

Influence of temperature and leaf-to-air vapor pressure deficit on net photosynthesis and stomatal conductance in red spruce (*Picea rubens*)

MICHAEL E. DAY

Department of Forest Ecosystem Science, University of Maine, 5755 Nutting Hall, University of Maine, Orono, ME 04469-5755, USA

Received March 3, 1999

Summary The roles of temperature (T) and leaf-to-air vapor pressure deficit (VPD) in regulating net photosynthesis (A_{net}) and stomatal conductance (G_s) of red spruce (*Picea rubens* Sarg.) were investigated in a field study and in a controlled environment experiment. Both A_{net} and G_s exhibited a relatively flat response to temperatures between 16 and 32 °C. Temperatures between 32 and 36 °C markedly decreased both A_{net} and G_s . Vapor pressure deficits above 2 kPa had significant effects on both A_{net} and G_s . The influence of VPD on A_{net} and G_s fit a linear response model and did not interact significantly with T effects.

Keywords: carbon gain, climate warming, drought, gas exchange, respiration, tree decline.

Introduction

In northeastern North America, red spruce (*Picea rubens* Sarg.) has historically been a major component of conifer and mixed hardwood–softwood associations and one of the most economically desirable species for lumber and fiber (Seymour 1995). However, recent USDA Forest Service inventory data (Griffith and Alerich 1996) indicate that red spruce has undergone a dramatic decline in the low-elevation northeastern forests and is being replaced by balsam fir (*Abies balsamea* Mill.) and several hardwood species (Seymour 1985). Harvesting practices or climatic changes that decrease the presence of microenvironments favorable for regeneration and early growth of the species may be contributing to this decline.

Several lines of evidence suggest that red spruce is sensitive to high air temperatures and low atmospheric humidity. Optimum conditions for regeneration of *P. rubens* have been associated with partially closed canopies (Davis 1991, Seymour 1992), indicating that environmental conditions under more open or absent overstory canopies may inhibit early growth. Recent palynological evidence suggests that, during warmer and drier periods of the Holocene, red spruce was restricted to refugia within the coastal fog belt that subtends the Bay of Fundy (Schauffler 1998). Intolerance of high temperatures and a requirement for high atmospheric humidity have been cited as common attributes of tree species currently restricted to coastal ranges (Laderman 1998).

Alexander et al. (1995) reported a temperature optimum for net photosynthesis of about 20 °C for understory *P. rubens* saplings. Vann et al. (1994) found significant inhibition of photosynthesis at air temperatures > 25 °C and related the response to current range limits and changes that might be associated with a warming climate. A 20 °C optimum for photosynthesis by C_3 species is predicted on the basis of the differential selectivity of ribulose-bisphosphate carboxylase/oxygenase (Rubisco) for current ambient CO_2 (300–350 $\mu\text{mol CO}_2 \text{ mol}^{-1} \text{ air}$) and O_2 (21%) and the effects of temperature on water solubility of the two gases (Ku and Edwards 1977a, Tolbert 1994).

Although no studies have been published on the effects of atmospheric humidity on carbon gain by *P. rubens*, work on related species suggests an influence. For example, in Sitka spruce (*P. sitchensis* (Bong.) Carr.), a species of the moist maritime forests of western North America, stomatal conductance decreases with increasing leaf-to-air vapor pressure deficits (VPD) (Ludlow and Jarvis 1971, Running 1976, Sanford and Jarvis 1986). Kaufmann (1976) reported a similar response for subalpine Engelmann spruce (*P. engelmannii* Engelm.). Research by Marsden et al. (1996) suggests that high VPD may inhibit growth of newly planted white spruce (*P. glauca* (Moench) Voss) seedlings.

In this study, I tested the hypothesis that increasing VPD and temperature, acting singly or interactively, reduce photosynthetic carbon gain in natural populations of *P. rubens*. A preliminary investigation determined responses under field conditions. This was followed by an experiment in a controlled environment to separate influences of VPD and temperature, which were highly correlated in the field study, and to examine possible interactive effects between the two variables.

Materials and methods

For the controlled environment experiment, nine trees were randomly selected from a population of 4-year-old, 0.5-m high, container-grown red spruce. The trees were placed in a greenhouse in mid-January after cold requirements had been met, repotted in 25-l pots containing a mixture of 50% peat, 25% sand, and 25% vermiculite, and fertilized with Osmocote (18,6,12; N,P,K; Sierra Chemical Co., Milpitas, CA) time-

release fertilizer at a rate of 0.124 kg m^{-3} . While in the greenhouse, soil was watered to field capacity every 3 days. New foliage had flushed by early February and was fully expanded with bark of twigs appearing lignified by the time of the experiment (May 1 through June 7, 1998). Because of inadequate environmental controls in the greenhouse, trees were subjected to a highly variable environment with daytime temperatures of 15 to 38 °C and vapor pressure deficits (VPD) ranging from near zero to over 3.5 kPa. Midday photosynthetic photon flux densities (PPFD) were typically 1200 to 1500 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ during clear weather.

