerated hardwood species; naturally regenerated herbaceous species; all two-way combinations; and the three-way combination of pine, hardwood, and herbaceous vegetation. Natural regeneration of hardwood and herbaceous species consisted of seed bank germination and stump and root sprouting. Herbaceous vegetation included annual and perennial forbs and graminoids, plus several species of blackberry (*Rubus* spp.), a genus of semiwoody perennials that we arbitrarily included in this category. Vegetation composition was maintained throughout the study primarily by hand weeding, but where possible, a 2% solution of glyphosate was sprayed directly on the leaves of unwanted plants. Vines were periodically removed, but were persistent in low levels.

For each plot, crown volume of woody plants and percent cover by herbaceous plants were measured using low-altitude, large-scale aerial photographs obtained for each plot via a helium-filled weather balloon. Photos were taken in June 1992 and September 1993; measures were determined by ground-truthed stereo photointerpretation (Pitt et al. 1996). In addition to total crown volume and herb cover, separate photo measures were made for crown volumes of each major woody plant species and for cover of annuals, perennials, grasses (including sedges), blackberry, and vines.

Root measurements

In February and March 1992, eight clear plastic minirhizotron tubes were installed in the inner 5 × 5 m area of each plot. A tractor-mounted Giddings probe (Giddings Machine Co., Fort Collins, Colo.) was used to make the holes and set the tubes. Tube locations were random. Each 1.6 m long tube was inserted at a 45° angle to limit the potential for root tracking along the soil tube interface (Bragg et al. 1983). The portion of the tubes extending above the soil surface was wrapped heavily in tape and capped using a PVC cap to prevent light and water entry. A gasket made of heavyweight plastic was also fitted around the tube at the soil surface to prevent near-surface light leaks (Levan et al. 1987).

Root density along the upper face of each minirhizotron tube was measured 11 times between May 1992 and June 1994 with a video camera (Bartz Technology, Inc. Santa Barbara, Calif.). For each 0.95 vertical soil depth, the number of root intersections with the bottom and right side of the video monitor was counted and recorded, which is an intersection count method for estimating root density (Böhm 1979; Buckland et al. 1993). Because of sparse data at lower depths, all measurements reported here are for the top 90 cm of soil.

Three tubes per plot were chosen at random for assessing live root fraction via UV light. In a previous laboratory study (Wang et al. 1995), roots collected from the same study site were successfully classified as live or dead by washing them, and then recording if they had fluorescence (i.e., were alive) under UV light in the laboratory. In situ, the microbes associated with dead roots may fluoresce under UV light, and thus our field assessment may overestimate live root fraction.

Root counts were converted to root length density (RLD) to make our final results more compatible with other studies (Buckland et al. 1993). To estimate RLD, color video images of all minirhizotron tubes were recorded on three of the sample dates (March 1993, September 1993, and June 1994). From each of the pure pine, pure hardwood, and pure herbaceous vegetation treatments, we randomly selected nine tubes from the September 1993 sample, three from the

March 1993 sample, and three from the June 1994 sample. The later dates were chosen to account for temporal variation if any existed. Root lengths for each image in each tube were traced using digital analysis software. Linear regression was then used to construct an equation for converting intersection counts made in the laboratory into RLD. To assess the possibility that errors were made in field root intersection counts, video images were examined in the laboratory to count root intersections along the bottom and right side (i.e., following the procedure used in the field), and these data were correlated with counts from the same images made during field sampling.

Soil water and inorganic nitrogen

From May 1992 to December 1993, volumetric soil moisture content was assessed by time domain reflectometry within the 0–20, 0–30, 0–40, and 0–80 depth zones using one set of paired stainless steel rods per depth per plot. Percent moisture readings were taken approximately monthly. Beginning in September 1993, we added a second set of rods per depth per plot. Variability within plots was large; therefore, in 1994 all rods from mixed functional type communities were pulled and used to increase replication within the pure (single) functional type treatment plots to four sets of rods per depth per plot. Soil temperature was measured at the 5, 15, 25, 35, 60, and 100 cm depths approximately once per month from May 1992 to April 1994. Each plot had one transducer per depth.

To sample nitrogen content of soil water, porous cup lysimeters mounted at the ends of PVC pipes were installed at 20, 40, 60, 100, 120, and 140 cm depths (one lysimeter per depth per plot). Soil water samples were collected six times in 1992 and two times in 1993. Each was analyzed for nitrate and ammonium concentration using an autoanalyzer. Sampling was suspended after September 1993, when it became clear that vegetation treatment differences were no longer significant.

Data analysis

Although we converted root counts to RLD for purposes of plotting our results, all analyses were conducted using raw root counts. Where data were heteroscedastic, observations were log transformed prior to analysis. Differences among vegetation treatments regarding root system production were assessed three ways: (1) root count change through time; (2) vertical root distribution in the soil profile; and (3) root productivity and mortality.

Changes in total root density over time were analyzed two ways. First we compared treatment (i.e., plot) effects using data from all root samples (i.e., 11 dates). Total root density increase in the top 90 cm of soil was regressed with time for each tube with the intercept fixed at zero. The slope estimates for each tube were then treated as subsamples within plots for nested analysis of variance (Merredith and Stehman 1991). Tukey's studentized range test (Zar 1984) was used to compare the seven vegetation composition treatments. The second method we used to assess density change over time was conducted for just the two dates that we had corresponding measures of aboveground vegetation (June 1992 and September 1993). For each date, total root counts in each plot (all eight tubes combined) were compared with photo samples of herbaceous cover and woody crown volume (independent variables) via multiple regression. Relationships between root counts and all measures of vegetation (total abundance and abundance for individual species or species groups) were explored by a maximum r^2 technique (SAS Institute Inc. 1988) followed by forward, backward, and stepwise multiple regression approaches (all leading to the same results). Only variables with significant slopes ($p < 0.05$) were accepted for the final models.

