Response of loblolly pine and sweetgum to intra- and inter-specific competition and influence of soil organic matter[1]

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Abstract: Loblolly pine (*Pinus taeda* L.) seedlings and sweetgum (*Liquidambar styraciflua* L.) sprouts were grown together for three growing seasons in a factorial combination of densities (additive series) on a formerly cultivated field that varied in organic matter (OM) in the upper 15 cm of the soil. Mean aboveground biomass per plant of each species at the end of each growing season was examined using a nonlinear yield–density model, incorporating soil OM as an index of soil productivity. In all years, competitive effects of sweetgum on itself and on loblolly pine were more than three times greater than effects of loblolly pine. However, the competitive effects of sweetgum relative to loblolly pine on response of both species decreased with time. Effects of density of one species declined with the increasing density of the other species. The effect of soil OM on biomass was positive for both species, being greater for sweetgum than for loblolly pine. The proportion of total variation in response explained by soil OM, after considering effects of plant density, decreased with age, becoming nonsignificant for loblolly pine by age 3. The magnitude of increases in mean plant biomass with increasing soil OM was density dependent, being greater at low plant densities.

Résumé : On a fait pousser ensemble des semis du pin à encens (*Pinus taeda* L.) et des rejets du liquidambar d'Amérique (*Liquidambar styraciflua* L.) durant trois saisons de croissance dans une combinaison factorielle de différentes densités (séries additives), dans un champ autrefois cultivé où la teneur en matière organique (MO) des 15 cm supérieurs du sol était variable. La biomasse épigée moyenne par plantule de chaque espèce, à la fin de chaque saison de croissance, était examinée à l'aide d'un modèle non linéaire de rendement en fonction de la densité, qui incorporait la MO du sol comme indice de productivité du sol. Au cours de toutes les années, les effets de compétition du liquidambar sur lui-même et sur le pin à encens étaient plus de trois fois plus grands que ceux du pin. Toutefois, les effets de compétition du liquidambar relatifs au pin, en réponse aux deux espèces, ont diminué avec le temps. Les effets de la densité d'une espèce diminuaient avec l'augmentation de la densité de l'autre espèce. L'effet de la MO du sol sur la biomasse était positif chez les deux espèces; il était cependant plus grand dans le cas du liquidambar que dans celui du pin. Après avoir considéré les effets de la densité des plantules, la proportion du total de la variation de la réponse attribuable à la MO du sol a décru avec l'âge, pour devenir non significative chez le pin à encens la troisième année. L'ampleur de l'augmentation de la moyenne de la phytomasse avec l'augmentation de la MO du sol dépendait de la densité; elle était plus grande lorsque la densité des plantules était faible.
[Traduit par la Rédaction]

Introduction

Plant density can have a great effect on the size of individual plants within a population as well as on total plant yield (Shinozaki and Kira 1956; Harper 1977; Watkinson 1980, 1981). Effects of increasing density in pure stands of trees have been observed to result in plant size decreasing in a negative hyperbolic fashion (Smith and DeBell 1974; Bormann and Gordon 1984; Shainsky and Radosevich 1991). Responses of mean tree size to increasing levels of interspecific competitors have also been noted to follow a negative hyperbolic pattern (Farmer et al. 1988; Shainsky and Radosevich 1991; Perry et al. 1993). Drew and Flewelling (1977), Shainsky and Radosevich (1991), and Zutter et al. (1998) provided reviews of mathematical models, commonly referred to as yield–density models, used to describe the effects of density on mean plant size in both monoculture and mixture.

Plant growth may be strongly influenced by a number of factors other than plant density. Light (Suehiro et al. 1985), soil nutrient levels (Hall 1974; Berendse 1982; Groninger et al. 1995), water (Suehiro et al. 1985; Groninger et al. 1995), salinity (Suehiro and Ogawa 1980), soil type (Firbank et al. 1990), plant spatial arrangement (Fowler 1984), and germination date (Fowler 1984; Cousens et al. 1987) can also have important effects, often interacting with plant density. Understanding the effects of these factors, in addition to the effects of density, is important to the development of predictive models of crop yield (Firbank et al. 1990) as well as to our understanding of dynamics of natural populations and ability to predict outcomes of competition in natural populations of plants (Tilman 1988).

Until recently, controlled experiments examining the interaction of two species of woody plants have been limited. Fredricksen et al. (1993*a*, 1993*b*), Jifon et al. (1995), and Groninger et al. (1995, 1996) examined the interaction of loblolly pine

Received May 8, 1997. Accepted October 9, 1997.

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(*Pinus taeda* L.) and sweetgum (*Liquidambar styraciflua* L.), red maple (*Acer rubrum* L.), or black locust (*Robinia pseudoacacia* L.) grown in both monocultures and mixtures at a constant total density. Cole and Newton (1986) quantified the interaction among Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and red alder (*Alnus rubra* Bong.) grown in monoculture and in 50:50 mixtures across a range of total plant density on several sites. Farmer et al. (1988) quantified the effects of competition among juvenile jack pine (*Pinus banksiana* Lamb.) and quaking aspen (*Populus tremuloides* Michx.) at different total densities and species proportions. Shainsky and Radosevich (1991, 1992) manipulated both total density and proportion of species in mixture by including a range of densities of Douglas-fir and red alder in a complete factorial design.

Utilizing an experimental approach similar to that of Shainsky and Radosevich (1991) with species from the southern United States would greatly enhance the understanding of the effects of density and species composition on early growth of tree species within the region. Mitchell et al. (1993) established an experiment of this kind using three species: loblolly pine, an evergreen conifer; sweetgum, a deciduous broadleaf tree; and broomsedge (*Andropogon virginicus* L.), a C4 grass, grown at a number of levels of total density in monoculture and multiple proportions in mixture. These species were selected because they are common associates during early secondary succession on artificially regenerated upland sites in the southeastern United States (Miller et al. 1987). This study examines the effect of two factors, plant density and soil organic matter (OM) (as a surrogate for soil nutrient level), on the mean plant size of loblolly pine and sweetgum in monoculture and mixture using data collected over a 3-year period from the study established by Mitchell et al. (1993). Specific objectives include (1) determining the relative effect of each species on itself and its interspecific competitor, (2) the importance of OM in influencing mean plant size, and (3) the impact of time on ranking of species effects and importance of OM. Fitting of yield–density models to the data and examining model parameters, generated response surfaces, and fit statistics will be used as the approach to satisfy the objectives.

