*Forest Science,* Vol. **41, No. 3.** pp. 513–530

# Evaluation of the Competitive Environment for White Pine (*Pinus strobus* L.) Seedlings Planted on Prescribed Burn Sites in the Southern Appalachians

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ABSTRACT. We evaluated the competitive environment around planted white pine (*Pinus strobus* L.) seedlings and monitored the response of seedling growth to competition from naturally regenerating herbaceous and woody species for 2 yr after prescribed burning. We evaluated the ability of distance-independent and distance-dependent competition indices to predict resource availability, determined if white pine seedlings responded to resource reduction by competitors, and identified species-specific contributions to the competitive environment through canonical correspondence analysis (CCA). Distance-independent measures of competition were not as well correlated with pine seedling growth as were distance-dependent measures. In 1991, competition was less important in 1991 than in 1992, and ordinating the species with CCA failed to improve the predictability of the competitive environment. By 1992, competition became more important, and individual species had differing effects on pine growth; we found that light was the most important resource limiting diameter growth and that the tall tree species were responsible for reduced light availability to pine seedlings. FOR. SCI. 41(3):513–530.

ADDITIONAL KEY WORDS. Competition indices, canonical correspondence analysis, disturbance, regeneration.

DISTURBANCE IS AN INTEGRAL PART OF MANY Southern Appalachian forests and defines their structure and composition. During precolonial times forest disturbances included windstorms, floods, landslides, insect and disease epidemics, and fires started by Native Americans and lightning. In particular, mixed pine/oak forest types on dry ridges (primarily composed of *Pinus rigida* Mill. and *Quercus prinus* L. in the overstory and ***Kalmia latifolia*** L. in the understory) depended on high intensity fires for their maintenance (Bar-den and Woods 1976). More recently, the selective removal of high quality trees in combination with fire protection changed the natural structure and composition of many mixed pine/oak forests. Substantial drought-related southern pine beetle (*Dendroctonus* ***frontalis*** Zimmermann) infestations contributed to further degradation of these forests (Smith 1991). The result has been a significant increase in the dominance and acreage of ***K.*** *latifolia,* which forms dense stands on upper, drier slopes and competes with woody and herbaceous vegetation.

Fire is currently prescribed as part of a silvicultural treatment to restore these

Reprinted from Forest ***Science,*** Vol. 41, No. 3, August 1995.

low-diversity, low-productivity sites. The treatment consists of: (1) chainsaw-felling all woody vegetation, (2) allowing stumps to sprout, (3) burning the sites with a high-intensity, low-severity fire, and (4) planting eastern white pine (*P. strobus* L.) at low density to provide a mixed-species stand. A major objective of the burning is to reduce competition around the planted seedlings; however, little is known about the effectiveness of this treatment.

Many studies have concentrated on the response of forest trees to competing vegetation and most conclude that the removal of competing vegetation results in increased growth and survival of conifer seedlings (e.g., Stewart et al. 1984, Ross and Walstad 1986). In the presence of competing vegetation, poor early growth can reduce the survival of planted trees or raise the cost of improving survival rates through vegetation management (Burdett 1990, Margolis and Brand 1990). For the purpose of this study, response to competition is defined as the relationship of some fitness component (such as growth) to resource availability, where resource availability depends on neighboring plants and the abiotic environment (Goldberg 1990). Thus, competition from neighboring plants can be demonstrated if the plants reduce the availability of some resource, creating an environmental change that reduces the growth of a target species (Goldberg 1990).

Recent research has concentrated on ways to assess competition under field conditions. The focus of many studies has been on a single competitor species, with a desired level of competition maintained by planting, weeding, or both (White and Elliott 1992, Morris et al. 1993). Other studies have measured the size and distance of species mixtures that compete with a target tree (e.g., Hix and Lorimer 1990, Holmes and Reed 1991, Wagner and Radosevich 1991, Biging and Dobbertin 1992). However, there have been few studies on interactions among size, distance, amount, and growth-form of competitors. These variables, especially growth-form, may be extremely important in determining the limiting resource and understanding competition effects. An example that illustrates the importance of growth-form would be a tall leafy herb, which intercepts light but has the same biomass as a short prostrate herb that does not intercept light. Natural regeneration provides multiple competitor species, sizes, and growth-forms that contribute to a complex species-environment gradient in competition levels (Goldberg and Werner 1983, Goldberg 1987).

The purpose of this study was to evaluate the competitive environment of planted white pine seedlings and to determine pine seedling growth response to competition from naturally regenerating herbaceous and woody species following a prescribed bum. Our objectives were to: (1) evaluate the ability of distance-independent and distance-dependent competition indices to determine whether competitors reduce resource availability, (2) determine whether pine seedlings respond to resource reduction by competitors, and (3) evaluate the species-specific contributions to the competitive environment.

## METHODS

### SITE DESCRIPTION

**Two** sites, approximately 5.25 ha each, were chosen from areas previously selected for prescribed burning in the Land Management Plan for the Wayah Ranger District (USDA Forest Service, National Forests in North Carolina). The two sites, Jacob Branch East and Jacob Branch West (JB sites), were within 0.4 km of each other in the Blue Ridge physiographic province of the Southern Appalachians (latitude 35°12′N, longitude 83°24′W). Jacob Branch East is on a west aspect and Jacob Branch West is on a south aspect. Midslope elevations are about 755 m. Soils are in the Cowee-Evard complex, which includes fine-loamy, mixed, mesic Typic Hapludults with only scattered rock outcrops and a clay loam layer at a depth of about 30-60 cm. The pretreatment overstory vegetation was mainly scattered ***P. rigida, Q. coccinea*** Muenchh., and Q. ***prinus.*** Basal areas ranged from 9 $m^2 ha^{-1}$ to 19 $m^2 ha^{-1}$. The shrub understory, which was dominated by ***K. latifolia,*** ranged in basal areas from 18 $m^2 ha^{-1}$ to 35 $m^2 ha^{-1}$. Vose and Swank (1993) describe pretreatment stand structure and biomass in detail.

### EXPERIMENTAL DESIGN

In the summer of 1989, five 0.05 ha plots (15 x 33 m) were established at each site for studying a variety of ecosystem processes (Swift et al. 1993), including those of interest in this competition study. Plots were located along steeply sloping (35–45% slope) midslope positions. Both sites were cut in 1990 with no merchantable products removed (Jacob Branch East completed by July 24 and Jacob Branch West completed by August 7). The sites were burned on September 18 and 19. Consumption of dry foliage, loose forest floor litter, and fine woody material was complete except along the shaded margins of the cut area (well outside of the established plots). In the upper centers of the two sites, the fire consumed or reduced most of the large woody material. Early the next spring (February and March), 2-yr-old bareroot ***P. strobus seedlings*** where planted at 5 x 5 m spacing on the burned sites.

