Effect of Daily Minimum Temperature on Photosynthesis in Eastern Hemlock (*Tsuga canadensis* L.) in Autumn and Winter*

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Abstract

Most coniferous trees are capable of photosynthesis throughout the year, but low temperatures and frozen soil limit winter photosynthesis in many regions. In eastern hemlock (*Tsuga canadensis* L.) in central Massachusetts, U.S.A., midday light saturated photosynthesis (P_{max}) in autumn was limited by subfreezing temperatures during the previous one to two nights. In autumn, minimum air temperature (T_{min}) during the previous 24 h had a strong effect on midday P_{max} only if T_{min} was below −2°C. P_{max} averaged about 5 μmol m^{-2} s^{-1} after T_{min} near −2°C, but fell to about 1 μmol m^{-2} s^{-1} after a T_{min} of −8°C. Maximum measured P_{max} in winter was about 2.5 μmol m^{-2} s^{-1} after a T_{min} of 7°C in mid-March, and P_{max} in winter was more strongly related to average T_{min} during the previous week than to the T_{min} just prior to measurement. However, no major mid-winter thaws, with several successive above-freezing minimum temperatures, occurred during this study. A model of annual carbon exchange for the hemlock forest showed that daily ecosystem carbon exchange in December through March was very sensitive to variation between −5 and 2°C in average daily T_{min} during the past 2 d. Fewer autumn frosts and prolonged winter thaws could increase annual photosynthesis and carbon storage in eastern hemlock forests in the northeastern United States.

Introduction

Year-round photosynthesis allows coniferous forests to fix substantially more carbon than deciduous forests with the same maximum photosynthetic rate and leaf area index. Alternatively, year-round carbon uptake can allow conifers to compensate for lower photosynthetic rates per unit leaf or ground area by extending the season for photosynthesis. In areas where extreme cold is rare, winter photosynthesis may play a major role in annual carbon fixation (Waring and Franklin, 1979). However, in cold-temperate and boreal forests, low temperatures and frozen soil limit photosynthesis for much of the year, reducing the advantage of evergreen foliage. In conifers of the Rocky Mountains, subfreezing night temperatures more than daytime temperatures impose a limit on stomatal conductance and presumably photosynthesis (Fahey, 1979; Smith et al., 1984; DeLucia and Smith, 1987). Low soil temperature appears to impose a secondary limit on conductance and photosynthesis when nights are above freezing (Smith, 1985), and both minimum air temperature and soil temperature are correlated with photosynthesis of red spruce saplings in spring and fall (Schwartz et al., 1997).

I became interested in cold-season photosynthesis in eastern hemlock (*Tsuga canadensis* L.) and the effect of night frost during the development of an ecosystem carbon exchange model for an old-growth eastern hemlock forest. The forest is about 200 yr old, in central Massachusetts, U.S.A. Foster et al. (1992) and Foster and Zebryk (1993) described this forest and its history.

Materials and Methods

This study was conducted during autumn and winter periods in 1997, 1998, and 1999. Gas exchange of attached current-year foliage was measured at intervals of 1 to 2 wk, and sometimes more often when large temperature changes occurred. All measurements were made from a canopy access tower, in the upper canopy of four trees at a height of 21 to 22 m. On each day a single shoot was measured on the S, W, N, or E side of each tree, depending on its position relative to the tower. Shoots were measured two or three times and then harvested to avoid damage from repeated handling. Needles were then removed from shoots, taped to acetate sheets, and photocopied. Projected needle areas were determined by NIH image computer software (U.S. National Institutes of Health, Bethesda, Maryland, U.S.A.) on scanned images of the photocopies.

Light-saturated net photosynthesis (P_{max}) and leaf conductance to water vapor (G_s) were measured with a CIRAS-1 photosynthesis system (PP Systems Inc., Herts, U.K.) at near-ambient air temperature and humidity. Measurements were taken between 1000 and 1500 h at a photosynthetic photon flux density (PFD) of about 1400 μmol m^{-2} s^{-1}. Light response curves taken in autumn 1997 and 1998 showed that net photosynthesis was light saturated at about 800 μmol m^{-2} s^{-1} PFD.

