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Winter photosynthesis of red spruce from three Vermont seed sources

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Summary We evaluated winter (January through March) carbon assimilation of red spruce (*Picea rubens* Sarg.) from three Vermont seed sources grown in a common garden in northwestern Vermont. Although CO_2 exchange rates were generally low, net photosynthetic rates increased during two prolonged thaws. Significant correlations between CO_2 exchange rates and multiday air temperature means supported our observations of enhanced gas exchange during extended periods of elevated temperature. Increases in photosynthesis during thaws occurred before observed increases in leaf conductance, indicating that initial changes in photosynthesis were probably not associated with changes in stomatal aperture. Results of correlations between photosynthetic rates and PAR suggested that solar irradiance did not have a strong effect on winter carbon capture.

Rates of net photosynthesis differed among seed sources. Trees from the Mt. Mansfield source had the highest average rates of photosynthesis and, at times, rates for individual trees from this source approximated those occurring during the growing season. Because seed sources differed in photosynthetic rates but not in leaf conductance, we conclude that differences in winter photosynthesis among seed sources were primarily attributable to factors other than changes in stomatal aperture.

Keywords: carbon assimilation, carbon exchange, genetic variation, leaf conductance, Picea rubens, stomatal aperture, temperature.

Introduction

Red spruce and other evergreens retain their foliage throughout the winter, thus they have the potential for year-round carbon assimilation. Neilson et al. (1972) suggested that conifers may compensate for low net assimilation rates during the normal growing season by photosynthesizing throughout the year. Snyder (1990) found that the total carbohydrate reserves of red spruce seedlings increased during winter, and he also reported an approximately 15% increase in sugar concentrations in needle tissue between February and March. These carbohydrate increases could have resulted from winter photosynthesis.

Field measurements of photosynthesis have shown that winter carbon assimilation can be significant in regions where winter climates are mild (Helms 1965, Ludlow and Jarvis 1971); however, field results from colder areas have been less consistent. For example, Freeland (1944) reported apparent photosynthesis for pine and spruce during a winter in northern Illinois, whereas Jurik et al. (1988) reported no photosynthetic activity for pine in Michigan from December to late April, and Parker (1961) found that, for pine measured in southern New England, winter photosynthesis was limited to a short period at the beginning of January. Laboratory-based assessments of photosynthetic capacity during winter reveal trends similar to the field studies, with trees growing in milder climates showing potential for photosynthesis (Neilson et al. 1972, Fry and Phillips 1977, Teskey et al. 1984), and trees from colder regions lacking this potential (Bourdeau 1959). It has been noted that the photosynthetic machinery of northern conifers can be altered during winter. Reported alterations include changes in chloroplast structure (Parker 1956, Perry and Baldwin 1966, Senser et al. 1975, Martin et al. 1978*a*, Fincher and Alscher 1992), reductions in chlorophyll content (McGregor and Kramer 1963, Perry and Baldwin 1966, Martin et al. 1978*a*, 1978*b*, Öquist et al. 1978*a*, 1978*b*), alterations in photosynthetic enzyme activity (Gezelius and Hallen 1980, Öquist et al. 1980), disruptions in photosynthetic electron transport (Martin et al. 1978*a*, 1978*b*, Öquist and Martin 1980, Öquist et al. 1980, Öquist 1983) and stomatal closure (Marchand 1991).

Although questions concerning winter carbon exchange exist for all northern conifers, information about the photosynthetic activity of red spruce may be of particular scientific interest. Since the mid-1960s, growth rates of red spruce in New England and northern New York have been declining (Siccama et al. 1982, Hornbeck and Smith 1985, Johnson et al. 1988). Numerous studies have emphasized the importance of winter injury to needles as a contributing factor in decline (Freidland et al. 1984, Evans 1986, Wilkinson 1990, Strimbeck et al. 1991, DeHayes 1992), but the exact mechanisms of injury have not been determined (DeHayes 1992). An increased understanding of the normal physiology of red spruce in winter could help in the assessment of potential mechanisms of dysfunction and injury.

