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

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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 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 1992) 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 competitor 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 site preparation fires are used before planting to reduce sprout vigor of *Kalnria 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 ashed 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 input to the forest floor. Soil temperatures on burned sites may be high where blackened 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 may increase vigor or mitigate other environmental stressors by improving photosynthetic capacity and plant water relations. Thus, an understanding of the relationships between multiple site resources and the physiology and growth response of planted *P. strobus* seedlings following prescribed fires is important to the evaluation of the 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 the climate by topography, aspect, and other localized phenomena, such as shading by 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 (Lauenroth et al. 1978, Mooney and Gulmon 1979, Chapin and Shaver 1985, Chapin et al. 1987). Incident radiation influences temperature, which affects metabolic rates and supplies energy to drive photosynthesis and transpiration (Kozlowski et al. 1991). Water stress reduces photosynthesis indirectly by causing stomatal closure and directly through effects on the photosynthetic apparatus (Brix 1962, 1972, 1979, Kozlowski 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 and C_4 plants (Natr 1975, Gulmon and Chu 1981, DeJong 1982, DeJong and Doyle 1985, Field and Mooney 1986, Chazdon and Field 1987, Hirose and Werger 1987, Sage

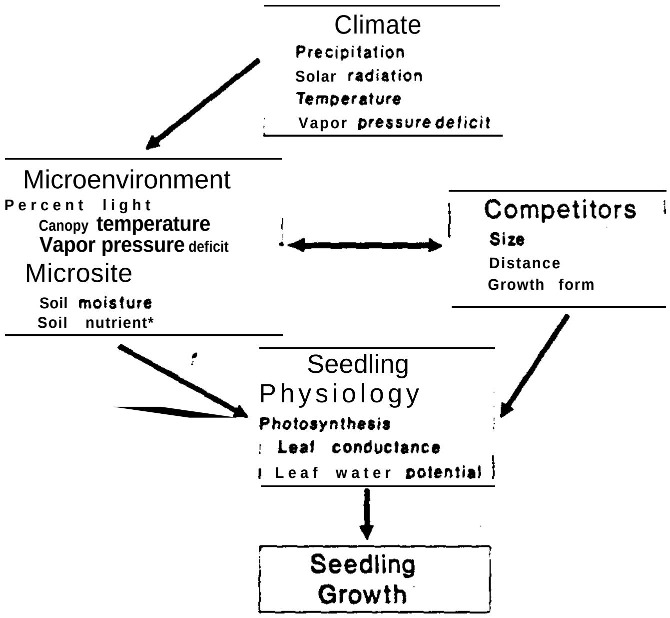


Figure I. Conceptual model of the interrelationships among climate, microenvironment, and competitors and how they affect pine seedling physiology and growth.

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, Sheriff 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 attributed the 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 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 300-600 mm. 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 0.05ha plots (15 x 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 x 5 m spacing on the burned sites.

A 2.0-m^2 circular subplot was established around six randomly chosen *P. strobus* seedlings per plot within each burned site. In all, 60 subplots (6 seedlings x 5 plots x 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^2 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.

Plant measurements

Diameter at ground level and height of each *P. strobus* seedling were measured at the time of planting (March 1991) and at the end of each growing season (September 1991, 1992). These measurements were used to calculate diameter growth (diameters? – diameter$_{91}$) and height growth (height$_{92}$ – heights]). 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 surface 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 competitor intensity.