A 2.0 $m^2$ circular subplot was established around randomly chosen ***P. strobus seedlings within*** each burned site. Fifty-three of the original 60 seedlings (6 seedlings x 5 plots x 2 sites) survived the study. One seedling per plot was randomly designated as zero-density, meaning that all vegetation within the 2.0 $m^2$ subplot was manually removed at the beginning of the study and as needed afterword.

### PLANT MEASUREMENTS

We measured diameter at ground level and height of each ***P. strobus seedling*** during planting (March 1991) and at the end of the 1991 and 1992 growing seasons. For each year we calculated diameter growth and height growth as the difference between beginning-of-year and end-of-year measurements. We used the product of stem diameter squared and stem height ($D^2H$) as a surrogate for total seedling biomass. For each year we calculated total seedling growth as the change in $D^2H$ from the beginning to the end of the year. On the circular subplots, we identified each competitor species, and we measured its distance from the target seedling, basal diameter, and height in late June-early July in 1991 and 1992. From these measurements, we estimated competitor biomass, using site and species-specific regression equations (Elliott and Clinton 1993).

### MICROENVIRONMENT MEASUREMENTS

We measured photosynthetically active radiation (PAR, 400–700 nm range) with a portable light meter (Sunfleck Ceptometer, Decagon Devices, Pullman, WA, USA). The light meter measures average PAR incident on 80 evenly spaced sensors along a narrow, 80-cm sampling bar. On mostly sunny days between 1100 and 1300 hr solar time, we recorded and averaged two PAR readings for each pine seedling, taking measurements at a 90” angle at the height of the terminal shoot. Immediately afterwards, we measured incoming solar radiation adjacent to the individual seedlings in open conditions above the plant canopy. The formula for calculating percent light available to pine seedlings was: PAR measured at the terminal of the seedling ÷ PAR measured in the open $*$ 100.

We measured soil moisture content near the monitored pines using time-domain reflectometry (1502B Metallic Time Domain Reflectometer, Tektronix, Beaver-ton, OR). A pair of 30-cm and 60-cm stainless steel rods were placed vertically at a distance of 10 cm from the base of each pine seedling. Xylem pressure potential (XPP), predawn ($XPP_{AM}$), and midday ($XPP_{PM}$, 1100-1300 hr solar time) were measured with a pressure chamber (PMS Instruments Co., Corvallis, OR, Scholander et al. 1965) on individual fascicles.

We repeated PAR, soil moisture content, and XPP measurements on the same day every month for three (1991) and five (1992) months. In September, the end of each growing season, we removed two fascicles of current needles per seedling to determine nitrogen concentration on a Per-kin-Elmer 2400 CHN Elemental Analyzer (Norwalk, CT).

### COMPETITION INDICES

We calculated both distance-dependent and distance-independent measures of competition (Martin and Ek 1984). Size-ratio competition indices are often weighted by distances of the subject tree to its competitors based on the assumption that competition increases as the distance between the subject tree to the competitor decreases (Hegyi 1974, Daniels 1976, Martin and Ek 1984, Daniels et al. 1986). Although most studies use ratios of diameters or heights, we chose $D_i$ for denominator in the ratio of our competition indices based on height or biomass. Seedling diameter has been shown to be more responsive to competition than height (e.g., Eissenstat and Mitchell 1983, Brand 1990, White and Elliott 1992) and provided as good or better models than height to predict diameter and $D^2H$ growth. The most common dimensions for calculating competition indices are diameter and height, although a few studies have substituted biomass (e.g., Doyle 1983, Thomas and Weiner 1989). The distance-dependent measures of competition within the subplots were competitor height ($CI_{height}$) and competitor biomass ($CI_{mass}$) of all plant species, and competitor height ($CI_{tree\ height}$) and competitor biomass ($CI_{tree\ mass}$) of tree species alone.

$$CI_{height} = \Sigma\ [H_j/D_i(Dist_{ij})]$$

$$CI_{mass} = \Sigma\ [Mass_j/D_i(Dist_{ij})]$$

where

$H,$ = height of competitor species (all or trees alone)

$D_i$ = diameter of subject tree

$Dist_{ij}$ = *distance* of subject tree $i$ from competitor $j$

$Mass_j$ = biomass of competitor species (all or trees alone)

The distance-independent measures of competition within the 53 subplots were either total biomass of all species or tree biomass alone. To determine how various measures of competitor abundance related to white pine seedling growth, we selected a nonlinear model ($Y = \beta_0 \exp^{(-\beta1 * Competition\ index)}$), which gave a random distribution of residuals and offered a better fit (larger approximate $r^2$) and a smaller mean square error than a linear model (PROC NLIN, SAS Institute 1987). To develop a conservative assessment of goodness-of-fit for each model we calculated approximate $r^2$ as 1 - (sums of squares residual/uncorrected total sums of squares) (Zar 1984, Chism et al. 1992). We used Pearson's product-moment correlations to relate pine seedling growth and competition indices to environmental variables (PROC CORR, SAS Institute 1987).

### CANONICAL CORRESPONDENCE ANALYSIS

We estimated the contribution of competitor species abundances to the competitive environment and to the growth of individual pine seedlings using canonical correspondence analysis (CCA; ter Braak 1986, 1988). This multivariate direct gradient analysis technique detects patterns of variation in community composition that are best explained by the environmental variables. Since weeded subplots were not a part of the CCA analysis, the sample size was 45 of the original 53 subplots. The parameters for the analysis were biomass of individual competitor species (Table 1), environmental variables (average percent light; average soil moisture; cumulative $XPP_{AM}$ and $XPP_{PM}$, calculated as $-$ CXPP; and needle nitrogen concentration), and pine seedling diameter growth.

Environmental variables were standardized to zero-mean and unit-variance before the analysis. This standardization removes arbitrariness in the units of measurement and allows comparisons of canonical coefficients without influencing other aspects of the analysis (CANOCO, ter Braak 1988).

The joint plot of species and environmental variables is a biplot (ter Braak 1983), chosen because of its ability to provide least squares approximations of weighted averages. The measure of goodness-of-fit [$100 * (\lambda_1 + \lambda_2) \div$ (sum of all eigenvalues); where $\lambda_1$ is the first eigenvalue and $\lambda_2$ is the second eigenvalue] is the percent variance of the weighted averages that the two-dimensional ordination could explain. The signs and relative magnitudes of the intraset correlations (correlations between individual environmental variables and the first two environmental axes) and the standardized canonical coefficients, formed the basis for estimating the relative importance of each environmental variable in the overall community composition. In the resulting ordination graph, plot points indicate species and arrows indicate environmental variables. The length of each arrow represents the rate of change in the weighted average as inferred from the biplot, showing how much the species distributions differ along that environmental variable. The most important environmental variables are those with the longest arrows.