To further our understanding of winter photosynthesis of red spruce (*Picea rubens* Sarg.), we evaluated carbon assimilation and needle conductance of trees from three Vermont seed sources during winter (January through March).

Methods

Plant material

Gas exchange rates were measured on 46 8-year-old red spruce trees growing in a common garden at the Vermont State Tree Nursery in Essex Junction, Vermont (elevation 104 m). To evaluate potential local genetic differences, measurements were made on trees from three Vermont seed sources: 22 trees from Wolcott (elevation 366 m), 12 trees from Mt. Mansfield, Stowe (975 m), and 12 trees from Camels Hump, Huntington (975 m).

Instrument evaluation

Commercially available instruments for measuring gas exchange are not normally designed for, or tested under, winter conditions. Consequently, we first assessed the feasibility of conducting winter field measurements of gas exchange with an LI-6200 portable photosynthesis instrument (Li-Cor Inc., Lincoln, NE) under simulated winter conditions. The LI-6200 calculates rates of photosynthesis and transpiration (used to calculate leaf conductance) by measuring cuvette air temperature, relative humidity and CO_2 concentration. We evaluated the accuracy and precision of the LI-6200 in measuring these parameters at three temperatures (24, 5 and –5 °C).

The LI-6200-generated air temperatures were compared to measurements taken with an alcohol bulb thermometer traceable to the National Institute of Standards and Technology. Average differences between bulb and LI-6200 measurements never exceeded 0.4 °C and were within the established tolerances of the thermometer. Relative humidities measured with the LI-6200 over a broad range of humidities were compared to values calculated from measurements of dew- or frost-point temperatures obtained with a dew point monitor (HYGRO MI PACER, General Eastern, Watertown, MA) with a 1211 H optical dew point sensor. Relative humidities measured with the LI-6200 closely approximated humidities determined with the monitor under all test conditions ($r^2 = 0.996$). Following calibration of the LI-6200 at room temperature, CO_2 concentrations of five reference gases (certified concentrations of 87, 180, 270, 360 and 449 ppm CO_2, Linde Specialty Gases, Union Carbide Corp., NJ) were determined. Carbon dioxide measurements of reference gases made with the LI-6200 were consistent over all temperatures tested ($r^2 = 0.988$). From these evaluations, we concluded that the LI-6200 provides accurate estimates of net photosynthesis and transpiration over a wide range of field temperatures, including winter temperatures as low as –5 °C.

Field measurement of net photosynthesis

Measurements were made on 11 days beginning January 28, 1991, and ending March 26, 1991. Sample days were chosen on the basis of weather: measurements were made on days when air temperatures were near or above freezing and no precipitation occurred. On each day, the sampling order of trees was completely random. Gas exchange was measured between 1100 and 1300 h. On each tree, one current-year, south-facing shoot (5 cm long) from the upper third of the crown was measured. Branches were maintained in their natural orientations during measurement. The same 46 shoots were used throughout the study. Gas exchange was measured with an LI-6200 with a 0.25-l cuvette. The LI-6200 was calibrated each day before field measurements using a span gas CO_2 concentration of 360 ppm. Zero settings of the infrared gas analyzer and flow meter were adjusted regularly in the field. Rather than using a fixed-concentration drawdown, a 60-s time-interval measurement of gas exchange was used because regular occurrences of low or negative rates of net photosynthesis were anticipated. Ambient photosynthetically active radiation (PAR) was recorded by the LI-6200 simultaneously with gas exchange measurements. At the end of the field season, sample shoots were harvested and projected needle areas were measured with a Li-Cor Model 3100 leaf area meter. Dry weights of needles were also determined. Photosynthetic rates were then expressed on both projected needle area and dry weight bases.

