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Site preparation burning to improve southern Appalachian pine-hardwood stands: photosynthesis, water relations, and growth of planted *Pinus strobus* during establishment[1]

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We examined the physiological performance and growth of ***Pinus strobus*** L. seedlings the first growing season after planting on two clear-cut and burned sites in the southern Appalachians. Growth of the seedlings was related to physiological measurements (net photosynthesis (P_N), transpiration. leaf conductance, and xylem water potential), soil water, foliar N, seedling temperature, and light environment using regression analysis. Diameter growth increased with increasing foliar N concentration and decreased as competitor biomass increased. Competition reduced growth by lowering foliar N, shading seedlings, and possibly reducing photosynthetic capacity. Increased temperature and lower available soil water may obscure these relationships on a harsh site.

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Nous avons examine la performance physiologique et la croissance de semis de ***Pinus strobus*** **L.** durant la premiere saison de croissance après plantation dans deux sites coupes à blanc et brûlés situées dans la partie sud des Appalaches. Selon les analyses de regression, la croissance des semis était reliée aux mesures physiologiques (photosynthese nette (P_N), transpiration, conductance foliaire et potentiel hydrique du xylème), à l'humidité du sol, à la concentration d'azote foliaire, à la temperature des semis et aux conditions lumineuses. La croissance en diamètre augmentait avec la concentration d'azote foliaire et diminuait avec l'augmentation de la biomasse des espèces competitrices. La competition réduisait la croissance en diminuant la concentration d'azote foliaire, en ombrageant les semis et, possiblement, en réduisant la capacité photosynthétique. L'augmentation de la temperature et la diminution de la disponibilité en eau du sol pourraient embrouiller ces relations sur un s&e de moins bonne qualité.

[Traduit par la redaction]

Introduction

Fire is now prescribed as a silvicultural treatment to restore low-diversity, low-productivity sites in southern Appalachian forests. Eastern white pine (*Pinus* strobus L.) is then planted on many of these sites to provide a mixed pine-oak forest type (see Swift et al. 1993). Fire reduces sprout vigor, which delays growth of ***Kalmia latifolia*** L., a common understory shrub competitor, and encourages tree species such as oak to sprout from the groundline and thereby produce oak that are less likely to develop rot (Van Lear 1991). A major objective of fire is to reduce competition to the planted seedlings; however, little is known regarding the effectiveness of the treatment.

Knowledge of the physiological performance and growth of planted tree seedlings during the first year of establishment is critical to improving management of plantations. The performance of a planted seedling is a function of genetic factors, competition from neighbors, and site condition. A lack of adaptation to the environmental conditions at the forest site, if not immediately fatal, impairs growth. In the presence of competing vegetation, poor early growth can reduce the survival of planted trees or increase the cost of ensuring tree survival through vegetation management (Burdett 1990; Margolis and Brand 1990).

Many studies have focused on the effects of competing vegetation on forest trees, with most concluding that the removal of competing vegetation results in increased growth and survival of conifer seedlings (Stewart et al. 1984; Ross and Walstad 1986). Response to competition can be defined as the relationship of some component of fitness (such as growth) to resource availability, where resource availability is determined by either neighboring plants and (or) the abiotic environment (Goldberg 1990). The impact of competition for resources on pine seedling growth may depend on the ability of seedlings to withstand stress such as low light, soil moisture, and nutrients.

In addition to competitive interactions, variation in the abiotic environment (e.g., soil nutrients, temperature, and soil moisture) may have direct effects on seedling fitness. Fire may affect soil nutrient status by ***(i)*** adding nutrients in ashed organic matter; ***(ii)*** altering the soil environment for microbial activity; and ***(iii)*** reducing plant competition for nutrients. In addition, removal of vegetation from these sites by cutting and prescribed burning increases soil moisture, soil temperature (see Swift et al. 1993). air temperature, and solar radiation input to the forest floor. For example, in a south-facing clear-cut watershed in the southern Appalachians, maximum temperatures at the forest floor exceeded 50°C (Swank and Vose 1988). Temperatures may even be greater on burned sites, where the blackened surface increases the fraction of radiation absorbed. These extreme temperatures may affect photosynthetic rate, carbohydrate reserves, and transpiration rates, all of which ultimately influence fitness. In contrast, increased nutrient and water availability may increase fitness or mitigate other environmental stresses by improving photosynthetic capacity and plant water relations.