Methods

Study area

The study utilized an area of approximately 2 ha located at Auburn University's E.V. Smith Research Center near Shorter, Ala., approximately 45 km southwest of the Auburn University campus. Prior to study establishment, the area had been in row crop production for more than 20 years, with the last crop, soybeans, being harvested in 1987. After laying fallow during 1988, the study area was chisel-plowed in early October 1988 to break up any plowpan created as a result of repeated tillage. To minimize the influence of other plant species, the entire area was sprayed with glyphosate (4.4 kg active ingredient·ha^{-1}) in early September, disked in mid-October, and then fumigated with 98% methyl bromide and 2% chloropicrin. The soils are of the Compass series (coarse–loamy, silicaceous, thermic Plinthic Paleudults) consisting of a 25- to 30-cm loamy sand surface layer overlying a sandy loam from about 30 to 80 cm and then a sandy clay loam layer to approximately 140 cm.

Experimental design and plot layout

The study was established as a complete factorial of loblolly pine and sweetgum each at densities of 0, 1, 2, and 4 plants/m^2. This additive series design (Cousens 1991) provides an array of total density, and species density and proportion (Firbank and Watkinson 1990), and data suitable for description of a response surface (Cousens 1991). Each combination of species and density occurred once per block in a randomized complete block design with four blocks.

Plots were approximately 490 × 898 cm. Plant layout and location was accomplished by first dividing the plot into 44 subplots measuring approximately 81.6 × 122.5 cm (an area of 1 m^2). Within each subplot, there were 24 potential plant locations, four rows of six locations each, with each location being 20.4 cm from an adjacent location within the subplot or an adjacent subplot. Within each subplot the locations of the appropriate number of plants of each species were randomly assigned and marked in the field with 15-cm plastic pot markers. This approach was utilized to overcome potential problems associated with systematic layout of plants in mixtures.

Plant establishment, measurement, and harvest

Bare-root 1-0 sweetgum seedlings grown from a seed source in the Upper Coastal Plain of Alabama were hand-planted in December 1988. Seedlings were part of a crop grown using typical nursery practices by a private forest industry nursery for internal use by the company (Union Camp Corporation, Franklin, Va.). During 1989, seedlings were allowed to grow and a minimal amount of hand-weeding was utilized to keep weed-free conditions for the developing sweetgum. In December 1989, sweetgum seedlings were cut at approximately 5 cm above the groundline and the tops were removed from the site. At the time of cutting, sweetgum survival exceeded 99% across the study site. Bare-root 1-0 loblolly pine seedlings were hand-planted in February 1990. Pine seedlings were grown by a local forest industry nursery (Union Camp Corporation, Union Springs, Ala.) using half-sib seed from an improved Upper Coastal Plain parent. Pine seedlings and sweetgum sprouts were allowed to grow during the 1990–1992 growing seasons.

Within each treatment plot, three 4-m^2 interior areas were designated for nondestructive measurements and (or) sequential destructive harvest of plants at the end of each growing season. Following planting of loblolly pine, one plant of each species was randomly selected from each 1-m^2 subplot within two of the 4-m^2 measurement/harvest plots. Selected attributes were measured on these eight plants of each species within each treatment plot. Total height was measured on both loblolly pine and sweetgum. Two basal diameters (perpendicular to each other) were recorded on each loblolly pine and two crown diameters (perpendicular to each other) on each sweetgum.

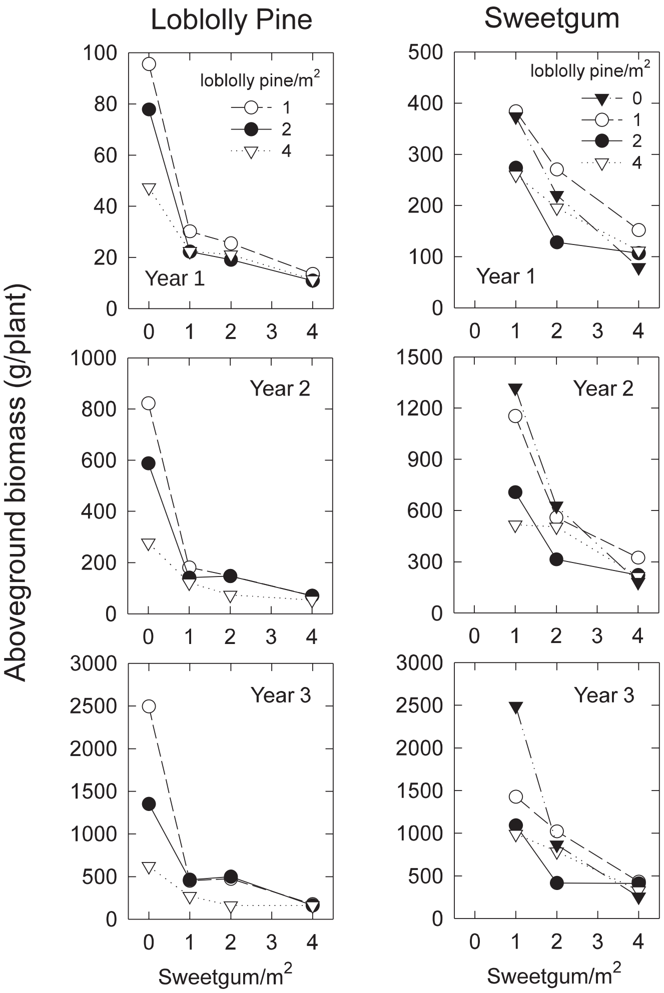
Aboveground biomass was determined for three plants of each species from the appropriate measurement/harvest plots within each treatment plot in late August to early September of each year ($n = 12$ plants per treatment, three plants per treatment plot × four treatment plots per treatment). After harvest, plants were dried at 60°C to a constant weight. Total height (both species), groundline diameters (loblolly pine), and crown diameters (sweetgum) of biomass sample plants were recorded to develop equations to estimate biomass of unharvested plants. Mean plant biomass was determined from estimates of individual plant biomass. Mean estimated values were used in the analysis.

Soil samples were collected at the end of the 1989 growing season from soil depths of 0–15 and 15–30 cm using a 2 cm diameter push tube soil probe. One sample was taken from the center of each subplot in the upper nondestructive plant measurement area and the samples from each soil depth combined to form a composite sample. The composite soil samples from each plot were analyzed for OM content using the loss on ignition method by the Auburn University Soil Testing Laboratory.

Data analysis

A nonlinear yield–density model to describe effects of density on mean plant size in a two-species mixture was introduced by Watkinson (1981) and presented by Firbank and Watkinson (1985) as

Fig. 1. Mean aboveground biomass per plant of loblolly pine and sweetgum by initial density levels of each species for years 1–3.



$$[1]\qquad w_1 = w_{m1}[1 + a_1(N_1 + \alpha N_2)]^{b_1}$$

$$w_2 = w_{m2}[1 + a_2(N_2 + \beta N_1)]^{b_2}$$

where subscripts 1 and 2 denote species 1 and 2, respectively, w_{m1} and w_{m2} are coefficients that provide an estimate of the mean mass of isolated plants, N_1 and N_2 are species densities, a_1 and a_2 are the coefficients representing the area required by the isolated plant to grow to its size, α and β are coefficients describing the degree of competitive equivalence between species, and b_1 and b_2 are coefficients giving an indication of resource use efficiency as density increases (Watkinson 1981).