Leaf conductance (m s^{-1}) was calculated for each gas exchange measurement by dividing the LI-6200-generated transpiration estimate (mmol m^{-2} s^{-1}) by the estimated absolute humidity gradient between the inside and outside of the needles (mmol m^{-3}). We assumed that leaf temperature equaled ambient cuvette temperature. Conductivity values were adjusted and expressed as mm s^{-1}.

Ambient air temperatures, used in correlation analyses with gas exchange rates, were recorded by the National Oceanic and Atmospheric Administration (NOAA), National Weather Service, at the Burlington International Airport, South Burlington, Vermont. This weather station is approximately 4 km from the study plantation.

Statistical analyses

Analyses of variance were used to test for differences among seed sources on individual sampling days, and repeated measures analyses of variance were used to test for differences among seed sources, days and seed source × day interactions for the entire sampling period. Where differences were detected, the Tukey-Kramer HSD test was used to determine differences among specific seed source and day-to-day means. Correlation analyses were used to evaluate relationships between foliar gas exchange, temperature and PAR. In all cases, differences were considered statistically significant if $P \leq 0.05$.

Results and discussion

Field photosynthesis and leaf conductance

Average net photosynthetic rates were generally low, but they were positive (net photosynthesis) on 7 of the 11 sample days (Figure 1). Several increases in assimilation rates occurred during the sampling period (Figure 1). Average rates ranged from a high of 0.81 µmol m^{-2} s^{-1} on February 8, to a low of –0.10 µmol m^{-2} s^{-1} on March 1. Although these average rates were relatively low, they reached 14% of the average rate reported for red spruce during the growing season (Gage and DeHayes 1992). Additionally, on days with the highest average assimilation, individual trees occasionally had photosynthetic

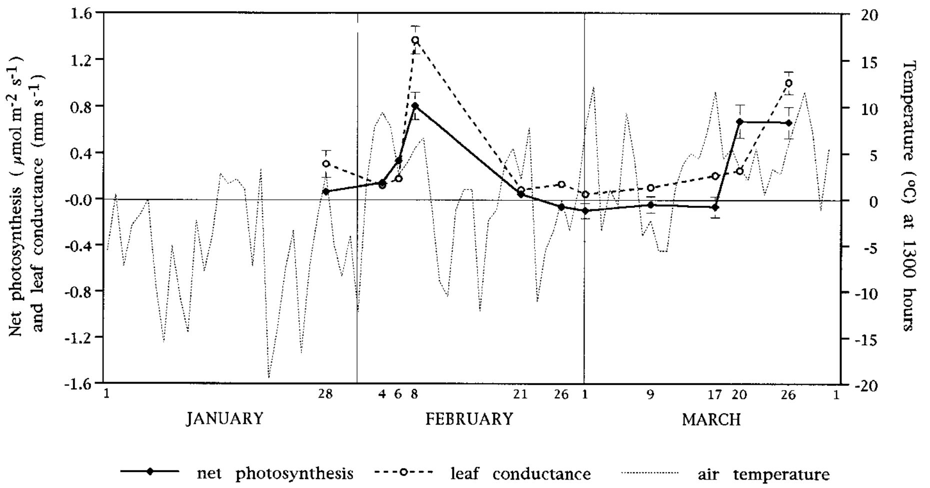

Figure 1. Average midday CO_2 exchange rates and leaf conductances for red spruce from three Vermont seed sources plotted with air temperatures at 1300 h for the sampling period (January through March 1991). Error bars are ± 1 SE from means for all seed sources combined.

rates comparable to those measured by Gage and DeHayes (1992) during the growing season. Because sampling was limited to days with favorable weather conditions (temperatures near or above freezing and no precipitation), measured photosynthetic rates do not characterize gas exchange for all winter conditions. Nonetheless, the data show that red spruce trees are capable of net photosynthesis during winter, and that, on certain days, rates of photosynthesis of individual trees can be as high as those measured during the growing season.