On the circular subplots, each competitor species was identified and its basal diameter and stem height were measured in late June and early September to estimate competitor biomass. Aboveground biomass of competitors was estimated by site- and 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, USA). The light meter measures average PAR incident on 80 sensors located at IO-mm 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 solar 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 time domain reflectometry (1502B Metallic Time Domain Reflectometer, Tektronix, Beaverton, OR). A set of stainless steel rods measuring at 300 and 600 mm depths 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 (ψ) and needle N were measured on all 30 pine seedlings. Potentials at predawn (ψ_{PD}) and midday (ψ_{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

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

Net photosynthesis (P_N), transpiration (E), and leaf conductance (g_l) of each seedling were measured monthly throughout the growing season (May-September 1992) with a portable photosynthesis system and a narrow-leaf Parkinson leaf chamber (ADC LCA-3, Analytical Development Co. Ltd., Hoddesdon, Hens, U.K.) operating in differential mode. Measurements were taken on clear sunny days between 1100 and 1300 h solar time when incoming PAR was above 800 μmol m^{-2} s-t, which represents light saturation for *P. strobus* (Maier 1990). On the first sampling date (May), only older foliage was sampled; on the second sampling date, both current-year and older foliage were sampled. On the last three sampling dates, 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 cases, measurements were taken under ambient conditions. Self-shading within the cuvette was minimized by ensuring that needles did not overlap. Needle surface area (all sides) was estimated by multiplying length x width x number of needles in the cuvette x 3 sides.

Statistical analysis

Relationships among physiological growth and environmental variables were determined 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 ψ_{PD} and ψ_{MD} to soil water content at 300 and 600 mm soil depth, to vapor pressure deficit (VPD; estimated from relative humidity data, collected from the climate station, and seedling temperatures), and to temperature measured in seedling crowns. Second, P_N and g_l were related to PAR, ψ_{PD} and ψ_{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 Ψ_{PD} and Ψ_{MD}; calculated as $-\Sigma\,\psi$ for the five sample dates, average soil water and VPD experienced by each seedling for the five sample dates), available light (indexed by average percent light 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 residual analyses, and comparisons of coefficients of determination (r^2) and mean square errors. To test for site differences, we included site as a dummy variable in all multiple regression models. Because microenvironment and plant physiological 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_l models, and the seedling size and growth models.

Results

Climate and microenvironment

Precipitation from June 18 (Day 169) through August 12 (Day 224) totalled only 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 the 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, and 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 soil 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 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 May (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 air 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 Ψ_{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 the 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 Ψ_{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

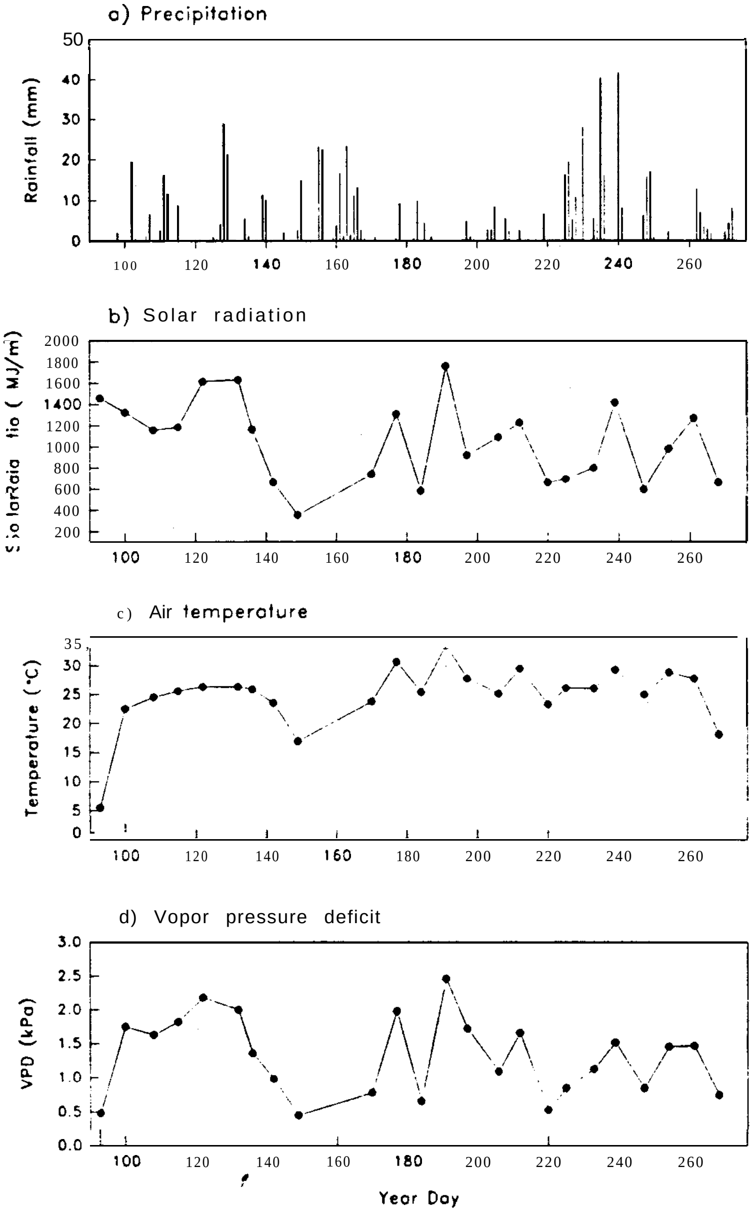
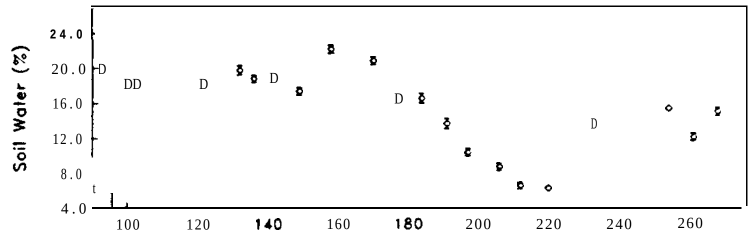


