

## Photosynthesis, water relations, and growth of planted *Pinus strobus* L. on burned sites in the southern Appalachians

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Received September 10, 1993

### Summary

We measured net photosynthesis, leaf conductance, xylem water potential, and growth of *Pinus strobus* L. seedlings two years after planting on two clear-cut and burned sites in the southern Appalachians. Multiple regression analysis was used to relate seedling net photosynthesis to vapor pressure deficit, seedling crown temperature, photosynthetically active radiation (PAR), needle N, xylem water potential, and soil water, and to relate seedling size and growth to physiological measurements (average net photosynthesis, leaf conductance, and cumulative xylem water potential), soil water, needle N, seedling crown temperature, and PAR. Seedling net photosynthesis was significantly related to vapor pressure deficit, midday water potential, crown temperature, and PAR ( $r^2 = 0.70$ ) early in the growing season (May) with vapor pressure deficit alone explaining 42% of the variation. As neighboring vegetation developed, light became more limiting and significantly reduced seedling net photosynthesis later in the growing season (July, August, and September). Final seedling diameter was significantly related to cumulative biomass, average photosynthetic rate, and needle N ( $r^2 = 0.68$ ).

*Keywords:* leaf conductance, microenvironment, seedling growth.

### Introduction

To create mixed stands of pine and oak, *Pinus strobus* L. is planted on dry ridge sites in the Southern Appalachians that have been clear-cut and burned. High-intensity prescribed fires are used before planting to reduce sprout vigor of *Kalmia latifolia* L. (Barden and Woods 1976), a common understory shrub, and to encourage tree species, such as oak, to sprout from the ground line and grow more vigorously (Van Lear 1991). Fire has both direct and indirect effects on site resource availability. For example, fire may affect soil nutrient status by: (a) adding nutrients in the form of organic matter, (b) altering the soil environment for microbial activity, and (c) reducing plant competition for nutrients. In addition, vegetation removal by clear-cutting and burning increases soil water, soil and air temperatures, and solar radiation to the forest floor. Soil temperatures on burned sites may be high where black surfaces increase radiant energy absorption. Extreme temperatures affect photosynthetic rates, carbohydrate reserves, and transpiration rates, all of which ultimately influence plant vigor. In contrast, increased nutrient and water availability increase vigor or mitigate other environmental stressors by improving photosynthetic capacity and plant water relations. Thus, an understanding of the relationship between multiple site resources and the physiology and growth response of planted *P. strobus* seedlings following prescribed fires is important to the evaluation of

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success of these mixed pine–oak forests.

Understanding the physiology and growth of planted pine seedlings requires knowledge of: (1) climate; (2) microenvironment, which is a modification of climate by topography, aspect, and other localized phenomena, such as shading from large logs or debris; (3) microsite variation in soil nutrient and water availability; (4) the presence of competing vegetation, which reduces essential resources such as nutrients, water, and light; and (5) internal controls or adaptations of the pine seedling to tolerate changes in resource availability. Thus, seedling growth is the result of complex, multivariate interactions among environmental variables and seedling physiology (Figure 1).

Much research has focused on plant responses and adaptations to single features of the environment, but plants in nature often encounter multiple stresses (Lauer et al. 1978, Mooney and Gulmon 1979, Chapin and Shaver 1985, Chapin et al. 1985). Incident radiation influences temperature, which affects metabolic rates and supplies energy to drive photosynthesis and transpiration (Kozłowski et al. 1991). Vapour stress reduces photosynthesis indirectly by causing stomatal closure and directly through effects on the photosynthetic apparatus (Brix 1962, 1972, 1979, Kozłowski et al. 1991). The availability of N has a large effect on the processes of initiation and leaf expansion as well as photosynthetic efficiency. There is considerable evidence that photosynthetic rate is strongly correlated with foliar N status in many  $C_3$  plants (Nair 1975, Gulmon and Chu 1981, DeJong 1982, DeJong and Doyle 1982, Field and Mooney 1986, Chazdon and Field 1987, Hirose and Werger 1987,

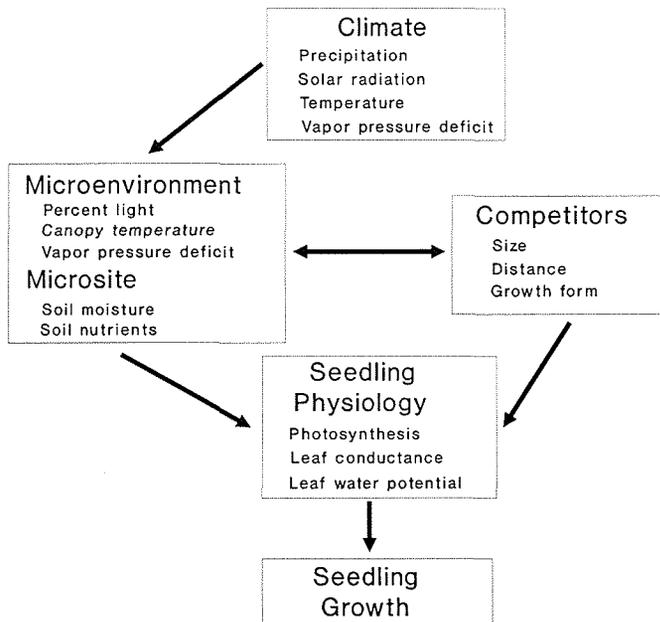


Figure 1. Conceptual model of the interrelationships among climate, microenvironment, and competitors, and how they affect pine seedling physiology and growth.