We used two approaches to compare root density depth profiles. First, we tested for differences among the three pure vegetation treatments using the Kolmogorov–Smirnov (K–S) test, a nonparametric method for comparing cumulative frequency distributions of paired samples (Sokal and Rohlf 1981). To control experiment-wide type I error rate, only the three single functional type groups were compared

at each of the three sample dates (July 1991, 1993 and June 1994) were compared with control the experiment-wide type I error rate. Prior to the K–S tests, data from all minirhizotron tubes within a given vegetation treatment were summed at each 1 cm depth increment. In our second analysis, we addressed the question: Do combinations of functional types lead to the same root distribution expected on the basis of root distributions in single functional type plots? Single functional type distributions were averaged to produce an expected root profile. Observed and expected profiles were compared using a G -test (Sokal and Rohlf 1981).

Root productivity and mortality were estimated using the decision matrix published by McClaugherty et al. (1982) and later revised by Fairley and Alexander (1985). Only data from tubes subject to UV light counts (three per plot) were used in this analysis. Although count data often have an underlying Poisson distribution, they can be used in an analysis of variance (ANOVA) if the counts are large, which is the case for our study (mostly greater than 100). Thus, we employed a nested ANOVA with individual tubes treated as multiple determinations within plots.

Soil moisture and temperature measurements were analyzed using multivariate ANOVA for repeated measures (Koch et al. 1980; Potvin et al. 1990). Each depth was analyzed separately. Because there were too many dates resulting in too few degrees of freedom for multivariate tests, the moisture data were divided into three data sets: (1) 1992–1993 growing season months (April–September inclusive); (2) 1992–1993 nongrowing season months; and (3) all 1994 measurements where replication was changed to four sets of rods per each of nine plots. Temperature data were divided into two sets: growing and nongrowing season. Two tests were of particular interest in these analyses: (1) main treatment effects, which were tested by a simple univariate ANOVA; and (2) treatment \times time interactions, which were tested using within-plot error in the multivariate ANOVA.

Nutrient data were unbalanced by missing observations (range of missing values within dates 38.2–54.2%); therefore, univariate analyses of variance were conducted for all dates combined within each depth. This approach violated the assumption of independence among observations, since some were repeated, and may have led to inflation of type II error rates; however, because very large treatment differences were detected (see below), the type II error rate was likely very small.

Results

Aboveground vegetation

The most common woody plant species (for all treatments combined) was water oak, which had 58% of the total woody plant crown volume in June 1992 and 49% in September 1993. Loblolly pine, black cherry (*Prunus serotina* Ehrh.), and sweetgum all had at least 10% of the total crown volume in at least one year. The most common herbs in the first growing season were annuals and blackberry (16.6 and 9.7% mean cover, respectively). By the end of the second growing season, annuals decreased to 4.9% cover, while blackberry increased to 10.8%. In 1993, perennials and graminoids had a cover of 2.1 and 1.6%; by 1994 they increased to 6.6 and 3.2%, respectively.

Weeding and herbicide treatments were effective in controlling functional type composition. By late in the second growing season (1993), no woody plant crown volume was recorded within herbaceous-only treatment plots and essentially no herbaceous cover was noted in exclusively woody plant plots (Table 1).

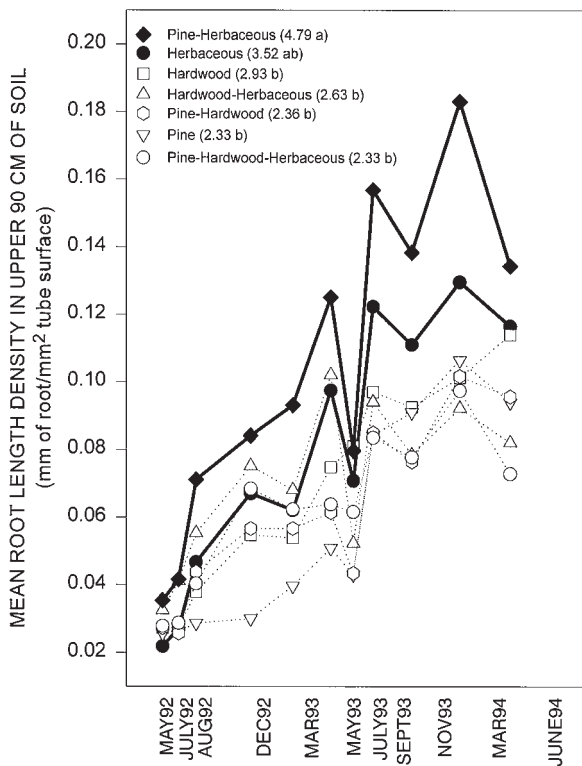
For all treatments with woody plants, crown volume increased from 1992 to 1993 (Table 1); and we observed further, substantial increases in 1994 (data not shown). Crown development was fastest in hardwood-only plots and decreased in

Table 1. Postdisturbance development of aboveground vegetation in 5 × 5 m measurement plots.