The purpose of this study was to (i) examine the direct effects of changes in the microenvironment on physiology and growth of ***P. strobus*** seedlings during establishment and ***(ii)*** examine the competitive effects of naturally regenerating vegetation on ***P. strobus*** seedlings planted after prescribed fire. This study is part of a larger, long-term project evaluating the effects of site preparation burning in low-productivity

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forests in the southern Appalachian Mountains. The long-term study is examining forest productivity and diversity, air, soil and stream chemistry, and soil microbiology.

Methods

Site description

Two sites, approximately *5.25* ha, were chosen from areas previously selected for prescribed burn in the Land Management Plan for the Wayah Ranger District of the Nantahala National Forest in North Carolina. The two sites, Jacob Branch East (JE) and Jacob Branch West (JW), were located in the Blue Ridge physiographic province of the southern Appalachians (35°12′N, 83°24′W). JE is located on a west aspect, and JW is located 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 about 30-60 cm depth. The original overstory vegetation was mainly scattered *Pinus rigida* Mill., Quercus *coccinea* Muenchh., and *Quercus prinus* L. with basal areas from 9 to 19 $m^2 \cdot ha^{-1}$. The shrub understory, which was dominated by *K. latifolia*, had basal areas of 18 to 35 $m^2 \cdot ha^{-1}$.

Experimental design

In the summer of 1989, five 0.05-ha plots (15 x 33.3 m) were established at each site. These plots were used for examining a variety of ecosystem processes (see Swift et al. 1993). including those of interest in the present study. Both sites were cut in summer 1990 with no merchantable products removed. JE was cut first, between June 20 and July 24, and JW was completed by August 7. Sites were burned on separate days (September 18 and 19, 1990). 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). Most of the large woody material was consumed or reduced by fire in the upper centers of the two sites. In early spring (February-March) of 1991, 2-year-old bare-root *P. strobus* seedlings were planted at 5 x 5 m spacing on the burned sites.

A $2.0\text{-}m^2$ circular subplot was established around six randomly chosen *P. strobus* seedlings per plot within each burned site. In all, there were 60 subplots (6 seedlings x 5 (15 m x 33.3 m) plots x *2* sites). One seedling per subplot was randomly selected as a zero-density subplot, where all vegetation within the $2.0\text{-}m^2$ subplot was manually removed at the beginning of the study and removed as needed thereafter.

Plant measurements

Diameter at ground level and height of each *P. strobus* seedling (30 seedlings/site) were measured at the time of planting and at the end of the growing season (1991). These measurements were used to calculate diameter growth (final diameter – initial diameter). Height growth was excluded as a response variable in this first-year analysis because height growth in *P. strobus* is determined during bud formation the previous year (Kozlowski et al. 1991).

Preliminary observations of planted seedlings indicated a wide variation in microsite factors, including proximity to partially burned logs, litter depth, surface blackness, and abundance of competing vegetation. This variation provided a gradient in environmental conditions and competition levels.

On the circular subplots, each species was identified, and its basal diameter and height of stem were measured in late June and early September to estimate competitor biomass. Biomass of competitors was estimated using species-specific regression equations derived from plants that occurred on the burned sites (r^2 values ranged from 0.62 to 0.99, $p < 0.05$, 49 species).

Microenvironment measurements

Availability of light and water were measured monthly. Photosynthetic photon flux density (PPFD, 400-700 nm range) was measured with a portable light meter (Sunfleck Ceptometer, Decagon Devices, Pullman, Wash.). The light meter measures average PPFD incident on 80 sensors located at l-cm intervals along a narrow, 80-cm sampling bar. Two measurements were taken at the height of the terminal shoot of individual pine seedlings at 90” angles and averaged to quantify seedling light environment. Samples were obtained at least once per month on clear days between 11:00 and 14:00 solar time.

Soil water content in the area of the 30 monitored pines per site (6 per plot x 5 plots per site) was measured using time domain reflectometry (1502B metallic time domain reflectometer, Tektronix, Beaverton, Oreg.). A set of stainless steel rods measuring 30 and 60 cm was placed around the base of the pine seedlings at a distance of 10 cm. Soil water was measured on the same day as the PPFD measurements.

Biweekly maximum and minimum temperatures at 20 cm above ground level were determined for each block with maximum–minimum thermometers. In addition, fine-wire thermocouples were placed in the midcrown of seedlings and temperature was measured at midday with a portable thermocouple thermometer.