and Pearcy 1987, Evans 1989, Hull and Mooney 1990), but studies on conifers are less conclusive (van den Driessche 1972, Brix 1981, Linder and Rook 1984, S et al. 1986, DeLucia et al. 1989, Karlsson 1991). High temperatures can have direct effects on photosynthesis and respiration rates and indirect effects through increases in leaf-to-air vapor pressure deficit that affect transpiration rates and stomatal aperture (Berry and Björkman 1980).

We have previously reported the response of *Pinus strobus* L. seedlings during the first year after planting on burned sites (Elliott and Vose 1993). We attribute differences in responses in photosynthesis and growth to variations in leaf N and photosynthetically active radiation (PAR), but found no effect of water stress on seedling net photosynthesis or growth. The present study builds on past work by: (1) examining the effects of multiple environmental factors on physiology and growth of established *P. strobus* seedlings under field conditions; and (2) examining the effects of competing vegetation on resource availability and *P. strobus* seedling physiology and growth.

## Methods

### *Site description*

The chosen sites have been described by Swift et al. (1993). Briefly, the two sites, Jacob Branch East (JE) and Jacob Branch West (JW), are in the Blue Ridge physiographic province of the southern Appalachians (latitude 35°12' N, longitude 83°24' W). Midslope elevations are about 755 m. Soils are in the Coweeta complex, which includes fine loamy, mixed, mesic Typic Hapludults with scattered rock outcrops and a clay-loam layer at a depth of about 300–600 cm. Precipitation, humidity, air temperature, and wind speed were measured at a climate station located on the site (see Swift et al. 1993).

### *Experimental design*

In the summer of 1989, five 0.05-ha plots (15 × 33.3 m) were established at each site. All woody stems were cut on both sites in summer 1990 with no merchantable products removed. Site JE was cut between June 20 and July 24 and Site JW between August 3 and August 7. Sites were burned on separate days (September 18 and 19, 1990). In early spring (February–March) of 1991, 1-year-old bare root *P. strobus* seedlings were planted at 5 × 5 m spacing on the burned sites.

A 2.0-m<sup>2</sup> circular subplot was established around six randomly chosen *P. strobus* seedlings per plot within each burned site. In all, 60 subplots (6 seedlings × 5 × 2 sites) were used to follow the growth and development of the pine seedlings. One seedling per plot was randomly selected as a zero-density subplot, where all vegetation within the 2.0-m<sup>2</sup> subplot was manually removed at the beginning of the study and at intervals thereafter. For the physiological measurements (photosynthesis, transpiration, and leaf conductance), a subset of seedlings was selected from the original 60 subplots (three seedlings per plot) subjected to no competitors (zero density), or a moderate or high density of competitors.

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### *Plant measurements*

Diameter at ground level and height of each *P. strobus* seedling were measured a time of planting (March 1991) and at the end of each growing season (September 1991, 1992). These measurements were used to calculate diameter growth ( $\text{diameter}_{92} - \text{diameter}_{91}$ ) and height growth ( $\text{height}_{92} - \text{height}_{91}$ ). Initial diameter and height were used as covariates in the regression analysis. We used stem diameter squared ( $D^2$ ) times stem height (H) as a surrogate for total seedling size. Total seedling growth was calculated as the change in  $D^2H$  (i.e.,  $D^2H_{92} - D^2H_{91}$ ).

Preliminary observations of planted seedlings indicated wide variation in microsite factors, including proximity to partially burned logs, litter depth, and soil blackness, as well as abundance of competing vegetation. This variation provided a range in environmental conditions and competition intensities. The plots with moderate and high competition were selected from this natural variation in competition intensity.

On the circular subplots, each competitor species was identified and its stem diameter and stem height were measured in late June and early September to estimate competitor biomass. Aboveground biomass of competitors was estimated by species-specific regression equations (Elliott and Clinton 1993).

### *Microenvironment measurements*

Photosynthetically active radiation (PAR, 400–700 nm range) was measured with a portable light meter (Sunfleck Ceptometer, Decagon Devices, Pullman, WA, U.S.). The light meter measures average PAR incident on 80 sensors located at 10-cm intervals along a narrow, 800-mm-long sampling bar. Two measurements were taken at the heights of the terminal shoots of individual pine seedlings at 90° angles and averaged to quantify seedling light environment. To determine incoming PAR radiation at the time of each individual seedling measurement, PAR was measured in the open area adjacent to each seedling. Samples were obtained between 1100 and 1400 h solar time on mostly sunny days.

Soil water content adjacent to the 30 monitored pines was measured by domain reflectometry (1502B Metallic Time Domain Reflectometer, Tektronix, Beaverton, OR). A set of stainless steel rods measuring at 300 and 600 mm depth were placed vertically in the soil at a distance of 0.10 m from the pine seedling. Soil water was measured on the same day as PAR. Fine-wire thermocouples were placed in the midcrown of seedlings and temperature was measured at midday with a portable thermocouple reader. Photosynthetically active radiation, soil water content, and seedling crown temperature were measured weekly.

