Seasonal air and soil temperature effects on photosynthesis in red spruce (Picea rubens) saplings

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Summary  Net photosynthesis and stomatal conductance were measured in ten red spruce (Picea rubens Sarg.) saplings, growing near Ithaca, New York, throughout the early spring and late-fall growing periods. Gas exchange and daily minimum and maximum soil and air temperatures were also measured. Linear regression analysis showed that rates of net photosynthesis were positively correlated with both minimum daily soil and air temperatures but that minimum soil temperature was a better predictor of net photosynthesis. Moreover, net photosynthesis was more sensitive to changes in soil temperature than to changes in air temperature, and photosynthesis was approximately twice as sensitive to temperature changes during the fall than during the spring.

Keywords: air temperature, climatic change, gas exchange, seasonal effects, temperature sensitivity.

Introduction

Evergreen coniferous trees growing in temperate climates become frost hardened and dormant during part of the winter (Levitt 1980, Kozlowski et al. 1991, Havranek and Tranquillini 1995). While dormant, they may show an almost total cessation of gas exchange (but see Schaberg et al. 1995). However, the evergreen habit affords the potential for year-round net photosynthesis. Furthermore, climatic change resulting in warmer winters may permit temperate conifers to continue photosynthesizing later in the fall and to begin photosynthesizing earlier in the spring, thereby extending their growing season. In the northeastern United States and eastern Canada, red spruce (Picea rubens Sarg.) is an important evergreen coniferous species in many montane and low-elevation forests (Blum 1990). The present study was undertaken to assess the possible influence of climatic warming on winter photosynthesis in red spruce by documenting the relationships between photosynthetic rates and soil and air temperatures during the spring and fall.

Previous studies of conifers native to western North America have demonstrated significant reductions in gas exchange rates on days following nights with near-freezing or sub-freezing air temperatures (e.g., Fahey 1979, Kaufmann 1982, Smith et al. 1984), and other field and laboratory studies have shown that low air temperatures can significantly limit gas exchange in conifers (e.g., Smith 1985, DeLucia 1987, DeLucia and Smith 1987, Carter et al. 1987). In addition, several studies have demonstrated the role of low soil temperatures in limiting gas exchange in conifers (DeLucia 1986, DeLucia and Smith 1987, Carter et al. 1987, Day et al. 1989, 1990, 1991, Lippu and Puttonen 1991).

Although recent observations of gas exchange in red spruce at low temperatures have been conducted in conjunction with studies of the species’ cold tolerance and susceptibility to winter injury (Fincher et al. 1989, DeHayes 1992, Fincher and Alschier 1992, L’Hirondelle et al. 1992, Amundson et al. 1993, Eamus 1993, Hadley et al. 1993), no systematic examination of the relative importance of air and soil temperatures in influencing photosynthesis of red spruce during spring and fall has been reported. Moreover, most studies of conifer gas exchange have focused on a single period during the growing season. In this study, we examined both the beginning and the end of the growing season. We hypothesized that gas exchange responses of red spruce to temperature differ between the fall and spring growing periods. In fall, air and soil temperatures decline in tandem, and subsequently trees undergo winter hardening. In spring, the presence of a snowpack may effectively decouple air and soil temperatures resulting in a more complex suite of cues leading to springtime recovery of gas exchange. The nature of these different temperature responses will be important in determining the effects of climatic change on a species’ performance.

Materials and methods

Site description and plant material

In April 1992, ten 7-year-old red spruce saplings were randomly selected from an even-aged plantation growing near Cornell University, Ithaca, New York. The stand was established in 1987 with 2-year old, greenhouse-grown seedlings from a South Range, Nova Scotia provenance collected in 1985 (Alschier et al. 1989). The plantation contained approximately 100 saplings planted in three rows in an east–west orientation. Rows were approximately 2.1 m apart, and spac-
ing within rows was approximately 0.9 m. Saplings were between one and two meters tall.