Precipitation, humidity, air temperature, and wind speed were measured at a climatic station located on the site (see Swift et al. 1993).

Physiological measurements

Xylem water potential (ψ) and foliar N were measured on all 30 pine seedlings per site. Predawn ψ (ψ_{PD}) and midday ψ (ψ_{MD}, 11:00–13:00 solar time) were measured monthly with a pressure chamber (PMS Instruments Co., Corvallis, Oreg.; Scholander et al. 1965) on individual fascicles. At the end of the growing season (September 29), two fascicles of current needles per seedling were removed to determine N concentration. Foliar N was determined on a Perkin-Elmer 2400 Cl-IN Analyzer (Norwalk, Conn.).

Photosynthesis (P_N), transpiration (E), and leaf conductance (g_l) were measured twice during the growing season (July 2 and September 4) on a subset of seedlings selected from each plot (three seedlings per plot) subjected to no, moderate, or high density of competitors. These sample periods coincided with measurements of competitor biomass (i.e., late June and early September). P_N, g_l, and *E were* measured using a portable photosynthesis system and a narrow-leaf Parkinson leaf chamber (ADC LCA, Analytical Development Co. Ltd., Hoddesdon, Herts, U.K.). On the first sampling date (July 2), four measurements were taken per seedling (two on current-year needles, two on older needles). On the last sampling date (September 4), older foliage on some of the seedlings had dry, brown tips. At that time, only current-year foliage was measured. Values were subsequently averaged to provide a mean value by needle age-class for each seedling. In all cases, measurements were taken under ambient conditions. Self-shading was minimized by ensuring that needles did not overlap inside the cuvette. Needle surface area (all sides) was estimated from length and number of needles in the cuvette using coefficients developed in an earlier study (J.M. Vose, unpublished data). Measurements were taken on clear sunny days between 11:00–13:00 solar time when incoming PPFD was above 800 $\mu mol \cdot m^{-2} \cdot s^{-1}$, which represents light saturation for *P. strobus* (Maier 1990). In addition, P_N of *P. strobus* seedlings was measured at 1-hr intervals from 10:00 to 15:00 on September 12 to verify the time of peak daily photosynthetic rate. P_N was highest between 11:00 and 14:00, after which time a marked decline in P_N occurred.

Statistical analysis

Relationships among physiological growth and environmental variables were explored through regression analysis (PROC GLM; SAS Institute Inc. 1987). Statistical analysis proceeded in a sequential fashion to relate physiological responses to environmental variables. First, we related ψ_{PD} and ψ_{MD} to soil water content at 30 cm and 60 cm soil depth and to vapor pressure deficit (VPD; estimated from relative humidity data collected from the climate station and seedling temperatures). Leaf conductance (g_l) was related to ψ_{MD} and VPD. Next, P_N was related to environmental variables (i.e., PPFD, foliar N as an index of N availability, soil water content at 30 and 60 cm soil depth, and seedling temperature). Competitor biomass was then

TABLE 1. Average environmental and physiological conditions of *P. strobus* seedlings on Jacob Branch East (JE) and Jacob Branch West (JW)

	July 2		August 2		September 4	
Variable	JE	JW	JE	JW	JE	JW
ψ_{PD} (MPa)	-0.70 (0.045)	-0.68 (0.091)	-0.89 (0.034)	-0.91 (0.047)	-0.72 (0.034)	-0.64 (0.028)
ψ_{MD} (MPa)	-1.29 (0.047)	-1.45 (0.072)	-1.31 (0.047)	-1.61 (0.077)	-0.96 (0.035)	-1.69 (0.072)
Soil MC_{30} (%)	23.8 (0.571)	22.8 (0.851)	19.2 (0.834)	16.2 (0.880)	17.99 (0.640)	17.48 (0.786)
Soil MC_{60} (%)	23.3 (0.819)	23.0 (0.647)	19.6 (0.666)	19.9 (0.609)	21.25 (0.581)	21.32 (0.636)
Temp. (°C)	25.3 (0.248)	33.2 (0.455)	25.1 (0.243)	30.7 (0.482)	21.9 (0.267)	29.6 (0.387)
PPFD ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	1111 (41.32)	1559 (46.85)	938 (50.41)	1509 (61.95)	636 (48.91)	969 (59.0)
Competitor (g)	98.6 (21.42)	179.7 (35.25)	—	—	207.4 (37.14)	272.5 (49.24)
Foliar N (%)	—	—	—	—	1.44 (0.061)	1.38 (0.068)
Current needles						
P_N ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	1.78 (0.193)	2.96 (1.190)	—	—	3.61 (0.439)	2.54 (0.289)
E ($mmol \cdot m^{-2}$)	2.18 (0.181)	2.52 (0.141)	—	—	1.13 (0.097)	1.26 (0.104)
g_l ($mol \cdot m^{-2} \cdot s^{-1}$)	0.27 (0.038)	0.29 (0.037)	—	—	0.15 (0.016)	0.09 (0.007)
Older needles						
P_N ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	1.50 (0.149)	3.03 (0.770)	—	—	—	—
E ($mmol\ m^{-2}$)	2.33 (0.126)	1.91 (0.208)	—	—	—	—
g_l ($mol \cdot m^{-2} \cdot s^{-1}$)	0.29 (0.030)	0.19 (0.029)	—	—	—	—