### *Physiological measurements*

Xylem water potential ( $\psi$ ) and needle N were measured on all 30 pine seedlings. Potentials at predawn ( $\psi_{PD}$ ) and midday ( $\psi_{MD}$ , 1100–1300 h solar time) were measured monthly with a pressure chamber (PMS Instruments Co., Corvallis, OR; Scholander et al. 1965) on individual fascicles. At the end of the growing season

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(September 29, 1992), two fascicles of current-year needles per seedling removed to determine N concentration. Needles were collected for N analysis in September to minimize destructive sampling. Needle N was determined Perkin-Elmer 20400 CHN Elemental Analyzer (Norwalk, CT).

Net photosynthesis ( $P_N$ ), transpiration ( $E$ ), and leaf conductance ( $g_l$ ) of seedling were measured monthly throughout the growing season (May–September 1992) with a portable photosynthesis system and a narrow-leaf Parkinson chamber (ADC LCA-3, Analytical Development Co. Ltd., Hoddesdon, Herts, operating in differential mode. Measurements were taken on clear sunny between 1100 and 1300 h solar time when incoming PAR was above  $800 \mu\text{mol m}^{-2} \text{s}^{-1}$ , which represents light saturation for *P. strobus* (Maier 1990). On the sampling date (May), only older foliage was sampled; on the second sampling both current-year and older foliage were sampled. On the last three sampling older foliage on some of the seedlings had dry brown tips so only current-year foliage was measured. Two measurements per needle age class were taken and subsequently averaged to provide a mean value by needle age class for each seedling. In all measurements were taken under ambient conditions. Self-shading within the chamber was minimized by ensuring that needles did not overlap. Needle surface area (sides) was estimated by multiplying length  $\times$  width  $\times$  number of needles  $\times$  3 sides.

#### *Statistical analysis*

Relationships among physiological growth and environmental variables were examined by multiple regression analyses performed with the SAS software package (SAS Institute, Inc., Cary, NC, 1987). Statistical analysis proceeded in a sequential fashion to relate physiological responses to microenvironment, and seedling size and growth to microenvironment, competitor biomass, and average  $P_N$  rate per seedling. First, we related  $\psi_{PD}$  and  $\psi_{MD}$  to soil water content at 300 and 600 mm soil depth, vapor pressure deficit (VPD; estimated from relative humidity data, collected at the climate station, and seedling temperatures), and to temperature measurements at seedling crowns. Second,  $P_N$  and  $g_l$  were related to PAR,  $\psi_{PD}$  and  $\psi_{MD}$ , soil water content at 300 and 600 mm soil depth, seedling temperature, VPD and needle N concentration. Third, the influences of competitor biomass on microenvironmental conditions of the *P. strobus* seedlings were examined by correlating competitor biomass with water availability (indexed by cumulative  $\Psi_{PD}$  and  $\Psi_{MD}$ ; calculated as  $-\sum \psi$  for the five sample dates, average soil water and VPD experienced by each seedling for the five sample dates), available light (indexed by average PAR experienced by each seedling for the five sample dates), and needle N (concentration of current-year needles collected in early September). Seedling size and growth were correlated with average values for each seedling's microenvironmental conditions and its average  $P_N$  rate over the 5-month growing season. Finally, stepwise multiple regression models were examined to assess the ability of multiple variables to predict seedling growth,  $P_N$ , and  $g_l$ . Models were evaluated based on graphical and regression analyses, and comparisons of coefficients of determination ( $r^2$ ) and mean

errors. To test for site differences, we included site as a dummy variable in multiple regression models. Because microenvironment and plant physiology processes are typically highly variable in field conditions, we chose a significant alpha level of 0.10 for variable entry into the  $P_N$  and  $g_1$  models, and the seedling and growth models.

## Results

### *Climate and microenvironment*

Precipitation from June 18 (Day 169) through August 12 (Day 224) totalled 64 mm. In the last week in August (Days 235–241), however, more than 100 mm of precipitation fell (Figure 2). In May (Days 137–138), 6.8 mm of rain fell 2 days before the measurement of  $P_N$ , but no additional rain fell within 7 days of measurement dates. In June (Days 170–171), only 0.5 mm of rain fell 3 days before  $P_N$  measurement. In July (Days 191–192), 1.0 mm of rain fell 3 days before measurement, and a total of 5.6 mm fell during the 7-day period. In August (Days 237–238), 16 mm of rain fell the day before  $P_N$  measurement, and a total of 95.5 mm fell in the 7-day period. Solar radiation and VPD fluctuated with rainfall events, both were higher without cloud cover. By mid-April, midday temperatures ranged from 17 to 34 °C with the highest temperatures occurring in late June and early July (Figure 2).