Average leaf conductance was low on all days except February 8 and March 26 (Figure1). Excluding these days, the range in daily average leaf conductance (0.05 to 0.31 mm s^{-1}) was below the range reported for *Abies amabilis* (Dougl.) Forbes. during the growing season (1.0 to 2.0 mm s^{-1}) by Teskey et al. (1984) and was lower than the range summarized by Nobel (1991) for trees with open stomata (0.5 to 3.0 mm s^{-1}). On February 8 and March 26, average leaf conductances increased to more than 1.0 mm s^{-1}; these increases occurred toward the end of prolonged thaws (Figure 1). Higher rates of photosynthesis on February 6 and, to a greater extent, on March 20 occurred without correspondingly large increases in leaf conductance (Figure 1). Assuming that the primary route for gas exchange is through stomata, then, for at least these days, increases in photosynthesis were not dependent on changes in stomatal aperture. In contrast, the increase in net photosynthesis on February 8 (the last day of the first thaw) occurred simultaneously with a significant increase in leaf conductance. For this day, increases in stomatal aperture may have promoted carbon capture.

Associations with temperature and light intensity

Sampling day was an important source of variation for photosynthesis (Table 1). A primary factor that varied among days was temperature (Figure 1), with maximum gas exchange rates recorded during periods with average temperatures above freezing, once at the beginning of February and again during mid- to late March (Figure 1). However, the correlation between cuvette temperatures and CO_2 exchange rates was not significant. There was also no significant correlation between either midday (1300 h) or average daily temperatures for sampling days and average CO_2 exchange rates. However, our data suggested a cumulative impact of temperature, with high rates of gas exchange occurring only after prolonged periods of elevated average temperature (Figure 1). Several investigators have noted that low temperatures on days preceding measurement may precondition trees and limit gas exchange (Parker 1953, Teskey et al. 1984, Jurik et al. 1988).

To test the influence of warm-day preconditioning, we correlated average sample-day photosynthetic rates with a series of multiday temperature means. These means were calculated by averaging sample-day temperatures with average temperatures for the days prior to sampling. For example, the 2-day mean was the average of temperatures for 2 days, the sample day and the day preceding sampling. For all days, average daily temperature was calculated as the mean of eight temperatures taken at 3-h intervals throughout the day at the

Table 1. Analysis of variance of winter photosynthetic rates for red spruce from three Vermont seed sources (* = $P > F = 0.05$, ** = $P > F = 0.01$, *** = $P > F = 0.0001$).

Sampling period	Source of variation	DF	MS	*F*
All days	Seed source	2	6.83	4.98*
	Tree	43	1.37	26.90***
	Day	10	7.80	3.34***
	Seed source × day	20	0.97	
	Tree × day	421	0.29	
	Total	496		
February 8	Seed source	2	2.83	3.63*
	Tree	43	0.78	
	Total	45		
March 20	Seed source	2	5.80	5.23**
	Tree	42	1.11	
	Total	44		
March 26	Seed source	2	5.96	6.64**
	Tree	41	0.90	
	Total	43		

Burlington, Vermont, NOAA weather station.

Correlations between average net photosynthetic rates and multiday temperature means support our hypothesis that significant gas exchange occurred primarily in association with prolonged periods of elevated temperature. Although correlations of photosynthetic rates with multiday temperature means were not significant for 2- and 3-day means, the correlation with 4-day temperature means was significant ($r^2 = 0.42$, $P \leq 0.03$), and the strength of correlations increased when 5-day and 6-day means were used ($r^2 = 0.49$, $P \leq 0.02$ and $r^2 = 0.51$, $P \leq 0.01$, respectively). Correlation strength decreased for associations with means beyond the 6-day average.

Although temperature was important in promoting net photosynthesis, it was not possible to discern from our data if specific critical temperatures were associated with enhanced winter gas exchange. But it is interesting to note that, although daytime temperatures remained above freezing during these thaws, night temperatures frequently dropped below 0 °C.