Treatment	Woody plant crown volume (m ³ /plot) by date		% herbaceous plant cover by date	
	June 1992	Sept. 1993	June 1992	Sept. 1993
Pine	1.485 (0.019)	31.454 (0.267)	4.60 (0.47)	0 (0)
Hardwood	28.748 (0.144)	86.481 (1.444)	5.10 (0.43)	0 (0)
Herbaceous	0.435 (0.036)	0 (0)	64.78 (2.18)	77.28 (2.66)
Pine–hardwood	22.848 (0.097)	69.567 (0.690)	10.45 (1.01)	0.08 (0)
Pine–herbaceous	1.022 (0.055)	8.877 (0.137)	85.29 (2.86)	75.51 (2.73)
Hardwood–herbaceous	22.663 (0.559)	63.675 (1.226)	46.95 (3.70)	20.76 (2.21)
Pine–hardwood–herbaceous	19.541 (0.116)	63.219 (0.707)	29.63 (2.25)	15.49 (1.13)

Note: Means (and standard errors) are shown for *n* = 3 plots per treatment.

Fig. 1. Mean root length density per treatment by sample date. Numbers in parentheses are estimated slopes for regression of counts (number per 90 cm depth) over time (days). Estimates followed by different letters are significantly different (*p* < 0.05) according to Tukey’s studentized range test (Zar 1984).



the following order: pine–hardwood, hardwood–herbaceous, pine–hardwood–herbaceous, pine, and pine–herbaceous.

Herb cover was least where hardwoods were present and greatest in pine–herbaceous and herbaceous-only plots (Table 1). Herb cover declined from 1992 to 1993 in plots with hardwoods, but remained more or less stable in all other treatments.

Where pines and hardwoods were mixed, strong negative interactions between functional types were apparent. For example, total woody crown volume was less on pine–hardwood plots than on hardwood-only plots (Table 1). Furthermore, although woody crown volume was similar in pine–hardwood–herbaceous and hardwood–herbaceous plots, herb cover was much lower in the former. Overall, the aboveground abundance measures suggest that hardwoods were the strongest competitors, followed by herbs and then pines.

Relationship between intersection count and root length

Counts of root intersections along the edges of video images were linearly related to root length within the images. The corresponding regression equation was

$$[1] \quad RL = 5.322 + 9.472C$$

where RL is the total root length (mm) for a video frame containing *C* root intersections (*R*² = 0.7369, *p* < 0.0001). The area of the video frame used for this equation was 243 mm². Therefore, a correction factor of RL/243 was needed to relate count to RLD as mm of root per mm² of tube surface area.

The relationship between field and laboratory counts of root intersections was very strong with a linear regression of

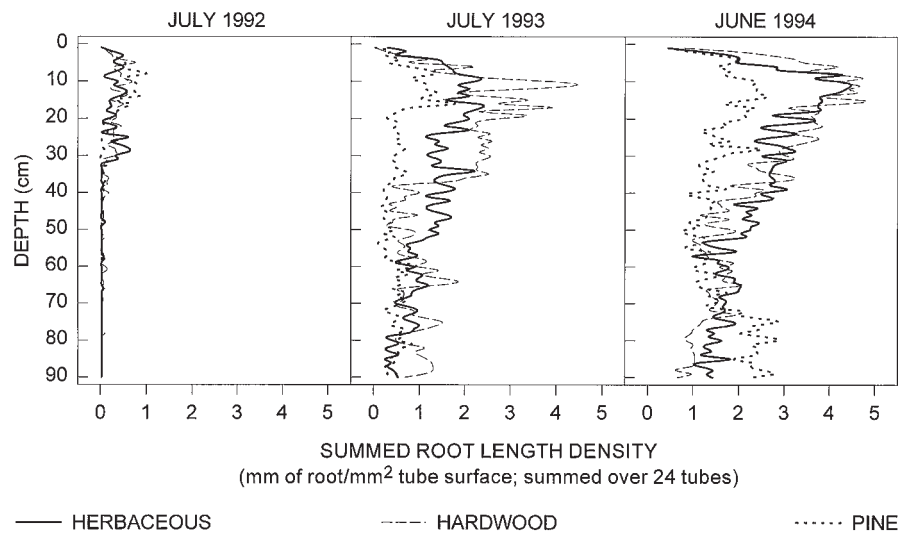
$$[2] \quad \text{field count} = 0.283 + 1.083(\text{lab count})$$

and an *R*² = 0.84 (*p* < 0.0001). A slope estimate of greater than 1.00 for this equation indicates that the field count was slightly higher than the lab count on average.

Total root density

Mean total RLD (live + dead roots) in the top 90 cm of soil increased linearly from May 1992 to June 1994 for all treatments (Fig. 1). Vegetation composition (treatment) significantly affected the rate of root density increase (ANOVA; *df* = 6, 14; *p* = 0.028), with the greatest rate occurring in the pine–herbaceous treatment. The pure herbaceous treatment was intermediate between pine–herbaceous and the other five treatments. The four lowest rates of increase, which were

Fig. 2. Depth distribution of root length density (summed over 24 tubes) for pure vegetation treatments. Lines were smoothed by graphics software.



statistically similar, included pine and the three-way combination of pine, hardwood, and herbaceous vegetation (Fig. 1). During the first year of the study, however, the pure pine treatment had distinctly fewer root intersections than all other treatments. Very rapid root growth occurred in the pine-only plots during the second and third years. Distinct peaks in root count occurred in May 1993, September 1993, and March 1994. Declines occurred for most treatments in July 1993, November 1993, and June 1994 (Fig. 1).

Herbaceous cover was a significant predictor of root density in 1992 and 1993. In the multiple regression of 1992 data (single date), cover of annuals explained 62.9% of the variability in total root density, and only one other variable, crown volume of water oak, was significant, explaining an additional 9.5%. Although annual cover was the best single variable for predicting total root count ($R^2 = 0.629$), total herb cover was a reasonable alternative ($R^2 = 0.343$). For the 1993 data, multiple regression identified two significant predictors of root density: total herb cover (38.4% of the variation in root count) and annuals (21.1%). The best single predictor of roots in 1993 was total herb density ($R^2 = 0.384$), but blackberry cover provided similar results ($R^2 = 0.380$).