Soil water content was around 20% through mid-June at both 300 and 600 mm depths. A decline in soil water content (Figure 3) coincided with the decrease in precipitation (Figure 2). From mid-June until August 7 (Day 219), soil water content declined from 16% to less than 8%. Enough precipitation fell in mid-August to replenish soil water. Vapor pressure deficit was highest in the first two weeks of June (Day 121 to Day 131) and again in July (Day 190), when the temperature peaked at 33 °C (Figure 3). Seedling crown temperatures averaged about 1.5 °C higher than soil temperatures throughout the growing season. Average light availability decreased from 95 to 75% of incoming PAR by May 21 (Figure 3) with the development of hardwood leaf area.

### *Seedling physiology related to microenvironment*

Average  $\Psi_{PD}$  was lowest on July 11, when average soil water at 300 mm soil depth was lowest and average temperatures in seedling canopies were highest (Table 1). Average PAR incident on seedlings increased from May to June, then declined in August and September with the development of competing vegetation. Average needle N (Table 1) was 74% of that found in these *P. strobus* seedlings during their first year after planting. Nitrogen concentrations ranged from 0.70 to 1.65% in 1992 compared to 0.67 to 2.20% in 1991 (Elliott and Vose 1993).

Predawn water potential was significantly related to VPD in June ( $r = 0.39$ ,  $P = 0.04$ ) and  $\Psi_{MD}$  was significantly related to percent soil water at 600 mm soil depth in July ( $r = 0.44$ ,  $P = 0.02$ ). No other significant relationships were found between

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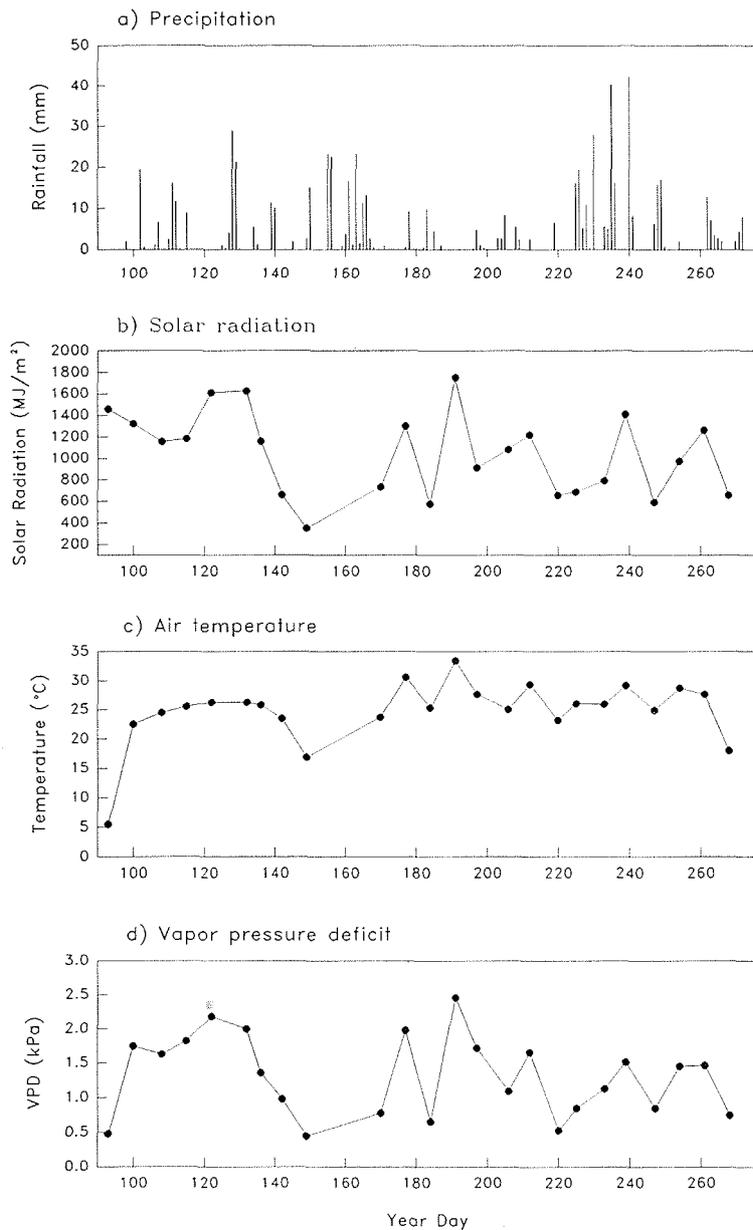


Figure 2. Growing season, April 2 (Day 93) to September 30 (Day 268), climate variables of the Branch sites: (a) daily precipitation; (b) average daily solar radiation; (c) average air temperature; (d) average vapor pressure deficit between 1100 and 1400 h solar time.