NOTE: Values in parentheses are standard errors of the mean. ψ_{PD}, predawn xylem water potential; ψ_{MD}, mid&y xylem water potential; soil MC_{30}, soil moisture content at 0-30 cm depth; soil MC_{60}, soil moisture content at 0-60 cm depth; PPFD, photosynthetic photon flux density measured at the terminal of the *P. strobus* seedlings; P_N, net photosynthesis; E, transpiration; g_l, leaf conductance.

related to environmental variables and P_N of pine seedlings to determine whether the competitive microenvironment affected the physiology of the seedlings. Finally, pine seedling diameter growth was related to environmental variables, P_N of pine seedlings, and competitor biomass. Stepwise multiple regression models were examined to assess the ability of multiple variables to predict seedling diameter growth and P_N. Models were evaluated based on graphical and residual analysis and comparisons of coefficients of determination (r^2). To test for site differences, we included site as a dummy variable in all the regression models. In all cases, we found that site was significant ($p < 0.05$), so further analyses were performed on data sets separated by sites. Significance was determined at an a level of 0.05.

Results

Microenvironment

Monthly precipitation was 12.93 cm in June, 6.12 cm in July, and 18.77 cm in August 1991 (see Swift et al. 1993). Soil moisture reflected these differences in precipitation; soil moisture was generally lower for the August 2 sample than for the July 2 or September 4 samples (Table 1). Average soil moistures (0-30 cm depth) was lower at JW than at JE for all sample dates (Table 1).

Average temperatures in seedling canopies were 5–7°C lower on JE than on JW (Table 1). Temperatures were higher on July 2 than on either August 2 or September 4 at JW, but temperatures were similar for all sample dates at JE. The average foliar N concentrations were similar at JE and JW (Table 1). PPFD measured at the terminal shoots of seedlings decreased over the growing season at both sites as competing vegetation grew (Table 1). The proportion of incoming PPFD available to seedlings (percent light expressed as: PPFD at the terminal/total incoming PPFD x 100) ranged from 17 to 100% at JE and from 6 to 100% at JW.

Average ψ_{PD} was similar between the two sites on all sample dates, with the lowest ψ_{PD} occurring on August 2. However, average ψ_{MD} was consistently lower at JW than at JE (Table 1). ψ_{PD} was not significantly related to soil water content on any of the site – sample date combinations. ψ_{MD} was not significantly related to soil water content or VPD at either site. Both g_l and E were lower on the August 2 sampling date than on June 2 at the two sites, with the lowest average g_l of seedlings on JW (Table 1). Although average g_l was lower at JW than at JE, the difference was not statistically significant ($p = 0.240$; PROC TTEST; SAS Institute Inc. 1987).

On September 4, P_N of *P. strobus* seedlings was significantly correlated with foliar N concentration at JE, but the relationship between P_N and foliar N was not significant at JW (Fig. 1). PPFD and P_N were positively correlated (Fig. 1) on September 4 at JW, but there was no relationship for the other sample dates at JW or for any date at JE. Adding independent variables such as PPFD and foliar N in multiple regression did not improve the predictability of P_N with multiple factors (e.g., PPFD and foliar N). The failure of multiple regression may be attributable to intercorrelations among environmental variables.