For each environmental variable, the direction of the arrow reflects the eigenvalues of the axes and the intraset correlations of that environmental variable with the axes. Each arrow represents a direction or axis in the diagram, realized by visually extending the arrow in both directions. The position of each species on the environmental axis can be determined by extending a perpendicular line from the plot point to the environmental axis. The endpoints of the perpendicular line

TABLE 1.

Frequency of occurrence (of a possible 45 plots), average weight (grams/plot), average height (cm), and average density (no. of individuals/plot) of species present in competitor plots on Jacob Branch East and Jacob Branch West. Code names are used in Canonical Correspondence Analyses in Figures 1 and 2.

| | | 1991 | | | | 1992 | | | |
|---|---|---|---|---|---|---|---|---|---|
| Genus and species | Code | Freq | Weight | Height | Den | Freq | Weight | Height | Den |
| Trees | | | | | | | | | |
| *Acer rubrum* L. | ACE RUB | 6 | 21.58 | 26.0 | 6.5 | 6 | 155.18 | 59.9 | 5.3 |
| *Amelanchier arborea* (Michaux f.) | AME ARB | — | — | — | — | 4 | 0.63 | 12.1 | 1.5 |
| *Betula lenta* L. | BET LEN | 4 | 2.57 | 19.3 | 5.0 | 3 | 44.36 | 43.2 | 4.3 |
| *Carya qlabra* (Miller) Sweet | CAR GLA | 7 | 43.48 | 42.4 | 3.1 | 7 | 70.29 | 41.8 | 2.4 |
| *Castanea pumila* Miller | CAS PUM | 8 | 94.70 | 46.1 | 7.0 | 8 | 435.27 | 76.4 | 5.3 |
| *Cornus florida* L. | COR FLO | — | | — | — | 2 | 84.11 | 84.8 | 1.5 |
| *Liriodendron tulipifera* L. | LIR TUL | 1 | 0.66 | 10.0 | 1.0 | 3 | 2.09 | 19.0 | 1.0 |
| *Nyssa sylvatica* Marshall | NYS SYL | 22 | 33.65 | 40.2 | 6.1 | 20 | 76.82 | 45.6 | 5.2 |
| *Oxydendrum arboreum* (L.) DC. | OXY ARB | 3 | 111.52 | 74.7 | 9.7 | 3 | 135.38 | 84.9 | 6.0 |
| *Quercus alba* L. | QUE ALB | 1 | 53.71 | 47.8 | 6.0 | 1 | 0.31 | 8.0 | 1.0 |
| *Quercus coccinea* Muenchh. | QUE COC | 10 | 37.30 | 24.6 | 3.1 | 14 | 69.96 | 23.9 | 4.7 |
| *Quercus prinus* L. | QUE PRI | 3 | 65.65 | 75.0 | 4.3 | 4 | 294.94 | 67.2 | 5.2 |
| *Quercus stellata* Wangenh. | QUE STE | — | — | — | | 1 | 155.84 | 46.2 | 10.0 |
| *Quercus velutina* Lam. | QUE VEL | 7 | 28.45 | 28.0 | 5.3 | 2 | 158.60 | 35.6 | 7.5 |
| *Robinia pseudoacacia* L. | ROB PSE | 2 | 1.49 | 18.5 | 2.0 | 2 | 57.02 | 99.8 | 1.5 |
| *Sassafras albidum* (Nutt.) Ness | SAS ALB | 26 | 17.33 | 24.6 | 5.2 | 23 | 37.80 | 43.2 | 6.8 |
| Shrubs | | | | | | | | | |
| *Aralia spinosa* L. | ARA SPI | 4 | 2.83 | 27.0 | 1.2 | — | — | — | |
| *Ceonothus americanus* L. | CEO AME | — | — | — | — | 3 | 2.81 | 27.0 | 1.7 |
| *Ilex ambigua* var. *montana* (Michaux) Torrey | ILE AMB | 16 | 11.49 | 27.9 | 3.8 | 12 | 24.34 | 29.3 | 4.6 |
| *Kalmia latifolia* L. | KAL LAT | 25 | 126.19 | 22.7 | 1.8 | 26 | 130.39 | 29.0 | 1.7 |
| *Pyrularia pubera* Michaux | PYR PUB | 14 | 1.34 | 11.7 | 1.9 | 12 | 3.09 | 14.9 | 2.0 |
| *Rhus glabra* L. | RHU GLA | — | — | — | — | 3 | 52.20 | 57.0 | 1.3 |
| *Rubus argutus* Link. | RUB ARG | 1 | 10.60 | 10.0 | 1.0 | 3 | 30.38 | 41.0 | 3.7 |
| *Rubus occidentalis* L. | RUB OCC | 10 | 3.13 | 16.2 | 3.3 | 13 | 14.32 | 41.6 | 2.9 |
| *Vaccinium stamineum* L. | VAC STA | 5 | 14.33 | 34.5 | 7.2 | 4 | 18.60 | 38.8 | 10.0 |
| *Vaccinium vacillans* Torrey | VAC VAC | 25 | 10.54 | 15.5 | 5.8 | 29 | 25.33 | 17.2 | 7.0 |
| *Vitis* spp. | VIT SPP | 2 | 0.18 | 10.0 | 1.0 | 3 | 5.02 | 58.0 | 1.0 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Herbs | | | | | | | | | |
| *Andropogan scoparius* Michaux | AND SCO | 9 | 0.79 | 22.7 | 1.3 | 2 | 17.81 | 35.5 | 1.0 |
| Aster *divaricatus* L. | AST DIV | 1 | 20.41 | 52.0 | 1.0 | — | | | |
| *Aureolaria laevigata* (Raf.) Raf. | AUR LAE | 1 | 0.04 | 26.3 | 3.0 | 2 | 1.91 | 75.8 | 2.0 |
| *Baptisia tinctoria* (L.) R. Br. | BAP TIN | 6 | 12.76 | 32.4 | 1.7 | 5 | 265.10 | 50.2 | 4.4 |
| *Carex* spp. | CAR SPP | 13 | 3.65 | 14.2 | 2.5 | 13 | 14.27 | 23.8 | 2.6 |
| *Cassia fasciculata* Michaux | CAS FAS | | | | | 1 | 2.87 | 13.8 | 4.0 |
| *Coreopsis* major Walt. | COR MAJ | 3 | 23.82 | 66.0 | 2.7 | 3 | 62.73 | 69.7 | 8.0 |
| Desmodium *cuspidatum* Muhl ex. Wiid. | DES CUS | 3 | 4.96 | 25.7 | 1.3 | 2 | 27.88 | 31.0 | 7.0 |
| Desmodium *rotundifolia* DC. | DES ROT | 1 | 0.12 | 0.5 | 1.0 | 1 | 30.18 | 69.6 | 5.0 |
| *Epigaea repens* L. | EPI REP | 1 | 1.15 | 2.0 | 3.0 | | — | | |
| *Erigeron canadensis* L. | ERI CAN | 2 | 7.84 | 27.0 | 2.5 | 33 | 6.32 | 18.1 | 22.1 |
| *Euphorbia corollata* L. | EUP COR | 2 | 11.40 | 45.0 | 1.0 | 1 | 43.87 | 74.5 | 2.0 |
| *Froelichia floridana* (Nutt.) Moq. | FRO FLO | 12 | 52.64 | 47.0 | 1.2 | 21 | 10.83 | 7.0 | 55.5 |
| *Galax aphylla* L. | GAL APH | 3 | 0.40 | 3.7 | 1.0 | 3 | 3.48 | 7.3 | 1.3 |
| *Helianthus atrorubens* L. | HEL ATR | — | — | — | — | 2 | 780.97 | 13.5 | 2.0 |
| *Houstonia purpurea* L. | HOU PUR | 2 | 5.29 | 13.5 | 1.0 | 6 | 21.24 | 20.6 | 11.7 |
| *Hypoxis hirsuta* (L.) Cov. | HYP HIR | | | | | 1 | 0.32 | 25.0 | 1.0 |
| *Lespedeza hirta* (L.) Hornem. | LES HIR | 11 | 4.82 | 27.6 | 2.6 | 10 | 27.18 | 36.8 | 9.0 |
| *Lespedeza* intermedia (Wats.) Britt. | LES INT | — | | — | — | 5 | 1.75 | 24.4 | 2.6 |
| *Lespedeza repens* (L.) Bart. | LES REP | 13 | 1.23 | 13.4 | 2.5 | 10 | 3.93 | 21.3 | 2.8 |
| *Lilium michauxii* Poir. | LIL MIC | — | — | — | — | 1 | 0.42 | 24.0 | 1.0 |
| *Melampyrum lineare* Desr. | MEL LIN | 1 | 3.92 | 53.5 | 2.0 | | — | | |
| *Panicum commutatum* Schultes | PAN COM | 38 | 8.04 | 11.8 | 7.3 | 36 | 90.54 | 35.0 | 7.5 |
| *Panicum dichotomum* Michaux | PAN DIC | 14 | 9.24 | 14.8 | 5.1 | 4 | 23.94 | 39.1 | 2.2 |
| *Phytolacca americana* L. | PHY AME | 13 | 48.11 | 32.2 | 2.8 | 15 | 31.48 | 18.4 | 5.4 |
| *Potentilla canadensis* L. | POT CAN | 4 | 5.23 | 28.5 | 3.0 | 3 | 183.65 | 44.1 | 7.7 |
| *Prenanthes trifoliolata* (Cassini) Fernald | PRE TRI | | | | | 2 | 1.70 | 18.0 | 2.0 |
| *Pteridium aquilinum* (L.) Kuhn | PTE AGU | 7 | 18.32 | 35.3 | 11.6 | 8 | 25.16 | 38.7 | 14.0 |
| *Scleria pauciflora* Vahl. | SCL PAU | — | — | — | — | 7 | 20.43 | 23.2 | 6.6 |
| *Scleria triglomerata* Michaux | SCL TRI | 8 | 1.83 | 33.0 | 6.9 | 11 | 3.38 | 38.7 | 5.8 |
| *Smilax glauca* Walt. | SMI GLA | 33 | 4.54 | 17.3 | 4.5 | 29 | 5.65 | 29.2 | 5.6 |
| *Smilax rotundifolia* L. | SMI ROT | 1 | 14.60 | 71.5 | 2.0 | | — | | |
| *Solidago odora* Ait. | SOL ODO | 6 | 29.36 | 36.9 | 2.7 | 4 | 75.99 | 68.2 | 8.5 |
| Trillium *catesbaei* EU. | TRI CAT | | | | | 1 | 3.22 | 16.0 | 2.0 |
| *Viola palmata* L. | VIO PAL | 4 | 0.68 | 7.3 | 2.0 | 4 | 9.11 | 7.3 | 1.7 |
| *Viola* pedata L. | VIO PED | 4 | 1.61 | 8.8 | 2.2 | 4 | 2.54 | 8.8 | 1.8 |