$\Psi_{PD}$  or  $\Psi_{MD}$  and percent soil water, VPD, or seedling crown temperature for other sampling date. Vapor pressure deficit and temperature were the only environmental variables that were significantly related to  $g_1$  (Table 2). Temperature explained 54% of the variability in  $g_1$  in May (Days 137 and 138), 36% in July

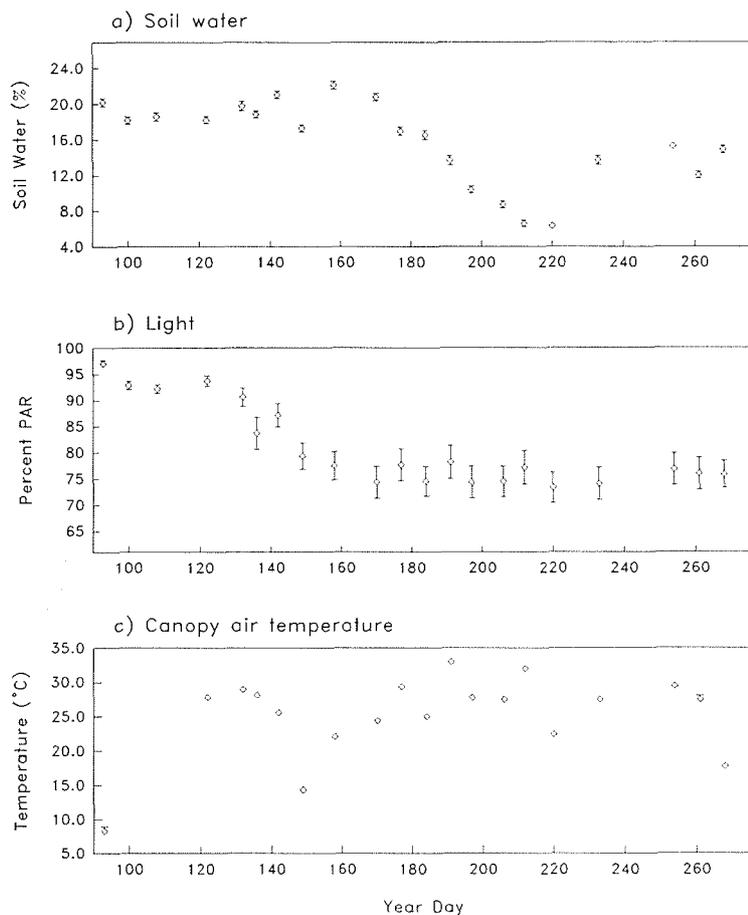


Figure 3. Growing season microenvironmental variables: (a) soil water content at 300 mm soil depth measured by time domain reflectometry; (b) percent potential photosynthetically active radiation ( $P_N$ ) and (c) seedling crown air temperature measured at midday. Soil water content at 600 mm soil depth not shown but followed the same pattern as soil water content at 300 mm. Average values with standard error bars of all seedlings are shown.

191 and 192), and 32% in August (Days 237 and 238) (Table 2).

Average  $P_N$  of current-year needles was highest in July (Days 191–192), and  $E_{g1}$  were lowest, indicating a potential uncoupling from environmental regulation. This was a result of developmental processes in the plant (Maier and Teskey 1992). Because water, precipitation, and  $\Psi_{PD}$  were lowest on Days 191–192, the data indicate that the  $P_N$  values may have been a result of internal controls rather than external environmental conditions (Teskey et al. 1986). It is likely that a strong sink for carbon provided by new growth resulted in the higher photosynthetic rates (Maier and Teskey 1992).

Seasonal variations in  $P_N$  of *P. strobus* seedlings were correlated with many factors whose relative importance changed as the growing season progressed. Thus, separa-

Table 1. Average environmental and physiological conditions of *Pinus strobus* seedlings. Values in parentheses are standard errors of the mean,  $n = 30$ . Abbreviations:  $\Psi_{PD}$  = predawn needle water potential;  $\Psi_{MD}$  = midday needle water potential; Soil WC<sub>300</sub> = soil water content at 0–300 mm depth measured with TDR; Soil WC<sub>600</sub> = soil water content at 0–600 mm depth measured with TDR; Temperature = temperature measured in the seedling crown; PAR = photosynthetically active radiation measured at the terminal of the *P. strobus* seedlings;  $P_N$  = net photosynthesis ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ );  $g_1$  = leaf conductance ( $\text{mol m}^{-2} \text{s}^{-1}$ ); ns = not sampled; na = not available.

Variable	Julian day				
	137 and 138	170 and 171	191 and 192	237 and 238	261 and 262
$\Psi_{PD}$ (MPa)	-0.43 (0.022)	-0.64 (0.036)	-0.82 (0.056)	-0.28 (0.016)	-0.56 (0.022)
$\Psi_{MD}$ (MPa)	-1.18 (0.043)	-1.43 (0.069)	-1.44 (0.089)	-1.30 (0.083)	-1.64 (0.054)
Soil WC <sub>300</sub> (%)	19.4 (0.415)	20.5 (0.354)	14.2 (0.742)	14.5 (0.579)	15.6 (0.415)
Soil WC <sub>600</sub> (%)	21.4 (0.601)	22.7 (0.749)	18.2 (0.545)	15.6 (0.520)	16.7 (0.520)
Temperature (°C)	28.1 (0.607)	24.6 (0.373)	33.7 (0.490)	27.7 (0.366)	18.3 (0.366)
PAR ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	908 (60.61)	989 (65.98)	966 (75.72)	820 (65.09)	624 (65.09)
Competitor biomass (g per 2.0 m <sup>2</sup> plot)	ns	384.7 (70.1)	ns	ns	483. (70.1)
Needle N (%)	ns	ns	ns	ns	1.07 (0.071)
$P_N$ (current needles)	na	3.48 (0.206)	6.08 (0.494)	3.48 (0.256)	3.65 (0.256)
$E$ (current needles)	na	1.43 (0.071)	0.40 (0.032)	1.18 (0.081)	1.15 (0.081)
$g_1$ (current needles)	na	0.099 (0.008)	0.033 (0.004)	0.151 (0.036)	0.091 (0.036)
$P_N$ (older needles)	5.38 (0.446)	2.23 (0.182)	na	na	na
$E$ (older needles)	0.37 (0.032)	1.15 (0.098)	na	na	na
$g_1$ (older needles)	0.036 (0.006)	0.076 (0.012)	na	na	na

