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Photosynthetic capacity of red spruce during winter

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Summary We measured the photosynthetic capacity (P_{max}) of plantation-grown red spruce (*Picea rubens* Sarg.) during two winter seasons (1993–94 and 1994–95) and monitored field photosynthesis of these trees during one winter (1993–94). We also measured P_{max} for mature montane trees from January through May 1995. Changes in P_{max} and field photosynthesis closely paralleled seasonal changes in outdoor air temperature. However, during thaw periods, field photosynthesis was closely correlated with multiple-day temperature regimes, whereas P_{max} was closely correlated with single-day fluctuations in temperature. There was a strong association between short-term changes in ambient temperature and P_{max} during the extended thaw of January 1995. Significant increases in P_{max} occurred within two days of the start of this thaw. Repeated measurements of cut shoots kept indoors indicated that temperature-induced increases in P_{max} can occur within 3 h. Although significant correlations between P_{max} and stomatal conductance (g_s) or intracelluar CO_2 concentration (C_i) raised the possibility that increases in P_{max} resulted from increases in stomatal aperture, fluctuations in g_s or C_i explained little of the overall variation in P_{max}. Following both natural and simulated thaws, P_{max} increased considerably but plateaued at only 37% of the mean photosynthetic rate reported for red spruce during the growing season. Thus, even though shoots were provided with near-optimal environmental conditions, and despite thaw-induced changes in physiology, significant limitations to winter photosynthesis remained.

Keywords: photosynthesis, Picea rubens, temperature, winter thaw.

Introduction

Northern red spruce (*Picea rubens* Sarg.) trees typically have relatively low rates of net photosynthesis in the fall and spring (Gage and DeHayes 1992) and have rates close to zero for much of the winter (Schaberg et al. 1995). However, red spruce can become photosynthetically active during winter thaws (Schaberg et al. 1995). Assimilation during thaws could be responsible for increases in total carbohydrates and foliar sugars reported for red spruce during winter (Snyder 1990), and these winter carbon reserves may help offset the metabolic costs of maintaining evergreen foliage. Any benefit of winter assimilation could increase in importance if the number or duration, or both, of winter thaws increases, as predicted by some climate models (MacCracken et al. 1991).

Increases in field-assessed winter photosynthesis require extended periods of elevated temperature (Schaberg et al. 1995). However, it is uncertain if this delay in photosynthetic response is primarily the result of a gradual restructuring of physiology or the progressive removal of environmental limitations to carbon capture. One way of assessing the degree to which environmental factors limit photosynthesis is to measure photosynthetic capacity (P_{max}; maximum photosynthetic rate measured in rehydrated shoots under near-optimal growing season temperature and light conditions). Reductions in field photosynthesis during winter could be associated with either temporary and reversible environmental limitations to carbon capture, or more profound alterations in the photosynthetic apparatus that are not easily reversed, or some combination of the two. In contrast, reductions in laboratory-based measurements of P_{max} are most likely attributable only to longer term alterations in the photosynthetic apparatus.

Although both short-term environmental and longer-lasting physiological impediments to winter photosynthesis probably exist (Havranek and Tranquillini 1995), a better understanding of the relative importance of these limitations would assist efforts to predict red spruce's response to potential climate change. To assess the degree to which short-term temperature, light and water limitations impede winter carbon capture, we measured P_{max} of young plantation-grown trees during two winters, and of mature montane trees for one winter. Repeated measurements of P_{max} during a protracted natural thaw allowed us to evaluate the magnitude and timing of thaw-induced changes in photosynthetic capacity. Comparisons of the response of field photosynthesis and P_{max} to thaw events allowed us to determine the relative responsiveness of these measurements to increases in temperature.

Methods

Plant material

During two winters, gas exchange measurements were recorded for red spruce in a plantation at the Vermont State Tree Nursery in Essex Junction, VT (elevation 104 m). The plantation was established in June 1986 with seed collected from a variety of sources in Vermont and germinated in 1985. Sea-

sonal measurements of P_{max} and field measurements of gas exchange were made on trees from four Vermont seed sources representing both high- and low-elevations. Sampling for all assessments of photosynthesis was evenly balanced among the four seed sources. From January through May 1995, photosynthetic capacity was also periodically assessed on mature trees growing at approximately 1000 m elevation on a southeast-facing slope of Mt. Mansfield, Stowe, VT.