The controlled experiment was carried out in an environmental chamber (I-37 Series, Percival Manufacturing Company, Boone, IA), where all components were maintained at the test temperature (T_e) to prevent condensation within the cuvette and control systems at high T and low VPD. It was possible to treat three trees per day in the controlled environment chamber. Temperatures were randomly assigned to each of 18 days. Three trees were assigned to each T_e without replacement; thus, each individual was tested at each T_e only once. Sampling order of trees within chamber runs was random. Trees were placed in the chamber the day before measurement and held for 16 h during the day at the T_e and for 8 h at night at the T_e less 7 °C. Four fluorescent lights provided 250–300 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ PPFD within the chamber during the 16-h photoperiod. Soil water was maintained near field capacity during the experiment. Twig samples removed following gas exchange measurements had a mean xylem pressure potential (Ψ_{xylem}) of -0.3 MPa (determined by pressure chamber method; Koide et al. 1989). There was no correlation between T_e and Ψ_{xylem} .

An LI-6400 photosynthesis system (Li-Cor, Inc., Lincoln, NE) equipped with a standard $2 \times 3 \text{ cm}$ leaf cuvette and a Li-Cor LI-6400-02B light source was used for gas exchange measurements. This system permitted accurate control of cuvette temperature and irradiance. Constant VPD within the leaf chamber was maintained with a Li-Cor LI-610 dew-point generator and a column of calcium sulfate desiccant in the input air stream. To compensate for changes in T_e , the IRGAs were calibrated to zero on a daily basis. The CO_2 and H_2O span values were calibrated weekly. Temperature control and VPD calculations were based on leaf temperature, measured by a fine wire thermocouple. Based on a preliminary determination of saturating irradiance at the shoot level, irradiance within the cuvette was maintained at $1400 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (photosynthetically active radiation, 400–700 nm).

Gas exchange was measured on attached terminal shoots of lateral branches from the upper one-third of the crown. The cuvette enclosed the central portion of a current-year shoot. Each measurement series began at 0900 h and was completed by 1430 h. Gas exchange was permitted to stabilize for approximately 40 min before measurements were made. A preliminary study indicated that stomatal conductance stabilized within 20 to 30 min. Before each measurement, stability of net photosynthesis and stomatal conductance was verified from the real-time strip chart output.

Measurements were made at six temperatures (16, 20, 24, 28, 32 and 36 °C) and three VPDs (2.0, 2.75 and 3.5 kPa). Be-

cause maximum VPD is constrained by temperature-related saturation vapor pressures, only a VPD of 2 kPa was tested at 20 and 16 °C, VPDs of 2 and 2.75 kPa were tested at 24 °C, and all VPDs were tested when T_e was ≥ 28 °C. During measurements, temperatures were maintained at ± 0.2 °C and VPDs at ± 0.1 kPa. In all cases, VPD was manipulated from low to high values, because adjustment of gas exchange to increasing humidity can require several hours, which precludes completing a series of measurements in a single day.

After gas exchange measurements were completed, leaf areas were determined by stripping all needles from the shoot section that was enclosed in the cuvette, scanning at high resolution, and analyzing the image with the computer program Needle 4.3b (Reagent Instruments, Quebec, P.Q., Canada). Because of the quadrate cross-sectional shape of red spruce needles, projected needle areas were converted to half-total areas based on a ratio of width to perimeter of 1.45, previously developed from analysis of 100 needle cross sections. These half-total needle areas were used to calculate net photosynthesis and stomatal conductance with the standard algorithms of Li-Cor's Open 3.2 operating system, with broad band correction for water vapor.

Field measurements were made in July 1996, on 1-year-old, randomly selected, upper-crown shoots from saplings (0.5 to 2 m high) growing in the Penobscot Experimental Forest, Bradley and Eddington, Maine. These trees were growing in the open after release by a shelterwood overstory removal cut two years before measurement. The same instrumentation (except that the light source was a Li-Cor LI-6400-02), calibration procedures, and methods for determining needle area as described for the chamber experiments were used to collect field data and calculate gas exchange rates. In this case, temperature was maintained at ambient and VPD was measured at ambient, 75% ambient, or 50% ambient (if saturation vapor pressure permitted). Single measurements were made on individual trees.

Correlations were examined with Pearson's product-moment correlation coefficients, and probabilities for $r = 0$ were tested after Bonferroni adjustment (Snedecor and Cochran 1989). Data from the controlled environment experiment were divided into subsets to test specific hypotheses by analysis of variance (ANOVA). In all analyses, each of the trees in a chamber run were considered subsamples and effects tested with the replicate-by-effect variable error term. Specific temperature effects over the range of 16 to 36 °C were analyzed by holding VPD constant at 2 kPa, a typical midday value for forest canopies in this region (unpublished data, Forest Ecosystem Research Program, University of Maine). To minimize threshold effects that occur between 32 and 36 °C, influences of VPD were evaluated based on the data for $T_e < 36$ °C. Interactive effects were assessed with a balanced 3×3 factorial design at temperatures of 28, 32 and 36 °C and VPDs of 2, 2.75, and 3.5 kPa. The SAS statistical package (Release 6.12, SAS Institute, Cary, NC) was used for all analyses. To meet the assumptions of ANOVA, analysis of A_{net} and G_s responses were performed on log-transformed data. The SAS GLM procedure was used for ANOVA to compensate for the

unbalanced design of the VPD response analysis. For T effects at VPD = 2 kPa, means were separated by Tukey's HSD test to control experiment-wise error rate with a large number of factor levels. Because of the small range of factor levels in the other analyses, the more sensitive Duncan's multiple range test was selected to separate means. Polynomial contrasts (Snedecor and Cochran 1989) were used to analyze the effects of increasing VPD on A_{net} and G_s .