For this study, the model of Firbank and Watkinson (1985) given in eq. 1, with $b = 1$, was chosen as the base model and rewritten as follows:

$$[2]\qquad w = \frac{a}{1 + cL + eS}$$

where w is the mean plant mass (grams), a is a parameter representing an estimate of the mass of an isolated plant, and c and e are parameters describing the effects of the densities of loblolly pine (L) and sweetgum (S). A comparison of the values of the parameters c and e provides a measure of relative competitive effects of the species. Attempts to fit the model of Watkinson (1981) where b was allowed to vary were not successful, possibly due to correlation among the b, and c, and e parameters noted as a potential problem by Cousens (1991).

Previous work by Zutter et al. (1998) showed that the effects of soil OM in monocultures might be incorporated by replacing a with $a + b$OM in the numerator. Incorporating this effect of soil OM into model 2, one obtains

$$[3]\qquad w = \frac{a + b\,\mathrm{OM}}{1 + cL + eS}$$

where variables are defined as in eq. 2. In this model, an estimate of the mass of an isolated plant is given by the numerator as in eq. 2, but the mass is dependent on the level of soil OM. Fitting of this model to the data allows relative effects of soil OM and density (level of competition) to be examined. Equations 2 and 3 were fitted to data from each species and year using the nonlinear regression procedure (NLIN) of the Statistical Analysis System (SAS Institute Inc. 1989). A fit index (FI), analogous to R^2 in linear models, was calculated for each nonlinear model as FI = 1 – (residual sum of squares)/(corrected total sum of squares).

Results

In general, sweetgum sprouts had a larger mean biomass than planted loblolly pine across the density combinations throughout the course of the study (Fig. 1). An exception to the general trend occurred by the end of the third growing season when mean biomass of each species grown in monoculture was approximately equal. Values for the a parameter from eq. 2, which reflects the size of an isolated plant, are larger for sweetgum compared with loblolly pine in years 1 and 2 and approximately equal by year 3 (Table 1), a trend consistent with the visual observations of the relative sizes of sweetgum and loblolly pine at the lowest density in monoculture, 1 plant/m² (Fig. 1). Scatter plots revealed densities of each species and soil OM to be important in influencing mean plant response of both loblolly pine (Fig. 2) and sweetgum (Fig. 3) in most years.

Equation 2, considering only species density, accounted for 84–93 and 55–78% of the variation in biomass of loblolly pine and sweetgum, respectively, with the percentage of variation explained increasing over time (Table 1). With the exception of year 3 for loblolly pine, inclusion of soil OM was significant ($p = 0.05$) and increased the percentage of variation in mean biomass explained by the equation for each species and year. The magnitude of the increases was greater for sweetgum than for loblolly pine and decreased for both species over time. Increases in the explained variation, in terms of FI, from the inclusion of soil OM were 0.151, 0.109, and 0.073 for sweetgum and 0.043, 0.006, and 0.002 for loblolly pine in years 1–3, respectively. The total variability in biomass explained by eq. 3, which included soil OM as well as species density, increased from 89 to 93% for loblolly pine and from 70 to 85% for sweetgum from years 1–3. The increase in biomass and the increasing effect of density of both species over time are illustrated in Fig. 4.

Effects of soil OM on growth were positive (or absent as in year 3 for loblolly pine), with the magnitude of effects generally increasing over time. Effects were greater in absolute magnitude for sweetgum compared with loblolly pine for the same year based on the sign and magnitude of values of the b parameter in eq. 3 (Table 1). Response surfaces for biomass of loblolly pine and sweetgum generated using eq. 3 (eq. 2 for loblolly pine in year 3, as soil OM was nonsignificant) at soil

Table 1. Estimated parameter values, standard errors (in parentheses), mean square error (MSE), and fit index (FI) for models 2 and 3 fitted to aboveground biomass for loblolly pine and sweetgum ($n = 48$ for each species).

			Parameter*					
Species	Year	Model	*a*	*b*	*c*	*e*	MSE	FI
Loblolly pine	1	2	138.63 (20.77)	—	0.4404 (0.1553)	2.9987 (0.6156)	130.1	0.842
		3	61.61 (17.24)	68.43 (16.42)	0.3362 (0.1019)	2.7465 (0.4424)	93.3	0.885
	2	2	1 832.5 (384.4)	—	1.1949 (0.4030)	1.3195 (1.7774)	4 813	0.919
		3	1 277.0 (341.9)	392.02 (205.02)	0.9961 (0.3157)	6.7119 (1.4705)	4 574	0.925
	3	2	14 501 (12 164)	—	5.0189 (4.9048)	23.005 (19.490)	35 421	0.926
		3	25 087 (35 021)	–3 596 (6876)	7.9049 (11.7877)	34.137 (45.940)	35 182	0.928
Sweetgum	1	2	762.21 (234.33)	—	0.1902 (0.1334)	1.2136 (0.5937)	6 720	0.553
		3	247.59 (94.88)	322.12 (78.97)	0.0338 (0.0165)	0.8261 (0.3005)	4 454	0.704
	2	2	4 049.2 (1965.1)	—	0.8437 (0.5080)	2.6615 (1.2277)	64 995	0.634
		3	681.83 (423.98)	1 383.1 (355.0)	0.2063 (0.1387)	1.1930 (0.5015)	46 784	0.743
	3	2	14 872 (10 965)	—	2.4251 (1.7682)	7.0973 (6.0693)	101 233	0.777
		3	2 238.4 (1092.0)	3 006.9 (772.7)	0.5776 (0.2326)	2.2381 (0.8698)	69 423	0.850

Note: Models 2 and 3 are as shown in the text.

*All parameters significant ($p = 0.05$) in years 1 and 2, except parameter *c* ($p < 0.10$) for sweetgum. No parameter significant ($p > 0.10$) in year 3 for loblolly pine. For sweetgum in year 3, all parameters significant ($p = 0.05$) for model 3 and none significant ($p > 0.10$) for model 2.

OM values of 1.5 and 0.5% illustrate effects of soil OM (Figs. 5A, 5B, 5D–5E, and 6A–6F). Higher soil OM resulted in greater mean per-plant aboveground biomass for any given density, with the magnitude of gains decreasing with increasing density of either or both species and the effect of soil OM increasing over time (Figs. 5F, 5G, and 6G–6I). The increase in biomass due to increases in soil OM may be expressed on a relative basis with respect to the biomass at the higher soil OM (i.e., values in Fig. 5F divided by corresponding values in Fig. 5A). Expressing the gain this way yields a constant value across all combinations of species densities within a given year. Relative increases in biomass of sweetgum attributed to soil OM were constant over time: 0.44, 0.50, and 0.45 for years 1–3, respectively. Relative increases in biomass of loblolly pine attributed to soil OM appear to be declining over time: 0.42 at year 1, comparable with that for sweetgum, and 0.21 at year 2 (and zero in year 3 if one considers the lack of a significant effect of soil OM).