**Temperature measurements**

For the first two sampling periods of the study (spring and fall 1992), calibrated thermistors were installed at four depths in the soil profile (1, 5, 10, and 20 cm) beneath the canopy of three of the saplings. Soil temperature measurements were made between 0800 and 0900 h on each day of gas exchange sampling, and it was assumed that these measurements approximated the minimum overnight soil temperatures. Minimum and maximum air temperatures for the preceding 24-h period were also recorded each morning with a Taylor min–max thermometer located in a weather shed at the site.

During the second year of the study (spring and fall 1993), a Campbell CR10 data logger (Campbell Scientific, Inc., Logan, UT) was installed to automate the collection of air and soil temperatures. Copper-constantan thermocouples were installed at soil depths of 1, 5, and 10 cm beneath the canopy of the same saplings measured during the previous year. An additional sensor measured air temperature and relative humidity. The data logger was programed to scan each sensor every 60 s, to calculate sample averages every 15 min, and to calculate 24-h minimum and maximum temperatures for each of the sensors.

**Gas exchange measurements**

Gas exchange was measured *in situ* on a single shoot selected from the south side of each of the ten saplings. The measurements were made with an LI-6200 Portable Gas Exchange System (Li-Cor, Inc., Lincoln, NE) equipped with a 0.25-liter cuvette. The rate of CO₂ depletion was measured over a 20-s interval after orienting the shoot normal to the direction of the sun. The same shoot from each of the saplings was used for all of the measurements during the sampling period. In a few cases, however, a shoot was accidentally damaged or broken, in which case a nearby shoot (usually on the same branch) was selected to take its place.

Two gas exchange sampling schedules were followed. Diurnal sampling sessions were scheduled periodically to measure net photosynthetic rate and stomatal conductance at hourly intervals on each of the three trees where the thermistors or thermocouples were located. These sampling sessions were used to characterize the diurnal pattern of gas exchange in the saplings. A total of six diurnal sessions during the two spring sampling periods and five sessions during the fall periods suggested that daily maximum photosynthesis and stomatal conductance occurred in the afternoon over a broad time period (1300–1600 h). Subsequent sampling sessions, during which all ten saplings were measured, were scheduled during these times. Sampling sessions were scheduled on sunny or partly cloudy days in an attempt to minimize the variation in irradiance. However, on four occasions over the two years, the sky became cloudy during a sampling session and irradiances were substantially reduced. In addition, late in the fall 1993 sampling period irradiances were reduced because of low sun angles.

Leaf areas for individual shoots were measured with a Li-Cor LI-3100 portable area meter. The shoot from each sapling was harvested at the end of the sampling period and then brought to the laboratory where the needles were stripped off and the projected leaf area measured. Three measurements were made for each shoot and a sample mean was used to calculate net photosynthetic rate and stomatal conductance on a projected needle area basis.

**Data analyses**

Sample means were computed for each of the following gas-exchange-related variables for each sampling session: daily maximum net photosynthesis ($A_{\text{net}}$), stomatal conductance ($g_s$), photosynthetically active radiation (PAR), and intercellular CO₂ concentration ($C_i$). Sample means were also computed for 24-h minimum and maximum soil temperatures at each of the sampled depths. Atmospheric vapor pressure deficit (VPD) at the time of the 24-h maximum air temperature was calculated for the two sampling periods (spring and fall 1993) for which the necessary relative humidity data were available. Pearson product-moment correlation coefficients were computed between average daily maximum $A_{\text{net}}$ and average PAR, 24-h maximum and minimum air temperatures, and average 24-h maximum and minimum soil temperatures at each soil depth. Minimum air temperature (min $T_{\text{air}}$), average minimum soil temperature measured at 5 cm depth (min$_5$ $T_{\text{soil}}$), and average minimum soil temperature measured at 10 cm depth (min$_{10}$ $T_{\text{soil}}$) were selected as independent variables in a multiple linear regression analysis because each variable had a substantive correlation coefficient in all four sampling periods. These three variables were also believed to represent best the thermal conditions within the canopy and rooting environments of the saplings. Combinations of the three variables were used to construct least squares linear regression equations to predict daily maximum $A_{\text{net}}$. In every case, adding more than one independent variable to the regression equation resulted in a nonsignificant slope coefficient and a reduction in the adjusted $r^2$ value. The likely explanation for this result is the strong linear association among the three temperature variables. Subsequently, a simple least squares linear regression was computed using only average min $T_{\text{soil}}$ and another using only min $T_{\text{air}}$. Although the regressions were based on time series data, a lack of autocorrelation in the residuals was verified by a Durbin-Watson test. For each regression, three sets of linear contrasts were computed to examine differences between the spring and fall sampling periods for both the slope coefficient ($\beta$) and the intercept ($\alpha$). Because the data failed to meet the assumption of homogeneity of variance among the four sampling periods, $t$-statistics were computed that incorporated the variance estimate for each sampling period. The estimated degrees of freedom for each of the comparisons were computed using Satterthwaite’s equation (Snedecor and Cochran 1980, p 228).
Results

