

COMPETITION AMONG SECONDARY-SUCCESSIONAL PINE COMMUNITIES: A FIELD STUDY OF EFFECTS AND RESPONSES

R. J. MITCHELL,¹ B. R. ZUTTER,² D. H. GJERSTAD,² G. R. GLOVER,² AND C. W. WOOD³

¹Jones Ecological Research Center, Route 2, Box 2324, Newton, Georgia 31770 USA

²School of Forestry, Auburn University, Auburn, Alabama 36849 USA

³Department of Agronomy, Auburn University, Auburn, Alabama 36849 USA

Abstract. Three common associates on secondary-successional pine sites (*Andropogon virginicus*, *Liquidambar styraciflua*, and *Pinus taeda*) were established in a field study in which a wide array of plant densities and species proportions were established using an additive series design. To mimic a specific competitive scenario (i.e., a managed early-successional *Pinus* stand), *Andropogon* and *Liquidambar* were established a year prior to the establishment of *Pinus*. Competitive effect (the attenuation of resources) and competitive response (the growth of each species as a function of resource availability) were determined.

Effect on soil water varied among species, depth of soil, and time. In the surface soil, soil water was largely influenced through non-uptake effects, while uptake effects were predominant in deeper portions of the solum. When competitor abundance was expressed on an aboveground biomass basis, rather than a density basis, species differences in effects on soil water were eliminated. Differences among the species in effects on soil water per unit leaf area or leaf biomass appear to be largely explained by differences in stomatal conductance. Predawn leaf-water potential was integrated over the season using a water-stress integral. Analysis of the water-stress integral suggested that *Liquidambar* and *Andropogon* both affected water available to *Pinus*; however, only *Liquidambar* affected *Andropogon*, and only *Andropogon* affected seasonal water available to *Liquidambar*. Light was most strongly influenced by *Liquidambar* density; however, as *Andropogon* density increased, the effects of *Liquidambar* were reduced.

Andropogon response was correlated with light but not with water stress or leaf nitrogen. This reflects high light requirements and high water use efficiency of C_4 plants. *Liquidambar* response was related to water stress and leaf nitrogen, perhaps reflecting the greater nitrogen requirements of hardwoods. *Pinus* response was significantly related to all three resources individually, i.e., water stress, light, and leaf nitrogen. *Pinus* response was better explained by a regression model that included light and water stress than by water stress or light alone. *Pinus* growth as a function of water stress and light indicated that communities dominated by *Liquidambar* largely reduced *Pinus* growth through reduction in light, while communities dominated by *Andropogon* reduced *Pinus* growth primarily by increasing water stress. In mixed communities of *Liquidambar* and *Andropogon*, pine growth was constrained more equally by light and water stress.

Key words: *Andropogon virginicus*; competitive effect; competitive response; *Liquidambar styraciflua*; mechanisms of competition; multiple resource limitation; *Pinus taeda*; plant competition; temporal resource heterogeneity.

INTRODUCTION

The nature of plant–plant interactions is diverse, with the potential net outcome of these interactions ranging from positive to negative (Goldberg 1990). Since plants are sedentary and require similar resources, plant–plant interactions are often competitive. Despite the amount of effort that has been expended in the study of plant competition, the mechanisms that account for competitive interactions in field environments are poorly understood (Goldberg and Barton 1992, Casper and Jackson 1997), in part because of the lack of attention paid to measuring both effects of competitors on resource

pools and responses of focal species in field environments (Goldberg 1990, Shainsky and Radosovich 1992, Gordon and Rice 1993, Mitchell et al. 1993, Burton and Bazzaz 1995).

Competitive interaction among plants can be viewed as a two-part process: competitive effect and competitive response (Goldberg and Fleetwood 1987, Miller and Werner 1987, Goldberg 1990, Mitchell et al. 1993, Mou et al. 1993, Burton and Bazzaz 1995). In the context of exploitation competition, competitive effect of plants can be mechanistically defined as the influence of plants in a neighborhood on resource availability, while response can be viewed as the relationship between the amount of a resource available to a plant and some component of fitness, such as growth, survival,

Manuscript received 25 June 1997; revised 1 March 1998; accepted 21 March 1998; final version received 5 May 1998.

and/or reproductive output (Goldberg 1990). Thus, for plant competition to occur, both the effects and responses must be significant and of proper direction.

The common resource requirements of plants have been suggested to result in an equivalence among plants with respect to competitive effects (Goldberg and Werner 1983, Goldberg 1987). Those studies that have investigated size-related competitive effects have concentrated for the most part on the ability to suppress; rarely have field experiments been conducted in which the effect on resources as a function of plant abundance (i.e., density, biomass, leaf area) is quantified. Characteristics other than size may determine the competitive abilities of species. Differences in phenology, morphology, and physiology that may result in a greater ability to reduce a limiting resource, or in increased efficiency in using resources to produce dry matter, enhance survival and/or reproduction (Pickett and Bazzaz 1976, Tilman 1982, 1988, Caldwell et al. 1985, Koppers 1985, Richards and Caldwell 1987, Gordon and Rice 1993, Tremmel and Bazzaz 1993). These differences may affect the ability to acquire resources, and thus influence competitive effect; however, we hypothesize that physiological differences among species will have only minor effects on resource use when size considerations are removed, but will strongly influence species-specific response components.

Upland loblolly pine (*Pinus taeda* L.) communities are extensive in the Southeast, and are among the most intensively managed ecosystems in North America (Vitousek and Matson 1985). Management typically results in removal of the overstory every 15–30 years, resulting in early-successional communities comprised of herbaceous plants, hardwood sprouts, and pine seedlings. For the most part, pine seedlings are planted into a community of established hardwood sprouts and a variety of herbaceous plants. This differential timing in establishment results in the possibility for asymmetry of competition to develop due to the occupation of space by well-established vegetation (Casper and Jackson 1997, McConnaughay and Bazzaz 1991) and the potential pre-emption of soil resources (Wilson and Tilman 1995). Although asymmetry due to the directional nature of light has been demonstrated for above-ground competition, the degree to which asymmetry occurs in belowground competition is less well understood (Casper and Jackson 1997). In the context of these upland pine communities in the southeast United States, we focus on two questions: (1) Does competitive effect on resource pools differ among commonly associated species in early-successional sites, and are these differences species dependent or simply size related? (2) Do species that commonly occupy the same site at the same stage in succession respond similarly to a limiting resource for that site, or do they differ in their response component?

METHODS

Study site and experimental design

The study site was located on an area of ~2 ha at Auburn University's E. V. Smith Research Center, ~50 km southwest of Auburn, Alabama, in the Coastal Plain physiographic region. The soils are classified in the Compass series (coarse-loamy, siliceous, thermic Plinthic Paleudults), and are representative of upland loblolly pine sites located in the Upper Coastal Plain of the southeastern United States. The study was established as a complete $4 \times 4 \times 3$ factorial arrangement of *Pinus taeda*, *Liquidambar styraciflua*, and *Andropogon virginicus*. *Pinus* and *Liquidambar* were each planted at densities of 0, 1, 2, and 4 plants/m², and *Andropogon* at a density of 0, 4, and 16 plants/m², for a total of 48 treatments. These three species were selected because they are frequent associates in early succession on cutover forest sites planted to *Pinus taeda* in the Southeast (Miller et al. 1995), and because competition has been shown to be an important determinant of stand development and ecosystem function in these species (Britt et al. 1991, Miller et al. 1991, Wood et al. 1992). The additive series design (Cousens 1991) used here provides an array of different densities and proportions of the three species, as suggested by Firbank and Watkinson (1990). The densities of plants selected in this study encompass the range of those previously observed on Coastal Plain sites after overstory removal (Miller et al. 1987, 1991). Each treatment (combination of species and density) occurred once per block in a randomized complete block design with four blocks. Blocks were placed across the study site based on subtle differences in surface slope and drainage patterns.

Treatment plots were ~4.9 × 9.0 m (Fig. 1). Plant layout was accomplished by dividing the treatment plot into 44 subplots measuring 81.6 × 122.5 cm, an area of 1 m². Within each subplot there were 24 potential planting locations, 4 rows of 6 locations each, with 20.4 cm spacing between locations. Within each subplot, the location of the appropriate number of plants of each species was randomly assigned. At the greatest density (i.e., 4 *Pinus*, 4 *Liquidambar*, and 16 *Andropogon* per square meter), all planting positions were occupied. This approach overcame difficulties inherent in systematic positioning of plants. Interior areas within each treatment plot were designated for nondestructive measurements (i.e., plant dimensional measurements, soil water, light, plant water potential, and stomatal conductance) and plant harvest (Fig. 1). Treatment plots were spaced 1 m apart in order to provide access to individual plots with minimal plant disturbance and to provide a buffer between treatments.