Results

The field data (Figure 1) indicated that both net photosynthesis (A_{net}) and stomatal conductance (G_s) were significantly correlated with leaf-to-air vapor pressure deficit (VPD) (Pearson's $r = -0.80$ and -0.78 , respectively; both $P < 0.0001$). However, VPD was also highly correlated with ambient temperature ($r = 0.76$, $P < 0.0001$), which varied from 16 to 29 °C. A strong correlation between A_{net} and G_s ($r = 0.91$, $P < 0.0001$) indicated that stomatal resistance provided significant control over gas exchange.

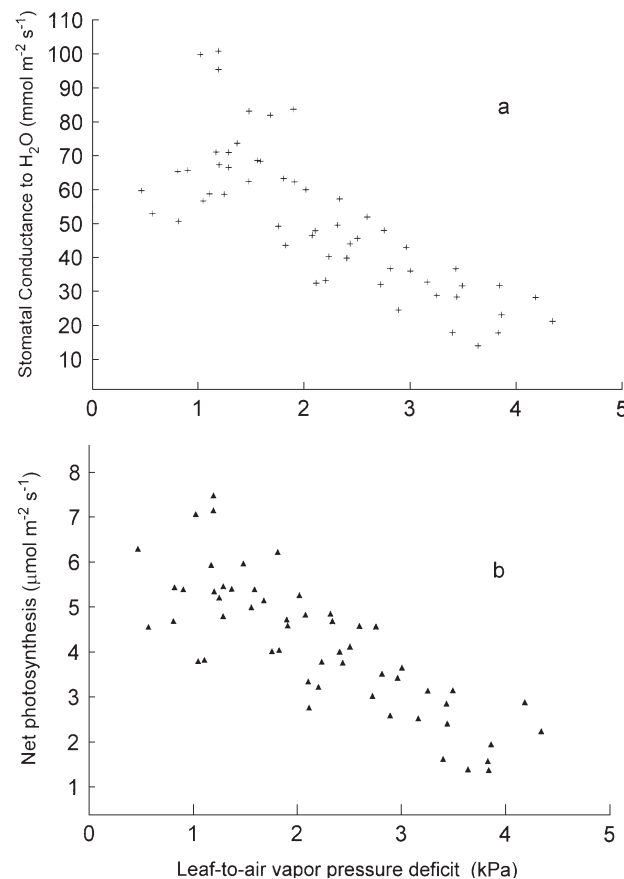


Figure 1. Relationships between leaf-to-air vapor pressure deficit and (a) stomatal conductance and (b) net photosynthesis for field-grown red spruce. Measurements were made on 1-year-old, upper crown foliage of 0.5–2-m-tall trees, growing in full sunlight ($n = 54$). Pearson's r for stomatal conductance = -0.80 ($P < 0.0001$), and for net photosynthesis $r = -0.78$ ($P < 0.0001$).

Because the scatter of the field data suggested that the influence of VPD on G_s was weaker at low VPDs than at high VPDs, I reanalyzed the data obtained at VPDs < 2 kPa together with measurements from that range of VPDs made during the growth chamber study (Figure 2). At VPDs < 2 kPa, neither data set showed a significant correlation between VPD and G_s ($r = -0.07$, $P = 0.75$ for field data and $r = -0.26$, $P = 0.27$ for growth chamber measurements). In Figure 2, the cloud of data points for the trees in the environmental chamber generally lies above that for the field population. This is probably because current-year needles were measured in the chamber experiment and 1-year-old foliage was measured in the field survey. In mature (upper canopy) *P. rubens*, mean differences in G_s of 46% between the two foliar cohorts have been observed (author's unpublished data) that are presumably related to buildup of waxes in epistomatal cavities.

In the controlled environment experiment with VPD held constant at 2 kPa, photosynthetic responses to temperature showed a broad temperature optimum (16–32 °C) (Figure 3) with a slight peak at 20 °C (statistically nonsignificant). There was a conspicuous decline in A_{net} between 32 and 36 °C. Although G_s appeared to decrease monotonically with increasing temperature (Figure 4), only the value at 36 °C was significantly less than the G_s values at lower temperatures, suggesting a response threshold at 32 °C or slightly above.

Figure 4 also indicates that the relationship between internal CO_2 concentration (C_i) and G_s is inconsistent. These findings suggest that the stomata were not responding in a predictable fashion to C_i during the experiment. The increase in C_i at