Competition relationships

The influences of competition on microenvironmental conditions were examined by correlating competitor biomass with percent light and foliar N. Competitor biomass was negatively correlated with percent light, foliar N, and P_N at JW for the September 4 sampling date, but there were no significant relationships with competitor biomass at JE (Fig. 2).

Diameter growth rate was significantly related to foliar N at both sites and to percent light at JW (Fig. 3). At JW, diameter growth rate was correlated with competitor biomass and P_N (Fig. 3). Diameter growth rate was not related to competitor biomass or P_N at JE.

Discussion

Microenvironment and physiological responses

During the 1991 growing season, it was not dry enough to detect relationships between soil moisture and seedling performance. Although we found no statistically significant rela-

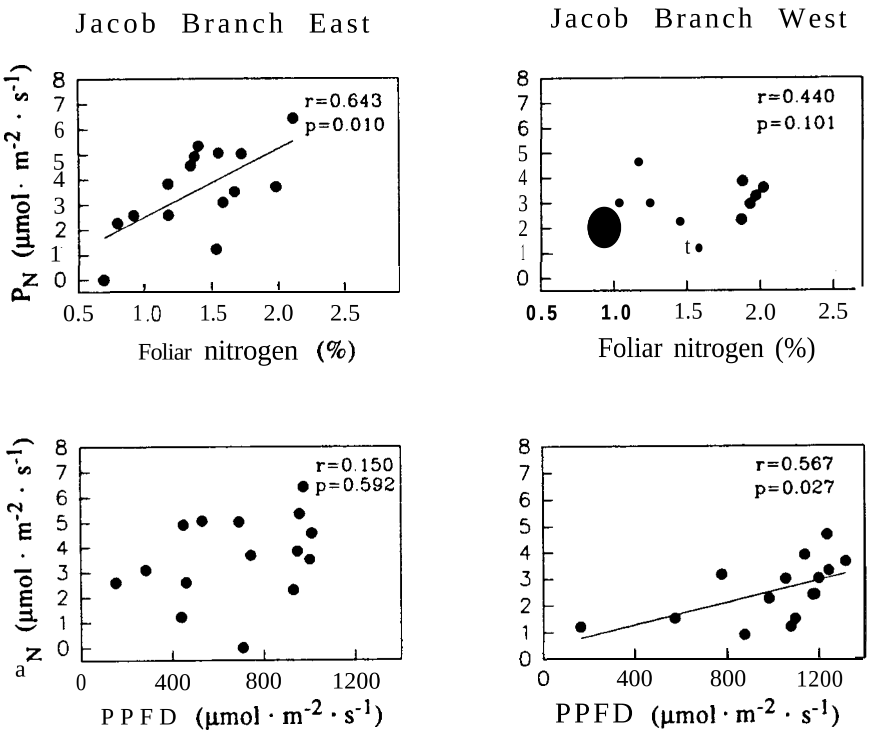

FIG. 1. Correlations of *P. strobus* seedling net photosynthesis (P_N) with photosynthetic photon flux density (PPFD, 400-700 nm range) and current needle nitrogen concentration at Jacob Branch East and Jacob Branch West.

tionships between ψ_{MD} and soil moisture or VPD, ψ_{MD} is typically a function of the supply of available soil moisture and evaporative demand (i.e., VPD) (Pallardy et al. 1991). Because temperature at JW averaged 5–7°C higher than at JE, evaporative demand was much higher at JW than at JE (VPD at JE and JW averaged 0.85 and 1.46 kPa, respectively). In September, g_l showed a similar trend to ψ_{MD}, with g_l being lower at the JW site than at the JE site. Lower g_l apparently resulted from lower ψ_{MD} and higher evaporative demand. In September, when soil moisture in the upper 30 cm had decreased to 17.5% and temperature was 29.6°C midday stomatal closure was apparent (Table 1).

The lack of a close relationship between ψ_{PD} and P_N is in contrast with other studies (Sands et al. 1984; Seiler and Cazell 1990; Pavlik and Barbour 1991); however, average ψ_{PD} values of -0.64 to -0.91 MPa in our study indicate relatively moderate conditions (Brix 1962; Sheriff and Whitehead 1984). A threshold response of P_N and g_l to decreasing water potentials is common in conifers; in some conifers a significant reduction of P_N does not occur until ψ_{PD} is below -1.5 MPa (Teskey et al. 1986; Pavlik and Barbour 1991; Running 1976). Drought during periods between sampling dates is unlikely because soil moisture increased after cutting (Swank and Vose 1988). regrowth of site leaf areas had not reached levels high enough to deplete soil moisture (Swank and Vose 1988), and the 1991 growing season received above-average precipitation for this region (see Swift et al. 1993).