Vertical root distribution

Roots increased in density and depth during the three growing seasons after disturbance. During the first growing season, most roots were within the upper 30 cm of soil (Fig. 2). By the middle of the second growing season, roots were detected along the entire length of the tubes (to 90 cm depth). Relatively few roots were detected in the top 10 cm of soil.

The three main functional type types (pine, hardwood, and herbaceous) differed both in root density profiles and in the way in which depth profiles developed over time (Fig. 2). Root density distributions were significantly different ($p < 0.01$) for eight of nine K-S tests comparing functional types on three dates. The only nonsignificant ($p > 0.05$) relationship was between the pure pine and pure hardwood treatments in July 1992, just 4 months after treatment establishment when few roots occurred along any of the minirhizotron tubes (Fig. 2).

Roots in the pure hardwood and pure herbaceous treatments were concentrated in upper soil depths (Fig. 2). Hardwood roots developed particularly rapidly, reaching relatively high densities by the second growing season, and changing little between the second and third growing seasons. Herbaceous plant roots continued to increase in density between the second and third years.

Pine root systems developed differently. In the second growing season, their distribution was nearly uniform across the 90-cm profile with a small peak (relative to hardwoods and herbs) in the upper 20 cm (Fig. 2). By the third growing season, pure pine plots still had a more uniform distribution of roots than did hardwoods and herbs; however, a peak in root density occurred between 70 and 90 cm.

When combined, pines and herbs had more roots than predicted on the basis of single functional type plots ($G = 4177$; $p < 0.001$; $df = 89$). The pine-herbaceous treatment had one peak of root density in the upper horizon and a second peak from 70 to 90 cm, and was the only mixed functional type treatment where observed root densities consistently exceeded predicted root densities based on averages of pure treatments (Fig. 3). In all other mixtures, observed root density profiles were less than predicted ($G \geq 330$; $p < 0.001$).

Root productivity and mortality

In general, herbs had the greatest mean root productivity and mortality, but differences among treatments changed over time. During the first year, treatment differences in production and mortality were significant (ANOVA; $p = 0.007$ and $p = 0.048$; $df = 6, 14$), and plots with herbaceous vegetation clearly had higher mean root productivity and greater mortality than plots without herbs (Fig. 4). By the second year, however, no significant treatment effect on productivity was found ($p = 0.116$), although plots with pines generally had the largest means (Fig. 4), reflecting the rapid increase in standing crop of pine roots (Fig. 1). Differences among treatments in mortality were significant in the second year ($p = 0.038$). Mortality patterns closely followed those for productivity, which is not surprising since mortality is a component of the productivity

Fig. 3. Depth distribution of root length density (summed over 24 tubes) for mixed vegetation treatments. Lines were smoothed by graphics software. Predicted values are the sum of root counts for each component functional type in a pure community divided by the number of component functional types in the mixed community.

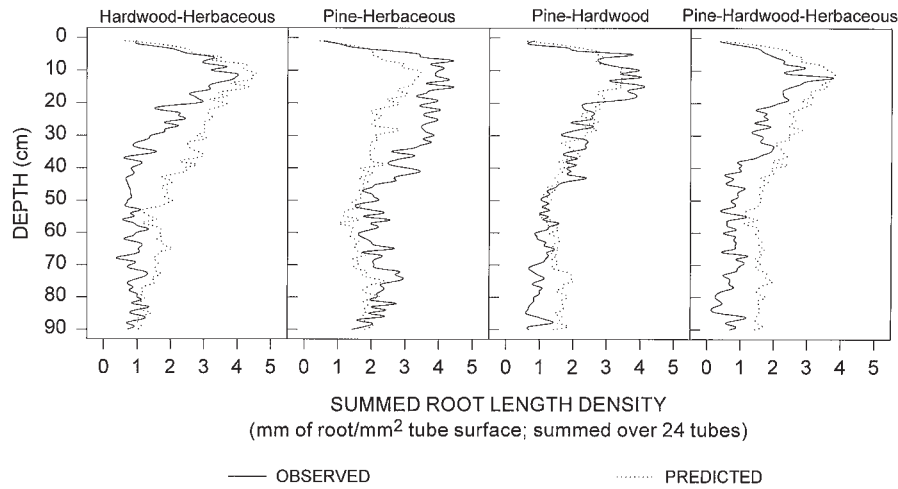
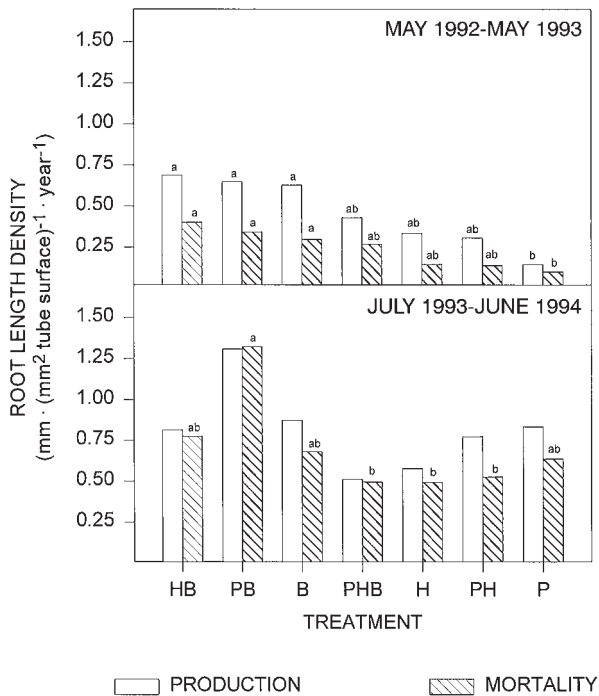


Fig. 4. Mean root production and mortality for pure and mixed vegetation treatments. Different lowercase letters indicate significant difference ($p < 0.05$, Tukey) among means within a given variable and year. Treatment codes: H, hardwoods; B, herbs; P, loblolly pine.



estimate (McClougherty et al. 1982; Fairley and Alexander 1985).