Note: Other minor species were *Acalypha rhomboidea* Raf and *Gnaphalium obtusifolium* L. Differentiation between trees and shrubs was based on growth from: tree = single main stem, large potential size at maturity (height ≥ 3 m), shrub = multiple stems from base, smaller potential size at maturity (Beard 1973).

indicate the relative position of the centers of the species distributions along the environmental axis; they indicate the relative value of each species' weighted average with respect to that particular environmental axis.

## RESULTS AND DISCUSSION

### COMPETITORS

We found 16 tree species, 11 shrub species, and 38 herbaceous species in the 45 subplots (Table 1); the subplots varied in the proportion of total plant biomass that each species contributed. Competitor biomass ranged from zero in the weeded subplots to 638 g/plot in 1991 and increased to a maximum of 2195 g/plot in 1992. Tree biomass ranged from zero in subplots containing only herbaceous competitors to 2121 g/plot in subplots dominated by trees (Table 2), most of which had grown from stump sprouts. ***Nyssa sylvatica*** and ***Sassafras albidum*** occurred most frequently in both years; however, ***Castanea pumila*** and Q. ***prinus*** had higher biomass per subplot than any other tree species in 1992. The tallest species were ***Robinea pseudoacacia, Oxydendrum arboreum,*** and ***Cornus florida,*** all of which had grown from stump sprouts. ***Panicum commutatum*** was the most abundant grass species occurring in 36 of the 45 competition plots with competitors. Although we did not find ***Helianthus atrorubens*** and ***Baptisia tinctoria*** **in** many of the competition plots, these tall herbaceous species showed the greatest increase in biomass from 1991 to 1992 (Table 1).

TABLE 2.