Measurements of photosynthetic capacity

During the 1993–94 winter, P_{max} was measured for trees on two consecutive days for each of five months: November and December 1993 and February, March and May 1994. During the 1994–95 winter, P_{max} was measured on three consecutive days for each of eight months: September, November and December 1994, and January through May 1995. Gas exchange was also measured on nine days in January 1995 during a prolonged thaw. Through December 1994, P_{max} was assessed on four current-year shoots per day. Sample size was increased to 24 shoots per day beginning January 1995. For all measurements, shoots were harvested at approximately 0700 h, sealed in shaded containers and immediately transported to a laboratory located 8 km from the site. Samples were kept at outside ambient air temperatures before photosynthetic assessment.

During the second season, P_{max} was measured on trees from Mt. Mansfield in addition to those at the Essex Junction Plantation. For the trees on Mt. Mansfield, gas exchange was measured on 11 days beginning January 17, 1995, and ending May 8, 1995. Sampling occurred at approximately 2-week intervals, except during the January thaw when collections were made every three or four days. On each date, measurements were recorded on two current-year shoots from each of 10 trees. Field collection and initial storage methods for these branches are detailed in Strimbeck et al. (1995). Immediately before all gas exchange measurements, shoots were brought to the laboratory, recut under water and attached to a supply of distilled water through latex tubing. Preliminary measurements indicated that current-year shoots processed in this manner reached stable photosynthetic maxima comparable to rates observed in freshly excised shoots within 20–40 min after initial illumination (data not shown). Gas exchange was measured for all shoots the day of sample collection. To evaluate the short-term impacts of above-freezing temperatures on P_{max}, gas exchange was remeasured on four current-year shoots from Essex Junction trees following 1, 2, 3, 4, 5, 6, 7 and 24 h indoors (at approximately 17 °C) on each of five days immediately before the January 1995 thaw.

Photosynthesis and transpiration were monitored simultaneously with an LI-6262 CO_2/H_2O IRGA (Li-Cor, Inc., Lincoln, NE) in an open-system configuration. The LI-6262 was calibrated each morning against a span gas CO_2 concentration of 310 ppm. Zero settings of CO_2/H_2O analyzers were adjusted every 20 min during operation. Air temperatures within cuvettes were maintained at 16.73 ± 0.15 °C and 110–130V/300W metal halogen lamps (General Electric Co., Cleveland, OH) were used to provide near-saturating photon flux densities (581.87 ± 15.89 μmol m^{-2} s^{-1}, Alexander et al. 1995). For each shoot, gas exchange was monitored for 40 min. For 1993 and 1994 measurements, gas exchange was measured using one leaf chamber. Beginning January 1995, the system was modified to accommodate three cuvettes. When multiple cuvettes were used, cuvettes were sequentially monitored for 1-min intervals during a 40-min sampling period. Data for the first 0.3 min of each 1-min reading were excluded from the calculations in order to isolate fully the measurements from each cuvette. Gas exchange data were subjected to curve fitting procedures following a variation of the Michaelis-Menten equation (JMP statistical software, SAS Institute, Cary, NC) to solve for the stabilized photosynthetic rate (P_{max}). Stomatal conductance (g_s) was calculated by the equations of von Caemmerer and Farquhar (1981), and intracellular CO_2 concentration (C_i) was calculated as described by Teskey et al. (1986).