Parameters *c* and *e*, describing the effects of density of loblolly pine and sweetgum, respectively, increased with age, a trend previously noted for parameters *a* and *b*. Effects of sweetgum density relative to that of loblolly pine density, as represented by the ratio of parameter *e* to parameter *c*, were greater on both itself and loblolly pine. In other words, intraspecific effects of sweetgum were greater (or more intense, sensu Weldon and Slauson 1986) than effects of interspecific competition with loblolly pine, and interspecific effects of sweetgum were greater on loblolly pine than intraspecific effects of other loblolly pine. The relative effects of sweetgum decreased with time as expressed by the ratios of parameter *e* to parameter *c* for eq. 3 (Table 1). Ratios were 8.2, 6.7, and 4.3 for loblolly pine response and 24.4, 5.8, and 3.9 for sweetgum response for years 1–3. The decreasing relative effects of sweetgum over time can also be thought of in terms of increasing relative effects of loblolly pine. Biomass response surfaces presented in Figs. 5A–5C and 6A–6C illustrate this increasing effect of loblolly pine relative to sweetgum over time. This is most easily seen by comparing the trends in the surfaces along the back vertical planes of the graphs: effects of loblolly pine along the left vertical plane and sweetgum along the right vertical plane. However, effects per plant are still smaller for loblolly pine than for sweetgum through year 3. Effects of density of either species were not independent. The effect of one species on the other was reduced as the density of the other species increased (Figs. 4–6).

Discussion

This study illustrates the response of both young loblolly pine and sweetgum grown in monoculture and mixed high-density stands to be dependent on plant density and soil OM. Levels of soil OM encountered in this study on a formerly row-cropped field were low, 0.95%, compared with a mean of 2.5% (range 1.0–3.6%) noted across 13 upland forested sites in the southeast by Miller et al. (1995).

Sweetgum and loblolly pine are capable of growth on a wide variety of soils and sites; however, productivity does depend on conditions of the site (Martindale 1958; Wahlenberg 1960). Sweetgum and loblolly pine grow best on rich, moist, alluvial clay and loam soils rather than lighter textured soils (Wenger 1952; Martindale 1958). Growth of sweetgum on surface soil with high OM was greater compared with subsurface soil with low OM (Davis et al. 1983). The positive response of each species to increasing soil OM may be related to increased availability of nitrogen due to mineralization. Growth of both sweetgum and loblolly pine during the first growing season was positively correlated with leaf nitrogen concentration (Mitchell et al. 1995). Leaf nitrogen concentration was positively correlated with soil OM content, being greater for sweetgum ($r = 0.672$, $p < 0.001$) than for loblolly pine ($r = 0.425$, $p = 0.001$). The higher correlation of leaf nitrogen concentration and soil OM for sweetgum and the greater effect of soil OM on sweetgum growth suggest that sweetgum is more site demanding than loblolly pine.

The decline in importance of soil OM over time in quantifying plant response may reflect an increased importance of resources such as light or water compared with soil nutrient availability. By year 3, the effect of soil OM on response of loblolly pine appears to have disappeared in the monoculture (Fig. 2). The strong response of sweetgum to increased soil

Fig. 2. Mean aboveground biomass per plant of loblolly pine by surviving plant density of loblolly pine and sweetgum and soil OM level class for years 1–3 (points represent plot means). Soil OM class levels selected to divide the data into three approximately equal parts.

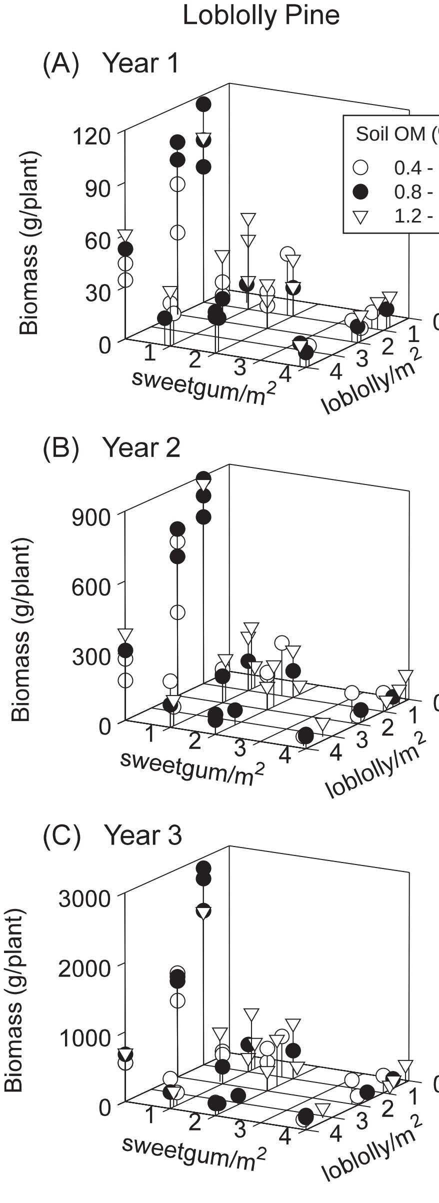
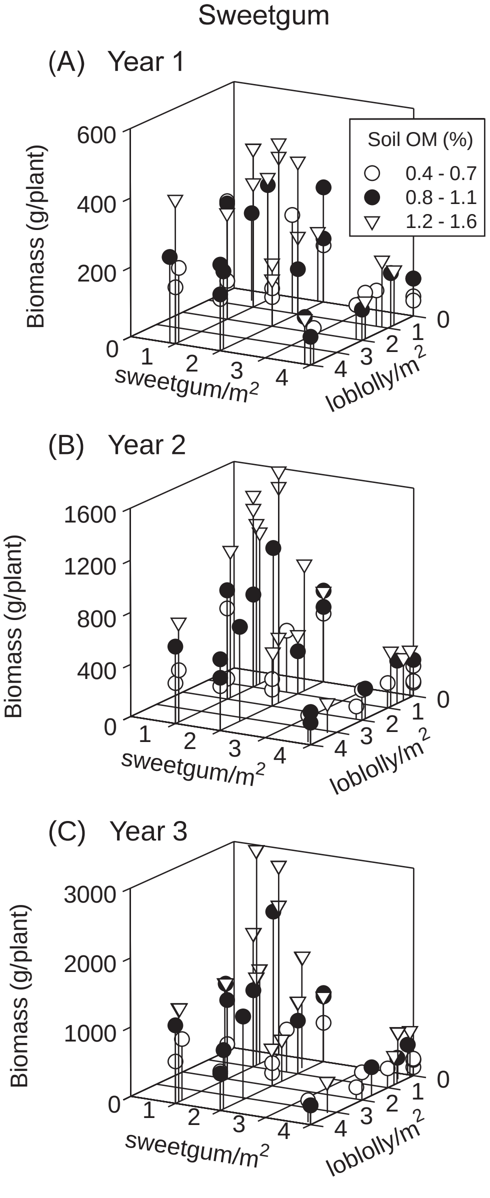