Average and range of white pine seedling growth measures, environmental conditions, and competitor biomass estimates.

| | 1991 | | 1992 | |
|---|---|---|---|---|
| **Variable** | Mean (SD) | Range | Mean (SD) | Range |
| Diameter growth (cm) | 0.19 (0.13) | 0–0.50 | 0.33 (0.16) | (M.72 |
| Height growth (cm) | 10.51 (4.87) | 0.10-20.80 | 17.14 (8.22) | 0.50–33.20 |
| $D^2H$ growth ($cm^3$) | 7.13 (5.26) | 0.25–22.59 | 33.02 (26.22) | 2.84-146.0 |
| XPP,, (MPa) | -0.74 (0.13) | −0.50– − 1.06 | − 0.55 (0.09) | −0.40– −0.76 |
| XPP,, (MPa) | − 1.38 (0.27) | -0.90-2.07 | − 1.43 (0.20) | −1.04– − 1.88 |
| % light | 79.0 (19.4) | 20.7-99.3 | 80.8 (18.4) | 23.2-99.0 |
| Needle N (%) | 1.43 (0.31) | 0.82-2.11 | 1.09 (0.22) | 0.62-1.68 |
| Soil moisture content (%) | 19.7 (3.2) | 11.5-24.8 | 15.7 (2.7) | 9.2-23.4 |
| Total biomass (g/plot) | 171.9 (147.0) | 0638.1 | 479.5 (451.1) | 0–2195 |
| Tree biomass (g/plot) | 66.4 (89.9) | 0-411.8 | 203.7 (365.5) | 0-2121 |

Note: $XPP_{AM}$, average predawn needle water potential; $XPP_{PM}$, average midday needle water potential; soil moisture content measured at 0–30 cm soil depth and averaged over the growing season; % light = percent light (photosynthetically active radiation measured at the terminal of the white pine seedlings ÷ photosynthetically active radiation measured in the open)*(100), averaged over the growing season. Values for 1991 are based on three measurement periods (July–September), and values for 1992 are based on five measurement periods (May-September); the total number of subplots is 53.

### ENVIRONMENTAL CONDITIONS

$XPP_{AM}$ per seedling averaged over the growing season ranged from − 0.50 MPa to − 1.06 MPa in 1991 and from -0.40 to -0.76 MPa in 1992 (Table 2). On some of the subplots, shading by competitors reduced light to as low as 21% in both 1991 and 1992. Needle N concentration ranged from 0.82% to 2.11% to 2.11% in 1991 and from 0.62% to 1.68% to in 1992. The average needle nitrogen concentration in 1992 was only 76% of the average in 1991. Although competitor biomass more than doubled from 1991 to 1992, average environmental conditions did not change by a comparable amount.

### COMPETITION INDICES

In 1991, distance-independent measures of competition were not as well related to pine seedling growth as the distance-dependent measures of competition (Table 3). $CI_{height}$ provided "better"models to predict diameter and $D^2H$ growth than $CI_{mass}$, with the relationship between $CI_{height}$ and pine diameter growth having the highest approximate $r^2$ (Table 3). Competition indices using height or biomass of

TABLE 3.

Nonlinear models for predicting white pine seedling growth in 1991 based on distance-dependent and distance-independent competition indices. Model = growth = $\beta_0 \exp^{(-\beta 1 * Competition\ Index)}$

Diameter growth

| Competition Index | $\beta_0$ (SE) | $\beta_1$ (SE) | $\sim r^2$ | MSE |
|---|---|---|---|---|
| *Distance-independent* | | | | |
| Total biomass | | no model | | |
| Tree biomass | | no model | | |
| ***Distance-dependent*** | | | | |
| $CI_{height}$ | *0.25341 (0.02920)* | *0.01494 (0.00582)* | *0.730* | *0.01438* |
| $CI_{mass}$ | | no model | | |
| $CI_{tree\ height}$ | | no model | | |
| $CI_{tree\ mass}$ | | no model | | |

$D^2H$ growth

| Competition Index | $\beta_0$ (SE) | $\beta_1$ (SE) | $\sim r^2$ | MSE |
|---|---|---|---|---|
| *Distance-independent* | | | | |
| Total biomass | | no model | | |
| Tree biomass | | no model | | |
| ***Distance-dependent*** | | | | |
| $CI_{height}$ | *10.182 (1.202)* | 0.01801 (0.00650) | 0.717 | 22.969 |
| $CI_{mass}$ | 9.581 (1.206) | 0.07846 (0.03425) | 0.698 | 24.484 |
| $CI_{tree\ height}$ | | no model | | |
| $CI_{tree\ mass}$ | | no model | | |

Note: $D^2H$, (diameter squared)*(height); $CI_{height}$, total competitor height; $CI_{mass}$, total competitor biomass; $CI_{tree\ height}$, height of tree species only; $CI_{tree\ mass}$, biomass of tree species only; MSE, mean square error. SE = asymptotic standard error; $\sim r^2$ or approximate $r^2 = 1 -$ (SS residual/SS uncorrected total), from nonlinear least squares (PROC NLIN, SAS Institute 1987).

tree species alone were not significantly related to pine seedling growth. None of the distance-independent measures of competition provided adequate models of pine seedling growth. In 1992, both distance-independent and distance-dependent measures of competition provided reasonable models for predicting pine seedling growth. However, the distance-dependent models were slightly better (e.g., higher approximate $r^2$ and lower mean square errors) than the distance-independent measures of competition. These results suggest that in 1991, the circular plot size of 2.0 $m^2$ may have been too large and many of the competitors were too far away to influence pine growth.

In 1992, competition indices based on competitor height performed better than those based on competitor biomass. $CI_{tree\ height}$ produced the best model for predicting diameter growth whereas $CI_{height}$ was the best model for predicting $D^2H$ growth based on its lower mean square error (Table 4). The importance of competitor height reflects reduced light availability to white pine seedlings by tall competitors. In a related study (Elliott and Vose 1993), we established that light is a major factor influencing white pine physiological processes in these mixed pine/oak systems. In addition, in 1992, percent light was significantly correlated to both diameter growth and $D^2H$ growth (Table 5). Needle N concentration was the only environmental variable significantly related to diameter growth and $D^2H$ growth in 1991; in 1992, its relationship to growth was not significant (Table 5).

TABLE 4.

Nonlinear models for predicting white pine seedling growth in 1992 based on distance-dependent and distance-independent competition indices. Model = growth = $\beta_0 \exp^{(-\beta_1 * \text{Competition Index})}$.