On forested sites that are cutover and reforested to southern pines, *Liquidambar* regeneration after disturbance is primarily from sprouts rather than seedlings, and herbaceous plants are often established before

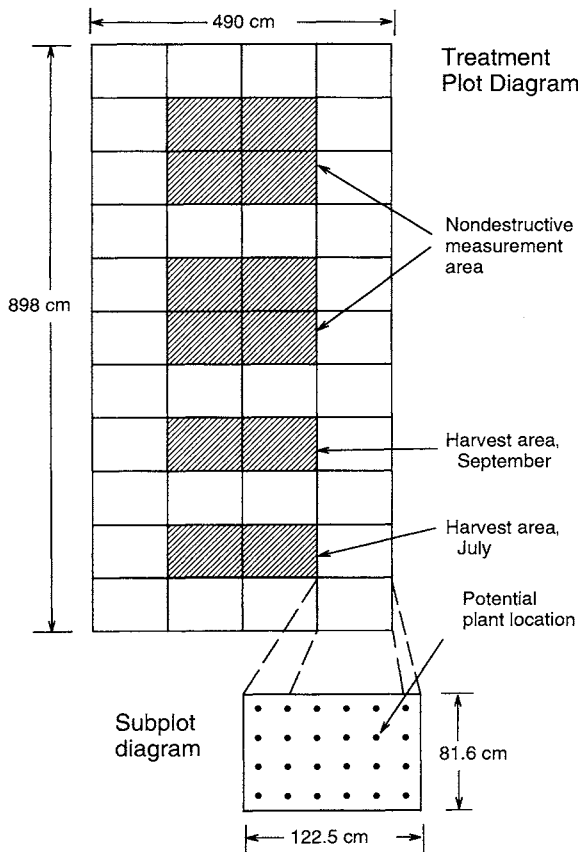


FIG. 1. Diagram of treatment plot showing sample areas (shaded) and subplot diagram showing potential locations of plants. Each of the 48 treatments was replicated four times in a randomized complete block design.

pinus are planted to or invade a site. To mimic this specific competitive situation, seedlings of *Liquidambar* and rooted tillers of *Andropogon* were established a year prior to planting of *Pinus*. *Liquidambar* seedlings were grown from seed (local source) for one year in a forest tree nursery and planted in December 1988. *Liquidambar* seedling stems averaged from 6.0 to 8.0 mm in basal diameter and 30 to 45 cm in height at the time of planting. *Andropogon* rooted tillers (<2 g total dry mass, ~3–4 cm in height) were excavated from an area adjacent to the study site as they initiated new shoot growth (February–March 1989) and were immediately planted. Both species were allowed to establish themselves throughout the 1989 growing season and then were severed near the ground line in December 1989 (this is similar to site preparation before planting of pines). At the end of the 1989 growing season, *Andropogon* survival exceeded 95% on three of the blocks and was greater than 90% on the remaining block. *Liquidambar* survival exceeded 99% throughout the study. Both species sprouted and grew vigorously during the 1990 growing season (Perry et al. 1993, 1994). *Pinus* seedlings were grown from seed (from a

commercial genetic source typically planted on these sites) for one growing season in a forest tree nursery and planted in February 1990. *Pinus* seedlings averaged 5 mm in basal diameter and 20 cm in height at the time of planting. This scenario may have resulted in placing *Pinus* seedlings in an inferior asymmetric competitive position, but it is representative of the competitive situation in these early-successional managed communities.

Data collection

Plant dimensional measurements and survival counts were made on eight interior subplots in each treatment plot during early July and early September 1990 (Fig. 1). Eight plants of each species, one randomly selected from each of the eight interior subplots, were chosen for collection of nondestructive dimensional measurements. All species were measured for height and crown diameter. In addition, basal diameter of *Andropogon* clumps and *Pinus* stems were recorded in order to provide better estimates of plant biomass from nondestructive measurements. At each date, three individuals of each species were randomly selected from designated subplots within each treatment plot (Fig. 1) for destructive harvest. Dimensional measurements on these destructive samples allowed for development of species and treatment-specific biomass equations ($n = 12$) based on nondestructive dimensional attributes. The equations were then used to estimate individual plant biomass of the eight nondestructively sampled plants and to compute mean plant biomass for each species in each treatment plot. Foliage from destructively sampled plants was composited by species within each treatment plot and foliar nitrogen determined using a CHN analyzer (LECO Corporation, St. Joseph, Michigan).

Soil water and predawn plant water potential measurements were measured every two weeks from early May through September 1990. Volumetric soil water content was estimated at a single point within each treatment plot (upper nondestructive measurement area, Fig. 1) using a Soil Moisture Equipment Corp. (Santa Barbara, California) Trase Unit (time domain reflectometry; Topp et al. 1980). Soil water was determined at four depths: 0–14, 14–30, 30–60, and 60–90 cm. Predawn xylem water potential of each species was assessed the morning following each soil water measurement using the pressure chamber method (Scholander et al. 1965). Three plants of each species were randomly chosen from the interior of each treatment plot. Water stress integral (WSI) was calculated as described by Myers (1988):

$$WSI = \sum_{i=0}^{i=t} |\Psi_{(i,i+1)} - C|N$$

where $\Psi_{(i,i+1)}$ is the mean predawn water potential for any interval ($i, i + 1$), C is the maximum predawn water potential measured for the entire study period,

and N is the number of days contained within the time interval.

Light was quantified within each treatment plot using a LI-COR quantum line sensor (LI-COR, Lincoln, Nebraska) averaging photosynthetically active radiation (PAR) across a 1-m length. These measurements were conducted between 1100 and 1300 solar time from 13 to 23 June 1990. Two 2-m transects were sampled at various heights in each treatment plot, one transect along the center of the long axis of each nondestructive measurement area (Fig. 1). Photon flux was measured starting at the ground line and proceeding upward in 25-cm increments to 1 m or until the height exceeded the tallest individual in the plot by at least 25 cm. Thus transects ran under, over, through, and between crowns of plants. Light at each sampled height was expressed as percentage of that above the plant canopy. An estimate of light at three-fourths the plant height of each species in a treatment plot was made by interpolating light values between the sample heights above and below three-fourths of the mean measured plant height for the species.

Stomatal conductance (g_s) was measured once each month from June through September 1990 using a LI-COR 1600 steady-state porometer. Due to the need to concentrate diurnal measurements within a short time period, a subset of treatments was measured. These treatments represented a factorial arrangement of *Pinus* and *Liquidambar* at 0 and 2 plants/m², and *Andropogon* at 0, 4, and 16 plants/m². Three individuals per treatment per block were measured at three times throughout the day (0900, 1200, and 1400 solar time). Due to the number of measurements, each block was sampled on a separate day. The order in which treatments were sampled with each block was randomized independently for each time period. Predawn and diurnal leaf-water potential of the same individuals were measured on the same days as stomatal conductance.

Data analysis

Effects on resources and response to resources as discussed by Goldberg (1990) were approached by first examining the effects of species density on resources using ANOVA and ANCOVA appropriate for a factorial treatment structure in a randomized complete block design (SAS Institute 1989). The treatment effect was partitioned into main effects of density of each species and two- and three-way interactions among species densities. Responses to resources were examined via correlation and regression analysis of relationships of aboveground biomass and indexes of resource availability. Soil water content and diurnal stomatal conductance data were each analyzed including date and depth (soil water) and hour of day (stomatal conductance) in the analysis as repeated factors as described by Moser et al. (1990) and Littell et al. (1991). Significant tests of sphericity ($P = 0.01$), indicating differing error variances across dates and soil depths, ne-

cessitated the use of multivariate repeated-measures ANOVA (Moser et al. 1990, Littell et al. 1991) in the analysis of soil water content (using date and depth as repeated measures). Diurnal stomatal conductance data was analyzed separately for each species by date using univariate ANOVA (using hour of day as repeated factor) because the test for sphericity was nonsignificant. Graphical presentation of ANOVA results are generally limited to significant main effects of species density, unless interactions were significant.

Comparisons of the relative effects of each species on soil water content in early July and light at the ground level in mid-June were examined as a function of density, aboveground biomass, foliage biomass, and leaf area in early July from monospecific plots and tested using ANCOVA. Although the relationship between effects and plant abundance may be curvilinear and asymptotic as abundance values approach zero (Miller and Werner 1987, Goldberg and Scheiner 1993), our data did not suggest such a relationship, and so a linear model with a common intercept was used. Tests of species by abundance (biomass, density, etc.) interaction were done by tests of inequality of slopes by species, and thus tested the per-individual, per-unit aboveground biomass, per-unit foliage biomass, and per-unit leaf area effects on soil water for each species.

Competitive responses (aboveground biomass) as a function of light, water, and nitrogen were examined for each plant species using simple correlation coefficients. In addition, response of *Pinus* to both light and water was examined by transforming values of each resource variable such that they were linearly related to *Pinus* response and by regressing *Pinus* response as a function of both transformed variables. Other species showed little to no improvement in the amount of variation of competitive response that was explained when response was regressed as a function of multiple resources.

RESULTS

Competitive effects on resources

Competitive effects on soil water content were complex (Fig. 2), with the exception that *Pinus* density was not noted to have a significant effect nor to interact with date, soil depth, and/or density of other species ($P > 0.20$ for all tests). Effects of density of *Andropogon* and *Liquidambar* were dependent on date, soil depth, and density of each other (i.e., significant two-way interactions between each species density and date or depth and three-way interactions among *Andropogon*, *Liquidambar*, and density or depth, all $P < 0.01$). Averaged across all dates and soil depths, *Liquidambar* density strongly influenced soil moisture ($F_{2,51} = 13.93$, $P < 0.001$).

The effect of *Andropogon* density on surface soil (0–14 cm) water was either neutral or positive. Positive effects were observed intermittently throughout the