models were needed for each sampling date to explain the variation in  $P_N$  during the growing season. In May (Days 137 and 138),  $P_N$  was significantly related to  $\Psi_{MD}$ , temperature, PAR and VPD. Vapor pressure deficit explained 42% of the variability in  $P_N$  and temperature, and  $\Psi_{MD}$  contributed an additional 21%. In June (Days 170 and 171),  $P_N$  was only related to  $\Psi_{PD}$ , which explained 18% of the variability. In July (Days 191 and 192), PAR became important in predicting  $P_N$ , explaining 17% of the variation. By August (Days 237 and 238), PAR explained 17% of the variability in  $P_N$  and crown temperature explained an additional 8%. The variability of  $P_N$  was not significantly related to needle N concentration.

In the seasonal models, crown temperature, VPD, and PAR explained 35% of the variability in  $P_N$ . Site,  $\Psi_{PD}$ , and VPD explained 12% of the variation in  $g_1$ .

#### *Competitors related to microenvironment, seedling physiology, and growth*

Competitor biomass was negatively correlated with average crown temperature, average percent light, and needle nitrogen; thus, it was negatively related to pine seedling diameter, height and D<sup>2</sup>H growth (Table 3). We found no significant relationship between competitor biomass and needle water potentials or soil water content (Table 3), indicating that competitors did not reduce available water. Average seedling diameter of each seedling was positively related to average seedling temperature and percent light. Seedling diameter and D<sup>2</sup>H growth were correlated with average percent light. Average VPD was positively related to seedling height growth (Table 3).

Table 2. Multiple regression models for *Pinus strobus* seedling photosynthetic rate ( $P_N$ ) and conductance ( $g_1$ ) for each sampling date. Abbreviations:  $\psi_{PD}$  = predawn needle water potential (abs value);  $\psi_{MD}$  = midday needle water potential (absolute value); VPD = vapor pressure deficit; P, photosynthetically active radiation; Temp = temperature measured in the seedling crown.

Julian day	Model	Partial $r^2$	P-value	Model $r^2$	
137 and 138	$P_N = 0.840667 - 3.62491 (\psi_{MD})$	0.116	0.007	0.699	
	+ 0.69146 (Temp)	0.103	0.084		
	- 0.00174 (PAR)	0.056	0.041		
	- 0.63323 (VPD)	0.424	0.0001		
	$g_1 = -0.05633 + 0.00788 (\text{Temp})$	0.358	0.0001		0.536
	- 0.00898 (VPD)	0.178	0.020		
170 and 171 <sup>1</sup>	$P_N = 3.57933 - 2.10915 (\psi_{PD})$	0.180	0.022	0.180	
	$g_1 = \text{no predictive model}$				
191 and 192	$P_N = 3.49452 + 0.00268 (\text{PAR})$	0.168	0.027	0.168	
	$g_1 = -0.022948 + 0.00339 (\text{Temp})$	0.080	0.083	0.361	
	- 0.00333 (VPD)	0.281	0.003		
237 and 238	$P_N = -6.20405 + 0.89880 (\text{Site})$	0.148	0.004	0.690	
	+ 0.22926 (Temp)	0.082	0.015		
	+ 0.002426 (PAR)	0.461	0.0001		
	$g_1 = -0.45642 + 0.05543 (\text{Temp})$	0.127	0.034	0.320	
	- 0.06250 (VPD)	0.194	0.015		
261 and 263	$P_N = -2.79206 + 0.26557 (\text{Temp})$	0.209	0.002	0.535	
	+ 0.00252 (PAR)	0.0326	0.001		
	$g_1 = \text{no predictive model}$				
Seasonal model <sup>2</sup>	$P_N = -0.5389 + 0.2888 (\text{Temp})$	0.216	0.0001	0.353	
	- 0.25147 (VPD)	0.114	0.0001		
	+ 0.00098 (PAR)	0.216	0.029		
	$g_1 = 0.23175 - 0.03725 (\text{Site})$	0.028	0.021	0.117	
	- 0.06033 ( $\psi_{PD}$ )	0.024	0.047		
	- 0.00432 (VPD)	0.028	0.027		

<sup>1</sup> Models for Days 170 and 171 were based on current foliage measurements of  $P_N$  and  $g_1$ .

<sup>2</sup> The seasonal model includes measurements from all sampling dates combined.