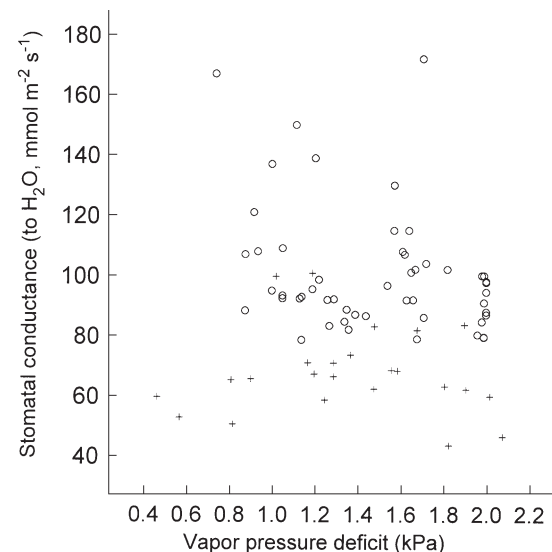


Figure 2. Effect of leaf-to-air vapor pressure deficit on stomatal conductance in red spruce. Symbols: + = 1-year-old foliage from the field population; and o = current-year needles from potted trees in an environmental chamber. Ambient air temperatures varied between 16 and 24 °C for both data sets. Pearson's r for the field data and environmental chamber data were 0.07 ($P = 0.75$) and -0.26 ($P = 0.27$), respectively. The generally higher stomatal conductance values of the environmental chamber foliage are largely attributable to effects of needle age on stomatal resistance.

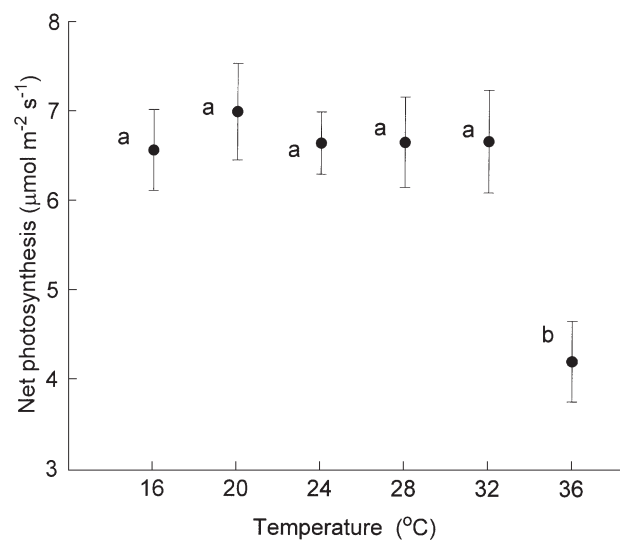


Figure 3. Effect of temperature on net photosynthetic rates of red spruce at a constant leaf-to-air vapor pressure deficit of 2 kPa. Bars indicate one standard error, and letters indicate Tukey's HSD groupings at $\alpha = 0.05$.

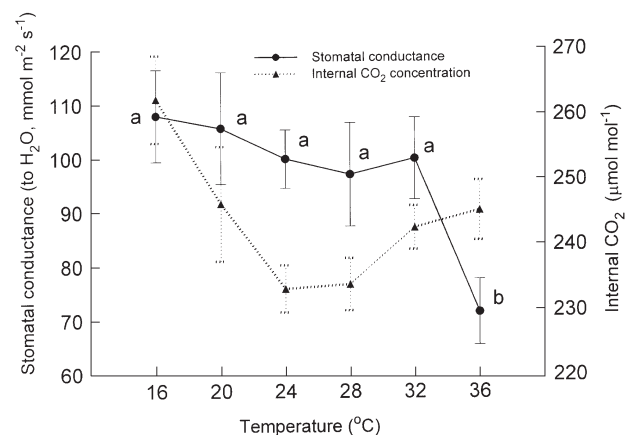


Figure 4. Responses of stomatal conductance (●) and internal CO₂ concentration (▲) to temperature at a constant leaf-to-air vapor pressure deficit of 2 kPa. Bars indicate one standard error, and letters indicate Tukey's HSD groupings at $\alpha = 0.05$.

higher temperatures implies that the rapid decrease in A_{net} above 32 °C was not caused by stomatal limitation of gas exchange.

Both A_{net} and G_s decreased in response to increasing VPD (Figure 5): however, the relative decrease in G_s was greater than that for A_{net} . Mean G_s decreased 43.6% between 2 and 3.5 kPa, whereas A_{net} declined by 26.3% over the same range. Thus A_{net} appears to be less sensitive than G_s to increasing VPD. A similar relationship between the two response variables was observed by Sanford and Jarvis (1986) for Sitka spruce. In that species, A_{net} decreased less than 30% between 0.5 and 2.0 kPa, whereas G_s declined by approximately 60%. Polynomial contrasts indicated that the responses of A_{net} and