Air and soil temperature

There was considerable day-to-day fluctuation in both 24-h minimum and maximum air temperatures (Figures 1a, 1b, 2a, and 2b) and in 24-h minimum soil temperature. The time series showed trends of gradually increasing temperature during the two spring sampling periods and gradually decreasing temperature during the two fall sampling periods. Exceptions to this general pattern were the air temperature data for the spring 1993 sampling, which showed little overall trend. Subfreezing nights were common throughout the spring of 1992 but occurred only once during spring 1993. There were frequent overnight frosts and steadily declining daytime temperatures during the fall sampling periods of both years.

Soil temperature tracked changes in air temperature, but the day-to-day fluctuation in soil temperature measured within the rooting zone (at a depth of 10 cm) was less than the fluctuation at the soil surface (at a depth of 1 cm). In spring 1992, soil temperature remained above freezing throughout the measurement period, whereas in 1993, soil surface temperatures dropped below 0 °C on several occasions during April before warming significantly in May. Throughout the four sampling periods, soil temperatures in the rooting zone were usually 1 to 2 °C higher than surface temperatures, and minimum surface soil temperatures were usually 3 to 6 °C higher than minimum air temperatures, except for spring 1993 when the average temperature difference was less than 1 °C.

Net photosynthesis

Seasonal patterns in peak, daily gas exchange rates during the four sampling periods are shown in the top half of Figures 1a, 1b, 2a, and 2b. Gas exchange rates were measured between early April and late May on 17 days during spring 1992 and 16
days during spring 1993. Fall measurements were begun in late September. In 1992, measurements ended in mid-November when average daily maximum net photosynthesis ($A_{\text{net}}$) reached approximately 0 µmol m$^{-2}$ s$^{-1}$ (a total of 19 days of measurements), whereas in 1993, measurements were made on 22 days because $A_{\text{net}}$ was positive until well into December. During the two fall periods, peak rates of photosynthesis occurred early in the sampling period (late September and early October), whereas the pattern was less clear during the spring periods. In spring 1992, the peak occurred midway through the sampling period (late September and early October), whereas in 1993 the peak occurred toward the end of the sampling period (mid- to late-May). During the spring 1992 sampling period, average daily maximum $A_{\text{net}}$ was consistently higher than the rates during the spring 1993 sampling period and both fall periods. In both fall periods, $A_{\text{net}}$ declined steadily and there were short-term reductions in gas exchange that corresponded with overnight frost events.

Overall, average daily maximum $A_{\text{net}}$ ranged from nearly 0 µmol m$^{-2}$ s$^{-1}$ in late fall to over 10 µmol m$^{-2}$ s$^{-1}$ in mid-April 1992. The patterns of $A_{\text{net}}$, stomatal conductance ($g_s$), and intercellular CO$_2$ concentration ($C_i$) varied considerably among trees. This variation was consistent within sampling periods and among sampling periods.