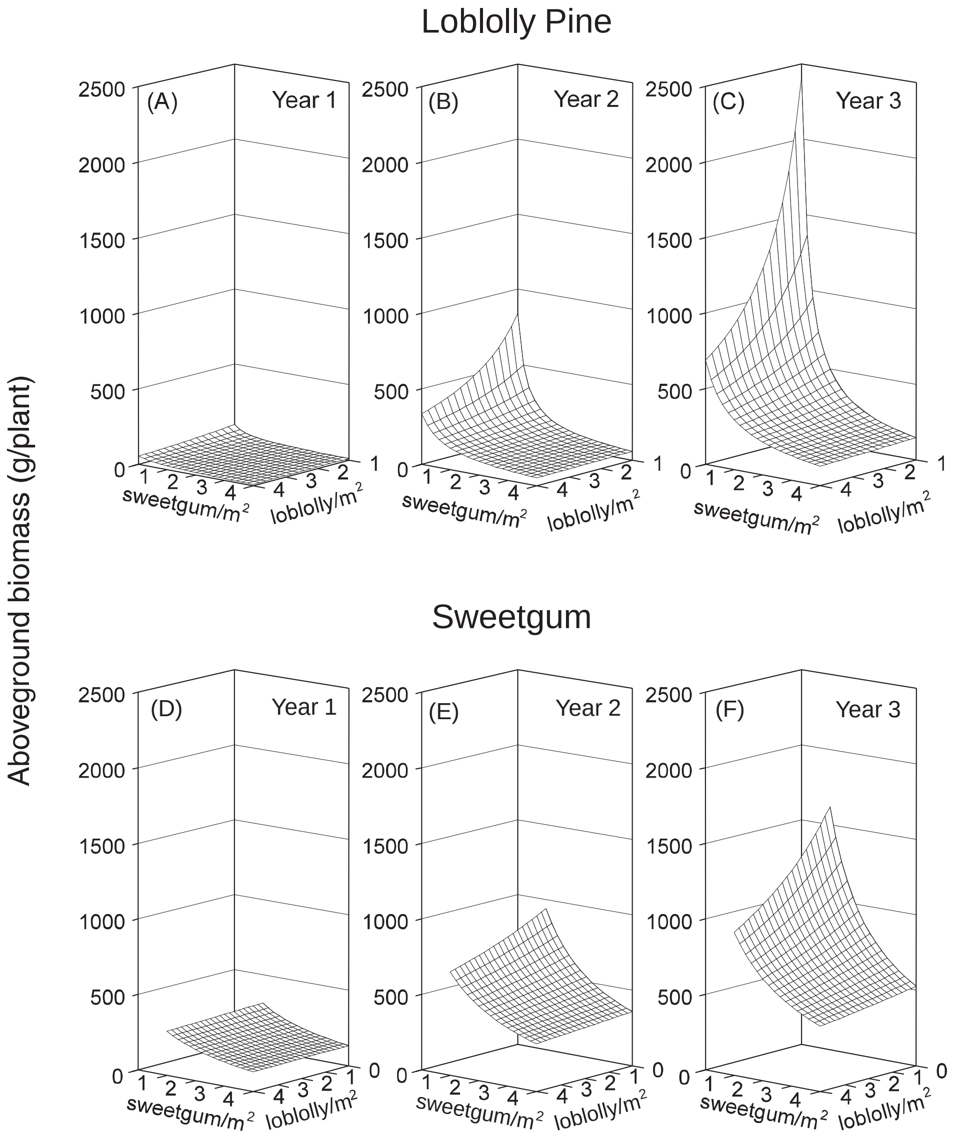
Fig. 3. Mean aboveground biomass per plant of sweetgum by surviving plant density of loblolly pine and sweetgum and soil OM level class for years 1–3 (points represent plot means). Soil OM class levels selected to divide the data into three approximately equal parts.



OM might, over time, lead to the development of an extensive canopy at high sweetgum densities and high soil OM such that light limitations would have a greater influence on the growth of loblolly pine than nutrient limitations at low levels of soil OM. Under such conditions, one might expect the relationship of loblolly pine response to soil OM to become negative. The decline and change in sign of the correlation of loblolly pine biomass and soil OM at 4 sweetgum/m^2 over time (across density levels of loblolly pine, $n = 12$) suggest that this might be the case. Values of the simple correlation coefficients were 0.824, 0.074, and –0.338 from age 1 through 3, respectively, although only the correlation at age 1 is statistically significant ($p = 0.05$).

Comparison of results of this study with those from other studies examining growth of sweetgum and loblolly illustrates the importance that early establishment and development can have on the effects of competition. In a similar study, Morris et al. (1993) observed reductions in groundline diameter of 17–28% after one and two growing seasons, respectively, whereas in this study, effects on diameters were much greater, 55–64%. Visual observations of sweetgum seedlings in mid-July of the first growing season from photographs in Morris et al. (1993) suggest that the greater reduction in the study reported here can be attributed to the larger size of sweetgum, in the form of sprouts, and thus, larger effects on resources both above and below ground. Groninger et al. (1995) noted that when sweetgum and loblolly pine were grown in pots at high-density 50:50 mixtures from simultaneously sown seed,