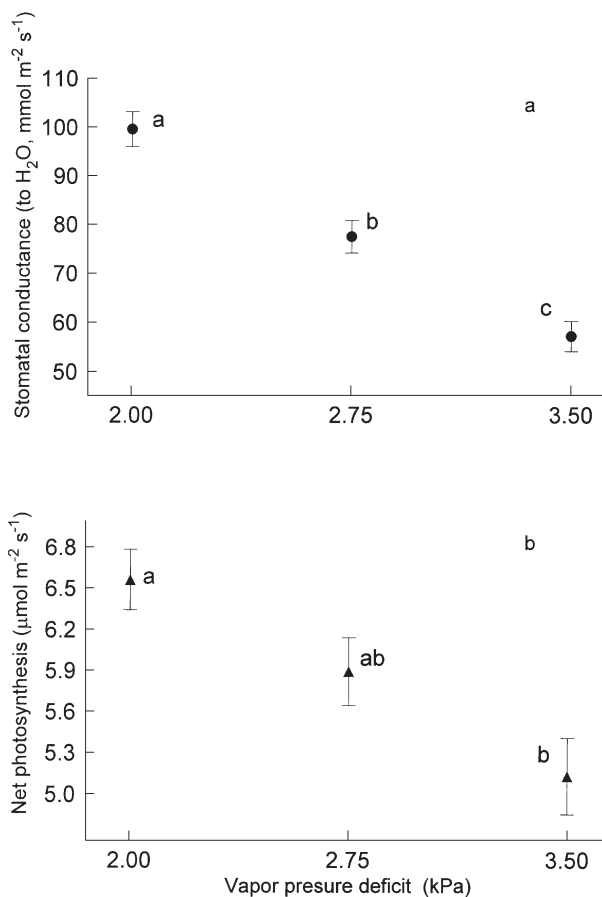


Figure 5. Effects of leaf-to-air vapor pressure deficit on (a) stomatal conductance and (b) net photosynthetic rate for the environmental chamber experiment. Bars indicate one standard error, and letters indicate Duncan's multiple range test groupings at $\alpha = 0.05$.

G_s to increasing VPD were best described as linear. Higher-order models tested as nonsignificant. Factorial analysis of T and VPD responses at 28, 32, and 36 °C provided nonsignificant interaction terms for both A_{net} and G_s (Table 1).

Discussion

Response to temperature

Red spruce, which is adapted to cool temperate climates, exhibited a broad temperature optimum (16–32 °C) for net photosynthesis (Figure 3). In contrast, Alexander et al. (1995) observed a peak in A_{net} at 20 °C followed by a decline to 47% of maximum at 30 °C. Alexander et al. (1995) attributed the decline in A_{net} with increasing temperature > 20 °C to increases in the proportion of photosynthate allocated to maintenance respiration (R_{dark}). The data of Alexander et al. (1995) indicate that, at 20 °C, shade-adapted saplings allocate approximately 18% of gross photosynthesis ($A_{\text{gross}} = A_{\text{net}} + R_{\text{dark}}$) to R_{dark} . This ratio increased to 28% at 25 °C and 52% at 30 °C. Over the temperature range from 20 to 30 °C, A_{gross} exhibited a slight decrease from 2.7 to 2.2 μmol m⁻² s⁻¹. These values are com-

Table 1. Summary of ANOVA of response of net photosynthesis and stomatal conductance to temperature (T) and leaf-to-air vapor pressure deficit (VPD). The experimental design was a 3×3 factorial with temperatures of 28, 32, and 36 °C and leaf-to-air vapor pressure deficits of 2, 2.75, and 3.5 kPa. Duncan's multiple range test groupings show significant differences between means at $\alpha = 0.05$.

Response variable	Source	df	Type III MS	F -value	$P > F$
$\text{Log}_{(e)}$ net photosynthesis	Temperature	2	1.8735	26.79	0.0048
	VPD	2	0.3876	119.71	0.0003
	$T \times \text{VPD}$	4	0.000945	0.16	0.9551
$\text{Log}_{(e)}$ stomatal conductance	Temperature	2	0.8399	8.36	0.0372
	VPD	2	1.6605	129.85	0.0002
	$T \times \text{VPD}$	4	0.00924	0.93	0.4925

Response variable	Temperature (°C)	Mean rate	Duncan Grouping	VPD (kPa)	Mean rate	Duncan Grouping
Net photosynthesis ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	28	5.91	a	2.0	5.58	a
	32	5.75	a	2.75	5.11	b
	36	3.70	b	3.5	4.40	c
Stomatal conductance ($\text{mmol m}^{-2} \text{s}^{-1}$)	28	74.96	a	2.0	86.05	a
	32	76.10	a	2.75	70.25	b
	36	55.66	b	3.5	52.55	c

parable with *in situ* rates ($2.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ at 20 °C) measured in shade-adapted *P. rubens* of similar size (0.5–1.5 m height) (author's unpublished data), although their ratio of $R_{\text{dark}}:A_{\text{gross}}$ is higher (18 versus 12.8%). In contrast, sunadapted foliage on open-grown saplings had an $R_{\text{dark}}:A_{\text{gross}}$ ratio of 6.6% (author's unpublished data), suggesting that temperature-induced increases in R_{dark} have a much smaller effect on A_{net} in sun-adapted foliage than in shade-adapted foliage.

An alternative explanation for the broad temperature optimum of A_{net} may be related to whole-tree respiratory demand, which would be expected to increase proportionally with temperature. Weak carbohydrate sink strength or reduced phloem loading can have a negative feedback effect on photosynthetic rates (e.g., Leverenz 1981, Stitt 1991). In the environmental chambers, only the shoot section used for gas exchange measurements received saturating irradiance. Because the balance of foliage was exposed to the low irradiances provided by growth chamber lamps it would be a relatively poor source for export of photosynthate.

Variation in temperature response among genetic lines or provenances and effects associated with plastic preconditioning may complicate comparisons across studies. Neilson et al. (1972) found that temperature optima varied within five provenances of Sitka spruce with one provenance showing little change in A_{net} between 15 to 28 °C. This provenance was from stock that had been subjected to long-term exposure to high temperatures. Neilson et al. (1972) also reported a correlation between time of year and T_{opt} , providing evidence of preconditioning effects. Trees used by Alexander et al. (1995) were collected from forest understories in Vermont, USA, at elevations of 380 and 945m, where temperature regimes would be expected to be moderately cool. In contrast, the greenhouse-maintained stock used in this experiment had

experienced temperatures greater than 30 °C on 10% of the days between initial budburst and sampling.