Diameter **growth**

| Competition Index | $\beta_0$ (SE) | $\beta_1$ (SE) | ~$r^2$ | MSE |
|---|---|---|---|---|
| *Distance-independent* | | | | |
| Total biomass | 0.41919 (0.03359) | 0.00052 (0.00017) | 0.858 | 0.02007 |
| Tree biomass | 0.39656 (0.02512) | 0.00112 (0.00038) | 0.870 | 0.01842 |
| *Distance-dependent* | | | | |
| $CI_{height}$ | 0.44335 (0.03358) | 0.00625 (0.00166) | 0.872 | 0.01807 |
| $CI_{mass}$ | 0.42738 (0.03037) | 0.02169 (0.00618) | 0.872 | 0.01804 |
| $CI_{tree\ height}$ | 0.42121 (0.02385) | 0.02709 (0.00665) | 0.893 | 0.01508 |
| $CI_{tree\ mass}$ | 0.41028 (0.02384) | 0.06392 (0.01854) | 0.886 | 0.01608 |

$D^2H$ growth

| Competition Index | $\beta_0$ (SE) | $\beta_1$ (SE) | ~$r^2$ | MSE |
|---|---|---|---|---|
| *Distance-independent* | | | | |
| Total biomass | 48.216 (6.226) | 0.00094 (0.00035) | 0.686 | 575.180 |
| Tree biomass | 42.488 (4.802) | 0.00193 (0.00096) | 0.683 | 580.576 |
| Distance-dependent | | | | |
| $CI_{height}$ | 54.174 (6.247) | 0.01222 (0.00343) | 0.728 | 498.198 |
| $CI_{mass}$ | 50.542 (5.938) | 0.04442 (0.01467) | 0.709 | 533.218 |
| $CI_{tree\ height}$ | 46.474 (4.712) | 0.04819 (0.01782) | 0.722 | 510.649 |
| $CI_{tree\ mass}$ | 45.394 (4.825) | 0.12957 (0.05574) | 0.710 | 532.457 |

Note: Abbreviations are the same as in Table 3.

TABLE 5.

Correlation coefficients relating diameter, height, and $D^2H$ growth of ***Pinus strobus*** L. seedlings, competition indices based on total competitor height ($CI_{height}$) and total competitor biomass ($CI_{mass}$), and competition indices based on height of tree species only ($CI_{tree\ height}$) and biomass of tree species only ($CI_{tree\ mass}$) to environmental variables.

1991

| | % light | Needle N | $-\Sigma XPP_{AM}$ | $-\Sigma XPP_{PM}$ | $SM_{30}\%$ |
|---|---|---|---|---|---|
| Diameter growth | 0.212 | 0.657*** | -0.004 | 0.145 | -0.108 |
| Height growth | 0.088 | 0.201 | -0.256 | 0.066 | 0.072 |
| $D^2H$ growth | 0.198 | 0.536*** | -0.124 | 0.106 | 0.008 |
| Total biomass | -0.340* | -0.234 | 0.233 | 0.106 | 0.206 |
| Tree biomass | -0.441*** | -0.328* | 0.164 | 0.332* | -0.017 |
| $CI_{height}$ | -0.403** | -0.497*** | 0.090 | 0.219 | 0.040 |
| $CI_{mass}$ | -0.545*** | -0.296* | 0.081 | 0.227 | -0.122 |
| $CI_{tree\ height}$ | -0.488*** | -0.429** | 0.110 | 0.215 | 0.005 |
| $CI_{total\ mass}$ | -0.446*** | -0.390** | 0.145 | 0.350* | -0.033 |

1992

| | % light | Needle N | $-\Sigma XPP_{AM}$ | $-\Sigma XPP_{PM}$ | $SM_{30}\%$ |
|---|---|---|---|---|---|
| Diameter growth | 0.511*** | 0.092 | -0.173 | -0.052 | -0.056 |
| Height growth | 0.209 | -0.242 | 0.162 | -0.005 | 0.076 |
| $D^2H$ growth | 0.459*** | -0.105 | -0.111 | -0.055 | -0.053 |
| Total biomass | -0.722*** | -0.125 | -0.007 | 0.012 | 0.125 |
| Tree biomass | -0.704*** | 0.023 | 0.184 | -0.198 | 0.005 |
| $CI_{height}$ | -0.494*** | -0.058 | -0.002 | 0.121 | 0.007 |
| $CI_{mass}$ | -0.742*** | -0.092 | 0.085 | -0.005 | 0.141 |
| $CI_{tree\ height}$ | -0.709*** | -0.001 | 0.164 | -0.166 | 0.040 |
| $CI_{tree\ mass}$ | -0.672*** | 0.071 | 0.203 | -0.201 | 0.020 |

Note: *,**, *** denotes significance at the 0.05, 0.01, and 0.001 level, respectively, number of subplots is 45. Abbreviations are the same as in Table 2.

Soil moisture content was not related to any of the competition indices in either year. Although competitors were taking up water, their shade was probably creating a reduction in seedling evapotranspiration.

Pine seedling height growth was not significantly related to any of the measures of competition in either year or to any of the environmental variables measured in this study. Many studies on a variety of coniferous species show the absence of consistent height response in the presence of competition (Eissenstat and Mitchell 1983, Brand 1990, Morris et al. 1990, White and Elliott 1992, Elliott and Vose 1993). Because shoot elongation in determinate species depends on the previous year's conditions (Kozlowski et al. 1991), height after two growing seasons would only reflect the first year's competition.

### EFFECTS OF INDIVIDUAL SPECIES

In addition to competitor size, the species of competitor can influence competition intensity (Goldberg 1990). We used CCA to identify species that had the greatest influence on pine seedling growth, water potential, light availability, soil moisture, and needle N concentration. The species-environment correlations were high in both years, suggesting that the six environmental variables (including pine diameter) reasonably explained the first two ordination axes (Tables 6 and 7). In 1991, the eigenvalues were 0.452 for the first axis and 0.306 for the second axis (Table 6). In 1992, the eigenvalues were 0.576 for the first axis and 0.438 for the second axis (Table 7). The cumulative variation explained by the first three axes of the species-environment relation in the CCA was 82% for 1991 and 74% for 1992.