Soil resources

Several expected soil moisture trends occurred: (1) moisture increased with soil depth; (2) moisture was lower during the growing season than during the nongrowing season; and (3) moisture was lower during the second (1993) growing season probably because of increased transpiration demand as

vegetation developed (Table 1) as well as differences in growing season precipitation (April–September precipitation was 604 mm in 1992 and 490 mm in 1993).

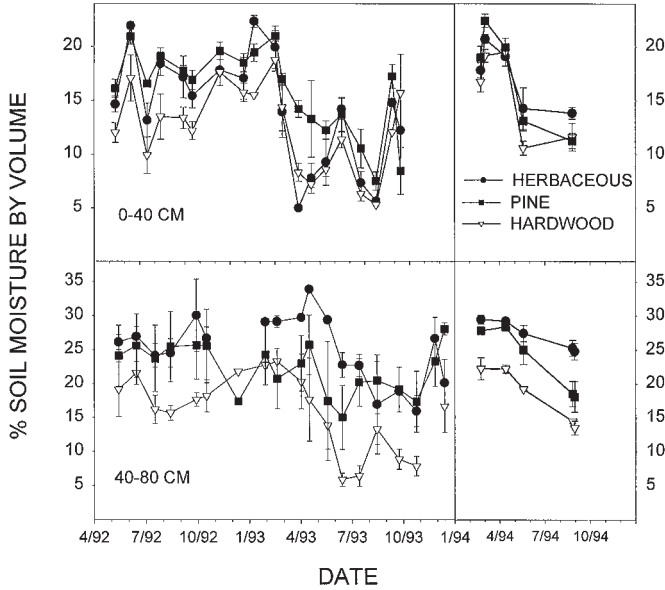
Vegetation treatments influenced soil moisture. Main vegetation treatment effects were significant once (0–80 cm depth during 1994; $p = 0.007$; univariate ANOVA) and nearly significant twice (0–40 and 0–80 cm depths during the growing season months of 1992–1993; $p = 0.054$ and 0.082) out of 12 total tests of vegetation effects (four soil depths and three time periods). Interactions between time and vegetation treatment were significant in 3 of the 12 tests (MANOVA; Wilk’s λ ; $p \leq 0.043$). The main difference was lower soil moisture in hardwood plots than in herb or pine plots, especially at lower depths (Fig. 5). This occurred despite the fact that herb plots had greater root density (Fig. 1).

The general soil temperature pattern included peaks during the growing season and decreased seasonal fluctuation with depth (Fig. 6). Pine-only plots had greater seasonal fluctuations, including higher peak temperatures in summer and lower minimum temperatures in winter (Fig. 6). However, according to univariate ANOVA, significant vegetation effects on temperature were detected in only 1 test out of 12 ($p = 0.021$ for the 15 cm depth in growing seasons months). MANOVA detected significant treatment \times time effects ($p \leq 0.05$) for only 3 out of 12 tests: the 15 cm depth during the growing season months, and the 25 cm depth in both the growing and nongrowing seasons months.

Soil water nitrate concentrations were elevated briefly at the beginning of the experiment, especially in the pine-only plots and in upper soil horizons (Fig. 7). A series of peak nitrate values occurred in summer 1992. The largest and earliest occurred at 20 cm, which was followed later by a smaller peak at 60 cm, and in pine-only plots, a third peak at 100 cm (Fig. 7). After 1992, no further seasonal peaks in soil nitrate were detected.

Mean nitrate on pine-only plots exceeded all others by one to two orders of magnitude depending on soil depth (Fig. 7). After log transforming the nitrate concentration data to control heteroscedastic variance, significant differences between treatments (entirely due to the pine plots) were detected at the

Fig. 5. Mean soil moisture after harvest and regeneration for pure functional type treatments only. For clarity, only two depths are plotted. Bars are standard errors and missing points represent missing data. Left panels $n = 1$ time domain reflectometry sample per plot; right panels $n = 4$ time domain reflectometry samples per plot.



60 cm depth (ANOVA; df 6, 14; $F = 4.21$; $p = 0.013$) and 120 cm depth ($p = 0.027$), and a nearly significant difference occurred at the 20 cm depth ($p = 0.067$). These tests are conservative because they integrate dates after the spikes in nitrate occurred and ignored some missing observations that occurred during the peaks. True differences between pines and all other plots may be greater than shown here.

During the summer of 1992, nitrate concentrations declined as root system densities increased, irrespective of vegetation treatment. In May, shortly after tubes were installed, log of nitrate in the top 60 cm of soil (where the nitrate peak occurred) was positively but not significantly correlated with log of root density $r^2 = 0.32$; $p = 0.36$; $n = 10$ plots). However, significant negative correlations occurred for nitrate measures made in July ($r^2 = -0.53$; $p = 0.02$; $n = 19$), September ($r^2 = -0.45$; $p < 0.05$; $n = 20$), and November ($r^2 = -0.69$; $p < 0.01$; $n = 17$).