Field measurements of gas exchange

Field measurements were recorded in the Essex Junction plantation on 23 days beginning November 18, 1993, and ending May 20, 1994. Gas exchange was measured between 1100 and 1300 h on days when air temperatures were near or above freezing and no precipitation occurred. Forty-eight trees were selected and, on each tree, one current-year, south-facing shoot (5 cm long) from the upper third of the crown was chosen for gas exchange measurement. These same 48 shoots were used throughout the field season. On each day, the sampling order of trees was random. Gas exchange was measured with a Li-Cor LI-6200 portable photosynthesis instrument equipped with a 0.25-l cuvette, as described by Schaberg et al. (1995). Gas exchange rates were expressed on a one-sided projected needle area basis. Needle areas were measured with a Li-Cor Model 3100 leaf area meter.

Ambient air temperatures reported for the Essex Junction plantation were recorded by the National Oceanic and Atmospheric Administration, National Weather Service (NOAA-NWS), at the Burlington International Airport, South Burlington, VT, approximately 4 km from the study plantation. Mean daily temperatures at the Mt. Mansfield site were estimated by linear interpolation, based on NOAA-NWS data for the south summit of Mt. Mansfield (1250 m) and data from a long-term monitoring site at 400 m on the west slope of Mt. Mansfield (Vermont Monitoring Cooperative).

Statistical analyses

Analyses of variance were used to test for differences between P_{max}, g_s and C_i means. Dunnett's Test was used to determine when thaw-associated changes in these parameters differed significantly from initial values. Correlation analyses were used to evaluate relationships among measurement parameters. Unless otherwise noted, differences were considered statistically significant if $P \leq 0.05$.

Results and discussion

Seasonal trends in P_{max} and field photosynthesis

Changes in photosynthesis generally paralleled seasonal changes in ambient temperature. For example, fall declines

and spring increases in field photosynthesis and P_{max} were coincident with seasonal temperature trends at the Essex Junction site during both seasons (Figures 1 and 2). However, the trends in temperature and carbon exchange differed between the two winter seasons. From mid-December 1993 through mid-March 1994, air temperatures were seldom above 0 °C and measurements of field photosynthesis and P_{max} remained close to 0 μmol m^{-2} s^{-1} (Figure 1). In contrast, during the 1994–95 winter, temperatures above 0 °C were common and mean P_{max} values were above 1 μmol m^{-2} s^{-1} for all dates except those portions of January and February that followed protracted periods of subfreezing temperatures (Figure 2). Data for Mt. Mansfield trees collected during 1995 indicated that montane red spruce also had the potential for photosynthetic activity when exposed to moderate winter temperatures: positive rates of P_{max} were recorded for these trees during or following protracted thaws (Figure 3).

Parallel trends in temperature and photosynthesis were supported by correlation analyses. For the 1993–94 winter season, correlations between mean daily temperatures and mean daily rates of field photosynthesis or P_{max} were both significant (r^2 = 0.582, $P \leq 0.001$ and r^2 = 0.665, $P \leq 0.001$, respectively). Correlations of mean daily temperature and P_{max} values were also significantly correlated for samples from the Essex Junction plantation (r^2 = 0.458, $P \leq 0.001$) and the Mt. Mansfield site (r^2 = 0.591, $P \leq 0.006$) during the 1994–95 winter season. Although field photosynthesis and P_{max} were both strongly correlated to seasonal trends in temperature, they were not equally responsive to changing temperature regimes during thaws.