Measuring air temperature rather than leaf temperature may bias the resulting response curve. In natural environments and gas-exchange cuvettes, conifer leaf temperature may diverge substantially from ambient air temperature at high irradiances. Vowinkel et al. (1974) reported that, at midday, leaf temperatures of *Picea mariana* (Mill.) BSP needles often exceeded air temperature by over 7 °C *in situ* and by 5 °C in cuvettes. In a previous study with detached shoots of red spruce, differentials of > 5 °C were observed in both naturally and artificially illuminated 0.25- to 1.0-l cuvettes that were equipped with circulating fans (author's unpublished data). Neither Alexander et al. (1995) nor Vann et al. (1994) report needle temperatures. If needle temperature was higher than ambient, their reported photosynthetic optima would show bias toward lower temperatures. Additionally, if needle temperature exceeded air temperature, VPD at the leaf surface might be higher than that calculated on an air temperature basis, providing the potential for VPD-induced limitations to G_s .

The threshold response to temperature that occurred just above 32 °C may indicate disruption of one or more components of the photosynthetic carboxylation pathway. However, this temperature is lower than the temperature generally associated with disruption of enzymatic and membrane systems (Kozlowski et al. 1991, Salisbury and Ross 1992). The temperature-dependent influence of photorespiration on A_{net} (Jolliffe and Tregunna 1968, Ku and Edwards 1977b, Monson et al. 1982) provides an alternative explanation. The solubility ratio of O_2 to CO_2 in the mesophyll symplast increases exponentially with temperature (Ku and Edwards 1977a), and Ogren (1984) has proposed that temperature and specificity of rubisco for O_2 are directly related. Tolbert (1994) predicted

that an atmospheric CO_2 concentration of 40 to 65 $\mu\text{mol mol}^{-1}$ is the effective compensation point (zero A_{net}) for C_3 plants at 20 °C, whereas compensation points for temperatures of 30 and 37 °C are 110 and 300 $\mu\text{mol mol}^{-1}$, respectively. Thus, at the highest temperature (36 °C) and a CO_2 concentration of 350–380 $\mu\text{mol mol}^{-1}$, the trees in this experiment were close to the predicted CO_2 compensation point. According to this conceptual model, the abrupt drop in A_{net} between 32 and 36 °C reflects a rapidly increasing $\text{O}_2:\text{CO}_2$ solubility ratio and perhaps shifts in the substrate affinity of rubisco. This interpretation is consistent with both the observed increase in C_i that accompanied the decrease in G_s at high temperatures (Figure 4) and the positive relationship between temperature and mesophyll resistance to CO_2 reported by Neilson et al. (1972) for *P. sitchensis*.

Increasing temperature also appeared to affect G_s independently of its effects on photosynthesis (Table 1). Although decreases in A_{net} are usually accompanied by decreases in G_s , mediated by increases in C_i (Mansfield 1985), the relationship between G_s and C_i (Figure 4) was not consistent with this pattern. A possible explanation may involve a stress-induced increase in abscisic acid (Weiler et al. 1982), perhaps mediated by changes in apoplastic pH (Wilkinson and Davies 1997) at the leaf level.

Effects of vapor pressure deficit

The negative responses of G_s and A_{net} to increasing VPD in red spruce (Table 1, Figures 1 and 5) have been described for several other members of the genus *Picea*. In general, red spruce appears to be less sensitive to low VPDs (Figure 2) than its congeners from western North America. Ludlow and Jarvis (1971), Running (1976), Sanford and Jarvis (1986), and Warkentin et al. (1992) all describe response curves for *P. sitchensis* that drop precipitously as VPD increases above 0.5 kPa. Kaufmann's (1976) curve for *P. engelmannii* shows a similar response. Darlington et al. (1997) reported that seedlings of *P. mariana*, a species that is closely related to and can hybridize with *P. rubens* in the sympatric portions of their ranges (Gordon 1976), showed no significant difference in biomass accumulation when grown in 0.3–0.8 kPa and 2.0–2.5 kPa VPD regimes. Although gas exchange rates were not measured by Darlington et al. (1997), their results are indicative of a relatively high threshold for the VPD response or a response curve with a low slope.

The pattern of response to VPD found in red spruce may be related to the comparatively low G_s in this species (Figures 1a and 5a; Eamus and Fowler 1990). In contrast, Sanford and Jarvis (1986) report that, in *P. sitchensis*, G_s approaches 300 $\text{mmol m}^{-2} \text{s}^{-1}$. Compared with its co-occurring conifer species and other members of the genus *Picea*, red spruce is relatively slow growing and its low G_s may reflect an adaptation to permit adequate gas exchange while minimizing water loss. The low G_s may explain the success of red spruce on drought-prone sites with shallow, primarily organic soils overlying bedrock or hardpan.

Decreased sensitivity to VPD at high humidities may represent an adaptation to the regional climate of northeastern

North America, where VPDs ≥ 2 kPa are common during the growing season. Data collected at a spruce plantation in the Penobscot Experimental Forest indicate that VPDs greater than 2 kPa occurred on 91% of days during July and August 1998, and on 83% of days under a partial canopy (unpublished data, Forest Ecosystem Research Program, University of Maine). This can be contrasted with the range of Sitka spruce in the Pacific Northwest where atmospheric VPDs of ≥ 1 kPa are rare (Warkentin et al. 1992).