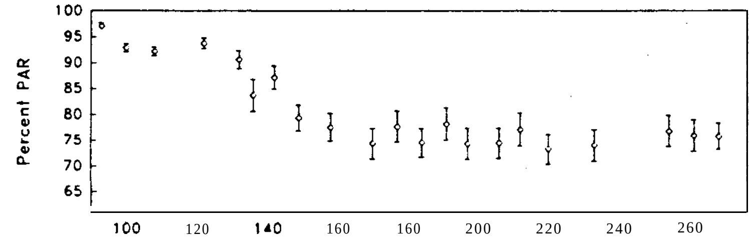
Figure 2. Growing season, April 2 (Day 93) to September 30 (Day 268), climate variables of the Jacob Branch sites: (a) daily precipitation (b) average daily solar radiation; (c) average air temperature between 1100 and 1400 h solar time; and (d) average vapor pressure deficit between 1100 and 1400 h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

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

a) Soil water



b) Light



c) Canopy air temperature

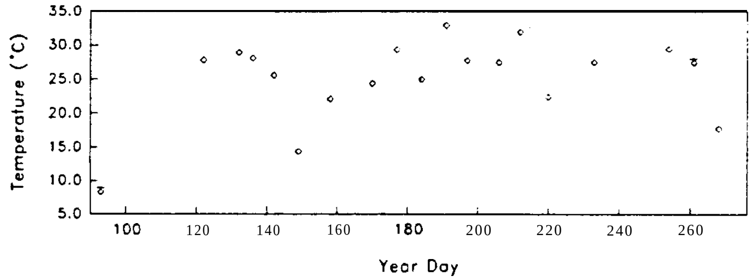


Figure 3. Growing season microenvironmental variables: (a) soil water content at 300 mm soil depth measured by time domain reflectometry; (b) percent potential photosynthetically active radiation (PAR); and (c) seedling crown air temperature measured at midday. Soil water content at 600 mm soil depth is 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 and g_l were lowest, indicating a potential uncoupling from environmental regulation as a result of developmental processes in the plant (Maier and Teskey 1992). Because soil water, precipitation, and Ψ_{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, separate

Table 1. Average environmental and physiological conditions of *Pinus strobus* seedlings. Values in parentheses are standard errors of the mean, $n = 30$. Abbreviations: ψ_{PD} = predawn needle water potential; ψ_{MD} = midday needle water potential; Soil WC_{300} = soil water content at 0-300 mm depth measured with TDR; Soil WC_{600} = 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 (μmol $m^{-2} s^{-1}$); E = transpiration (mmol $m^{-2} s^{-1}$); g_l = leaf conductance (mol $m^{-2} s^{-1}$); ns = not sampled; na = not available.