Foliar N concentrations in our study were within the range others have observed for many temperate pine species (Timmer and Morrow 1984; Bockheim et al. 1986; Adams et al. 1987; Elliott 1991). Swan (1972) determined for *Pinus resinosa* Ait. seedlings that a moderate range of N deficiency occurred at 1.3–1.0% foliar N and acute N deficiency occurred below 1.0%. In our study, when seedling percent foliar N was below 0.70, the seedlings exhibited symptoms of N deficiency (i.e., chlorotic needles) and subsequently died by the end of the growing season. Photosynthetic rate – leaf nitrogen relationships for deciduous species are generally strong (DeJong 1982; DeJong and Doyle i985; Field and Mooney 1986; Karlsson 1991). while for evergreen conifers they are inconsistent (van den Driessche 1972; Brix 1981; Linder and Rook 1984; Sheriff et al. 1986; DeLucia et al. 1989). P_N – foliar N relationships found in our study are not as explanatory as has been found in other studies (Natr 1975; Field and Mooney 1986; Evans 1989; Hull and Mooney 1990) possibly because of other factors of the seedling environment. For example, Reich and Schoettle (1988) found that percent leaf N explained between 68 and 84% of the variance in P_N of *P. strobus* seedlings when P was not limiting. However, in soil subgroups with low available P there were no significant relationships between percent leaf N and P_N.

PPFD decreased from July to September, reflecting the growth of competing vegetation near the pine seedlings. Total incoming PPFD at JE was less than at JW between 11:00 and 13:00. Differences in slope and aspect between the two sites influenced the solar incidence angle. For example, on September 4, PPFD input ranged from 800 to 1100 and 1100 to 1400 µmol · m^{-2} · s^{-1} for JE and JW, respectively. These differences in solar radiation alone should not have directly influenced P_N between the two sites, since P_N of *P. srrobus* is saturated at 600 µmol · m^{-2} · s^{-1}, but the indirect effect on temperature and VPD would be influenced by the different solar radiation inputs.