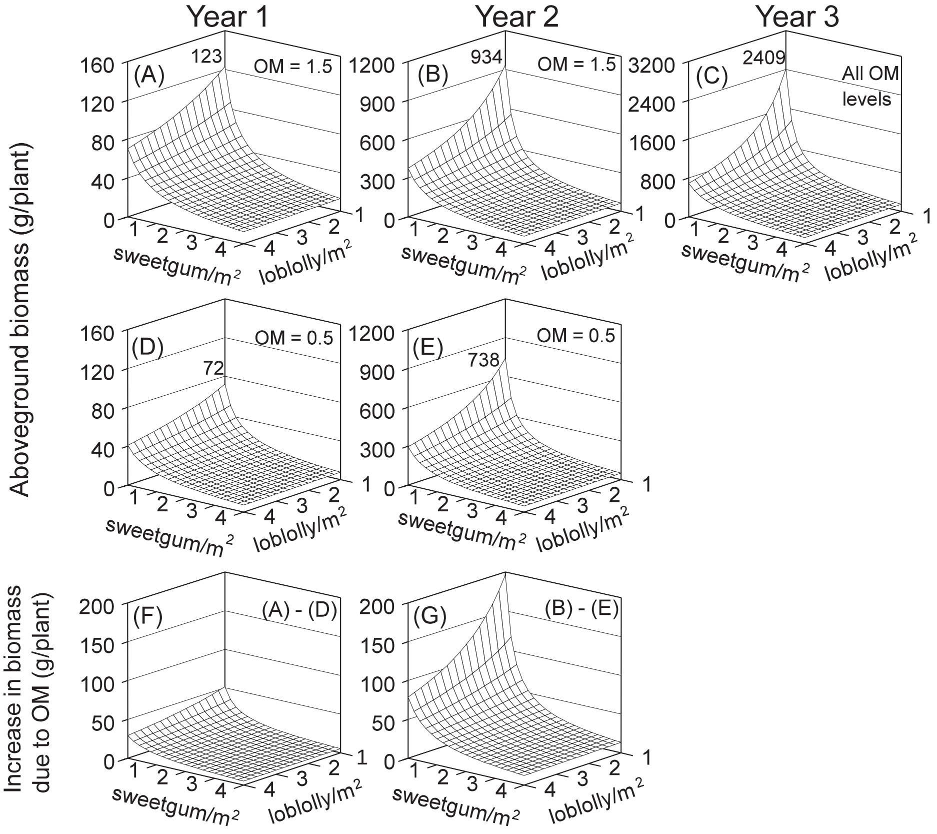
Fig. 4. Relationships between plant density and aboveground biomass of (A–C) loblolly pine and (D–F) sweetgum at a soil OM of 1.0%. Values for loblolly pine generated from model 3 in years 1 and 2 and from model 2 in year 3 using parameter values in Table 1. Values for sweetgum generated from model 3 for each year using parameter values in Table 1.



sweetgum had about twice the biomass of loblolly pine under well-watered conditions and about equal biomass under drought stress conditions. This is in contrast with observations in this study where sweetgum had approximately 13, 7, and 10 times the aboveground biomass of loblolly pine at the three 50:50 mixtures (1, 2, and 4 plants of each species/m^2) at the end of 1 year.

For competition for resources to occur, Goldberg (1990) stated that there should be (1) evidence that there is depletion of resources associated with the abundance of plants (competitive effects) and (2) a positive correlation between the abundance of resources and plant response such as survival, growth, and (or) reproductive output (competitive response). Work by Cole and Newton (1986, 1987) and Shainsky and Radosevich (1991, 1992) demonstrated that the relationship of density to the growth and development of Douglas-fir and red alder was related to quantifiable changes in resource availability which were dependent on density and species composition. During the first growing season in the present study, sweetgum density had strong negative effects on both light available to loblolly pine and soil water whereas loblolly pine did not have significant effects on light available to sweetgum or soil water (Mitchell et al. 1995). The minimal effect on resources by loblolly pine during the first growing is reflected in the smaller effects of loblolly pine density on the biomass response of both itself (Figs. 5A and 5D) and sweetgum (Figs. 6A and 6D). Limitations in light and water interacted to strongly influence loblolly pine growth and physiology (e.g., plant water potential and stomatal conductance). Since sweetgum formed the main canopy of these experimental stands, sweetgum growth and physiology appeared to be primarily limited by water and nutrients rather than by light (Mitchell et al. 1995). Photosynthesis of both sweetgum (Tolley and Strain 1985; Pezeshki and Chambers 1986; Groninger et al. 1996) and loblolly pine (Tolley

Fig. 5. Relationships between aboveground biomass of loblolly pine and species density for a soil OM content of (A and B) 1.5% and (D and E) 0.5% and (F and G) the increase in aboveground biomass of loblolly pine due to an increase from 0.5 to 1.5% soil OM for years 1 and 2. Data generated from model 3, except data in (C) year 3 generated from model 2 using parameter values in Table 1.



and Strain 1985; Groninger et al. 1996) has been shown to decrease with water stress or lower levels of soil water.

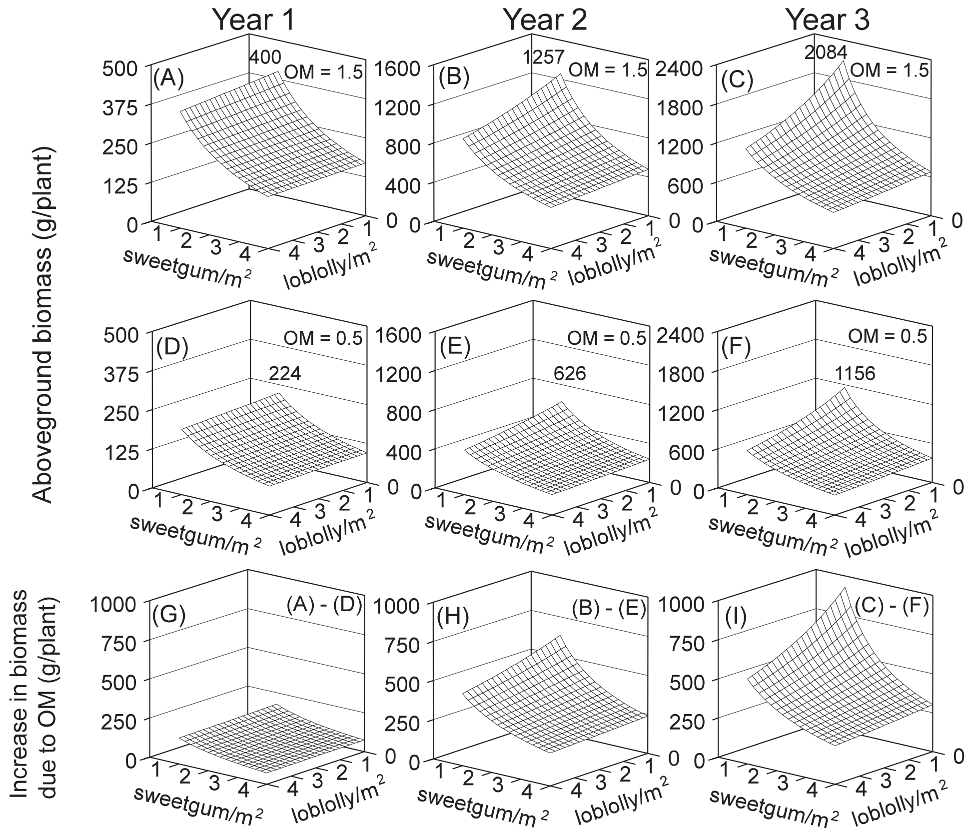
Temporal patterns of fitted model parameters in this study were as expected based on previous work with other species (Watkinson 1984; Shainsky and Radosevich 1991). Shainsky and Radosevich (1991), in their study of yield–density relationships in planted monocultures and mixtures of Douglas-fir and red alder, observed red alder to assume a dominant canopy position relative to Douglas-fir similar to that observed with sweetgum relative to loblolly pine in this study. Density effects of each species on itself and on its interspecific competitor increased with time, as noted here for sweetgum and loblolly pine. Red alder behaved somewhat similarly to sweetgum in this study by having greater effects on itself as well as on its interspecific competitor, Douglas-fir. However, relative effects of red alder compared with Douglas-fir increased over time, compared with a decreasing trend for sweetgum relative to loblolly pine in this study. They also noted the effects of density of one species to be negative and the magnitude of effects to be dependent on the density of the other species for most combinations of density and species.