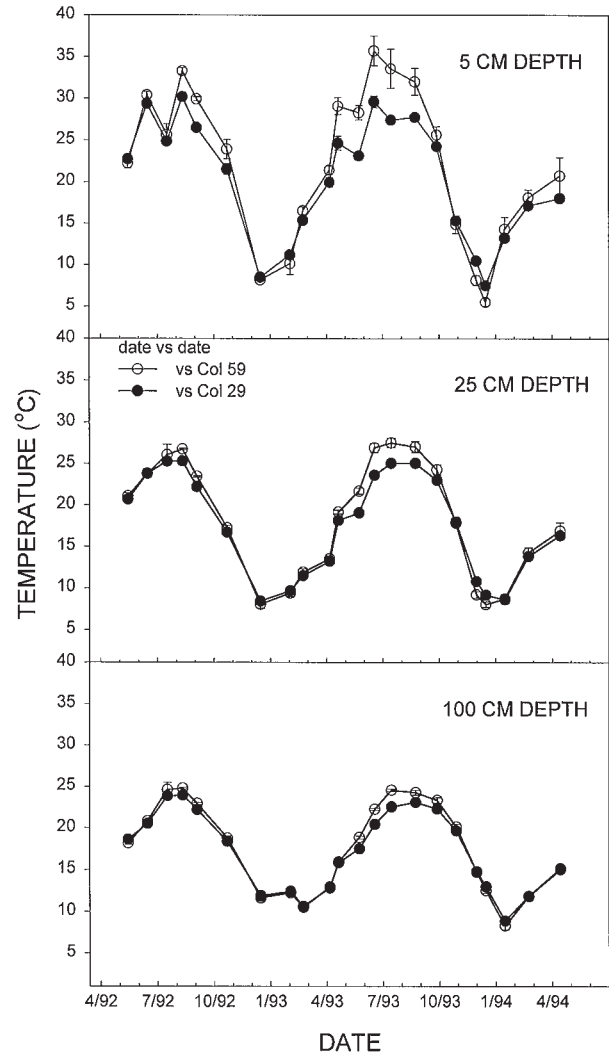
Soil water ammonium concentrations were generally low throughout the measurement period, with no significant differences among functional types or soil depths (Fig. 7). Furthermore, no correlations between ammonium concentrations and root densities were found.

Discussion

Root production

Herbaceous plants were important for rapid re-establishment of roots after disturbance. Herbs had the greatest root productivity and greatest root densities by year 3 of the three functional types tested (Fig. 1). Other studies comparing herbs with woody plants have found the same (Bowen 1985; Caldwell 1987). Herbs had greater root densities than hardwoods despite the fact that hardwoods had many more, and much larger, root-

Fig. 6. Mean daytime soil temperatures for pine-only plots versus all other plots for three soil depths.

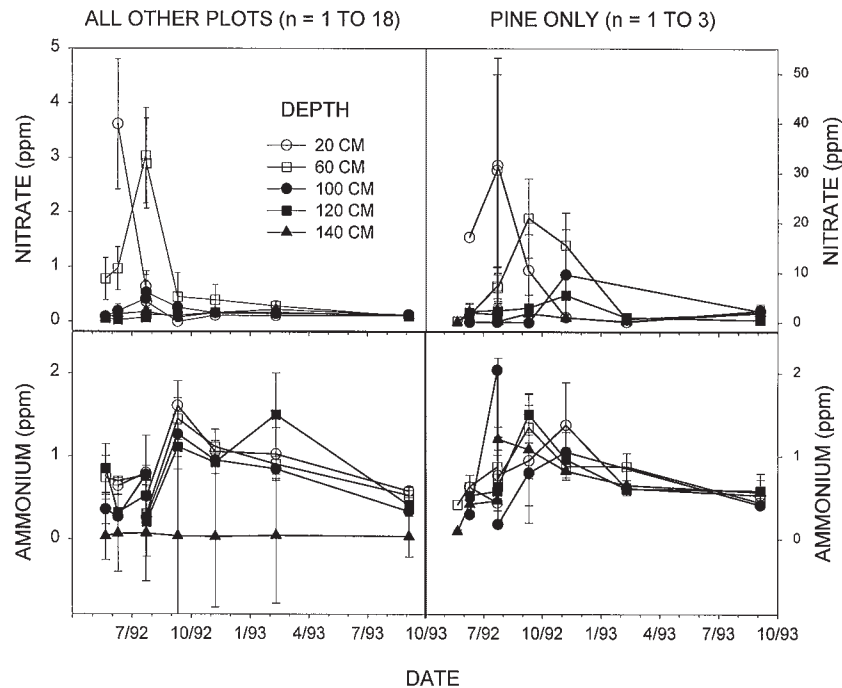


stocks at the time of harvest. This result reflects a greater capacity for root production among herbs, and possibly a temporary shift in carbon allocation within hardwood root stocks to favor aboveground growth after the stems were removed.

Annuals were strong contributors to new root system development. Cover of annuals was the most important predictor of root production during the first year and was still highly correlated with root production in the second year. The importance of annuals was somewhat surprising, since they constituted only half of total herb cover in 1992 and one third in 1993. On the other hand, Grime's plant strategy theory (1979) predicts that annuals should grow faster than perennials. Yet one study of 25 herbaceous species failed to show consistent differences among annuals, biennials, and perennials in terms of overall growth rates or allocation of carbon to root versus shoot growth (Gleason and Tilman 1994). A repeat of our experiment with separate perennial and annual herb plots may be needed to test whether these two groups of plants are truly different functional types in upland pine-oak ecosystems.

Initially, pines did not provide rapid recolonization of plots with roots (Fig. 1). This makes sense considering their small

Fig. 7. Nutrient concentrations in soil water sampled by lysimeter immediately after harvest and regeneration of upland forest. Bars are standard errors.



size and low density at the time of planting compared with the larger size and densities of hardwood rootstocks, and the greater density of herbs (100s to 1000s of stems per plot versus about 50 pines per plot).