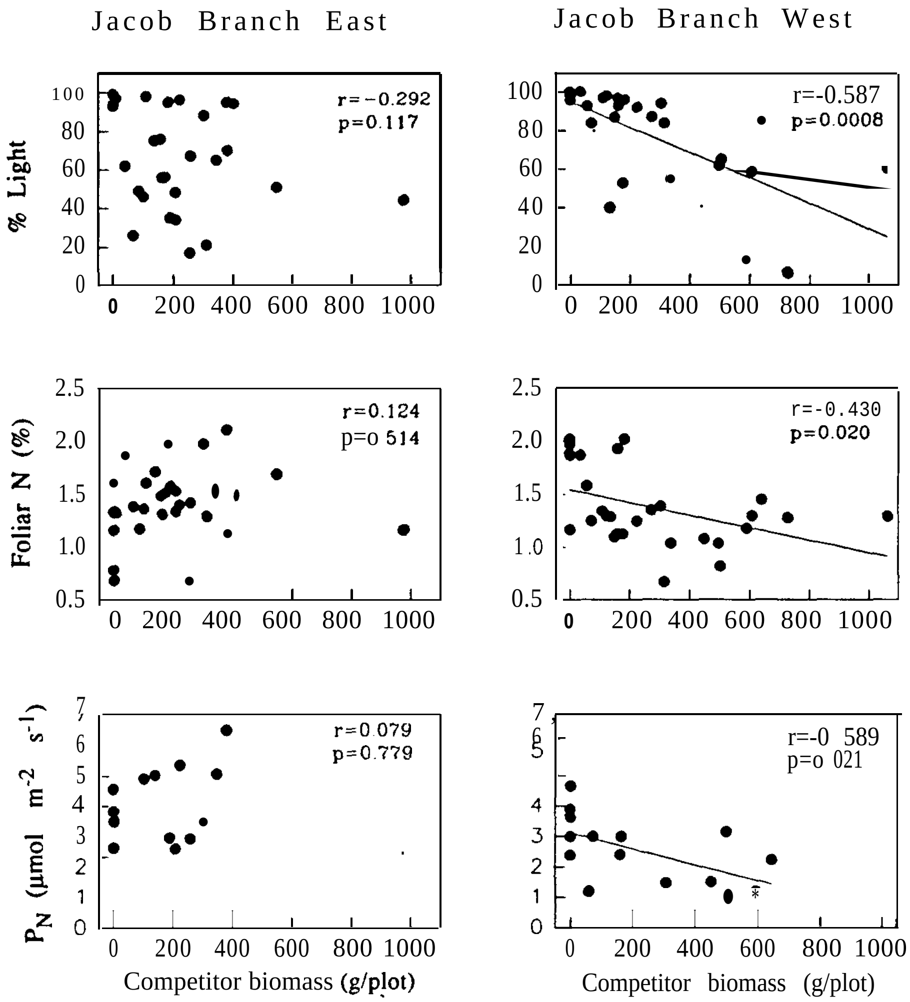

FIG. 2. Correlations of biomass of competitors within 2.0-m^2 circular plots and percent photosynthetic photon flux density, PPFD (% Light, expressed as (PPFD, 400-700 nm range, at the terminal/total incoming PPFD) x 100); current needle nitrogen concentration; and net photosynthesis (P_N) of ***P. strobus*** seedlings at Jacob Branch East and Jacob Branch West.

Competitive effects on physiology and growth

Competitor biomass was ***45%*** less at JE than at JW on July 2 and ***24% less*** on September 4. These differences are attributable to the contrasting intensities of the prescribed fires (Swift et al. 1993). The JE site had the greatest preburn biomass and was cut first. Thus, it had the longest drying cycle and the largest amount of fuel. Peak flame temperatures averaged 803°C on JE but only 672°C on JW. The significant relationships between competitor biomass and percent light at JW indicate that competitors reduced available light to ***P. strobus*** seedlings, which presumably resulted in a decrease in P_N. However, competitors around ***P. strobus*** seedlings at JE were not tall enough to reduce light availability to the seedlings.

The relationship between competitor biomass and diameter growth was significant at JW, but the explanatory power was relatively low. The response of ***P. strobus*** seedlings to competition on the two sites was explained by differences in competition intensity. At JW, competitors near ***P. strobus*** seedlings reduced light and may have reduced available nitrogen as indicated by low foliar N concentrations. Diameter growth of ***P. strobus*** seedlings increased as percent light and percent foliar N increased at JW. At JE, the significant relationship between leaf N and photosynthesis resulted from factors other than competing vegetation. Possible explanations for the gradient in leaf N concentration at JE include microsite variability in N availability, variation in seedling quality, and variation in establishment of root systems after transplanting. During the first growing season, slow establishment of root-soil contact of bare-root seedlings can limit the absorption of nutrients and water (Burdett et al. 1983; Grossnickle and Blake 1987; Burdett 1990). In addition, mortality was higher at JE than at JW (36 and 12%, respectively), and most of the mortality occurred in May and early June, indicating that root establishment may have been a problem on JE.

Summary and conclusions

Although we had only three sampling periods in this first growing season after planting ***P. strobus*** seedlings, we found significant relationships between microenvironment and seedling 'physiology, between seedling P_N and diameter growth, and between competitor biomass and seedling physiology and growth. Both nitrogen and light were the dominant factors limiting P_N and diameter growth of ***P. strobus*** seedlings. Although these relationships were not consistent over all time