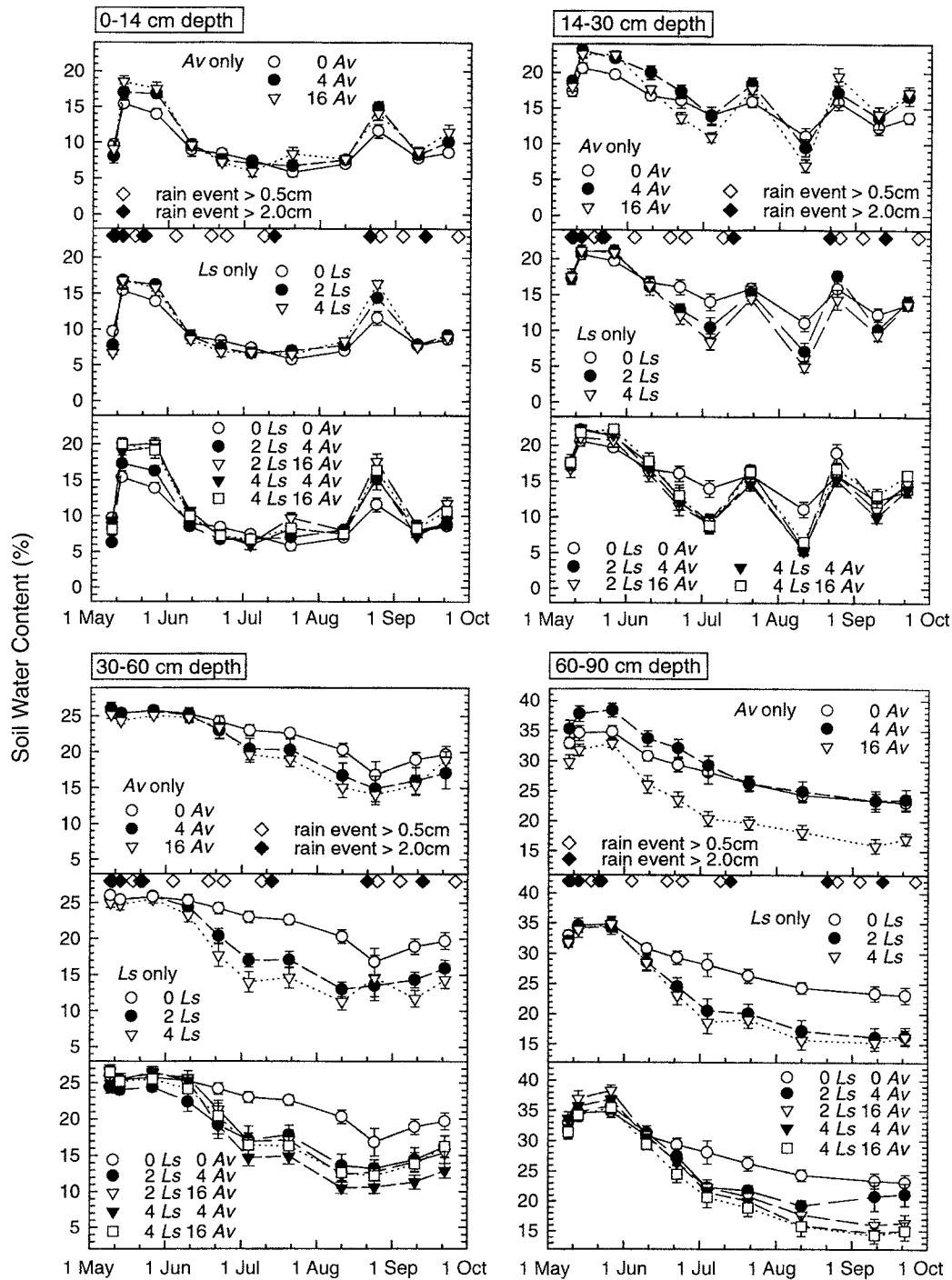


FIG. 2. Soil water content (mean across all densities of *Pinus taeda* \pm 1 SE, $n = 9$) at four depths over time by planting density (no. plants/m²) of *Liquidambar styraciflua* (*Ls*) and/or *Andropogon virginicus* (*Av*). Significant rain events are noted by diamonds along upper x-axis in middle graph at each depth. Measurements were made in 1990.

growing season (11 and 25 May, 19 July, and 22 August) after significant precipitation events (Fig. 2, upper panel of 0–14 cm depth). After drought periods (i.e., 3 July, 9 August), effects of *Andropogon* density on surface soil water were not significant. At the 14–30

cm depth, effect of *Andropogon* density on soil water was either positive or negative depending on time since rain. After a precipitation event, soil water increased dramatically at 4 and 16 *Andropogon* plants/m² (11 May, 19 July, and 22 August) relative to no *Andro-*

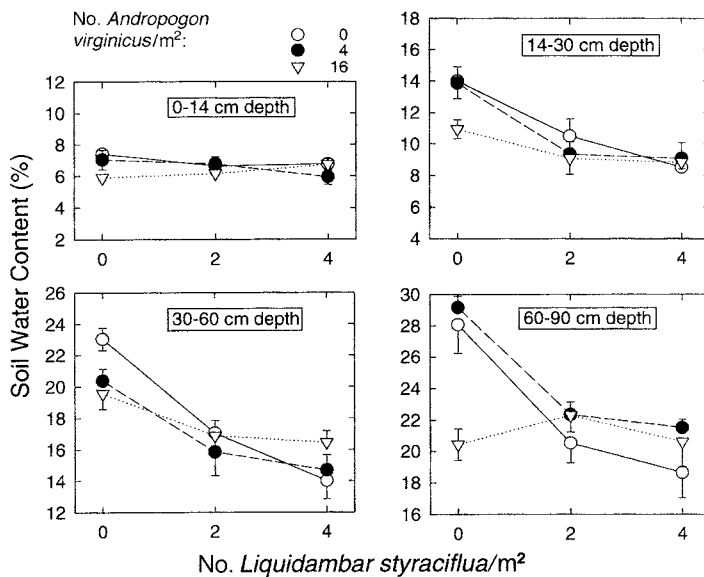


FIG. 3. Soil water content (mean across all densities of *Pinus taeda* \pm 1 SE, $n = 9$) at four depths on 2 July by planting density of *Liquidambar styraciflua* and *Andropogon virginicus*.

pogon (Fig. 2, upper panel of 14–30 cm depth). The rate of decline in soil water in the time periods between rainfall increased with *Andropogon* density (early June to early July, mid-July to early August). Below the 30 cm depth, soil water decreased as *Andropogon* density increased, and the general decline in soil water throughout the growing season tended to be less dynamically influenced by precipitation events (i.e., a gradual decline from high soil water at the beginning of the growing season to lower soil water with time). *Liquidambar* density effects on soil moisture followed similar patterns (Fig. 2, middle panels at each soil depth); however, the positive influences of *Liquidambar* density after precipitation events at the soil surface were less pronounced than those observed for *Andropogon*, and the negative effects of *Liquidambar* density were greater with increasing soil depth.

The interaction between *Liquidambar* and *Andropogon* in effects on soil water was particularly evident during drought periods (Fig. 3). On 2 July, the interaction between *Liquidambar* and *Andropogon* densities in effects on soil water was significant ($F_{4,51} = 5.23$, $P < 0.0001$). Effects of *Liquidambar* were dependent upon soil depth ($F_{6,98} = 7.28$, $P < 0.0001$). Effects of *Liquidambar* and *Andropogon* on soil water content were absent in the surface soil layer (Fig. 3) where the surface soil was uniformly dry. At greater soil depths, soil water decreased with increasing *Liquidambar* density in the absence of *Andropogon*, but the reduction was not as strong at high *Andropogon* density. Effects of *Andropogon* density were also negative below the 14 cm depth, but only when *Liquidambar* was absent (Fig. 3).

Soil water content (0–60 cm, 2 July) in monospecific plots generally decreased with increasing plant abundance, whether expressed as density, aboveground bio-

mass, foliage biomass, or leaf area (Fig. 4). Rates of decline in soil water content differed by species for the variables of increasing density, foliage biomass, and leaf area, but not for aboveground biomass (Table 1, Fig. 4). *Liquidambar* effects per plant and per unit foliage biomass and leaf area on soil water were greater than those for *Pinus* or *Andropogon* (per plant, $F_{2,18} = 12.43$, $P = 0.0004$; per unit foliage biomass, $F_{2,18} = 4.07$, $P = 0.0348$; per unit leaf area, $F_{2,18} = 6.61$, $P = 0.0070$).

Seasonally integrated measures of predawn water stress (WSI) varied among species, and were influenced by density of associate competitor species (Fig. 5). *Pinus* experienced greater water stress (more negative values for WSI) throughout the season followed by *Andropogon* and lastly *Liquidambar*. WSI values for *Pinus* were negatively affected by both *Andropogon* ($F_{2,34} = 6.59$, $P = 0.0038$) and *Liquidambar* ($F_{2,34} = 8.92$, $P = 0.0008$) in a linear relationship with density (Fig. 5 A, D). Values of WSI for *Andropogon* also decreased linearly ($F_{1,34} = 8.46$, $P = 0.0064$) with increasing *Liquidambar* density (Fig. 5C). Effects of *Andropogon* density on WSI of *Liquidambar* were significant ($F_{2,34} = 4.72$, $P = 0.0155$); however, WSI of *Liquidambar* decreased from 0 to 4 *Andropogon*/m², but did not change from 4 to 16 *Andropogon*/m² (Fig. 5B).

Competitive effects on light received by a species at three-fourths total height was dependent upon species density and combinations of species as given by significant main effects and interactions of species densities (Table 2). Associate competitor species influenced light available to an individual through direct influences (attenuation) on light availability and potentially through reducing height growth of the focal plant and thus its position in the canopy (Fig. 6). Light

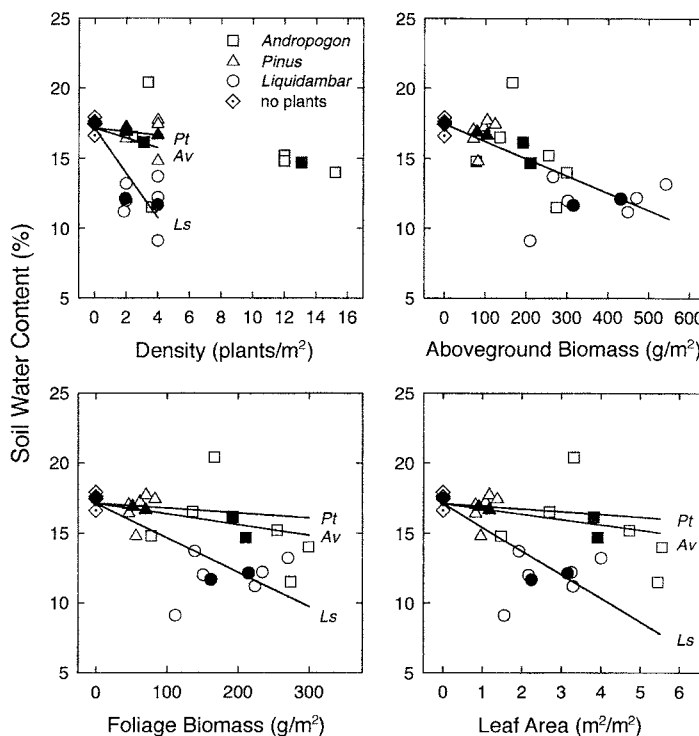


FIG. 4. Relationship of soil water content (0–60 cm layer, 2 July) to density, aboveground biomass, foliage biomass, and leaf area for monospecific stands of *Pinus taeda* (Pt), *Liquidambar styraciflua* (Ls), and *Andropogon virginicus* (Av). Treatment means are denoted by filled symbols, plot means by open symbols. A common regression line is presented if the competition measure \times species interaction is not significant (Table 1).

reaching the *Pinus* canopy was strongly reduced by *Liquidambar* density, with the effect lessening at higher *Andropogon* density (Table 2, Fig. 7 A, B). *Andropogon* effects on light available to *Pinus* were influenced by *Liquidambar* density. In the absence of *Liquidambar*, *Andropogon* at 16 plants/m² decreased light available to *Pinus*; however, at 4 *Liquidambar* plants/m², light available to *Pinus* was greatest at 16 *Andropogon* plants/m². Light reaching *Liquidambar* crowns was most strongly affected by *Andropogon* (Fig. 7C–E). High *Andropogon* density strongly reduced the devel-

opment of *Liquidambar* crown height (Fig. 6) and width, and thus increasing light was observed at three-fourths total height of *Liquidambar* at greater *Andropogon* densities. Effects of associate species and densities on light available to *Andropogon* were similar to those noted for *Pinus* (Table 2, Fig. 7 F–H), due in part to their similarity in height (Fig. 6).