Shainsky and Radosevich (1991) also observed an increasing amount of variation in size (stem volume index) to be explained by the yield–density model over time, noting that their models explained 85–90% of the variation by year 3. Increases in the amount of variation explained by the yield–density equations over time are likely due to increased interactions among plants as individual plants increase in size and resources become more limited across the range of densities.

A couple of general concepts may be deduced from this study that seem applicable to the management of sweetgum and loblolly pine in mixtures. First, effects of each species on mean plant biomass are not additive. Effects of interspecific competition are greatest at lower densities of the response plant species. And similarly, effects of intraspecific competition will be greatest in the absence of interspecific competitors. A second concept is suggested by responses observed with increases in soil OM, namely, that the magnitude of effects of competition on mean plant biomass may be greater at higher levels of productivity.

Because this study examined high-density plantings over a short period of time, specific results of this study seem more directly applicable to naturally established stands of similar density. In stands typically managed for timber production, there is a greater spatial distribution of trees (lower densities) and a longer time frame for interaction. This greater spatial distribution of plants can be a particularly important factor. This is illustrated by examining response in a nearby field study (Tallassee COMP study site, Miller et al. 1995) following clear-cutting of a mixed pine–hardwood stand, chop and burn site preparation, and planting of loblolly pine. In that study, hardwood density (75% in sweetgum) averaged 0.52 rootstock/m^2 and planted pines 0.13 stem/m^2 at year 1 where herbaceous plants were controlled (Miller et al. 1995).

Fig. 6. Relationships between aboveground biomass of sweetgum and species density for a soil OM content of (A–C) 1.5% and (D–F) 0.5% and (G–I) the increase in aboveground biomass of sweetgum due to an increase from 0.5 to 1.5% soil OM for years 1–3 as generated from model 3 using parameter values in Table 1.



The hardwood basal area at age 5 was nearly 4 $m^2 \cdot ha^{-1}$, a value that foresters would regard as a high level of hardwood on an upland site. Reductions in pine groundline diameter from hardwoods at the Tallassee COMP site compared with those in this study at the lowest density, loblolly pine and sweetgum each at $1 \cdot m^{-2}$, were lower each year during the first 3 years: 25 vs. 41% at age 1, 36 vs. 48% at age 2, and 42 vs. 51% at age 3. In addition, intraspecific effects of pine are also likely to be greater in the present study. Thus, the “trading of space for time” through the use of high-density plantings examined over a short period of time would appear to have limited value in terms of understanding development of planted pine stands if one is simply examining plant response.

Future research should consider extending the study approach used here to establish trees at wider spacings and examine dynamics over longer time-frames. Such investigations should more closely approximate spatial and temporal relationships in operational stands, making results more readily applicable to such situations.

Acknowledgments

Funds for this research were provided by the Alabama Agricultural Experiment Station, USDA/CSRS Grants Program in Forest Biology and Weed Science, and gifts from Rayonier Inc., Union Camp Corporation, and Westvaco Corporation. The authors thank Dr. Robert H. Jones and Dr. Greg L. Somers for their helpful comments on an earlier draft of the manuscript.

References

Berendse, F. 1982. Competition between plant populations with different rooting depths. II. Pot experiments. Oecologia (Heidelb.), **53**: 50–55.

Bormann, B.T., and Gordon, J.C. 1984. Stand density effects in young red alder plantations: productivity, photosynthate partitioning, and nitrogen fixation. Ecology, **65**: 394–402.

Cole, E.C., and Newton, M. 1986. Nutrient, moisture, and light relations in 5-year-old Douglas-fir plantations under variable competition. Can. J. For. Res. **16**: 727–732.

Cole, E.C., and Newton, M. 1987. Fifth-year responses of Douglas-fir to crowding and nonconiferous competition. Can. J. For. Res. **17**: 181–186.

Cousens, R. 1991. Aspects of the design and interpretation of competition (interference) experiments. Weed Technol. **5**: 664–673.

Cousens, R., Brain, P., Donovan, J.T., and O’Sullivan, P.A. 1987. The use of biologically realistic equations to describe the effects of density and relative time of emergence on crop yield. Weed Sci. **35**: 720–725.

Davis, E.A., Young, J.L., and Linderman, R.G. 1983. Soil lime level and VA-mycorrhiza effects on growth responses of sweetgum seedlings. Soil Sci. Soc. Am. J. **47**: 251–256.

Drew, T.J., and Flewelling, J.W.. 1977. Some recent Japanese theories of yield–density relationships and their application to Monterey pine plantations. For. Sci. **23**: 517–534.

Farmer, R.E., Morris, D.M., Weaver, K.B., and Garlick, K. 1988. Competition effects in juvenile jack pine and aspen as influenced by density and species ratios. J. Appl. Ecol. **25**: 1023–1032.

Firbank, L.G., and Watkinson, A.R. 1985. On the analysis of competition within two-species mixtures of plants. J. Appl. Ecol. **22**: 503–517.

Firbank, L.G., and Watkinson, A.R. 1990. On the effects of competition: from monocultures to mixtures. *In* Perspectives on plant competition. *Edited by* J.B. Grace and D. Tilman. Academic Press, Inc., San Diego, Calif. pp. 165–192.

Firbank, L.G., Cousens, R., Mortimer, A.M., and Smith, R.G.R. 1990. Effects of soil type on crop yield – weed density relationships between winter wheat and *Bromus sterilis*. J. Appl. Ecol. **27**: 308–318.

Fowler, N.L. 1984. The role of germination date, spatial arrangement, and neighbourhood effects in competitive interactions in *Linum*. J. Ecol. **72**: 307–318.

Fredricksen, T.S., Zedaker, S.M., and Seiler, J.R. 1993*a*. Interference interactions in simulated pine–hardwood seedling stands. For. Sci. **39**: 383–395.

Fredricksen, T.S., Zedaker, S.M., Smith, D.W., Seiler, J.R., and Kreh, R.E. 1993*b*. Interference interactions in experimental pine–hardwood stands. Can. J. For. Res. **23**: 2032–2043.