Competitor biomass and needle N explained 53% of the variability in final seedling diameter and 48% of the variability in D<sup>2</sup>H growth of seedlings (Table 4). Average percent light explained 31% of the variability in diameter growth. Competitor biomass, average VPD, and needle N explained 49% of the variability in height growth. In four of the six models, needle N concentration explained more than 2% of the variation in the seedling size and growth (Table 4). Although competitor biomass was inversely related to needle N, inclusion of N concentration reduced  $r^2$  of multiple regression models (Table 4). Average  $P_N$  accounted for less than 2% of the variation in final diameter, but accounted for 14% of the variation in final height (Table 4).

Table 3. Correlation coefficients relating competitor biomass and cumulative needle water potential (absolute value), soil water content, temperature, light, vapor pressure deficit (VPD), and net photosynthesis ( $P_N$ ), averaged over the growing season, and needle N and seedling growth. Abbreviations: diameter growth (diameter<sub>92</sub> – diameter<sub>91</sub>); GRH = height growth (height<sub>92</sub> – height<sub>91</sub>); GRD = diameter<sup>2</sup> × height growth (D<sup>2</sup>H<sub>92</sub> – D<sup>2</sup>H<sub>91</sub>); BIOM = competitor biomass measured in June; % light = (photosynthetically active radiation measured in the open/photosynthetically active radiation measured at the terminal of each seedling) × 100, averaged over the growing season. Other abbreviations are the same as in Table 1.

Variable	BIOM	GRD	GRH	GRD <sup>2</sup> H	$P_N$
$\Sigma\Psi_{PD}$	-0.119	-0.197	-0.141	-0.241	-0.12
$\Sigma\Psi_{MD}$	0.090	-0.081	-0.062	-0.110	-0.12
Soil WC <sub>300</sub>	0.057	-0.056	0.081	-0.002	-0.12
Soil WC <sub>600</sub>	0.184	0.019	-0.133	-0.122	0.18
Temp	-0.349*	0.228	0.107	0.180	0.40
% light	-0.571***	0.561***	0.337	0.497**	0.56
VPD	-0.173	0.209	0.365*	0.292	0.01
$P_N$	-0.297	0.351*	0.308	0.321	–
Needle N	-0.502**	-0.005	-0.277	-0.208	0.11
BIOM	–	-0.482**	-0.369*	-0.467**	-0.29
GRD	-0.482**	–	–	–	0.35
GRH	-0.369*	–	–	–	0.30
GRD <sup>2</sup> H	-0.467**	–	–	–	0.32

\*, \*\*, \*\*\* denote  $P < 0.05$ , 0.01, and 0.001, respectively.

Table 4. Multiple regression models for *Pinus strobus* seedling size and growth ( $n = 30$ ). Abbreviations: BIOM = competitor biomass (g per 2.0 m<sup>2</sup> plot) measured in June 1992;  $P_N$  = net photosynthesis (m<sup>-2</sup> s<sup>-1</sup>) averaged over the growing season; % light = (photosynthetically active radiation measured in the open/photosynthetically active radiation measured at the terminal of each seedling) × 100, averaged over the growing season; VPD = vapor pressure deficit averaged over the growing season; GRD = diameter<sup>2</sup> × height.

Model	Partial $r^2$	$P$ -value
Diameter = 1.220986 + 0.844386 (initial diameter)	0.106	0.011
– 0.000464 (BIOM)	0.294	0.002
+ 0.060639 ( $P_N$ )	0.044	0.077
– 0.620042 (Needle N)	0.236	0.001
Diameter growth = -0.1845488 + 0.006349 (% light)	0.315	0.001
Height = 3.254881 + 44.633375 (initial diameter)	0.126	0.040
+ 4.961099 ( $P_N$ )	0.145	0.038
Height growth = 28.195286 – 0.013139 (BIOM)	0.136	0.045
+ 1.245138 (VPD)	0.062	0.088
– 22.62129 (Needle N)	0.286	0.001
D <sup>2</sup> H = 136.00480 + 93.56069 (initial diameter)	0.068	0.055
– 0.065731 (BIOM)	0.215	0.010
– 95.31681 (Needle N)	0.279	0.001
D <sup>2</sup> H growth = 147.38055 – 0.058296 (BIOM)	0.218	0.009
– 81.96911 (Needle N)	0.262	0.001

## Discussion

Total rainfall appeared adequate for the 5-month growing season, but periods of precipitation reduced soil water content for several consecutive weeks. We found VPD was important in regulating  $g_1$  and  $P_N$  of seedlings early in the growing season even when soil water was relatively high. However, the amount and duration of precipitation before measurement of  $P_N$  early in the growing season were much less than in August and September. The significant relationship between  $\Psi_{MD}$ , VPD, and  $P_N$  early in the growing season suggests a closer coupling of the photosynthetic apparatus and seedling water relations (Sands et al. 1984, Seiler and Cazell 1990, Pavlik Barbour 1991, Pallardy et al. 1991) than was observed in pine seedlings sample 1991 (Elliott and Vose 1993). In 1991, no significant relationship between  $P_N$  and needle water potential was found. By midseason, water stress was alleviated by increased precipitation, and PAR explained more of the variation in  $P_N$  because of the increasing leaf area of the hardwood competitors. Although the same variables (i.e., VPD, crown temperature, and PAR) were as important in the seasonal models for individual dates, the seasonal models for  $P_N$  and  $g_1$  were more explanatory.