Light reaching the soil surface in monospecific stands decreased with increasing plant density, aboveground biomass, foliage biomass, and leaf area (Fig. 8). Species-specific differences in rates of decline were

TABLE 1. Analysis of effects of species identity and various measures of competition on soil water content at mid-season (0–60 cm depth, 2 July) in monospecific treatments.

Factor	df	SS	MS	F	P
Block	2	23.26	11.63	4.08	0.0346
Density	1	37.20	37.20	13.04	0.0020
Density \times Species	2	70.88	35.44	12.43	0.0004
Error	18	51.33	2.85		
Block	2	23.26	11.63	3.41	0.0555
Aboveground biomass	1	92.55	92.55	27.13	0.0001
Aboveground biomass \times Species	2	5.45	2.73	0.80	0.4651
Error	18	61.41	3.41		
Block	2	23.26	11.63	3.51	0.0516
Foliage biomass	1	72.83	72.83	21.99	0.0002
Foliage biomass \times Species	2	26.96	13.48	4.07	0.0348
Error	18	59.62	3.31		
Block	2	23.26	11.63	3.40	0.0558
Leaf area	1	52.66	52.66	15.40	0.0010
Leaf area \times Species	2	45.20	22.60	6.61	0.0070
Error	18	61.54	3.42		

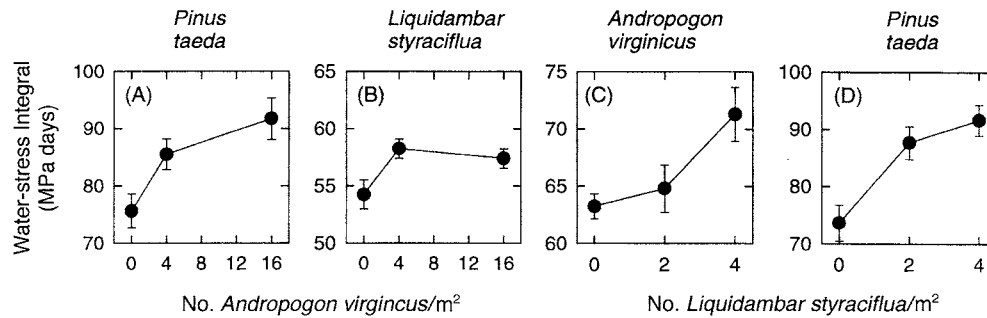


FIG. 5. Water-stress integral for (A) *Pinus taeda* and (B) *Liquidambar styraciflua* by density of *Andropogon virginicus* (mean across all dates and densities of *Pinus taeda* and *Liquidambar styraciflua* ± 1 SE, $n = 180$), and for (C) *Andropogon virginicus* and (D) *Pinus taeda* by density of *Liquidambar styraciflua* (mean across all dates and densities of *Pinus taeda* and *Andropogon virginicus* ± 1 SE, $n = 180$).

noted for density, foliage biomass, and leaf area, but not for aboveground biomass (Table 3, Fig. 8).

Leaf N concentration of *Pinus* was marginally affected by *Liquidambar* density ($F_{2,50} = 2.49$, $P = 0.0934$; Fig. 9A). *Liquidambar* foliar N declined linearly with increasing *Andropogon* density ($F_{2,50} = 4.19$, $P = 0.0460$; Fig. 9B) and declined or remained constant across densities of *Pinus* depending upon its own den-

sity ($F_{2,50} = 2.85$, $P = 0.0674$; Fig. 9C). *Andropogon* foliar N was dependent upon density of itself and *Liquidambar* ($F_{1,32} = 4.73$, $P = 0.0371$ for *Andropogon* main effect; $F_{2,32} = 2.79$, $P = 0.0765$ for interaction of *Liquidambar* and *Andropogon*). Foliar N of *Andropogon* at 4 plants/m² decreased with increasing density of *Liquidambar*. At 16 plants/m², foliar N of *Andropogon* was constant from 0 to 2 *Liquidambar* plants/m² and increased from 2 to 4 *Liquidambar* plants/m².

Stomatal conductance values varied by species, date, time of day, density, and species of competitors (Figs. 10, 11). In general, *Liquidambar* tended to have the greatest stomatal conductance, *Andropogon* was intermediate, and *Pinus* had the least (Fig. 10). This ranking in stomatal conductance corresponds to ranking of each species in per-unit-foliage-area effects on soil water noted in early July (Fig. 4). At each sample date, stomatal conductance for a given species differed by time of day ($P < 0.001$ for all tests) with no interaction between time of day and species density ($P > 0.25$ for all tests). Stomatal conductance of *Pinus* in June and August (Fig. 11 A, D) decreased linearly with increasing density of *Andropogon* (June, $F_{1,10} = 7.29$, $P = 0.0223$; August, $F_{1,10} = 7.00$, $P = 0.0245$) and *Liquidambar* (June, $F_{1,10} = 13.12$, $P = 0.0047$; August, $F_{1,10} = 8.30$, $P = 0.0164$). *Liquidambar* ($F_{2,10} = 5.69$, $P = 0.0223$; Fig. 11B) and *Andropogon* ($F_{1,14} = 5.31$, $P = 0.0371$; Fig. 11D) stomatal conductance also decreased with increasing *Andropogon* density in August. In addition, *Andropogon* stomatal conductance decreased with increasing *Liquidambar* density in July ($F_{1,14} = 6.94$, $P = 0.0337$) and August ($F_{1,14} = 4.21$, $P = 0.0594$; Fig. 11E).

Relationship between effects on resources and responses

Aboveground biomass response of *Pinus* was significantly correlated with water-stress integral (WSI), light (relative light received), and leaf N concentration, while response of *Liquidambar* was correlated to WSI and leaf N (Fig. 12). *Andropogon* response was only

TABLE 2. Analysis of relative light (percentage of above-canopy light) to *Pinus taeda*, *Liquidambar styraciflua*, and *Andropogon virginicus* at three-fourths plant height in mid-June, as influenced by densities of each species.

Source†	df	MS	F	P
<i>Pinus taeda</i>				
Block	2	492.3	3.90	0.0300
A	2	245.4	1.94	0.1590
L	2	6 825.6	54.01	0.0001
A × L	4	755.7	5.98	0.0009
P	1	241.3	1.91	0.1761
A × P	2	453.6	3.59	0.0385
L × P	2	85.9	0.68	0.5136
A × L × P	4	221.9	1.76	0.1606
Error	34	126.4		
<i>Liquidambar styraciflua</i>				
Block	2	136.8	4.76	0.0151
A	2	175.7	6.11	0.0054
L	1	196.2	6.82	0.0133
A × L	2	110.1	3.83	0.0316
P	2	9.7	0.34	0.7162
A × P	4	104.0	3.62	0.0147
L × P	2	148.3	5.16	0.0111
A × L × P	4	60.4	2.10	0.1024
Error	34	28.8		
<i>Andropogon virginicus</i>				
Block	2	492.5	5.20	0.0107
A	1	484.1	5.11	0.0304
L	2	4 071.7	42.95	0.0001
A × L	2	601.5	6.35	0.0046
P	2	2.5	0.03	0.9743
A × P	2	47.8	0.50	0.6086
L × P	4	130.5	1.38	0.2627
A × L × P	4	389.5	4.10	0.0081
Error	34	94.8		

† A = *Andropogon virginicus*, L = *Liquidambar styraciflua*, P = *Pinus taeda*.

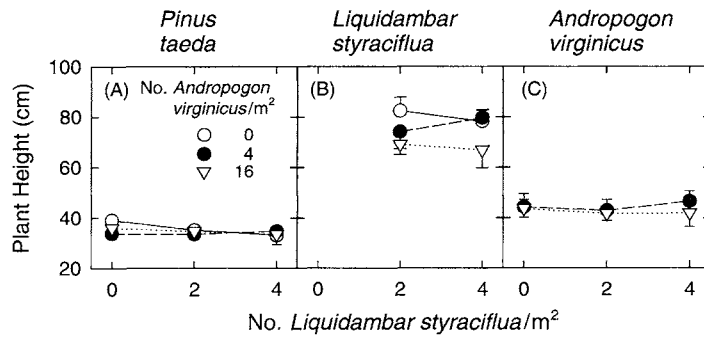


FIG. 6. Height (mean \pm 1 SE, $n = 3$) of (A) *Pinus taeda*, (B) *Liquidambar styraciflua*, and (C) *Andropogon virginicus* by planting density of *Liquidambar styraciflua* and *Andropogon virginicus*.

correlated with light. Sixty-eight percent of the variation in response of *Pinus* could be explained by the regression model using both light and WSI as independent variables (Fig. 12), with approximately 54 and 50% explained by the transformed variables of light and WSI singularly.