The fluctuations in root density observed toward the latter part of the study may reflect a seasonal pattern. Two density peaks occurred in spring months and one in an early fall month, and two troughs occurred in summer months plus another in late fall (Fig. 1). Seasonal changes are common in forests (Vogt et al. 1981; Keyes and Grier 1981; McClaugherty et al. 1982; Farrish 1991; Hendrick and Pregitzer 1992; Fahey and Hughes 1994) and have been explained as responses to seasonal cycles in soil temperature, moisture or nutrients, or timing of shoot growth (Farrish 1991; Aber et al. 1985). We do not have data to link peaks with specific internal physiological processes, and we are reluctant to declare the observed peaks a true pattern different from random fluctuation. However, peak root densities did correspond roughly to greater soil moisture availability (data not shown). It is unlikely that root growth in central Alabama would be halted by cold temperatures during winter, although it may be slowed (Vogt et al. 1986).

The inference space for the root production portion of our study is limited by the fact that we only counted roots during the first three growing seasons after a major disturbance. Further, we usually counted total root densities instead of separate live and dead root densities, and when we did estimate live root fractions, the estimates could have been inflated if the dead roots along our minirhizotron tubes fluoresced under UV light. Nevertheless, our study is somewhat unique because it compared plants grown in a natural soil system with similar climate conditions for all plots. Many past studies of this type have compared plants from different natural ecosystems (Bowen 1985; Caldwell 1987; Jackson et al. 1996) or have

used greenhouse experiments (Hunt et al. 1987; Fitter et al. 1988; Gleeson and Tilman 1994).

Root depth distribution

When root systems were viewed across the soil profile, niche separation was apparent. Herbs and hardwoods had most of their roots in the uppermost soil horizons, a pattern frequently demonstrated for these two functional types in humid regions (Kalisz et al. 1987; Atkinson 1991). This depth distribution may reflect (1) the influences of soil texture, which is increasingly finer with depth at our study site; (2) inherent root system architecture; or (3) an affinity for growth in nutrient-rich portions of the soil. In contrast with herbs and hardwoods, pines developed proportionally more deep fine roots (Fig. 2). Similar depth distribution differences have been noted in other ecosystems. In deserts, phreatophytes and shrubs are often more deeply rooted than grasses (Reynolds and Fraley 1989; Bonham and Mack 1990; Atkinson 1991; Lee and Lauenroth 1994; Jackson et al. 1996). Mou et al. (1995) found that loblolly pine roots had a greater affinity for shallower depths than sweetgum roots in 3-year-old monocultures; however, soil below 60 cm was not excavated and thus, deeper pine roots may have been missed. Van Rees and Comerford (1986) found that both slash pine and saw palmetto (*Serenoa repens* (Bartr.) Small) in northern Florida were more deeply rooted than co-occurring shrubs and herbs. Ludovici and Morris (1996) found proportionally deeper rooting for loblolly pine than for sweetgum and crabgrass (*Digitaria* sp.) grown in rhizotrons.

Several factors may have caused the increased pine-root density at the 70–90 cm depth. One is the presence of a dense plinthite layer at approximately 1 m depth. If the plinthite caused a perched zone of moisture to form, the pine roots may have proliferated in that zone to extract the water resource, much as desert phreatophytes do (Rundel and Nobel 1991).

Table 2. Loblolly pine crown volume (m³/plot) for pine-containing treatments listed in order of greatest to least.

Treatment	Crown volume	
	1992	1993
Pine	1.253	31.454
Pine-herbaceous	0.856	8.273
Pine-hardwood	0.597	4.435
Pine-hardwood-herbaceous	0.478	2.183

Van Rees and Comerford (1986) found that slash pine roots proliferated at the top of an argillic horizon (at 105 cm), where water was presumably abundant. Fine-scale root proliferation in soil patches rich in water or nutrient concentrations is well documented (Gross et al. 1993; Caldwell 1987; Harper et al. 1991; Robinson 1994). Although our greenhouse and field studies show that loblolly pine roots are less sensitive to nutrient-rich soil patches than sweetgum, sensitivity to soil moisture heterogeneity has not been explicitly tested (Mou et al. 1995). A second possibility is that pine roots were unable to penetrate the plinthite layer and thus increased in density just above it.

The low root densities observed for all treatments in the upper 10 cm of soil may have been caused by the minirhizotron tubes (Vos and Groenwold 1987; Levan et al. 1987; Bragg et al. 1983; Upchurch and Ritchie 1983). Tubes can inhibit root growth near the soil surface via light leaks (Levan et al. 1987) or suppression of soil moisture (Vos and Groenwold 1987). However, other minirhizotron studies have found good correlations between minirhizotron and soil core data, even at shallow depths (Bragg et al. 1983; Bland and Dugas 1988). Since we did not core the soil, we are unable to determine whether our minirhizotrons underestimated or accurately estimated root density at the shallowest depths.

Niche partitioning and competition

Certain combinations of functional types enhanced total plot production, while others did not. In particular, pines and herbs grown together had greater than predicted root production (Fig. 3) and aboveground abundance. Although other studies have contended that differences in root distributions should lead to reduced competitive interactions (Sands and Nambiar 1984; Jonsson et al. 1988; Bonham and Mack 1990; Franco and Nobel 1990; Mou et al. 1995), our study is one of a few (e.g., Melgoza and Nowak 1991) that support this contention via plant response data in pure and mixed natural communities.