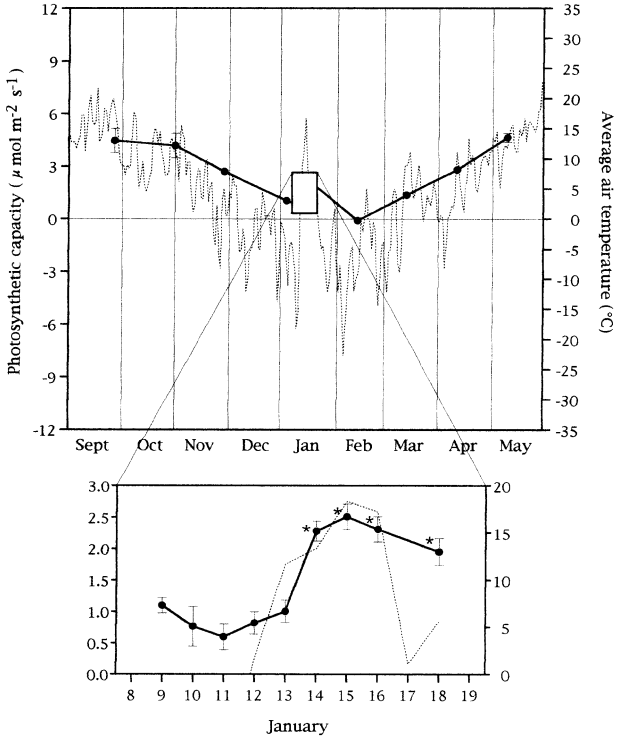

Figure 2. Mean photosynthetic capacities (●) for red spruce trees from the Essex Junction Plantation plotted with mean daily air temperatures from September 1994 to May 1995. An asterisk (*) identifies means that are significantly different ($P \leq 0.05$) from the pre-thaw (January 11, 1995) mean, as determined by Dunnett's Test. Error bars are ± 1 SE of means for all seed sources combined.

Thaw-associated changes in P_{max} and field photosynthesis

To test the relative influence of temperature on field photosynthesis and P_{max} during thaws, we correlated mean daily photosynthetic rates with a series of multiday temperature means. Correlations between temperature and field photosynthesis were based on data from the thaw that began in March 1994. Temperature means for this assessment were calculated by averaging temperatures for the days of photosynthetic assessment with temperature means for days immediately before this. For example, the 2-day mean was the average of temperatures for two days, the day of photosynthetic assessment and

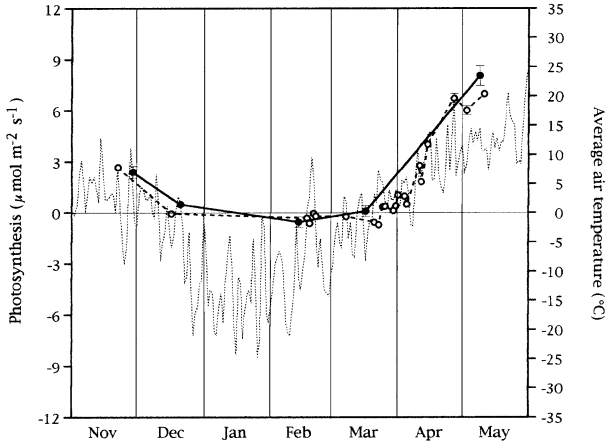

Figure 1. Mean photosynthetic capacity (●) and field photosynthetic (○) rates for red spruce trees from the Essex Junction Plantation plotted with daily mean air temperatures from November 1993 to May 1994. Error bars are ± 1 SE of means for all seed sources combined.

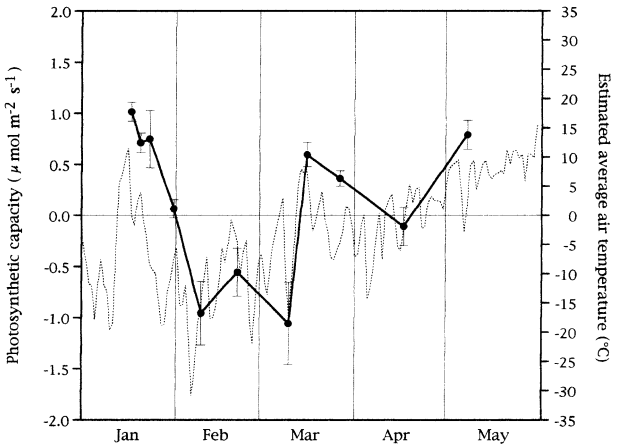

Figure 3. Mean photosynthetic capacities (●) for red spruce trees from Mt. Mansfield plotted with estimated mean air temperatures for the period from January to May 1995. Error bars are ± 1 SE of daily means.

the day immediately preceding this. Correlations between temperature and P_{max} were based on data obtained from the Essex Junction plantation for the January 1995 thaw. Temperature means for this assessment were computed as described above, except that mean temperatures for the day of P_{max} measurement were not included because shoots were collected in the morning before they were exposed to the influence of daytime temperatures. For all calculations, mean daily temperature was computed from eight temperatures taken at 3-h intervals at the NOAA-NWS station, Burlington, VT.