The model was used to generate a contour plot of *Pinus* biomass response with respect to WSI and light and then overlain with mean values for WSI and light for each treatment (denoted by density of *Liquidambar* and *Andropogon* only, since *Pinus* did not significantly affect either WSI or light). This graph demonstrates the interplay of both light and water on response and gives insight as to the relative effects of associate competitor composition on light and water stress (Fig. 13). Similar biomass response of *Pinus* may result across a range of water stress or light availability as one factor decreases and the other increases (and vice versa), with the range in effects on resources increasing as both

become more limiting (and biomass decreases). *Liquidambar* alone had very strong effects on light and slightly lesser effects on water available to *Pinus* (0-00 to 2-00 and 4-00, Fig. 13), whereas the effects of *Andropogon* alone (0-00 to 0-04 and 0-16) were primarily on water. The effect of adding *Liquidambar* to *Andropogon* alone at low density (0-04 to 2-04 to 4-04) was to increase water stress and strongly decrease light, whereas adding *Liquidambar* to high densities of *Andropogon* (0-16 to 2-16 to 4-16) had less of an effect on light and water stress (Fig. 13).

DISCUSSION

Resource preemption may be an important mechanism in early-successional managed *Pinus* communities, and can result in strong asymmetry in competition. Differences in the magnitude of competitive effects between our report and the findings of the full study of Morris et al. (1993) may be explained by the manner

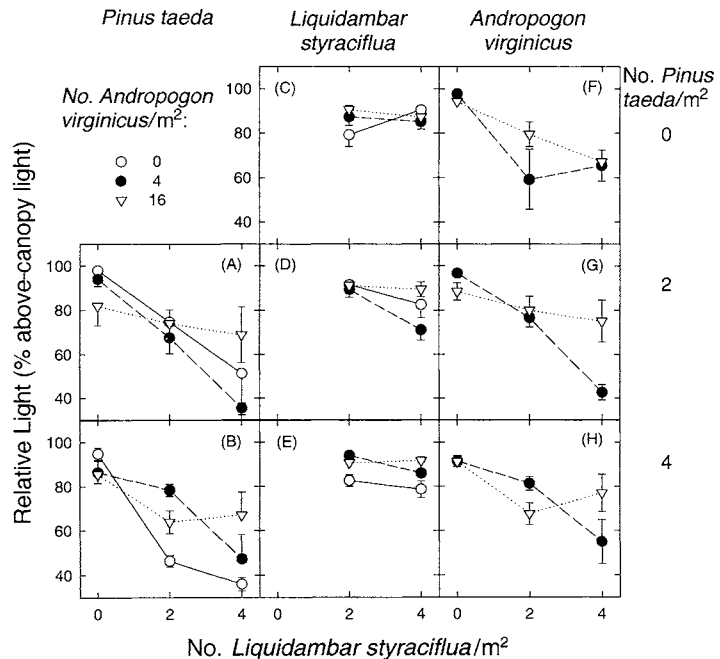


FIG. 7. Relative light (percentage of above-canopy light) in mid-June at three-fourths plant height (mean \pm 1 SE, $n = 3$) of (A, B) *Pinus taeda*, (C-E) *Liquidambar styraciflua*, and (F-H) *Andropogon virginicus* by planting density of each species.

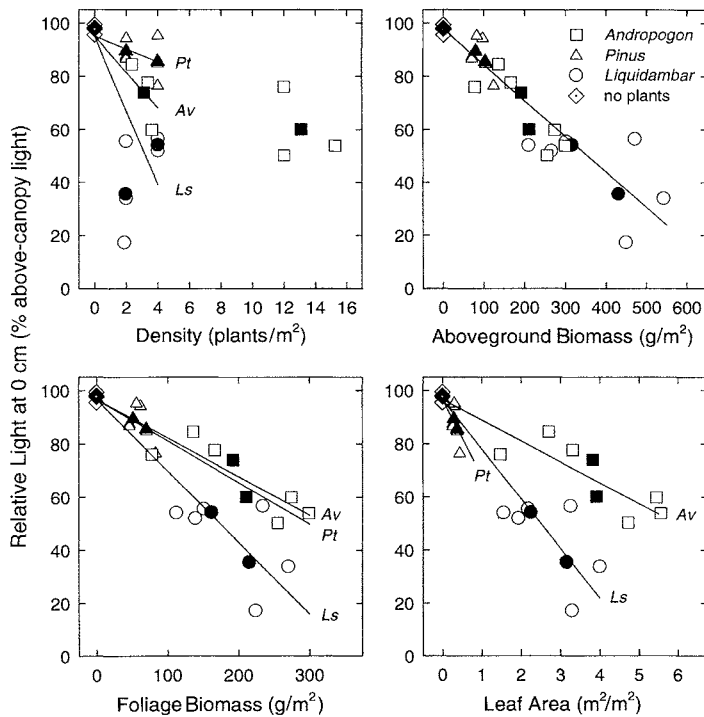


FIG. 8. Relationship of relative light (percentage of above-canopy light) in mid-June at 0 cm (ground level) to density, aboveground biomass, foliage biomass, and leaf area for monospecific stands of *Pinus taeda* (Pt), *Liquidambar styraciflua* (Ls), and *Andropogon virginicus* (Av). Treatment means are given by filled symbols, plot means by open symbols. A common regression line is presented if the competition measure \times species interaction is not significant (Table 3).

in which plants were established. In the study reported here, *Liquidambar* and *Andropogon* were established the year before *Pinus*, while Morris et al. (1993) planted seedlings of each species at the same time. Thus, in the field in which competitors are established earlier than *Pinus taeda*, greater reductions in growth occur than if they are established simultaneously. Once differences in resource acquisition rates are established, plants that can acquire greater resources grow more rapidly and suppress the growth of plants less able to initially access resources. Thus, a positive feedback

between growth and resource capture tends to magnify differences in competition (Weiner 1986, 1990).

Asymmetry in competition may be accentuated when resource supply is directional, as in competition for light. Plants that grow taller will shade plants lower in stature, but shorter plants have lesser or no impact on light reaching taller plants (Weiner 1986). Soil water availability can also have directional properties. In many, but not all communities, soil water availability deeper in the profile is greater than at the surface horizons during periods of drought. Thus, deeper rooted

TABLE 3. Analysis of effects of species identity and various measures of competition on relative light (percentage of above-canopy light) at 0 cm (ground level) in mid-June in monospecific treatments.

Factor	df	ss	ms	F	P
Block	2	433.4	216.7	0.85	0.4419
Density	1	3 033.1	3 033.1	11.97	0.0019
Density \times Species	2	4 062.5	2 031.2	8.01	0.0032
Error	18	4 562.5	253.5		
Block	2	707.9	353.9	7.84	0.0036
Aboveground biomass	1	2 068.1	2 068.1	45.79	0.0001
Aboveground biomass \times Species	2	66.2	33.1	0.73	0.4944
Error	18	813.0	45.2		
Block	2	675.8	337.9	8.05	0.0032
Foliage biomass	1	2 435.6	2 435.6	58.06	0.0001
Foliage biomass \times Species	2	1 899.8	949.9	22.64	0.0001
Error	18	755.1	42.0		
Block	2	674.6	337.3	8.55	0.0025
Leaf area	1	1 031.9	1 031.9	26.15	0.0001
Leaf area \times Species	2	3 851.2	1 925.6	48.81	0.0001
Error	18	710.2	39.5		

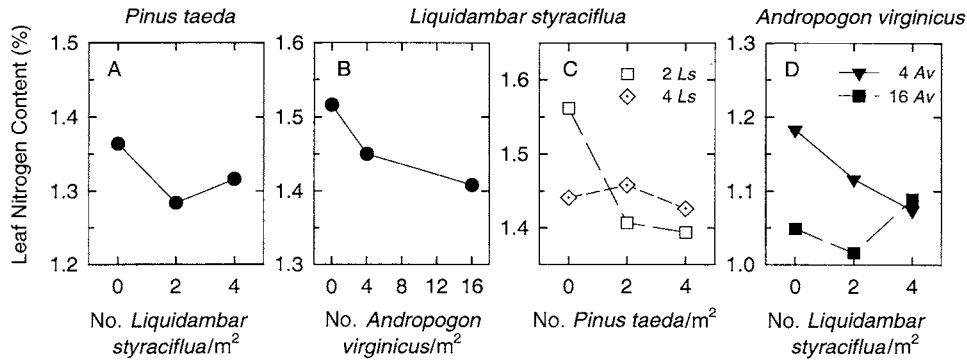


FIG. 9. Mean leaf nitrogen concentration at the end of the growing season for (A) *Pinus taeda* by density of *Liquidambar styraciflua* (means across levels of *Pinus taeda* and *Andropogon virginicus* \pm 1 SE, $n = 36$); (B) *Liquidambar styraciflua* by density of *Andropogon virginicus* (means across levels of *Pinus taeda* and *Liquidambar styraciflua* \pm 1 SE, $n = 36$); and (C) combinations of densities of itself (*Ls*) and *Pinus taeda* (means across levels of *Andropogon virginicus* \pm 1 SE, $n = 12$), and (D) *Andropogon virginicus* by combinations of densities of itself (*Av*) and *Liquidambar styraciflua* (*Ls*) (means across levels of *Pinus taeda* \pm 1 SE, $n = 12$).

species could function in ways analogous to tall plants in competition for light. For example, deeply rooted plants (such as *Liquidambar* sprouts) may reduce soil water in the rooting zone of more shallow-rooted species (establishing *Pinus* seedlings), but the latter species would not affect the soil water available to deeply rooted neighbors. In this way, asymmetry in both above- and belowground resources can develop.

Goldberg (1990) predicts that traits related to species success in competitive environments depend on the size

structure of the competing populations. If target individuals are small relative to their neighbors, they are unlikely to significantly reduce resources to neighbors, thus their ability to suppress neighbors should be reduced. This is likely to create greater neighbor effects on target species. This appears to have been the case with *Liquidambar* and *Andropogon*, established prior to *Pinus* in this study.