Competitors reduced light availability, and light was the primary environmental factor limiting pine seedling growth (Table 3). However, both needle N (pine) and competitor biomass were significant variables in the regression models. An interaction of light and N or other unexplained factors may also be important in determining pine seedling growth and size. Competitor biomass and percent leaf N were significantly correlated, but competitor biomass enters the models for diameter,  $D^2H$ , and  $D^2H$  growth rather than light, and needle N enters as a negative parameter. Our data suggest that something related to competitor biomass other than environmental variables measured in this study may be contributing to the variability in *P. strobus* growth. Hence, competitor biomass in these models is an indirect integrator of light availability and additional factors not explained by the environmental variables measured.

Within a range of competitor biomass, seedling size and growth decreased as needle N concentration increased. At a fixed level of competitor biomass, needle N concentration had a negative effect on diameter, possibly because of variation in the vertical structure of the competitors. When tall competitors shade seedlings, N is concentrated in foliage, whereas when short competitors do not shade seedlings, growth dilution of N may occur. Dilution of percent leaf N may occur as carbon is imported into the leaf for expansion and as a result of variation in starch content of the needles or both (Linder and Flower-Ellis 1992). In the high biomass plot (> 900 g per plot) with tall competitors and low irradiance, needle N concentration was consistently higher. Most studies report a positive relationship between nitrogen concentration (see Field and Mooney 1986, Field 1991, and Reich et al. 1992 for reviews) and photosynthetic rate under saturating light intensity, which subsequently result in greater diameter growth at higher N concentrations. However, in low light, carbon assimilation is reduced and as a result, N may concentrate

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foliage. Shaded plants invest large quantities of N in light-harvesting pigment proteins, but make only small investments in ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) and other CO<sub>2</sub>-processing enzymes (Björkman and Evans 1989). Many woody species have shown higher N concentrations in shaded environments than in open environments (Margolis et al. 1988, McDonald 1992, Midgley et al. 1992, Elliott and White 1993, Morris et al. 1993). For example, Margolis et al. (1988) found that nitrogen concentration was 55% higher in *banksiana* Lamb. seedlings in low-light (shade cloth; 50% reduction in photosynthetic density) treatments than in high-light treatments. From our data, however, it is uncertain whether growth dilution or a nutrient imbalance (Linder and Rook 1986) was responsible for the negative relationship of needle nitrogen concentration and seedling growth. We did not measure soil nutrient availability or foliar nutrient concentrations.

Developmental components as well as environmental controls contribute to the photosynthesis of *P. strobus* seedlings. Seedling  $P_N$  was highest in early July, when soil water was low and VPD was high, but was not related to any measure of water stress. At this time, internal control of  $P_N$  may have been more important than environmental controls. Maier and Teskey (1992) found strong internal control of photosynthesis during the period of new foliage growth for mature *P. strobus* compared two days, with similar environmental conditions, when current-year foliage was actively growing (June 21) and when current-year foliage was expanded (July 20). When foliage and branches were growing, midday  $P_N$  increased, particularly in 1-year-old foliage. However,  $P_N$  in 1-year-old foliage began to decline when new foliage was 70 to 80% expanded. This pattern of photosynthetic rate during foliar growth was similar for both 1986 and 1987, despite differences in rainfall.

Although photosynthesis is the primary source of carbon for growth, the differences between photosynthesis and productivity are often not statistically significant (Gifford and Evans 1981, Kuppens et al. 1988, Nelson 1988). Productivity is dependent on a variety of variables including carbon uptake, respiration, photosynthate partitioning, leaf area index, leaf life span, light interception and utilization, and stress tolerance. Net photosynthesis was positively correlated with diameter growth (Elliott and Vose 1993). However, we found that average photosynthetic rate and diameter growth were not as well correlated in 1992 as in 1991 ( $r = 0.35$  versus  $0.69$ ). The ratio of photosynthetic to nonphotosynthetic tissue in seedlings is typically large compared to ratios in saplings and trees; thus, proportionately less photosynthate is lost in woody respiration. As seedlings grow, partitioning of photosynthate to maintenance respiration becomes increasingly important and respiration assumes an increasing fraction of the gross photosynthesis (Waring and Schlesinger 1985).

The empirical models developed in our study emphasize the importance of environmental factors (biotic and abiotic) influences on *P. strobus* physiology and growth. Climate factors have both a direct and an indirect influence on growth, and these influences are modified by climatological and site conditions. Our study represents an

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attempt to integrate the factors outlined in Figure 1. However, a more mechanistic modeling approach that accounts for multi-factor influences and includes above- and below-ground partitioning, respiration, and leaf area will be necessary to develop a more complete understanding of *P. strobus* growth and physiological processes.

#### Acknowledgments

We thank Patsy Clinton for her help in collecting field data. This manuscript was improved by comments from Drs. Paul J. Hanson, Martha R. McKeivlin, John Seiler, Chris A. Maier, Wayne T. Swank and anonymous reviewers.

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