Above-canopy air temperature and sapwood temperature in 24 branches were measured every 10 to 60 s by copper-constantan thermocouples made from 24- or 20-gauge wire. Air temperature was measured beneath an inverted white plastic cup on the north side of the 22-m canopy access tower, just below the top of the tower. Sapwood temperatures were measured at about 1 cm depth in 24 branches in the upper, middle, and lower canopy of the trees. Average, maximum, and minimum values were calculated every hour and stored in a CR-10 datalogger (Campbell Scientific, Logan, Utah, U.S.A.). Statistical models for net
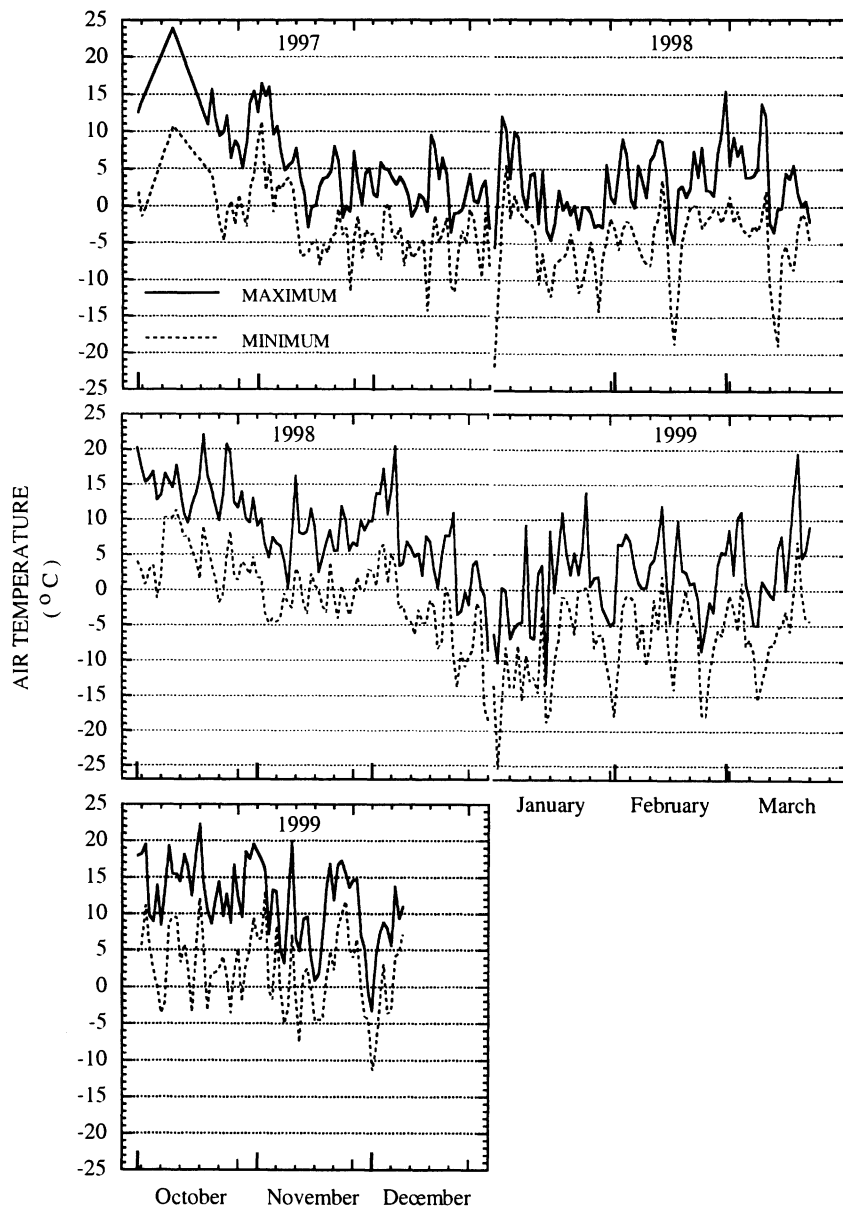
FIGURE 1. Maximum and minimum air temperatures in the upper canopy of the hemlock forest (22 m above ground) during the period of this study. Some data from October 1997 are missing due to a datalogger failure.

photosynthesis were developed as part of a whole-ecosystem carbon exchange model for the hemlock forest (Hadley, unpublished data). Net photosynthesis was one of four components of this model, which also estimated foliar respiration, wood respiration and soil respiration (see Appendix). Soil temperatures for the model were measured using 20-gauge copper-constantan thermocouples at 10 cm depth. All statistical analyses were done in SYSTAT v. 5.0 for Macintosh (SYSTAT Inc., Evanston, Illinois, U.S.A.).