Effects on resources varied among species, but in complex ways. *Liquidambar* and *Andropogon* signifi-

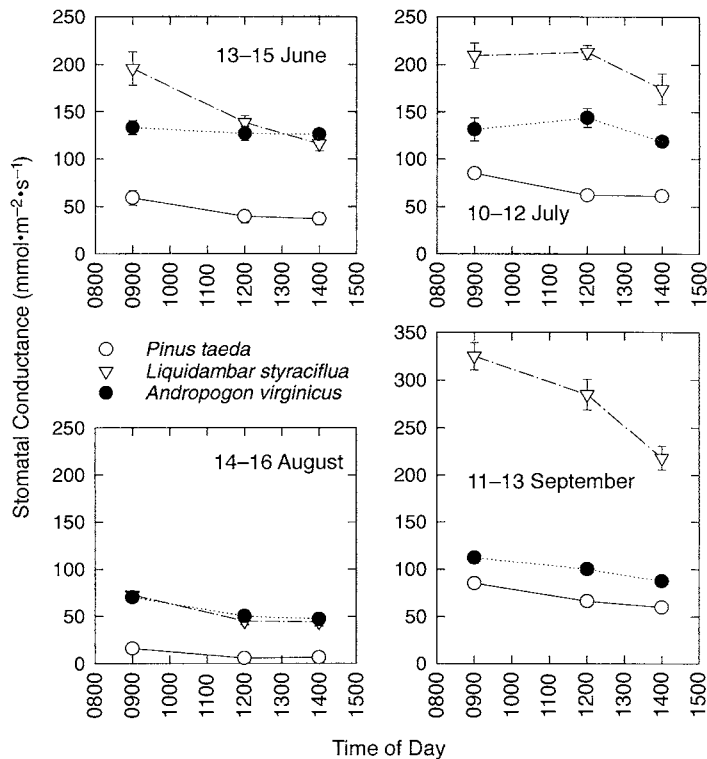


FIG. 10. Stomatal conductance for each species over hour of day by sample date (mean \pm 1 SE; $n = 12$ for *Pinus taeda* and *Liquidambar styraciflua* on 10-12 July, $n = 18$ for other dates; $n = 16$ for *Andropogon virginicus* on 10-12 July, $n = 24$ for other dates).

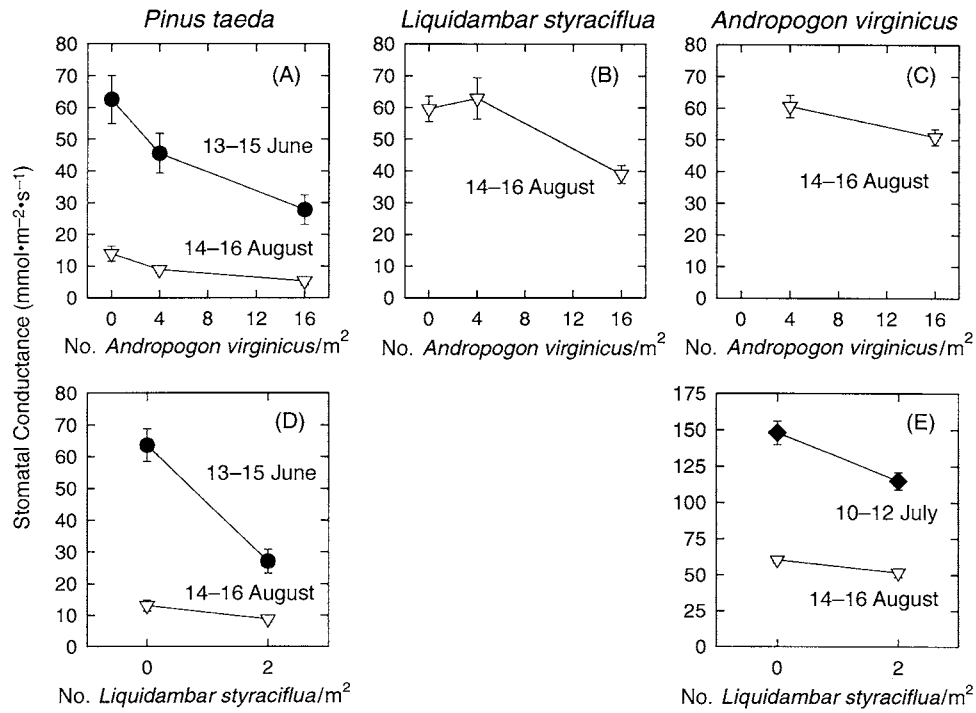


FIG. 11. Stomatal conductance for (A) *Pinus taeda*, (B) *Liquidambar styraciflua*, and (C) *Andropogon virginicus* by planting density of *Andropogon virginicus* (mean ± 1 SE; n = 18 for *Pinus* and *Liquidambar*, n = 36 for *Andropogon*) by sample date; and for (D) *Pinus taeda* and (E) *Andropogon virginicus* by planting density of *Liquidambar styraciflua* (mean ± 1 SE; n = 27 for *Pinus*, n = 24 for *Andropogon* on 10–12 July, and n = 36 for *Andropogon* on 14–16 August) by sample date.

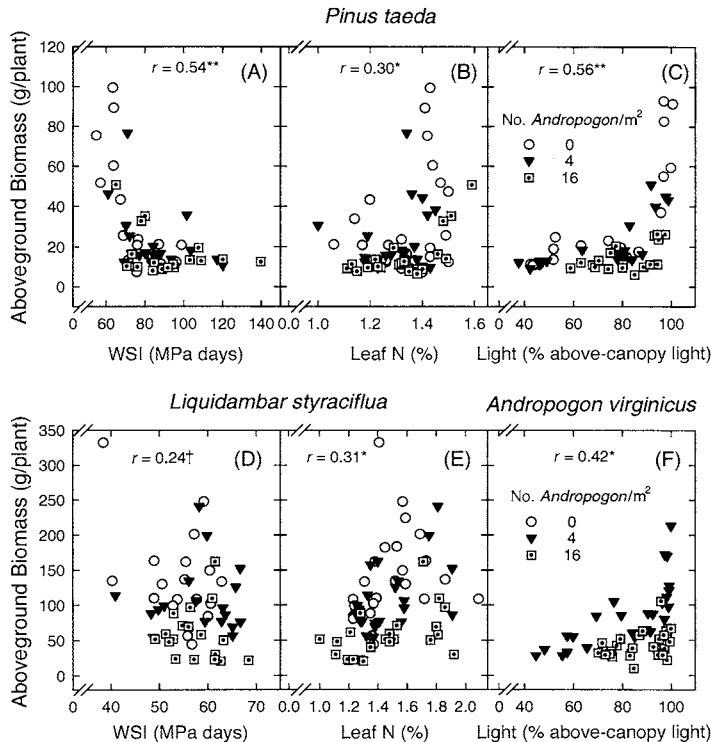


FIG. 12. Aboveground biomass as a function of water-stress integral (WSI) for (A) *Pinus taeda* and (D) *Liquidambar styraciflua*; as a function of leaf nitrogen concentration for (B) *Pinus taeda* and (E) *Liquidambar styraciflua*; and as a function of relative light (percentage of above-canopy light) in mid-June at three-fourths plant height for (C) *Pinus taeda* and (F) *Andropogon virginicus*. Values on each graph are r values and level of significance († P < 0.10, * P < 0.05, ** P < 0.01).

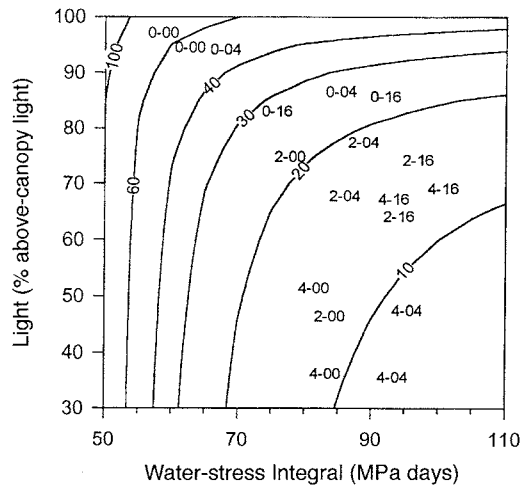


FIG. 13. Contour plot of aboveground biomass (g) of *Pinus taeda* from fitted model based on relative light (percentage of above-canopy light) in mid-June at three-fourths plant height (LT). Also shown are water-stress integral (WSI) and mean values ($n = 3$) of LT and WSI for combinations of densities of *Liquidambar styraciflua* (before hyphen) and *Andropogon virginicus* (after hyphen) overlaid on the contour plot. Model: biomass = $-9.3 + 504.7/(110 - LT) + 522.85/(WSI - 45)$ ($n = 54$, $R^2 = 0.68$; all parameters are significant at $P < 0.01$).

cantly affected soil moisture, but their effects depended on the time of the measurement and the depth of the soil that was measured. After a rain, soil water increased in the surface horizons with increasing competitor density. This non-uptake effect of competitor abundance on soil moisture has been previously reported (Gill and Marks 1991, Mitchell et al. 1993), and has been attributed either to reduced evaporation or to greater rates of infiltration, or both. However, at no time in this study did increasing competitor density decrease water stress of any of the three species. De Steven (1991a, b) showed that the presence of neighbor plants facilitated the establishment of *Pinus taeda* immediately after germination, but that strong competitive effects were apparent on seedling growth. Thus, non-uptake effects on soil water at the surface may not affect the water relations of *Pinus* seedlings after the critical establishment period.