We have no direct information about the physiological mechanisms involved in the observed response of red spruce to winter thaws, but there are several possible physiological conditions that would tend to result in increased net photosynthetic rates after periods of extended winter thaw. Reductions in gas exchange have been associated with low root temperatures (Turner and Jarvis 1975, DeLucia 1986, Day et al. 1991). Because soils have great thermal mass, prolonged periods with high air temperatures are needed to raise soil temperatures significantly. Prolonged winter thaws might allow soils and roots to warm enough to promote enhanced physiological activity. In addition, the process of winter hardening induces changes in chloroplast structure that also decrease photosynthetic efficiency (Senser and Beck 1977, Martin et al. 1978*a*, Öquist et al. 1978*a*, 1980, Öquist 1982). Prolonged warming trends may initiate tissue dehardening and chloroplast restructuring, resulting in increased photosynthetic activity (Steffen and Palta 1987).

Comparisons of mean photosynthetic and leaf conductance rates showed that initial increases in photosynthesis during thaws were not associated with changes in stomatal aperture (Figure 1). This is consistent with Parker's (1963) contention that winter photosynthesis is limited more by internal factors than by stomatal closure. Parker (1963) concluded that, in winter, photosynthetic capacity may be directly related to changes in leaf biochemistry associated with the induction and maintenance of cold hardiness.

Average PAR values for sampling days ranged from 174 μmol m^{-2} s^{-1} on February 21 to 1702 μmol m^{-2} s^{-1} on March 20 (data not shown). Correlations between net photosynthetic rates and PAR measurements for the entire sampling period were not significant, even during the thaw periods. For the first thaw (February 4–8), photosynthesis and PAR measurements were not significantly correlated, and for the second thaw (March 17–26), there was a weak negative relationship ($r^2 = 0.04$, $P \leq 0.03$).

Differences among seed sources

Although the pattern of photosynthetic response over the entire sampling period was similar for all seed sources, the magnitude of response frequently differed among seed sources (Figure 2A).

Significant differences in photosynthetic rates among seed sources were found for the entire sampling period and for each of the 3 days with the highest average photosynthesis (February 8, March 20 and 26) (Table 1). These differences were evident regardless of whether photosynthesis was expressed on an area basis or a dry weight basis. In general, seed source differences were attributable to the higher photosynthetic rates of the Mt. Mansfield source. For the days with the highest average carbon capture, photosynthetic rates for the Mt. Mansfield source were approximately 23% of the average rate reported for red spruce during the growing season (Gage and DeHayes 1992). Seed source × day interactions were an important source of variation in net photosynthetic rate (Table 1). Partitioning of the sums of squares for the interaction term using orthogonal contrasts further highlighted the physiological response of Mt. Mansfield trees to warming trends; over 69% of the total variability of the interaction was accounted for by contrasting the daily pattern of the Mt. Mansfield source with those of the other two sources combined. It is interesting to note that, although we found significant differences in winter carbon assimilation among seed sources, Gage and DeHayes (1992) found little consistency from one sampling period to the next in photosynthesis of provenances in a range-wide test and no significant differences between provenance means for the entire growing season. The reasons for these differences between growing season and winter responses are unknown.

The relative magnitude of leaf conductance among seed sources showed no consistent pattern (Figure 2B). No significant differences in leaf conductance among seed sources were found for the entire sampling period, and although seed source differences in leaf conductance were significant on February 26 and March 20, these were days of low leaf conductance, and there was no consistent pattern in these differences (data not shown). Because seed sources differed in their photosynthetic rates but not in their leaf conductances, differences in photosynthesis among seed sources probably resulted from the influence of nonstomatal factors.