Variable	Julian day				
	137 and 138	170 and 171	191 and 192	237 and 238	261 and 263
ψ_{PD} (MPa)	-0.43 (0.022)	-0.64 (0.036)	-0.82 (0.056)	-0.28 (0.016)	-0.56 (0.038)
ψ_{MD} (MPa)	-1.18 (0.043)	-1.43 (0.069)	-1.44 (0.089)	-1.30 (0.083)	-1.64 (0.086)
Soil WC_{300} (%)	19.4 (0.415)	20.5 (0.354)	14.2 (0.742)	14.5 (0.579)	15.6 (0.489)
Soil WC_{600} (%)	21.4 (0.601)	22.7 (0.749)	18.2 (0.545)	15.6 (0.520)	16.7 (0.540)
Temperature (°C)	28.1 (0.607)	24.6 (0.373)	33.7 (0.490)	27.7 (0.366)	18.3 (0.328)
PAR (μmol $m^{-2} s^{-1}$)	908 (60.61)	989 (65.98)	966 (75.72)	820 (65.09)	624 (36.40)
Competitor biomass (g per 2.0 m^2 plot)	ns	384.7 (70.1)	ns	ns	483.7 (84.2)
Needle N (%)	ns	ns	ns	ns	1.07 (0.039)
P_N (current needles)	na	3.48 (0.206)	6.08 (0.494)	3.48 (0.256)	3.65 (0.187)
E (current needles)	na	1.43 (0.071)	0.40 (0.032)	1.18 (0.081)	1.15 (0.038)
g_l (current needles)	na	0.099 (0.008)	0.033 (0.004)	0.151 (0.036)	0.091 (0.003)
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_l (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 and g_l during the growing season. In May (Days 137 and 138), P_N was significantly related to Ψ_{MD}, temperature, PAR and VPD. Vapor pressure deficit explained 42% of the variability in P_N and temperature, and Ψ_{MD} contributed an additional 21%. In June (Days 170 and 171), P_N was only related to Ψ_{PD}, which explained 18% of the variation. 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 46% of the variability in P_N and crown temperature explained an additional 8%. The value of P_N was not significantly related to needle N concentration.

In the seasonal models, crown temperature, VPD, and PAR explained 35% of the variation in P_N. Site, Ψ_{PD}, and VPD explained 12% of the variation in g_l.

Competitors related to microenvironment, seedling physiology, and growth

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

Table 2. Multiple repression models for *Pinus strobus* seedling photosynthetic rate (P_N) and leaf conductance (g_l) for each sampling date. Abbreviations: ψ_{PD} = predawn needle water potential (absolute value); ψ_{MD} = midday needle water potential (absolute value); VPD = vapor pressure deficit; PAR = photosynthetically active radiation; Temp = temperature measured in the seedling crown.