The results of the CCA for 1991 (Figure 1, Table 6) showed that the main variation in vegetation (AXIS 1) was explained by average percent light (LIGHT). On the first axis, *Baptisia tinctoria* and *K. latifolia,* left of the ordination diagram, were the species that represented a high light condition, and *Acer rubrum* and 0. *arboreum, in* the upper right, represented low light. Although *B. tinctoria* is a tall herb, it is sparsely foliated resulting in light penetration through its canopy. Pine seedling $XPP_{PM}$ was the second most important variable related to SPEC AXIS 1 and SPEC AXIS 2. Pine seedlings occurring with *Desmodium rotundifolia, Rubus argutus,* and *Euphorbia corollata* exhibited the lowest xylem pressure potentials (XPP is in absolute value; a higher value represents greater water

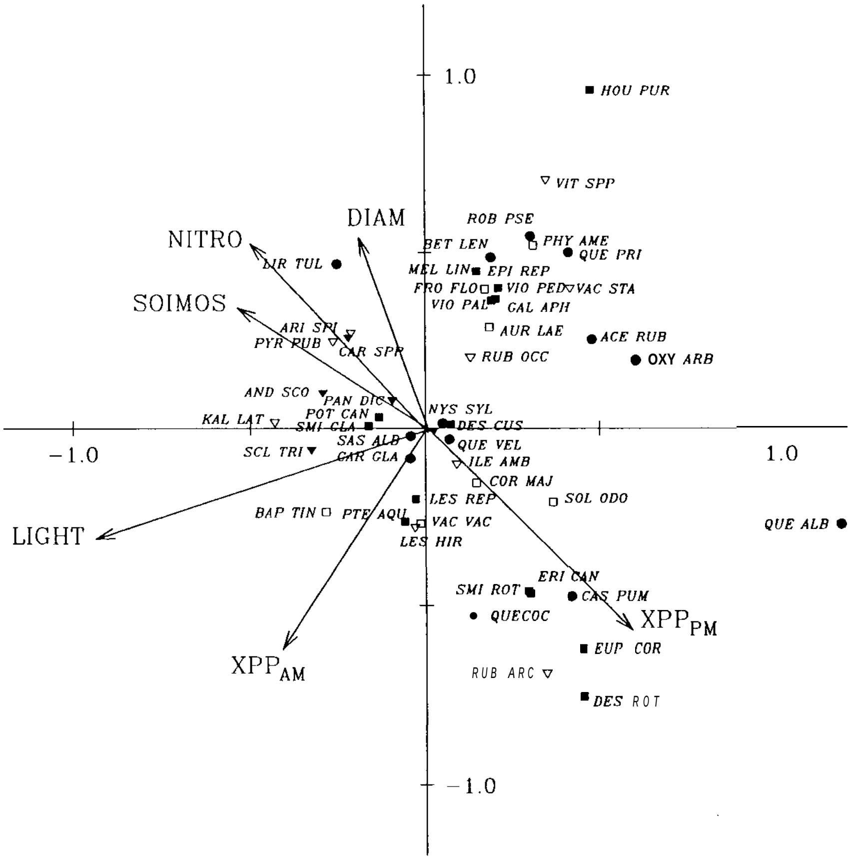

FIGURE 1. Jacobs Branch competitor data for 1991: CCA ordination diagram with plant species. Note: trees (filled circles), shrubs (open triangles), tall herbs (open squares), short herbs (filled squares), and grasses (tilled triangles); and environmental variables (bold arrows). First axis horizontal; second axis vertical. Abbreviations for species are given in Table 1. Abbreviations for environmental variables are given in Table 6.

## TABLE 6.

Weighted correlation matrix for species axes, environmental axes, and environmental variables for competitor plots on Jacob Branch sites (*n* = 45) for 1991.

| | SPEC AX1 | SPEC AX2 | SPEC AX3 | ENVI AX1 | ENVI AX2 | ENVI AX3 |
|---|---|---|---|---|---|---|
| SPEC AX1 | | | | | | |
| SPEC AX2 | − 0.0370 | | | | | |
| SPEC AX3 | -0.0018 | − 0.0388 | | | | |
| ENVI AX1 | 0.8316 | 0.0000 | 0.0000 | | | |
| ENVI AX2 | 0.0000 | 0.7680 | 0.0000 | | | |
| ENVI AX3 | 0.0000 | 0.0000 | 0.7249 | | | |
| DIAM | -0.1176 | 0.3253 | 0.1317 | -0.1414 | 0.4236 | 0.1816 |
| $XPP_{AM}$ | − 0.2894 | -0.4178 | 0.1638 | − 0.3480 | − 0.5440 | 0.2260 |
| $XPP_{PM}$ | 0.4981 | -0.4170 | -0.2857 | 0.5990 | − 0.5430 | − 0.3942 |
| SOIMOS | − 0.3046 | 0.2392 | − 0.0265 | − 0.3663 | 0.3114 | − 0.0365 |
| LIGHT | − 0.6988 | − 0.3075 | − 0.1075 | − 0.8403 | -0.4004 | − 0.1483 |
| NITRO | − 0.2783 | 0.2996 | − 0.3200 | − 0.3347 | 0.3901 | − 0.4414 |
| **Eigenvalues** | 0.452 | 0.306 | 0.267 | | | |

Note: DIAM = diameter growth: XPP,, = $-\Sigma XPP_{AM}$ and XPP,, = $-\Sigma XPP_{PM}$, calculated as the cumulative sum of seedling xylem pressure potential for the growing season; SOIMOS = average percent soil moisture content at 30 cm soil depth; LIGHT (average percent light) = (photosynthetically active radiation measured at the terminal of the *Pinus strobus seedlings* ÷ photosynthetically active radiation measured in the open)*(100); NITRO = percent needle nitrogen concentration.

stress or lower needle xylem pressure potential). Pine seedling diameter growth (DIAM) and needle N concentration (NITRO) were related to the second species axis (Table 6). Needle N and seedling diameter growth were higher with ***Liriodendron tulipifera, Aralia spinosa, Pyrularia pubera,*** and ***Carex*** spp. (i.e., near the end of the environmental vectors); and lower with species such as ***E. corollata, Castanea pumila,*** and ***R. argutus*** (i.e., in the lower right of the ordination diagram; visualize a projection of the NITRO and DIAM vectors in the opposite direction, Figure 1). In this study, the ***Liriodendron tulipifera*** were small because they had germinated from seeds the first spring after the clearcut and burn treatment rather than from stump sprouts, which characteristically have faster growth rates.