Conclusions

Winter net photosynthetic rates and leaf conductances of red spruce were generally low but increased during two prolonged thaws. Increased photosynthetic capture was not correlated with cuvette temperature but was positively correlated with higher temperatures on days preceding CO_2 exchange measurement. During thaws, photosynthetic rates increased prior to increases in leaf conductance, indicating that initial changes in photosynthesis were not associated with changes in stomatal aperture. The lack of correlations between photosynthetic rates and PAR suggest that solar irradiance had little effect on winter carbon capture.

Rates of photosynthesis differed among seed sources; maximum average photosynthetic rates were observed for trees

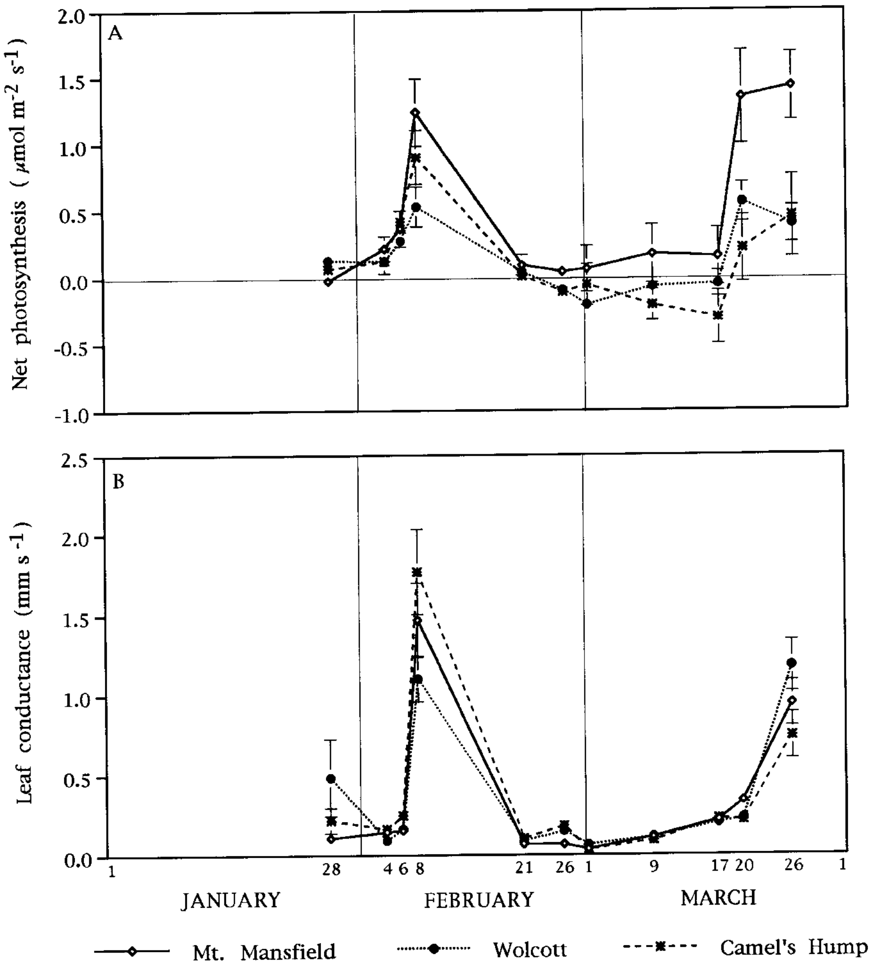

Figure 2. Average winter net photosynthetic rates (A) and leaf conductances (B) for red spruce from three Vermont seed sources. Error bars are ± 1 SE from seed source means.

from the Mt. Mansfield source. Rates for individual trees from this source were, at times, comparable to those measured during the growing season. Consistent differences in photosynthetic rates among seed sources contrasted with reports of genetic homogeneity in red spruce photosynthesis during the growing season. Because seed sources differed in their photosynthetic rates but not in their leaf conductances, it seems likely that differences in photosynthesis among seed sources were primarily attributable to factors other than changes in stomatal aperture.

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