Implications for population dynamics and management

The relatively small responses of A_{net} and G_s to increasing temperature reported here suggest that modest increases in daytime temperatures during the growing season are unlikely to hinder gas exchange in *P. rubens*. However, daytime maxima that result in needle temperatures in excess of 32 °C could have a dramatic effect on carbon gain. Increases in overnight temperatures may elevate losses to dark respiration, which would be expected to have a greater negative effect on shade-adapted individuals than on sun-adapted individuals. Also, small changes in carbon balance stress may have long-term indirect consequences for population dynamics by limiting reproductive output (Harper and White 1974) or increasing susceptibility to pests or pathogens (Warkentin et al. 1992).

This study supports the hypothesis that current decreases in the abundance of *P. rubens* in low-elevation forests are more a consequence of harvesting practices and inter-specific competition than a response to unfavorable environmental variables. Although red spruce commonly regenerates under partially closed canopies, based on its gas exchange responses to temperature and VPD it also appears to be capable of tolerating the environments found in large canopy openings. In canopy gaps, high solar irradiance could maximize growth, whereas low nighttime temperatures (Childs and Flint 1987, McCaughey 1989) would reduce losses to R_{dark} . In a study of transects running from intact forests into clearcuts, Hughes and Bechtel (1997) found that *P. rubens* saplings furthest from overstory shade had the greatest stem diameters. Nevertheless, differences in physiology of sun- and shade-adapted foliage and preconditioning appear to be important determinants of this species' ability to take advantage of environments with high irradiance.

Acknowledgments

The author thanks J. Brissette, M. Greenwood, R. Jagels, R. Seymour, and A. White, for their critical reviews of this manuscript; The Northeastern Forest Experiment Station, USDA Forest Service, for use of research sites on the Penobscot Experimental Forest; and A. Simmons and S. Gourde for assistance with field and growth chamber studies, respectively. Support for this research was provided by a McIntire-Stennis grant to the Forest Ecosystem Research Program of the University of Maine. This paper is Maine Agriculture and Forest Experiment Station publication number 2361.