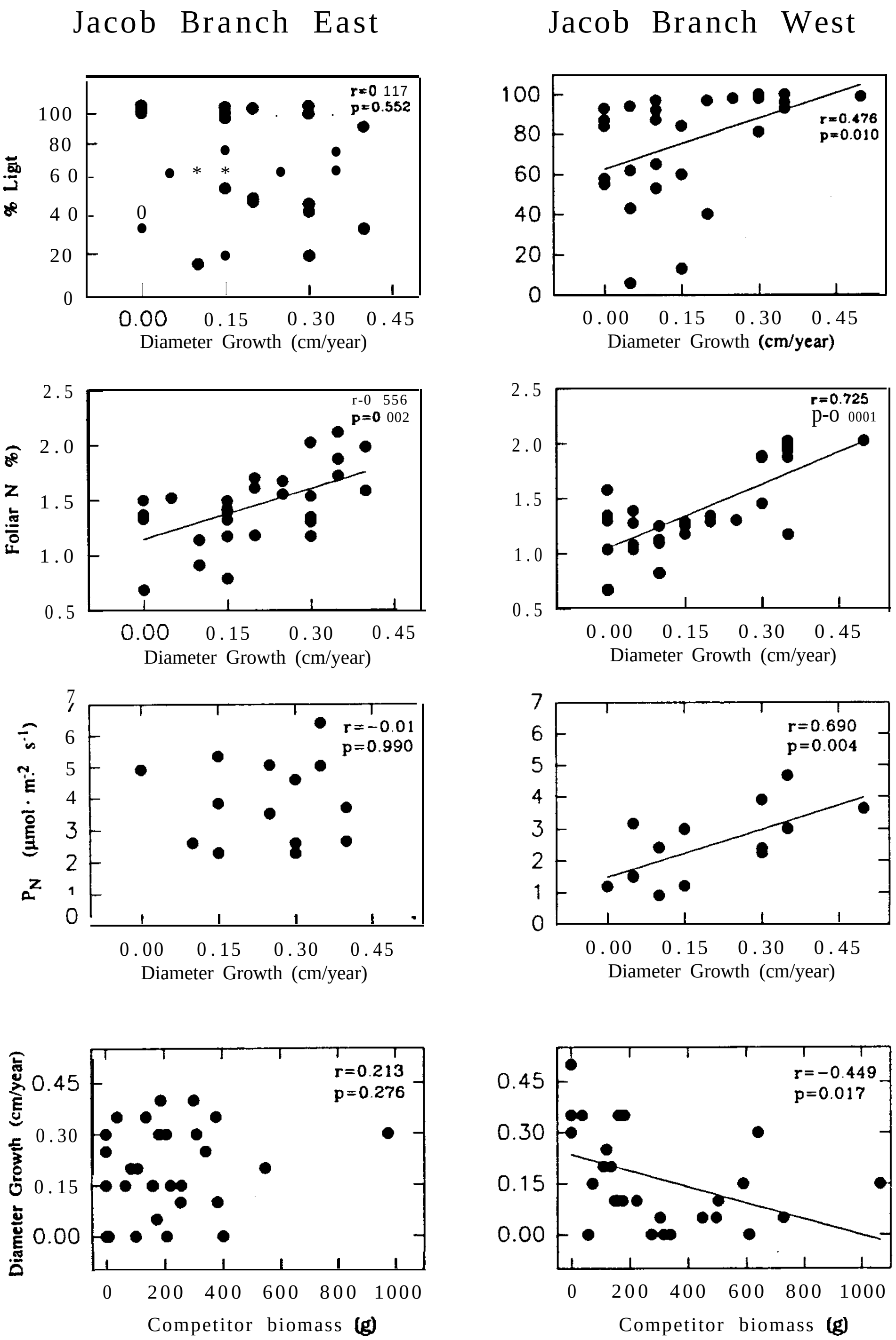

FIG. 3. Correlations of diameter growth with percent photosynthetic photon flux density, PPFD (% Light, expressed as (PPFD, 400–700 nm range, at the terminal/total incoming PPFD) x 100); current needle nitrogen concentration; net photosynthesis (P_N) of *P. strobus* seedlings, and competitor biomass at Jacob Branch East and Jacob Branch West

periods, total carbon gain per seedling may have been reduced by low soil N and reduced light availability. Water stress was not an important factor determining P_N and growth at the Jacob Branch sites during the measurement periods examined in our study possibly owing to the relatively frequent rainfall. Competition from neighboring vegetation reduced resource availability at the JW site, decreasing P_N and diameter growth. Competition did not appear to be as important at JE, since competitors did not reduce light, N, or P_N of seedlings.

Further studies are needed to understand the effect of complex environmental variables on photosynthesis and growth of plants under field conditions. Most research to date has focused on plant responses and adaptations to single features of the environment, but plants in nature often encounter multiple stressors (Lauenroth et al. 1978; Mooney and Gulmon 1979; Chapin and Shaver 1985; Chapin et al. 1987). Environmental changes during the first year after planting strongly influence seedling survival and growth because the ability of seedlings to successfully adjust to environmental stresses is lowest during the first growing season (Sands 1984; Sheriff et al. 1986; Brand 1990). In subsequent growing seasons, competing vegetation may be increasingly important and demands of the planted trees for resources will change. Those changes are of little consequence, however, for seedlings that are **not** well established by the end of the first growing season.

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