**Functional relationship between temperature and $A_{\text{net}}$**

Daily maximum $A_{\text{net}}$ and the various temperature variables were highly correlated. The association between average daily maximum $A_{\text{net}}$ and average PAR was not as strong as the association between $A_{\text{net}}$ and temperature (Table 1); however, the spring 1992 coefficient for PAR appears to be anomalous. The fall data displayed stronger correlations than the spring
Table 1. Pearson product-moment correlation coefficients calculated between average daily maximum $A_{\text{net}}$ and various environmental factors: PAR, photosynthetically active radiation; $\max T_{\text{air}}/\min T_{\text{air}}$, maximum/minimum daily air temperature during the preceding 24 h; VPD, atmospheric vapor pressure deficit at time of $\max T_{\text{air}}$; $\max T_{\text{soil}}/\min T_{\text{soil}}$, maximum/minimum daily soil temperature measured at a soil depth of 1 cm during the preceding 24 h; $\max T_{\text{soil}}$, maximum daily soil temperature measured at a soil depth of 5 cm during the preceding 24 h; $\max T_{\text{soil}}$, maximum daily soil temperature measured at a soil depth of 10 cm during the preceding 24 h.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Spring</th>
<th>Fall</th>
<th>Spring</th>
<th>Fall</th>
</tr>
</thead>
<tbody>
<tr>
<td>PAR</td>
<td>0.145</td>
<td>0.498</td>
<td>0.137</td>
<td>0.180</td>
</tr>
<tr>
<td>$\max T_{\text{air}}$</td>
<td>0.680</td>
<td>0.728</td>
<td>0.603</td>
<td>0.728</td>
</tr>
<tr>
<td>VPD</td>
<td>0.315</td>
<td>0.315</td>
<td>0.315</td>
<td>0.315</td>
</tr>
<tr>
<td>$\max T_{\text{soil}}$</td>
<td>0.953</td>
<td>0.956</td>
<td>0.953</td>
<td>0.956</td>
</tr>
<tr>
<td>$\min T_{\text{soil}}$</td>
<td>0.928</td>
<td>0.928</td>
<td>0.928</td>
<td>0.928</td>
</tr>
<tr>
<td>$\min T_{\text{air}}$</td>
<td>0.065</td>
<td>0.065</td>
<td>0.065</td>
<td>0.065</td>
</tr>
</tbody>
</table>

Minimum $T_{\text{air}}$ was a significant predictor of $A_{\text{net}}$ ($P < 0.005$) only during the two fall sampling periods, and it explained only 30 to 70% of the variation. The regression summaries indicate that the least squares regression model fits the fall data better than the spring data and that the model fits the 1993 data better than the 1992 data. None of the environmental variables provided a significant linear relationship for the spring 1992 data, and scatter plots of average daily maximum $A_{\text{net}}$ and other variables did not suggest other functional relationships.

Although the regression slope coefficient for soil in spring 1992 (Table 2) was similar to the one in 1993, the regression itself was not significant. Moreover, the magnitude and range of measurements in 1992 were considerably higher than those during the same period in 1993. The measurements were also considerably higher than published values for many conifers (Teskey et al. 1995). This discrepancy suggested a potential calibration problem with the LI-6200, and the unit was subsequently re-calibrated by Li-Cor, Inc. Given these uncertainties, the spring 1992 data were removed from further analyses.

There was a significant, positive linear relationship between average minimum $T_{\text{soil}}$ measured at 5 cm depth and average daily maximum $A_{\text{net}}$ and between minimum $T_{\text{air}}$ and average daily maximum $A_{\text{net}}$ (Table 3). Furthermore, the results suggest that the linear relationship with minimum $T_{\text{soil}}$ was significantly different between the spring 1993 sampling period and the two fall periods, and that the relationship between the two fall periods for both predictors was not significantly different. In contrast, no seasonal differences were observed for the relationship between $A_{\text{net}}$ and minimum $T_{\text{air}}$.