Uptake effects on soil water were also present, but again they varied with the time of measurement and the depth. During droughts the surface soil was uniformly dry regardless of competitor type or density. However, at subsurface soil layers both density and species of competitors influenced soil water availability. Effects on soil water were consistent among species on the basis of aboveground biomass. Furthermore, soil water differences among species as a function of leaf biomass and leaf area appear to be related to differences among species in stomatal conductance: *Liquidambar* had the greatest stomatal conductance and the greatest slope of leaf area and soil water, while *Pinus* had the

least. In addition, the dynamics of soil water throughout the year varied with depth. In the deeper portions of the soil, increasing competitor density of either *Andropogon* or *Liquidambar* decreased soil water, and this effect was more pronounced with time. In contrast, soil layers closer to the surface (0–14, 14–30 cm) were more dynamic, responding to rainfall events as well as competitor density. Since sympatric species often differ considerably in rooting depth (Burton and Bazzaz 1995, Burch et al. 1997), relating these complex patterns in competitive effects to responses can be problematic (Mitchell et al. 1993).

Fahey and Young (1984) suggest that predawn water potential of individuals represents soil moisture availability integrated across the root zone of individuals. However, relating competitive effects to responses requires not only that the vertical heterogeneity in soil moisture be integrated (as was done by measuring predawn water potential) but also that variation through time also be incorporated into the effects measure. Schultze et al. (1980a) and Linder et al. (1987) calculated a parameter termed “deficit time” that represented the accumulated predawn water potential measured every two weeks throughout a growing season. They showed that this parameter was strongly related to maximum net photosynthesis, and also to net photosynthesis per day (Schultze 1980a, b) and *Pinus* needle length. Since both development of leaf area (Britt et al 1990, 1991) and photosynthetic rates (Burton and Bazzaz 1995) have been reported to be related to competitive response, the accumulation of water potential may be a better index of competitive effect than measurement of plant water status at any particular date. Myers (1988) and Myers and Landsberg (1989) used a similar approach, the water-stress integral, which approximates the area bound by the least stress encountered by an individual in the experiment and the pattern of predawn water potential measured throughout the growing season. They found that a water-stress integral successfully related long-term water deficits to growth of *Pinus radiata* and *Eucalyptus*.

Using a water-stress-integral approach, *Pinus taeda* was demonstrated to be significantly affected by both *Liquidambar* and *Andropogon*, *Liquidambar* to be affected by *Andropogon*, and *Andropogon* to be affected by *Liquidambar*. The presence of interspecific competitive effects and the absence of intraspecific competitive effects between *Liquidambar* and *Andropogon* are worthy of note. Questions related to the intensity of intra- versus interspecific competition in plant communities have been the subject of debate (see reviews by Goldberg and Barton 1992, Shipley and Keddy 1994). With respect to competitive effects on water, the greater intensity of interspecific competition on soil moisture was perhaps due to complex interactions among species determining net competitive effects. *Liquidambar* consistently was less water stressed than the other species, most likely due to the deep-rooted

nature of sprouts, as noted by Burch et al. (1997). Competition from *Andropogon* reduced aboveground growth, and may have reduced belowground growth in ways that reduced access to deeper, more plentiful supplies of water. Thus, *Andropogon* may have indirectly affected the level of stress experienced by *Liquidambar*. On the other hand, *Liquidambar* (due to its large development of leaf area and its high stomatal conductance) most likely reduced soil moisture in the rooting zone of *Andropogon*. Much greater emphasis on documenting belowground architectural development of roots and understanding root function will be required to gain a greater mechanistic understanding of belowground responses of plants to competition.

Competitive effects on light were dominated by *Liquidambar*. *Liquidambar* was the tallest of the three life-forms in this study, primarily due to its establishment a year prior to *Pinus* and the rapid growth of sprouts. At midday in our study, *Pinus* seedlings only received 60% of incoming radiation at the same *Liquidambar* density. *Liquidambar* also strongly affected light reaching *Andropogon*. However, an interaction between *Liquidambar* and *Andropogon* density on light availability was observed. This was most likely due to indirect effects of *Andropogon* reducing the size of *Liquidambar* crowns, and thus reducing the effect of *Liquidambar* at high densities of *Andropogon*. Tremmel and Bazazz (1993) indicate that local crowding can strongly influence the architecture of crowns of annuals and influence competitive outcomes. This study suggests that changes in crown structure can be affected by increased density of plants of low stature, thus affecting the acquisition of light.

Competitive effects on N, as measured by foliar N levels of the species, tended to show that N effects were less apparent than were those of either light or water. Morris et al. (1993) showed moderate effects of competitive neighborhoods on foliar N concentration of *Pinus*, comparable in range to those reported in this study. In addition, they fertilized with N and with NPK fertilizers, but showed no *Pinus* response. These reports are consistent with earlier reports by Carter et al. (1984) that showed no foliar N response of pine to manipulation of sweetgum and broomsedge in neighborhoods of established *Pinus taeda* seedlings, and that of Nambiar and Zed (1980), which reported that *Pinus radiata* response to competition control was more strongly related to water stress than N availability (as measured by foliar N content). Collectively, these findings suggest that early-successional *Pinus* communities are more often limited by light and soil water than by N.

Competitive responses to resources differed among the three species included in this study. *Pinus* seedlings showed a significant relationship between growth and light, WSI, and foliar N. *Liquidambar* response was significantly correlated to leaf N and WSI, while *Andropogon* growth was only correlated with light. Competitive response appears to be a reflection of physi-

ological responses of species to their environment and the ability to acquire resources. *Liquidambar* and *Andropogon* had the advantage of root establishment on site before *Pinus* seedlings were planted. This allowed for greater rates of resource acquisition early in the growing season, and these differences were accentuated through time (Perry et al. 1993). In addition, *Pinus* was the only target species to be related to all three resources. This may be due to the fact that plants of low stature have more access to resources in low-intensity competitive environments (low density of small plants) compared to high-intensity competitive environments (greater density of larger plants).

In the few studies that have attempted to relate competitive effect on resources to response (Goldberg 1990, Gordon and Rice 1993, Mitchell et al. 1993, Burton and Bazazz 1995), response was correlated to a single resource. However, if plants are not optimal foragers for both above- and belowground resources, multiple limitations to plant growth can occur (Rastetter and Shaver 1992, Canham et al. 1996). We attempted to empirically analyze the effects and response component of competition to light and water stress for *Pinus taeda*. Nearly 70% of the variation in *Pinus* response could be explained by a multiple regression model of light and water stress, whereas ~50% of the variation in pine growth could be explained by light or water stress (WSI) alone. Plotting isopleths of *Pinus* growth as a function of both WSI and light and overlaying composition of plots at their mean WSI and light values indicated that communities dominated by *Liquidambar* had the greatest effect on *Pinus* growth through reduction in light, while pure *Andropogon* communities reduced *Pinus* growth by increasing *Pinus* water stress; in mixed communities *Pinus* growth was constrained more equally by both light and water stress.

Liquidambar, the tallest of the three species included in this study, only responded to N and water stress. Deciduous plants often have leaves with higher N requirements and respond more robustly to nutrient availability than do evergreen plants (Chapin 1980). *Andropogon*, a C₄ bunchgrass, is able to reduce water-loss rates (i.e., low stomatal conductance), but maintain high photosynthetic rates, culminating in greater water-use efficiency due to its photosynthetic pathway (Bazazz 1979). Thus, it is not unexpected that *Andropogon* was the least sensitive species to moisture limitations on the site. In addition, *Andropogon*'s competitive ability has been reported to be reduced by fertilization; thus, it appears to be adapted to low nutrient conditions. However, most C₄ grasses are only photosaturated at radiance levels close to full sunlight, thus the significant response of *Andropogon* to light is consistent with the physiological nature of this species.

In summary, species-specific competitive effects on resources were strong when density was used as an abundance measure, but few differences among species were noted in resource attenuation as a function of

aboveground biomass. Species-specific effects on water appeared to be largely related to differences in stomatal conductance. The response component of competition differed among the three species tested. *Pinus* showed a significant response to light, water stress, and foliar nitrogen. Soil water and light collectively explained a greater percentage of variation in pine response than either alone. When *Pinus* was grown in *Liquidambar* communities, response was greatest to light, while *Pinus* grown with *Andropogon* responded mostly to competition for soil water. When grown in mixtures, *Pinus* response was regulated by multiple resource limitations. In contrast, *Andropogon* response was correlated only with light, reflecting the higher light requirements and greater water use efficiency of C_4 plants. *Liquidambar* response was related to water stress and leaf nitrogen, perhaps reflecting the greater nitrogen requirements of hardwoods. This work suggests that competitive effects and responses can be used in field environments to understand mechanisms regulating plant-plant interactions if spatial and temporal heterogeneity of resources are accounted for and multiple resource limitations are examined.

ACKNOWLEDGMENTS

We would like to thank D. Goldberg for extensive comments and improvement of an earlier draft of this manuscript. In addition, D. DeSteven and three anonymous reviewers provided many useful criticisms that have also improved the manuscript. Statistical assistance was provided by G. Somers and J. Williams. We thank C. Brewer, P. D'Anieri, and T. Green for assistance with data collection. The study was partially funded by grants through USDA/NRI Weed Science, and Forest, Rangeland, and Agricultural Ecosystems Programs and the National Council of the Paper Industry for Air and Stream Improvement, Incorporated. (NCASI).