In 1992, the results of the CCA (Figure 2, Table 7) showed that the main variation in vegetation was explained by percent light and pine seedling diameter growth. Light was highly correlated to the first species axis ($r = -0.8689$), with high light at the left of the ordination diagram and low light at the right, where tall, stump sprouting tree species such as C. ***pumila, A. rubrum,*** and Q. ***prinus*** occurred. Diameter growth was also significantly related to SPEC AXIS 1 ($r = -0.6512$). Diameter growth was highest in the presence of ***Andropogon scoparius, E. corollata,*** and ***K. latifolia*** (low stature species), and lowest with Q. ***prinus,***

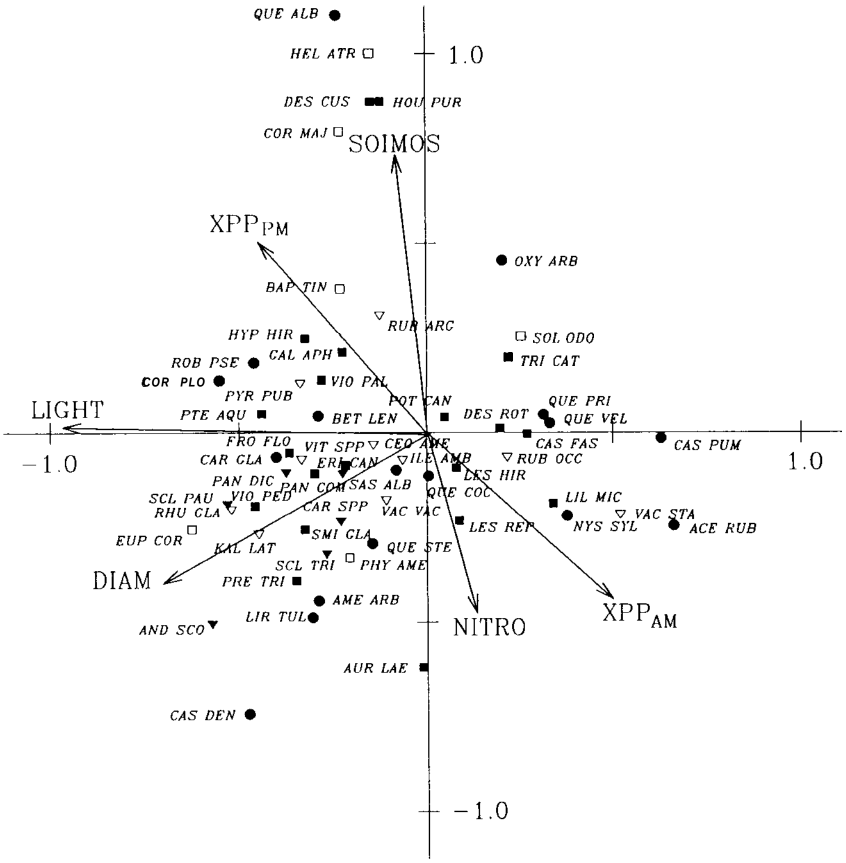

FIGURE 2. Jacobs Branch competitor data for 1992: CCA ordination diagram with plant species. Symbols, axes, and labels are the same as in Figure 1.

TABLE 7.

Weighted correlation matrix for species axes, environmental axes, and environmental variables for competitor plots on Jacob Branch sites ($n$ = 45) for 1992.

| | SPEC AX1 | SPEC AX2 | SPEC AX3 | ENVI AX1 | ENVI AX2 | ENVI AX3 |
|---|---|---|---|---|---|---|
| SPEC AX1 | | | | | | |
| SPEC AX2 | 0.0188 | | | | | |
| SPEC AX3 | 0.0612 | 0.0293 | | | | |
| ENVI AX1 | 0.9361 | **0.0000** | *0.0000* | | | |
| ENVI AX2 | 0.0000 | 0.8077 | *0.0000* | | | |
| ENVI AX3 | 0.0000 | 0.0000 | 0.7436 | | | |
| DIAM | −0.6512 | −0.3251 | 0.0654 | −0.6956 | −0.4026 | 0.0879 |
| XPP$_{AM}$ | 0.3663 | −0.3329 | 0.5095 | 0.3913 | -0.4122 | −0.6851 |
| XPP$_{PM}$ | −0.3652 | 0.4106 | 0.1282 | −0.3901 | 0.5084 | 0.1724 |
| SOIMOS | −0.0455 | 0.5812 | -0.1076 | −0.0486 | 0.7196 | -0.1447 |
| LIGHT | −0.8689 | 0.0011 | 0.1830 | −0.9282 | 0.0013 | 0.2461 |
| NITRO | 0.0571 | −0.3657 | −0.3931 | 0.0609 | −0.4528 | -0.5286 |
| Eigenvalues | 0.576 | 0.438 | 0.262 | | | |

Note: Abbreviations are the same as in Table 6.

***Q. velutina,*** and *Solidago ordora* (two tall tree species and a tall herb). Soil moisture content (SOIMOS) was significantly related to the SPEC AXIS 2. ***R. argutus*** represented the high end of the soil moisture gradient and ***Lespedeza repens*** and Q. ***stellata*** occurred at the low end of the soil moisture gradient (Figure 2).

## CONCLUSIONS

Our goals were to measure the intensity of competition to white pine seedlings and understand how limited resources and the species composition of competitors influence seedling growth. The white pine seedlings were considered phytometers, and the effects of multiple species were treated as diffuse competition (*sensu* Keddy 1990). The competitive environment and resources affecting pine seedling growth changed from 1991 to 1992. Although competitors reduced available light in 1991, light was not significantly related to pine seedling growth. Nitrogen was the most important resource limiting pine seedling growth, based on needle N concentration. In 1992, light was the most important resource limiting pine seedling diameter growth, and the tall tree species were responsible for that reduction in light availability to pine seedlings.

Distance-dependent measures of competition provided better models to estimate pine seedling growth than distance-independent models. We used both height and biomass of competitors and found that $CI_{height}$ usually was more highly correlated with pine seedling growth than $CI_{mass}$ ***in*** both years. In 1991, competition was not as important as in 1992; ordinating the species did not improve the predictability of the competitive environment. Overall, the relationship of diameter growth to SPEC AXIS 1 in the CCA for 1992 (Table 7) was weaker than the models developed to predict diameter growth based on various measures of competition (Table 4) without taking species of competitor into account. This suggests that knowing which species make up competitor biomass does not improve the predictability of the influence of competitors. However, the ordination of the species-environment relationship can help evaluate the community structure of the competitive environment. For example, species ordination was more closely related to diameter growth in 1992 than in 1991 and succeeded in identitying the species of competitors contributing to the reduction in growth of pine seedlings.

Because height is easier to measure than biomass and competition indices based on competitor height were better at evaluating the effects of competition on white pine seedling growth than models using competitor biomass, from a practical perspective, we suggest than competitor height and pine seedling diameter may be useful variables for evaluating early competitive effects.

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**Manuscript received May 10, 1994**

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Katherine J. Elliott and James M. Vose are research ecologists with Coweeta Hydrologic Laboratory, Southeastern Forest Experiment Station, USDA Forest Service, Otto, NC 28763. The authors thank Patsy Clinton, Barry Clinton, and James Buchanan for their help in collecting the field data. The manuscript was improved by comments by Alan S. White, David White, Wayne T. Swank, and two anonymous reviewers.