**Discussion**

Both minimum air and soil temperatures appeared to influence the pattern of photosynthesis during the spring and fall. During fall, short-term reductions in daily maximum $A_{\text{net}}$ that were superimposed on a trend of steadily declining gas exchange (Figures 2a and 2b) were associated with overnight frost events and are consistent with the results of others (Fahey 1979,
Smith et al. 1984, DeLucia 1987). Together with the strong relationships between \( A_{\text{net}} \) and \( T_{\text{soil}} \) in the fall sampling periods, these results suggest a simple model of environmental regulation of photosynthesis: the gradual decline in \( A_{\text{net}} \) may be driven by root-zone soil temperature, whereas short-term reductions are associated with overnight freezing. Such a model is consistent with the observations of DeLucia and Smith (1987) and Carter et al. (1987) who indicated that, for Rocky Mountain Engelmann spruce (\( Picea engelmannii \) (Parry)), low soil temperatures are more limiting to net photosynthesis and stomatal conductance than low air temperatures only when air temperatures are above freezing. However, maximum \( T_{\text{soil}} \) was also highly correlated with fall \( A_{\text{net}} \) (Table 1), suggesting that a model for red spruce photosynthetic performance under declining temperatures may be more complex than the simple model proposed above. In addition, maximum \( T_{\text{air}} \) was strongly correlated with \( A_{\text{net}} \) during the two fall sampling periods (Table 1). This is likely to be related to the fact that maximum daily air temperatures during the fall measurement periods (15–30 °C) (Figures 2a and 2b) were in the optimal range for photosynthesis in conifers (Belous 1986, as cited in Teskey et al. 1995, p 114).

The regulation of \( A_{\text{net}} \) in red spruce during the spring appears to be more complex than during the fall, and the results of the present study do not provide a clear picture of the environmental controls. Although air and soil temperatures were significant predictors of \( A_{\text{net}} \), in spring 1993, possible effects of sub-freezing nights were not demonstrated because only one overnight frost occurred during the sampling period. This may explain, in part, the weaker relationship between minimum \( T_{\text{air}} \) and \( A_{\text{net}} \) that was observed during the spring 1993 sampling period compared with the spring 1992 sampling period (Figure 1b). Moreover, in spring 1992, the pattern of daily maximum \( A_{\text{net}} \) differed greatly from the pattern in 1993 with the highest photosynthetic rates observed early in the spring (Figure 1a).

In a laboratory study, DeLucia (1986) reported sharp declines in photosynthesis in Engelmann spruce seedlings after soil temperatures dropped below 8 °C. In another laboratory study, Day et al. (1991) reported sharp reductions in \( A_{\text{net}} \) in loblolly pine (\( Pinus taeda \) L.) seedlings when soil temperatures dropped below 10 °C, and Lippu and Puttonen (1991) reported significant reductions in \( A_{\text{net}} \) in Scots pine (\( Pinus sylvestris \) L.) seedlings in an 8 °C soil temperature treatment relative to a 12 °C treatment. Moreover, both DeLucia (1986) and Day et al. (1991) reported an overall curvilinear response in \( A_{\text{net}} \) to changes in soil temperature, but the response was linear when soil temperature fell below 10 °C. In the present study, minimum subsurface soil temperatures during the two fall sampling periods and the spring 1993 period were generally below 10 °C, and the data for these three periods suggest a linear response of \( A_{\text{net}} \) to minimum soil temperature.

The high degree of covariance between air and soil temperatures in our field studies makes it difficult to separate the effects of these factors on gas exchange in spring and fall. In general, minimum soil temperature explained more of the variation in average daily maximum \( A_{\text{net}} \) than did minimum \( T_{\text{air}} \). The sensitivity suggests that, during both the fall cooling period and the spring warming period (1993), minimum soil temperature may not only be a better predictor of daily maximum \( A_{\text{net}} \) than minimum \( T_{\text{air}} \), but that photosynthesis may be more limited by minimum soil temperature than by minimum air temperature. Jurik et al. (1988) also concluded that soil temperature was a better predictor of \( A_{\text{net}} \) than air temperature during the springtime recovery of photosynthesis in white pine (\( Pinus strobus \) L.). Thus, after accounting for the effects of sub-freezing nights, it would seem that models of environmental control of fall (and probably spring) net photosynthesis in conifers in cold temperate regions should focus on soil temperatures.