Correlations between mean rates of field photosynthesis and multiday temperature means (Table 1) supported our previous findings that increases in field photosynthesis during winter occurred primarily during extended periods of elevated temperature (Schaberg et al. 1995). For the current study, correlations of field photosynthesis and multiday temperature means were not significant for 1-, 2-, 3-, and 4-day means (Table 1); however, the correlation with the 5-day mean was positive and significant ($P \leq 0.088$), and the strength of the correlations increased for the 6- and 7-day temperature means (Table 1). In contrast, P_{max} values were better correlated with temperature regimes close to the date of gas exchange assessment: photosynthetic capacity was significantly correlated with 1-, 2-, 3-, and 4-day ($P \leq 0.069$) temperature means, but not with means beyond the 4-day mean (Table 1). The relationship between P_{max} and temperature was particularly strong for associations with temperature means for the two days closest to the date of photosynthetic assessment (Table 1).

These correlations indicate that P_{max} was more responsive to short-term temperature changes, whereas field photosynthesis was better related to multiday temperature regimes. The delayed response of field photosynthesis to temperature suggests that environmental limitations retarded the photosynthetic response to thaw. Because environmental limitations were minimal when photosynthetic capacity was measured, P_{max} reflected short-term temperature-dependent alterations in the plant's ability to fix carbon. In contrast, field photosynthesis was probably influenced not only by these same short-term alterations, but also by temperature-dependent changes in the availability of critical environmental resources, especially water. Winter photosynthesis is not generally light limited (Schaberg et al. 1995), and air temperatures during thaws can approach the photosynthetic optimum for red spruce (Alexander et al. 1995). However, because plant water availability is reduced at low and subfreezing temperatures (Kramer 1983, Marchand 1991), particularly when soil freezing prevents water uptake, prolonged periods with high air temperatures may be needed to thaw well-insulated root environments and increase water availability. If temperature-induced changes in field water availability were delayed relative to alterations in the photosynthetic apparatus, or if an alteration in water availability was itself the stimulus for physiological change, then increases in field photosynthesis would lag behind increases in ambient temperature.

Rapid increases in P_{max}

The impact of short-term increases in temperature on P_{max} was particularly evident during the extended thaw of January 1995 (Figure 2). With the exception of a 12-h period when temperatures dipped to –1.1 °C, air temperatures near the Essex Junction plantation remained above freezing for 10 days, reaching a high of 18.3 °C. On January 11, 1995, the day before the onset of thaw, mean P_{max} for trees in the Essex Junction plantation was 0.60 μmol m^{-2} s^{-1}. Within two days of the start of the thaw, there were significant increases in P_{max} compared with P_{max} measured on January 11 (Dunnett's Test; Figure 2) and maximum mean P_{max} (2.51 μmol m^{-2} s^{-1}) occurred after three days. Although pre-thaw values of P_{max} were not measured for Mt. Mansfield trees, their P_{max} values were high during the January thaw relative to other winter values (Figure 3). The highest mean P_{max} for these trees (1.01 μmol m^{-2} s^{-1}) occurred on the warmest thaw day, with comparable values occurring after only a short thaw in March (0.60 μmol m^{-2} s^{-1}) and following the onset of spring in May (0.79 μmol m^{-2} s^{-1}).

To determine the minimum response time of P_{max} to a sustained higher temperature, we collected 20 shoots from the Essex Junction plantation in January 1995 and measured P_{max} at hourly intervals following 0 to 7 h of exposure to temperatures of approximately 17 °C, and again after 24 h of exposure to this temperature. Under these experimental conditions, there was a significant increase in P_{max} within 3 h (Figure 4A). These data demonstrate that increases in photosynthetic capacity can occur sooner than the 24 h previously reported by Hadley et al. (1993).