References

- Alexander, J.D., J.R. Donnelly and J.B. Shane. 1995. Photosynthetic and transpirational responses of red spruce understory trees to light and temperature. *Tree Physiol.* 15:393–398.
- Childs, S.W. and L.E. Flint. 1987. Effect of shade cards, shelterwoods, and clearcuts on temperature and moisture environments. *For. Ecol. Manag.* 18:205–217.
- Darlington, A.B., A. Halinska, J.F. Dat and T.J. Blake. 1997. Effects of increasing saturation vapor pressure deficit on growth and ABA levels in black spruce and jack pine. *Trees* 11:223–228.
- Davis, W.C. 1991. The role of advance regeneration of red spruce and balsam fir in east central Maine. *In* Proc. Conference on Natural Regeneration Management. Ed. C.M. Simpson. Forestry Canada Maritimes Region, Fredericton, New Brunswick, pp 157–168.
- Eamus, D. and D. Fowler. 1990. Photosynthetic and stomatal conductance responses to acid mist of red spruce seedlings. *Plant Cell Environ.* 13:349–357.
- Harper, J.L. and J. White. 1974. The demography of plants. *Annu. Rev. Ecol. Syst.* 5:419–463.
- Hughes, J.W. and D.A. Bechtel. 1997. Effect of distance from forest edge on regeneration of red spruce and balsam fir in clearcuts. *Can. J. For. Res.* 27:2088–2096.
- Griffith, D.M. and C.L. Alerich. 1996. Forest statistics for Maine, 1995. USDA Forest Service Northeast Forest Experiment Station Resource Bulletin NE-135, 134 p.
- Gordon, A.G. 1976. The taxonomy and genetics of *Picea rubens* and its relationship to *Picea mariana*. *Can. J. Bot.* 54:781–813.
- Jolliffe, P.A. and E.B. Tregunna. 1968. Effect of temperature CO₂ concentration and light intensity on oxygen inhibition of photosynthesis in wheat leaves. *Plant Physiol.* 43:902–906.
- Kaufmann, M.R. 1976. Stomatal response of Engelmann spruce to humidity, light, and water stress. *Plant Physiol.* 57:898–901.
- Koide, R.T., R.H. Robichaux, S.R. Morse and C.M. Smith. 1989. Plant water status, hydraulic resistance and capacitance. *In* Plant Physiological Ecology: Field Methods and Instrumentation. Eds. R.W. Pearcy, J.R. Ehleringer, H.A. Mooney and P.W. Rundal. Chapman and Hall, New York, pp 161–183.
- Kozłowski, T.T., P.J. Kramer and S.G. Pallardy. 1991. The physiological ecology of woody plants. Academic Press, New York, 657 p.
- Ku, S.B. and G.E. Edwards. 1977a. Oxygen inhibition of photosynthesis. II. Kinetic characteristics as affected by temperature. *Plant Physiol.* 59:991–999.
- Ku, S.B. and G.E. Edwards. 1977b. Oxygen inhibition of photosynthesis. I. Temperature dependence and relation to O₂/CO₂ solubility ratio. *Plant Physiol.* 59:986–990.
- Laderman, A.D. 1998. Freshwater forests of continental margins. *In* Coastally Restricted Forests. Ed. A.D. Laderman. Oxford University Press, New York, pp 3–35.
- Leverenz, J.W. 1981. Photosynthesis and transpiration in large forest grown Douglas-fir: Interactions with apical control. *Can. J. Bot.* 59:2568–2576.
- Ludlow, M.M. and P.G. Jarvis. 1971. Photosynthesis in Sitka spruce (*Picea sitchensis* (Bong.) Carr.) . I. General characteristics. *J. Appl. Ecol.* 8:925–953.
- Mansfield, T.A. 1985. Porosity at a price: The control of stomatal conductance in relation to photosynthesis. *In* Photosynthetic Mechanisms and the Environment. Eds. J. Barber and N.L. Baker. Elsevier Science Publishers, New York, pp 419–452.
- Marsden, B.J., V.J. Lieffers and J.J. Zwiazek. 1996. The effect of humidity on photosynthesis and water relations of white spruce seedlings during the early establishment phase. *Can. J. For. Res.* 26:1015–1021.
- McCaughey, J.H. 1989. Energy exchange for a forest site and a clear-cut site at Chalk River, Ontario. *Can. Geogr.* 33:299–311.
- Monson, R.K., M.A. Stidham, G.W. Williams, III, G.E. Edwards and E.G. Uribe. 1982. Temperature dependence of photosynthesis in *Agropyron smithii* Rydb. I. Factors affecting net CO₂ uptake in intact leaves and contribution from ribulose-1,5-bisphosphate carboxylase *in vivo* and *in vitro*. *Plant Physiol.* 69:921–928.
- Neilson, R.E., M.M. Ludlow and P.G. Jarvis. 1972. Photosynthesis in Sitka spruce (*Picea sitchensis* (Bong.) Carr.) II. Response to temperature. *J. Appl. Ecol.* 9:721–745.
- Ogren, W.L. 1984. Photorespiration: Pathways, regulation, and modification. *Annu. Rev. Plant Physiol.* 35:415–442.
- Running, S.W. 1976. Environmental control of leaf water conductance in conifers. *Can. J. For. Res.* 6:104–112.
- Salisbury, F.B. and C.W. Ross. 1992. Plant physiology, 4th Edn. Wadsworth Publishing Co., Belmont, CA, 682 p.
- Sanford, A.P. and P.G. Jarvis. 1986. Stomatal responses to humidity in selected conifers. *Tree Physiol.* 2:89–103.
- Schauffler, M. 1998. Paleocology of coastal and interior *Picea* (spruce) stands in Maine. Ph.D. Thesis, University of Maine, Orono, Maine. 125 p.
- Seymour, R.S. 1985. Where has all the spruce-fir gone? *Habitat* 9/10:24–29.
- Seymour, R.S. 1992. The red spruce–balsam fir forest of Maine: evolution of silvicultural practice in response to stand development patterns and disturbances. *In* The Ecology and Silviculture of Mixed-Species Forests: A Festschrift for David M. Smith. Eds. M.J. Kelty, B.C. Larson and C.D. Oliver. Academic Press, Boston, pp 217–244.
- Seymour, R.S. 1995. The northeastern region. *In* Regional Silviculture of the United States. Ed. J.W. Barrett. Wiley and Sons, New York, pp 31–79.
- Snedecor, G.W. and W.G. Cochran. 1989. Statistical methods, 8th Edn. Iowa State University Press, Ames, Iowa, 503 p.
- Stitt, M. 1991. Rising CO₂ levels and their potential significance for carbon flow in photosynthetic cells. *Plant Cell Environ.* 14:741–762.
- Tolbert, N.E. 1994. Role of photosynthesis and photorespiration in regulating atmospheric CO₂ and O₂. *In* Regulation of Atmospheric CO₂ and O₂ by Photosynthetic Carbon Metabolism. Eds. N.E. Tolbert and J. Preiss. Oxford University Press, New York, pp 8–36.
- Vann, D.R., A.H. Johnson and B.B. Casper. 1994. Effect of elevated temperatures on carbon dioxide exchange in *Picea rubens*. *Tree Physiol.* 14:1339–1349.
- Vowinkel, T., W.C. Oechel and W.G. Boll. 1974. The effect of climate on the photosynthesis of *Picea mariana* at the subarctic tree line. I. Field measurement. *Can. J. Bot.* 53:604–620.
- Warkentin, D.L., D.L. Overhulser, R.I. Gara and T.M. Hinckley. 1992. Relationships between weather patterns, Sitka spruce (*Picea sitchensis*) stress, and possible tip weevil (*Pissodes strobi*) infestation levels. *Can. J. For. Res.* 22:667–673.
- Weiler, E.W., H. Schnabl and C. Hornberg. 1982. Stress-related levels of abscisic acid in guard cell protoplasts of *Vicia faba* L. *Planta* 154:24–28.
- Wilkinson, S. and W.J. Davies. 1997. Xylem sap pH increase: A drought signal received at the apoplastic face of the guard cell that involves the suppression of saturable abscisic acid uptake by the epidermal symplast. *Plant Physiol.* 113:559–573.