We found a significant difference in the photosynthetic response of red spruce to changes in temperature between the spring and fall periods. The linear contrasts in Table 3 indicate that the difference between the spring 1993 slope estimate for minimum \( T_{\text{soil}} \) (the predictor variable) and the average of the two fall estimates was highly significant \( (P < 0.005) \). However, the difference between the spring 1993 slope estimate for minimum \( T_{\text{air}} \) and the average of the two fall estimates was not significant \( (P < 0.1) \). Furthermore, although the regression equation between \( A_{\text{net}} \) and minimum \( T_{\text{soil}} \) for spring 1992 was

<table>
<thead>
<tr>
<th>Linear contrast</th>
<th>( \min_{\text{soil}} T_{\text{soil}} ) Coefficient</th>
<th>( P )-value</th>
<th>( \min_{\text{air}} T_{\text{air}} ) Coefficient</th>
<th>( P )-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>1(Spring 93) – 1/2(Fall 92 + Fall 93)</td>
<td>( \alpha )</td>
<td>( \approx 0.005 )</td>
<td>( \alpha )</td>
<td>( &lt; 0.1 )</td>
</tr>
<tr>
<td>0(Spring 93) + 1(Fall 92) – 1(Fall 93)</td>
<td>( \beta )</td>
<td>( &lt; 0.005 )</td>
<td>( \beta )</td>
<td>( &lt; 0.1 )</td>
</tr>
<tr>
<td>1/3(Spring 93 + Fall 92 + Fall 93)</td>
<td>( \alpha )</td>
<td>( n.s. )</td>
<td>( \alpha )</td>
<td>( &lt; 0.025 )</td>
</tr>
<tr>
<td></td>
<td>( \beta )</td>
<td>( &lt; 0.025 )</td>
<td>( \beta )</td>
<td>( n.s. )</td>
</tr>
<tr>
<td></td>
<td>( \alpha )</td>
<td>( &lt; 0.001 )</td>
<td>( \beta )</td>
<td>( &lt; 0.001 )</td>
</tr>
</tbody>
</table>
not significant, the slope estimate for spring 1992 was similar to the estimate for spring 1993 (Table 2). Because of the uncertainties in the spring data, these results are tentative; however, they suggest that the sensitivity of net photosynthesis to changes in soil temperature during the spring was approximately half of that during the fall. This result is consistent with the hypothesis that the photosynthetic response of red spruce to temperature differs between the fall and spring.

The simplest regression-type model, based solely on \( T_{air} \) and \( T_{soil} \), may be inadequate for predicting the photosynthetic response of red spruce to changes in the spring warming and fall cooling periods of the growing season. In particular, the sensitivity of \( A_{net} \) to changes in temperature depends on the particular physiological mechanisms that may constrain \( A_{net} \) during these periods, and these constraints probably differ between spring and fall. Changes in chloroplast thylakoid structure, chlorophyll content, photosynthetic enzyme activity, and electron transport (see reviews by Öquist 1983, Havranek and Tranquillini 1995, Teskey et al. 1995 and references therein) are associated with winter hardening, and although the relationships among these physiological changes is unclear, it is believed that these changes in combination with stomatal closure are largely responsible for the winter decline in net photosynthesis (Öquist 1983, Havranek and Tranquillini 1995, Teskey et al. 1995). Limitations to the springtime recovery of photosynthesis, on the other hand, have been associated with photoinhibition (Lundmark et al. 1988, Ottander and Öquist 1991, Strand and Lundmark 1995), insufficient soil water associated with soil thawing (Fahey 1979, Smith 1985, Jurik et al. 1988, Day et al. 1990), root hormones and mycorrhizal activity (Havranek and Tranquillini 1995). Thus, an improved model of photosynthetic sensitivity to temperature will depend on experimental work to isolate the relevant mechanisms and to describe their seasonal dependence on air and soil temperatures. Finally, although warmer air and soil may delay the onset of winter hardening and hasten springtime recovery, the significance of extending the growing season must be assessed in terms of whole-plant responses and overall carbon balance.

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References