Compared with other studies, stomatal conductance values were low (Figure 4B), and the range in mean g_s (5.1 to 14.9 mmol m^{-1} s^{-2}) was lower than the range summarized by Nobel (1991) for trees with open stomata (20 to 120 mmol m^{-1} s^{-2}). Although low g_s values may indicate some stomatal limitation to gas exchange, several lines of evidence suggest that this was not the dominant factor limiting carbon gain. For example,

Table 1. Correlation coefficients (*P*-values) for relationships between mean field photosynthesis or P_{max} values and multiday air temperature means for transitional periods that include days before and during thaws.

	Number of days included in temperature mean						
	1	2	3	4	5	6	7
Field photosynthesis	–0.3812	0.2886	0.2635	0.4383	0.5993	0.6584	0.7657
Mar. 21–Apr. 5, 1994 (n = 9)	(0.3114)	(0.4514)	(0.4933)	(0.2380)	(0.0881)	(0.0538)	(0.0160)
P_{max}	0.9230	0.9543	0.8617	0.7179	0.6003	0.5712	0.6241
Jan. 11–18, 1995 (n = 7)	(0.0030)	(0.0008)	(0.0127)	(0.0692)	(0.1541)	(0.1804)	(0.1342)

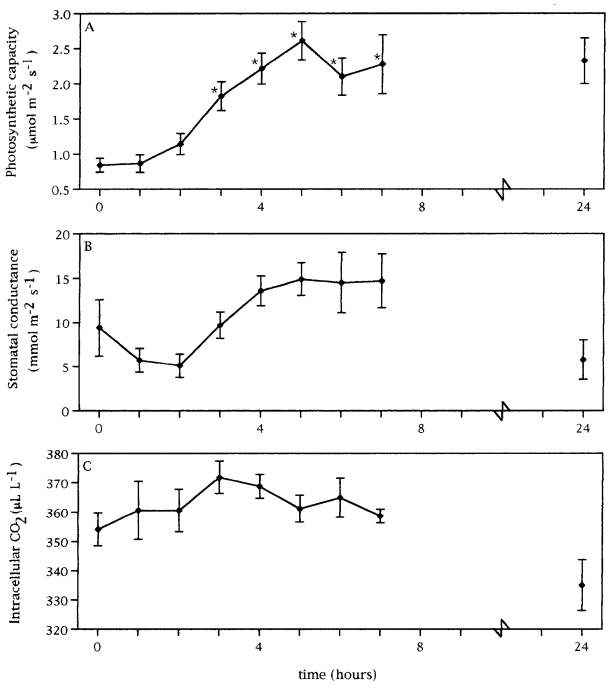

Figure 4. Short-term changes in midwinter photosynthetic capacity (A), stomatal conductance (B) and intracellular CO_2 concentration (C) for red spruce shoots during an experimental exposure to 17 °C. An asterisk (*) identifies means that are significantly different ($P \leq 0.05$) from each other as determined by the Tukey-Kramer HSD Test. Error bars are ± 1 SE of hourly means.

results of the Dunnett's Test indicated that exposure of shoots to 17 °C had no effect on g_s, indicating that the temperature-induced changes in P_{max} (Figure 4A) were not caused by changes in g_s. However, the Dunnett's test may have underestimated potential increases in g_s because the 0-h values were comparatively high (potentially a sign of surface moisture/frost on foliage when brought indoors). If the 0-h data are excluded, then g_s tended to increase over time, and the increase was most pronounced between 2 and 3 h after exposure of the shoots to the 17 °C treatment, which is the time when increases in P_{max} were first detected (Figure 4A). Nevertheless, correlations between P_{max} and g_s suggest that the overall influence of changing stomatal conductance on photosynthetic capacity was not great. There was little correlation between P_{max} and g_s for individual readings ($r^2 = 0.050$, $P \leq 0.01$, $n = 143$), or between mean hourly values of P_{max} and g_s ($r^2 = 0.085$, $P \leq 0.415$, $n = 9$). At 24 h after exposure of shoots to the 17 °C treatment there was no correlation between P_{max} and g_s; P_{max} remained high, whereas g_s values were among the lowest recorded (Figures 4A and 4B).