Julian day	Model	Partial r^2	P-value	Model r^2	n
137 and 138	P_N = 0.840667 − 3.62491 (ψ_{MD})	0.116	0.007	0.699	30
	+ 0.69146 (Temp)	0.103	0.084		
	− 0.00174 (PAR)	0.056	0.041		
	− 0.63323 (VPD)	0.424	0.0001		
	g_l = − 0.05633 + 0.00788 (Temp)	0.358	0.0001	0.536	30
	− 0.00898 (VPD)	0.178	0.020		
170 and 171[1]	P_N = 3.57933 − 2.10915 (ψ_{PD})	0.180	0.022	0.180	30
	g_l = no predictive model				
191 and 192	P_N = 3.49452 + 0.00268 (PAR)	0.168	0.027	0.168	29
	g_l = − 0.022948 + 0.00339 (Temp)	0.080	0.083	0.361	
	− 0.00333 (VPD)	0.281	0.003		
237 and 238	P_N = − 6.20405 + 0.89880 (Site)	0.148	0.004	0.690	30
	+ 0.22926 (Temp)	0.082	0.015		
	+ 0.002426 (PAR)	0.461	0.0001		
	g_l = − 0.45632 + 0.05543 (Temp)	0.127	0.034	0.320	30
	− 0.06250 (VPD)	0.194	0.015		
261 and 263	P_N = − 2.79206 + 0.26557 (Temp)	0.209	0.002	0.535	30
	+ 0.00252 (PAR)	0.0326	0.001		
	g_l = no predictive model				
Seasonal model[2]	P_N = − 0.5389 + 0.2888 (Temp)	0.216	0.0001	0.353	149
	− 0.25147 (VPD)	0.114	0.0001		
	+ 0.00098 (PAR)0.216	0.022	0.029		
	g_l = 0.23175 − 0.03725 (Site)	0.028	0.021	0.117	149
	− 0.06033 (ψ_{PD})	0.024	0.047		
	− 0.00432 (VPD)0.028	0.065	0.027		

[1] Models for Days 170 and 171 were based on current foliage measurements of P_N and g_l.

[2] 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^2H 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 20% 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 the r^2 of multiple regression models (Table 4). Average P_N accounted for less than 5% 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: GRD = diameter growth (diameter$_{92}$ – diameter$_{91}$); GRH = height growth (height$_{92}$ – height$_{91}$); GRD^{2}H = diameter^2 x height growth (D^{2}H$_{92}$ – D^{2}H$_{91}$); BIOM = competitor biomass measured in June 1992; % light = (photosynthetically active radiation measured in the open/photosynthetically active radiation measured at the terminal of each seedling) x 100, averaged over the growing season. Other abbreviations are the same as in Table 1.

Variable	BIOM	GRD	GRH	GRD^{2}H	P_N
$\Sigma\Psi_{PD}$	-0.119	-0.197	-0.141	-0.241	-0.122
$\Sigma\Psi_{MD}$	0.090	-0.081	-0.062	-0.110	-0.124
Soil WC$_{300}$	0.057	-0.056	0.081	-0.002	-0.126
Soil WC$_{600}$	0.184	0.019	-0.133	-0.122	0.189
Temp	**–0.349***	0.228	0.107	0.180	**0.404***
% light	**–0.571*****	**0.561*****	0.337	**0.497****	**0.564****
VPD	-0.173	0.209	**0.365***	0.292	0.016
P_N	-0.297	**0.351***	0.308	0.321	
Needle N	**–0.502****	**–0.005**	-0.277	-0.208	0.116
BIOM		**–0.482****	**–0.369***	**–0.467****	-0.297
GRD	**–0.482****				**0.351***
GRH	**–0.369***	–	–	–	0.307
GRD^{2}H	**–0.467****				0.321

*, **, *** 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^2 plot) measured in June 1992; P_N = net photosynthesis (µmol m^{-2} s^{-1}) averaged over the growing season; % light = (photosynthetically active radiation measured in the open/photosynthetically active radiation measured at the terminal of each seedling) x 100, averaged over the growing season; VPD = vapor pressure deficit averaged over the growing season; D^{2}H = (diameter^2 x height).