Goldberg, D.E. 1990. Components of resource competition in plant communities. *In* Perspectives on plant competition. *Edited by* J.B. Grace and D. Tilman. Academic Press, Inc., San Diego, Calif. pp. 27–49.

Groninger, J.W., Seiler, J.R., Zedaker, S.M., and Berrang, P.C. 1995. Effects of elevated CO_2, water stress, and nitrogen level on competitive interactions of simulated loblolly pine and sweetgum stands. Can. J. For. Res. **25**: 1077–1083.

Groninger, J.W., Seiler, J.R., Zedaker, S.M., and Berrang, P. 1996. Photosynthetic response of loblolly pine and sweetgum seedling stands to elevated carbon dioxide, water stress, and nitrogen level. Can. J. For. Res. **26**: 95–102.

Hall, R.L. 1974. Analysis of the nature of interference between plants of different species. II. Nutrient relations in a Nandi *Setaria* and greenleaf *Desmodium* association with particular reference to potassium.Aust. J. Agric. Res. **25**: 749–756.

Harper, J.L. 1977. The population biology of plants. Academic Press Limited, London, U.K.

Jifon, J.L., Friend, A.L., and Berrang, P.C. 1995. Species mixture and soil-resource availability affect the root growth response of tree seedlings to elevated atmospheric CO_2. Can. J. For. Res. **25**: 824–832.

Martindale, D.L. 1958. Silvical characteristics of sweetgum. USDA For. Serv. Stn. Pap. SE-90.

Miller, J.H., Zutter, B.R., Zedaker, S.M., Cain, M., Edwards, M.B., Xydias, G.K., Applegate, A.R., Atkins, R.L., Campbell, S., Daly, E., Hollis, C., Knowe, S.A., and Paschke, J. 1987. A regionwide study of loblolly pine seedling growth relative to four competition levels after two growing seasons. *In* Proceedings of the Fourth Biennial Southern Silvicultural Research Conference, 4–6 Nov. 1986, Atlanta, Ga. *Edited by* D.R. Phillips. USDA For. Serv. Gen. Tech. Rep. SE-42. pp. 581–591.

Miller, J.H., Zutter, B.R., Zedaker, S.M., Edwards, M.B., and Newbold, R.A. 1995.A regional framework of early growth response for loblolly pine relative to herbaceous, woody, and complete competition control: the COMProject. USDA For. Serv. Gen. Tech. Rep. SO-117.

Mitchell, R.J., Zutter, B.R., Green, T.H., Perry, M.A., Gjerstad, D.H., and Glover, G.R. 1993. Spatial and temporal variation in competitive effects on soil moisture and pine response. Ecol. Appl. **3**: 167–174.

Mitchell, R.J., Zutter, B.R., Gjerstad, D.H., and Glover, G.R. 1995. Competition among three perennial species in the southeastern United States. *In* Popular Summaries of the Second International Conference on Forest Vegetation Management, 20–24 Mar. 1995, Rotorua, New Zealand. *Edited by* R.E. Gaskin and J.A. Zabekewicz. N.Z. For. Res. Inst. Bull. 192. pp. 40–42.

Morris, L.A., Moss, S.A., and Garbett, W.S. 1993. Competitive interference between selected herbaceous and woody plants and *Pinus taeda* L. during two growing seasons following planting. For. Sci. **39**: 166–187.

Perry, M.A., Mitchell, R.J., Zutter, B.R., Glover, G.R., and Gjerstad, D.H. 1993. Competitive responses of loblolly pine to gradients in loblolly pine, sweetgum, and broomsedge densities. Can. J. For. Res. **23**: 2049–2058.

Pezeshki, S.R., and Chambers, J.L. 1986. Stomatal and photosynthetic response of drought-stressed cherrybark oak (*Quercus falcata* var. *pagodaefolia*) and sweetgum (*Liquidambar styraciflua*). Can. J. For. Res. **16**: 841–846.

SAS Institute Inc. 1989. SAS/STAT user's guide, version 6, edition 4. Vol. 2. SAS Institute Inc., Cary, N.C.

Shainsky, L.J., and Radosevich, S.R. 1991. Analysis of yield–density relationships in experimental stands of Douglas-fir and red alder seedlings. For. Sci. **37**: 574–592.

Shainsky, L.J., and Radosevich, S.R. 1992. Mechanisms of competition between Douglas-fir and red alder seedlings. Ecology, **73**: 30–45.

Shinozaki, K., and Kira, Y. 1956. Intraspecific competition among higher plants. VII. Logistic theory of the C-D effect. J. Inst. Polytech. Osaka City Univ. **D7**: 35–72.

Smith, J.H.G., and DeBell, D.S. 1974. Some effects of stand density on biomass of red alder. Can. J. For. Res. **4**: 335–340.

Suehiro, K., and Ogawa, H. 1980. Competition between two annual herbs, *Atriplex gmelini*, C. A. Mey and *Chenopodium album* L., in mixed cultures irrigated with seawater of various concentrations. Oecologia (Heidelb.), **45**: 167–177.

Suehiro, K., Ogawa, H., and Hozumi, K. 1985. Growth analysis of artificially mixed populations under different levels of a growth factor. *In* Origin and evolution of diversity in plants and plant communities. *Edited by* H. Hara. Academia Scientific Book, Tokyo. pp. 363–376.

Tilman, D. 1988. Plant strategies and the dynamics of plant communities. Princeton University Press, Princeton, N.J.

Tolley, L.C., and Strain, B.R. 1985. Effects of CO_2 enrichment and water stress on gas exchange of *Liquidambar styraciflua* and *Pinus taeda* seedlings grown under different irradiance levels. Oecologia (Heidelb.), **65**: 166–172.

Wahlenberg, W.G. 1960. Loblolly pine: its use, regeneration, protection, growth and management. School of Forestry, Duke University, Durham, N.C.

Watkinson, A.R. 1980. Density-dependence in single-species populations of plants. J. Theor. Biol. **83**: 345–357.

Watkinson, A.R. 1981. Interference in pure and mixed population of *Agrostemma githago*. J. Appl. Ecol. **18**: 967–976.

Watkinson, A.R. 1984. Yield–density relationships: the influence of resource availability on growth and self-thinning in populations of *Vulpia fasciculata*. Ann. Bot. **53**: 469–482.

Weldon, C.W., and Slauson, W.L. 1986. The intensity of competition versus its importance: an overlooked distinction and some implications. Q. Rev. Biol. **61**: 23–44.

Wenger, K.F. 1952. Effect of moisture supply and soil texture on the growth of sweetgum and pine seedlings. J. For. **50**: 862–864.

Zutter, B.R., Glover, G.R., Mitchell, R.J., and Gjerstad, D.H. 1998. Influence of plant density and soil organic matter on the first-year growth of loblolly pine and sweetgum. For. Sci. In press.