LITERATURE CITED

- Bazzaz, F. A. 1979. The physiological ecology of plant succession. *Annual Review of Ecology and Systematics* **10**: 351-371.
- Britt, J. R., R. J. Mitchell, B. R. Zutter, D. B. South, D. H. Gjerstad, and G. R. Glover. 1991. The influence of herbaceous weed control and seedling diameter on six years of growth of loblolly pine—a classical growth analysis approach. *Forest Science* **37**:655-668.
- Britt, J. R., B. R. Zutter, R. J. Mitchell, D. H. Gjerstad, and J. F. Dickson. 1990. Influence of herbaceous interference on growth and biomass partitioning in planted loblolly pine. *Weed Science* **38**:497-503.
- Burch, W. H., R. H. Jones, P. Mou, and R. J. Mitchell. 1997. Root system development of single and mixed plant functional types communities following harvest in a pine-hardwood forest. *Canadian Journal of Forestry Research* **27**: 1753-1764.
- Burton, P. J., and F. A. Bazzaz. 1995. Ecophysiological responses of tree seedlings invading different patches of old-field vegetation. *Journal of Ecology* **83**:99-112.
- Caldwell, M. M., D. M. Eissenstat, J. H. Richards, and M. F. Allen. 1985. Competition for phosphorus: differential uptake from dual-isotope-labeled soil interspaces between shrub and grass. *Science* **229**:384-386.
- Canham, C. D., A. R. Berkowitz, V. R. Kelly, G. M. Lovett, S. V. Ollinger, and J. Schnurr. 1996. Biomass allocation and multiple resource limitation in tree seedlings. *Canadian Journal of Forest Research* **26**:1521-1530.
- Carter, G. A., J. H. Miller, D. E. Davis, and R. M. Patterson. 1984. Effect of vegetative competition on moisture and nutrient status of loblolly pine. *Canadian Journal of Forest Research* **14**:1-9.
- Casper, B. B., and R. B. Jackson. 1997. Plant competition underground. *Annual Review of Ecology and Systematics* **28**:545-570.
- Chapin, F. S., III. 1980. The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics* **11**:233-260.
- Cousens, R. 1991. Aspects of the design and interpretation of competition (interference) experiments. *Weed Technology* **5**:664-673.
- De Steven, D. 1991a. Experiments on mechanisms of tree establishment in old-field succession: seedling emergence. *Ecology* **72**:1066-1075.
- . 1991b. Experiments on mechanisms of tree establishment in old-field succession: seedling survival and growth. *Ecology* **72**:1076-1088.
- Fahey, T. J., and D. R. Young. 1984. Soil and xylem water potential and soil water content in contrasting *Pinus contorta* ecosystems, southeastern Wyoming, USA. *Oecologia* **61**:346-351.
- Firbank, L. G., and A. R. Watkinson. 1990. On effects of competition: from monocultures to mixtures. Pages 165-192 in J. B. Grace and D. Tilman, editors. *Perspectives on plant competition*. Academic Press, New York, New York, USA.
- Gill, D. S., and P. L. Marks. 1991. Tree and shrub seedling colonization of old-fields in central New York. *Ecological Monographs* **61**:183-206.
- Goldberg, D. E. 1987. Neighborhood competition in an old-field plant community. *Ecology* **68**:1211-1223.
- . 1990. Components of resource competition in plant communities. Pages 27-49 in J. B. Grace and D. Tilman, editors. *Perspectives in plant competition*. Academic Press, New York, New York, USA.
- Goldberg, D. E., and A. M. Barton. 1992. Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. *American Naturalist* **139**:771-801.
- Goldberg, D. E., and L. Fleetwood. 1987. Competitive effect and response in four annual plants. *Journal of Ecology* **75**:1131-1143.
- Goldberg, D. E., and S. M. Scheiner. 1993. ANOVA and ANCOVA: Field competition experiments. Pages 69-93 in S. M. Scheiner and J. Gurevitch, editors. *Design and analysis of ecological experiments*. Chapman and Hall, New York, New York, USA.
- Goldberg, D. E., and P. A. Werner. 1983. Equivalence of competitors in plant communities: a null hypothesis and a field experimental approach. *American Journal of Botany* **70**:1098-1104.
- Gordon, D. R., and K. J. Rice. 1993. Competitive effects of grassland annuals on soil water and blue oak (*Quercus douglasii*) seedlings. *Ecology* **74**:68-82.
- Kuppers, M. 1985. Carbon relations and competition between woody species in a Central European hedgerow. IV. Growth form and partitioning. *Oecologia* **66**:343-352.
- Linder, S. M., L. Benson, B. J. Meyers, and R. J. Raison. 1987. Canopy dynamics and growth of *Pinus radiata*. I. Effects of irrigation and fertilization during a drought. *Canadian Journal of Forest Research* **17**:1157-1165.
- Littell, R. C., R. J. Freund, and P. C. Spector. 1991. SAS system for linear models. SAS Institute Incorporated, Cary, North Carolina, USA.
- McConnaughay, K. D. M., and F. A. Bazzaz. 1991. Is physical space a soil resource? *Ecology* **73**:94-103.
- Miller, J. H., et al. 1987. A region-wide study of loblolly pine seedling growth relative to four competition levels after two growing seasons. Pages 581-591 in D. R. Phillips,

- editor. Proceedings of the Fourth Biennial Southern Silviculture Research Conference, November 4–6, 1986, Atlanta, Georgia. USDA Forest Service General Technical Report **SE-42**.
- Miller, J. H., B. R. Zutter, S. M. Zedaker, M. B. Edwards, J. D. Haywood, and R. A. Newbold. 1991. A regional study on the influence of woody and herbaceous competition on early pine growth. *Southern Journal of Applied Forestry* **9**:11–15.
- Miller, J. H., B. R. Zutter, S. M. Zedaker, M. B. Edwards, J. D. Haywood, and R. A. Newbold. 1995. Early plant succession in *Pinus* plantations as affected by vegetation management. *Southern Journal of Applied Forestry* **19**:1–18.
- Miller, T. E. and P. A. Werner. 1987. Competitive effects and responses between plant species in a first-year old-field community. *Ecology* **68**:1201–1210.
- Mitchell, R. J., B. R. Zutter, T. H. Green, M. A. Perry, D. H. Gjerstad, and G. R. Glover. 1993. Spatial and temporal variation in competitive effects on soil moisture and pine response. *Ecological Applications* **3**:167–174.
- Morris, L. A., S. A. Moss, and W. S. Garbett. 1993. Competitive interference between selected herbaceous and woody plants and *Pinus taeda* L. during two growing seasons following planting. *Forest Science* **39**:166–187.
- Moser, E. B., A. M. Saxton, and S. R. Pezeshki. 1990. Repeated measure analysis of variance application to tree research. *Canadian Journal of Forest Research* **20**:524–535.
- Mou, P., R. J. Mitchell, and R. H. Jones. 1993. Ecological field theory model—a mechanistic approach to simulate plant–plant interactions in southeastern forest ecosystems. *Canadian Journal of Forestry* **23**:2180–2193.
- Myers, B. J. 1988. Water stress integral—a link between short-term stress and long-term growth. *Tree Physiology* **4**:315–323.
- Myers, B. J., and J. J. Landsberg. 1989. Water stress and seedling growth of two eucalyptus species from contrasting habitats. *Tree Physiology* **5**:207–218.
- Nambiar, E. K. S., and P. G. Zed. 1980. Influence of weeds on the water potential, nutrient content and growth of young radiata pine. *Australian Journal of Forest Research* **10**:279–288.
- Perry, M. A., R. J. Mitchell, B. R. Zutter, G. R. Glover, and D. H. Gjerstad. 1993. Competitive responses of loblolly pine to gradients in loblolly, sweetgum and broomsedge densities. *Canadian Journal of Forestry Research* **23**:2049–2058.
- Perry, M. A., R. J. Mitchell, B. R. Zutter, G. R. Glover, and D. H. Gjerstad. 1994. Seasonal variation in competitive effect on water stress and pine responses. *Canadian Journal of Forestry Research* **24**:1440–1449.
- Pickett, S. T. A., and F. A. Bazzaz. 1976. Divergence of two co-occurring successional annuals on a soil moisture gradient. *Ecology* **57**:169–176.
- Rastetter, E. B., and G. R. Shaver. 1992. A model of multiple element limitation for acclimating vegetation. *Ecology* **73**:1157–1174.
- Richards, J. H., and M. M. Caldwell. 1987. Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. *Oecologia* **73**:486–489.
- SAS Institute. 1989. SAS/STAT user's guide, version 6. Fourth edition, volume 2. SAS Institute Incorporated, Cary, North Carolina, USA.
- Scholander, P. F., H. T. Hammel, E. D. Bradstreet, and E. A. Hemmingsen. 1965. Sap pressure in vascular plants. *Science* **148**:339–346.
- Schultze, E.-D., A. E. Hall, O. L. Lange, M. Evenari, L. Kappen, and U. Buschbom. 1980a. Long-term effects of drought on wild and cultivated plants in the Negev desert. I. Maximum rates of photosynthesis and daily carbon gain. *Oecologia* **45**:11–18.
- Schultze, E.-D., O. L. Lange, M. Evenari, L. Kappen, and U. Buschbom. 1980b. Long-term effects of drought on wild and cultivated plants in the Negev desert. I. Diurnal patterns of photosynthesis and daily carbon gain. *Oecologia* **45**:19–25.
- Shainsky, L. J., and S. R. Radosevich. 1992. Mechanisms of competition between Douglas-fir and red alder seedlings. *Ecology* **73**:30–45.
- Shipley, B., and P. A. Keddy. 1994. Evaluating the evidence for competitive hierarchies in plant communities. *Oikos* **69**:340–345.
- Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey, USA.
- . 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, New Jersey, USA.
- Topp, G. C., J. L. Davis, and A. P. Annan. 1980. Electromagnetic determination of soil water content: measurement in coaxial transmission lines. *Water Resource Research* **16**:579–582.
- Tremmel, D. C., and F. A. Bazzaz. 1993. How neighbor canopy architecture affects target plant performance. *Ecology* **74**:2114–2124.
- Vitousek, P. M., and P. A. Matson. 1985. Disturbance, nitrogen availability, and nitrogen losses in an intensively managed loblolly pine plantation. *Ecology* **66**:1360–1376.
- Weiner, J. 1986. How competition for light and nutrients affects size variability in *Ipomoea tricolor* populations. *Ecology* **67**:1425–1427.
- . 1990. Asymmetric competition in plant populations. *Trends in Ecology and Evolution* **5**:360–364.
- Wilson, S. E., and D. Tilman. 1995. Competitive responses of eight old-field plant species in four environments. *Ecology* **76**:1169–1180.
- Wood, C. W., R. J. Mitchell, B. R. Zutter, and C. L. Lin. 1992. Loblolly pine plant community effects on soil carbon and nitrogen. *Soil Science* **154**:410–419.