The compatibility of pines and herbs may reflect partitioning of soil profiles whereby herbs concentrated roots in upper horizons and pines had proportionally deeper roots. Herbs and hardwoods, in contrast, had more or less similar root system distributions (Fig. 2) and therefore greater chance for competition. The poor performance of pines in hardwood plots, even though the two had different root depth profiles in pure culture, may be the result of relatively strong aboveground competition as hardwoods undoubtedly cast much more shade than did herbs. The total impact of hardwoods on pines was twice as strong as the impact of herbs on pines, as seen by crown volumes (Table 2). The even slower growth observed in the three-way combination may reflect strong competitive interactions

both above and below ground among the functional types. These presumed competitive interactions, however, rest on the assumption that root overlap alone is a strong indicator of belowground competition. Model simulations have shown that exploitation of different soil depths can reduce potential competition (Franco and Nobel 1990). However, even where roots overlap, competitive interactions may be strongly affected by interplant differences in uptake rates per unit of root surface, fine-scale foraging for nutrients, interactions with microbes, allelopathy, total plant size, and positive effects of plants on soil resources (Caldwell 1987; Goldberg 1990; Caldwell et al. 1991b; Grime et al. 1991; Vaughan and Ord 1991; Mitchell et al. 1993, 1996). The specific effects of plants on resources, as well as on other intermediaries, must be carefully defined before the mechanisms of competitive interaction can be revealed (Goldberg 1990). A recent study by R.J. Mitchell et al. (1997, see footnote 3) and a review therein suggests that pines respond most strongly to reductions in light and water than to reduced nitrogen availability. Since effects of hardwoods on both water (measured) and light (presumed) were greater than were the similar effects of herbs, it is not surprising that hardwoods had the greater competitive impact on pines.

Effects of functional types on soil environment

During the first few months after disturbance, a nitrate pulse occurred. The pulse moved downward through the soil profile, which suggests that (1) the pulse originated at the surface and then the nitrate diffused through the soil over time or (2) a zone of elevated nitrification moved downward over time. Very similar patterns have been predicted by simulating a surface fertilization followed by repeated irrigation events (Habib and Lafolie 1991), which suggests that the first explanation may be more likely.

The high degree of nitrate leaching in the pine plots may have been caused by increased mineralization or reduced uptake. Although soil temperatures (Fig. 6) and soil moisture (Fig. 5) were relatively high in pine-only plots, differences among vegetation treatments were relatively small; thus, reduced uptake was probably more important than increased mineralization. Uptake can be by plants or microbes. In a harvested pine plantation, Vitousek and Matson (1985) reported that microbes associated with organic debris immobilized nitrogen and strongly limited nitrate loss. Since we distributed approximately equal quantities of organic debris on each plot after the harvest and burn, we speculate that the reduced uptake by pine plots in our study was mainly due to a lack of roots. Because nitrification rates were not measured in our study, we cannot make a stronger statement.

The lack of trends for soil ammonium was somewhat surprising because other studies have shown that ammonification rates and soil ammonium concentrations can be increased by forest harvesting and affected by type of site preparation treatment (Vitousek and Matson 1985; DiStefano and Gholz 1989). Since this ion is much less mobile than nitrate, it is possible that concentrations increased in the horizons above our shallowest lysimeter (20 cm), yet little or none leached downward to reach our lysimeters.

Our finding of reduced soil moisture beneath hardwoods (Fig. 5) has been noted elsewhere. Morris et al. (1993) found that volumetric moisture in the upper 80 cm of soil was usually lower in plots dominated by sweetgum than in plots dominated

by loblolly pines or three species of herbs. R.J. Mitchell et al. (1997, see footnote 3) demonstrated lower soil moisture beneath sweetgum than beneath loblolly pine or broomsedge (*Andropogon virginicus* L.) whether the relationship was expressed per unit of plant density or aboveground biomass. If equal uptake per unit of root density is presumed, both hardwoods and herbaceous plants should have had similar impacts on soil water. The lower moisture levels beneath hardwoods may therefore reflect greater uptake capacity per unit of root length or greater interception losses in the hardwoods. Hardwood canopies were much taller with much greater surface area to capture precipitation than were pine or herbaceous canopies. During 1994, we noted that pines began to deplete soil water to similar levels as hardwoods, which may reflect the rapid growth and subsequent evapotranspiration demand of pure pine plots towards the latter part of the study.

Management implications

Our study has implications for choice of tree regeneration technique. Obviously, to maximize long-term pine growth rates, competing functional types should be reduced or controlled (Miller et al. 1991; Glover and Zutter 1993; Lauer et al. 1993; Morris et al. 1993). The choice of control method can be made using a financial analysis pitting growth gains against costs of control. The kind of competing functional types present may be important; hardwoods had a greater impact on pine than did herbs in our study, although the reverse has been demonstrated (Morris et al. 1993).

To minimize potential net ecosystem nitrogen loss or groundwater pollution, however, the best regeneration techniques may be those that promote the most rapid production of roots. In our study, root density was inversely correlated with nitrate concentration. Herbs had the greatest belowground growth rates and may be the best functional type for retaining nitrogen. The elevated soil nitrate we observed, however, was ephemeral and diluted with depth; thus, we believe that none of our treatments indicate a serious threat to total ecosystem nitrogen supply. However, other studies have shown greater or more prolonged periods of nitrate leaching during forest regeneration, especially on sites that are nitrogen-rich or fertilized, where organic debris is lost with a concomitant loss of microbial biomass or where vegetation regrowth is suppressed (Bormann and Likens 1979; Vitousek et al. 1982; Vitousek and Matson 1985; DiStefano and Gholz 1989). We have observed regeneration sites where herbicides are repeatedly applied to facilitate planting in the second dormant season after tree harvest. We recommend a cautious approach that allows for establishment of at least some herbaceous plants during the first two growing seasons after harvest. If a mixed functional type community is desired, the optimal combination in terms of crop tree growth and nitrogen retention would be pines plus herbs.

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