Analysis of the C_i data further supports the conclusion that stomatal limitations were not a major influence on photosynthetic capacity. Low stomatal aperture can prevent the full recharge of CO_2-enriched air from outside the leaf following photosynthetic CO_2 drawdown and result in low C_i (Farquhar and Sharkey 1982). Thus, increases in C_i would accompany the relaxation of stomatal limitations to photosynthesis. There was a tendency for C_i to increase during the first 3 h after exposure of shoots to the 17 °C treatment, however, the effect was not significant. There was little correlation between P_{max} and C_i for individual readings ($r^2 = 0.12$, $P \leq 0.01$, $n = 143$), and no correlation between mean hourly P_{max} and C_i values ($r^2 = 0.006$, $P \leq 0.84$, $n = 9$). At 24 h after exposure of the shoots to the 17 °C treatment, C_i concentrations were lowest whereas photosynthetic rates were among the highest recorded.

Although we have no direct information about the physiological mechanisms responsible for these thaw-induced increases in P_{max}, the potential rapidity of this response (within 3 h) appears to exclude certain mechanisms. For example, alterations in chloroplast structure (Parker 1957, Senser et al. 1975, Fincher and Alscher 1992), thylakoid membrane composition and associated photosynthetic electron transport (Martin et al. 1978*a*, 1978*b*, Öquist 1982, 1983, Öquist and Ögren 1985), and chlorophyll content (McGregor and Kramer 1963, Perry and Baldwin 1966, Öquist et al. 1978*a*, 1978*b*), have all been causally linked to the low photosynthetic rates typical of the cold season. However, it is unlikely that these types of anatomical and physiological limitations would be rapidly reversible. In contrast, increases in photosynthesis following rehydration (Epron and Dreyer 1992), or temperature-sensitive alterations in foliar sugar concentrations and their influence on the feedback inhibition of photosynthesis (Azcón-Bieto 1983) can occur within hours.

Whatever the mechanism for thaw-related increases in P_{max}, our data show that this increase can be substantial and rapid. Photosynthetic capacity quadrupled in magnitude and stabilized at approximately 2.3 ± 0.1 μmol m^{-2} s^{-1} following 48 h of natural thaw (Figure 2). Increases in P_{max} occurred more rapidly (3 h), but plateaued at a similar rate (2.2 ± 0.1 μmol m^{-2} s^{-1}) when exposed to a simulated thaw (Figure 4A). This apparent plateau in winter P_{max} (± 2.2 μmol m^{-2} s^{-1}) is about 37% of the mean photosynthetic rate reported for red spruce during the growing season (Gage and DeHayes 1992). Thus, despite thaw-induced increases in P_{max}, photosynthetic capacity remained depressed during winter. Long-term reductions in P_{max} may be under the influence of endogenous rhythms (Havranek and Tranquillini 1995), although it is also possible that extended periods of above-freezing temperatures are needed to repair structural and biochemical alterations in chloroplasts that are induced by freezing (Havranek and Tranquillini 1995).

Conclusions

Changes in P_{max} and field photosynthesis closely paralleled seasonal changes in temperature. However, during thaw periods, field photosynthesis was closely related to multiday temperature regimes, whereas P_{max} was closely related to short-term changes in temperature. The close relationship between short-term changes in ambient temperature and photosynthetic capacity was particularly evident during the extended thaw of January 1995, when significant increases in P_{max} occurred within two days of thaw initiation. Exposure of cut shoots to a constant temperature of 17 °C indicated that temperature-induced increases in P_{max} can occur within 3 h.

Although significant correlations between P_{max} and g_s or C_i concentrations raised the possibility that increases in P_{max} resulted from increases in stomatal aperture, fluctuations in g_s or C_i explained little of the overall variation in P_{max}. Following both natural and simulated thaws, P_{max} increased considerably but plateaued at 37% of the mean photosynthetic rate reported for red spruce during the growing season. Thus, even though shoots were provided with near-optimal environmental conditions, and despite thaw-induced changes in physiology, significant limitations to winter photosynthesis remained.

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