Model	Partial r^2	P-value	Model r^2
Diameter = 1.220986 + 0.844386 (initial diameter)	0.106	0.011	0.679
– 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	0.315
Height = 3.254881 + 44.6’33375 (initial diameter)	0.126	0.040	0.271
+ 4.961099 (P_N)	0.145	0.038	
Height growth = 28.195286 – 0.013139 (BIOM)	0.136	0.045	0.485
+ 1.245138 (VPD)	0.062	0.088	
– 22.62129 (Needle N)	0.286	0.001	
D^{2}H = 136.00480 + 93.56069 (initial diameter)	0.068	0.055	0.562
– 0.065731 (BIOM)	0.215	0.010	
-95.31681 (Needle N)	0.279	0.001	
D^{2}H growth = 147.38055 – 0.0582% (BIOM)	0.218	0.009	0.480
– 81.96911 (Needle N)	0.262	0.001	

Discussion

Total rainfall appeared adequate for the 5-month growing season, but periods of low precipitation reduced soil water content for several consecutive weeks. We found that VPD was important in regulating g_l and P_N of seedlings early in the growing season, even when soil water was relatively high. However, the amount and duration of rain before measurement of P_N early in the growing season were much less than in August and September. The significant relationship between Ψ_{MD}, VPD, and P_N early in the growing season suggests a closer coupling of the photosynthetic apparatus with seedling water relations (Sands et al. 1984, Seiler and Cazell 1990, Pavlik and Barbour 1991, Pallardy et al. 1991) than was observed in pine seedlings sampled in 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 model as in the models for individual dates, the seasonal models for P_N and g_l were less explanatory.

Competitors reduced light availability, and light was the primary environmental factor limiting pine seedling growth (Table 3). However, both needle N (pine) and biomass (competitors) were significant variables in the regression models. The interaction of light and N or other unexplained factors may also be important in determining pine seedling growth and size. Competitor biomass and percent light were significantly correlated, but competitor biomass enters the models for diameter, D^2H, and D'H growth rather than light, and needle N enters as a negative parameter. Our data suggest that something related to competitor biomass other than the 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 may concentrate 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 plots (> 900 g per plot) with tall competitors and low irradiance, needle N concentration was consistently higher. Most studies report a positive relationship between leaf nitrogen concentration (see Field and Mooney 1986, Field 1991, and Reich et al. 1992 for reviews) and photosynthetic rate under saturating light intensity, which may 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 in foliage. Shaded plants invest large quantities of N in light-harvesting pigments and proteins, but make only small investments in ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) and other CO_2-processing enzymes (Björkman 1981, Evans 1989). Many woody species have shown higher N concentrations in shaded environments than in open environments (Margolis et al. 1988, McDonald et al. 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 *Pinus banksiana* Lamb. seedlings in low-light (shade cloth; 50% reduction in photon flux density) treatments than in high-light treatments. From our data, however, it is not certain whether growth dilution or a nutrient imbalance (Linder and Rook 1984, Sheriff et al. 1986) was responsible for the negative relationship of needle N and seedling growth. We did not measure soil nutrient availability or foliar nutrients other than N.

Developmental components as well as environmental controls contribute to photosynthesis off. *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 external environmental controls. Maier and Teskey (1992) found strong internal control of photosynthesis during the period of new foliage growth for mature *P. strobus*. They compared two days, with similar environmental conditions, when current-year foliage was actively growing (June 21) and when current-year foliage was fully expanded (July 20). When foliage and branches were growing, midday P_N sharply increased, particularly in l-year-old foliage. However, P_N in l-year-old foliage began to decline when new foliage was 70 to 80% expanded. This pattern of peak 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 correlations between photosynthesis and productivity is often not statistically significant (Gifford and Evans 1981, Kuppers 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 $r = 0.69$). The ratio of photosynthetic to nonphotosynthetic tissue in seedlings is relatively large compared to ratios in saplings and trees; thus, proportionately less carbon is lost in woody respiration. As seedlings grow, partitioning of photosynthate and loss to maintenance respiration become increasingly important and respiration consumes an increasing fraction of the gross photosynthesis (Waring and Schlesinger 1985).

The empirical models developed in our study emphasize the importance of multifactor (biotic and abiotic) influences on *P. strobus* physiology and growth. Competitors have both a direct and an indirect influence on growth, and these influences are modified by climatological and site conditions. Our study represents an initial attempt to integrate the factors outlined in Figure I. 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 off. *strobus* growth and physiological processes.

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