Results

MAXIMUM AND MINIMUM AIR TEMPERATURES

The autumn and winter months during this study had generally above average air temperatures at Harvard Forest, with only one minimum temperature below −20°C during each of the winters 1997–98 and 1998–99 (Fig. 1). Typically, air temperature maxima were 5 to 15°C in autumn, with a few days 20°C or warmer, and 0 to 15°C in winter. Daily minimum temperatures were mostly −10 to 5°C in autumn and −20 to 0°C in winter (Fig. 1).

PHOTOSYNTHESIS AND LEAF CONDUCTANCE IN AUTUMN (15 SEPTEMBER–10 DECEMBER)

Minimum daily air temperatures (T_{min}) prior to measurements ranged from −8.5 to 12°C. The largest number of measurements was made in autumn 1999, which showed declining trends in T_{min}, P_{max}, and G_s over time (Fig. 2). There was, however, great variation above and below the seasonal trends and only the seasonal declines in P_{max} and G_s were statistically significant. A regression of T_{min} versus P_{max} for all three years on days with of $T_{min} \leq −2°C$ explained about 60% of the variation and was highly significant (Fig. 3a). The regression of T_{min} versus P_{max} for all three years on days with of $T_{min} > −2°C$ explained only about 20% of the variation and had a much lower slope, although it was also statistically significant (Fig. 3a). Leaf conductance showed similar trends, but the regression of T_{min} versus G_s on days with of $T_{min} > −2°C$ was not statistically significant (Fig. 3b).

Stepwise multiple regression of P_{max} versus day of year, time of day and T_{min} showed that for days with $T_{min} \leq −2°C$, only T_{min} was a significant predictor of P_{max}. In contrast, on days with $T_{min} > −2°C$ all three variables significantly affected P_{max}.
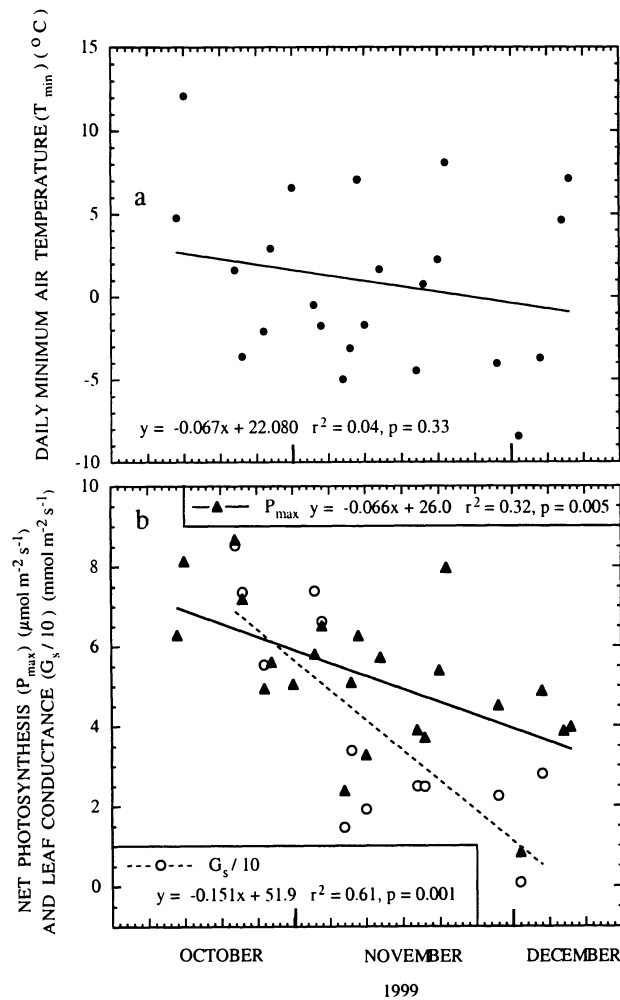
FIGURE 2. Changes in (a) daily minimum air temperature (T_{min}) and (b) mid-day light-saturated net photosynthesis (P_{max}) and leaf conductance (G_s) during autumn 1999. Each P_{max} or G_s value is the average of four measurements, one from each of four trees. Regression lines and equations indicate linear least-squares fits to the data. The variable x in the regressions is Julian date (or day of year).
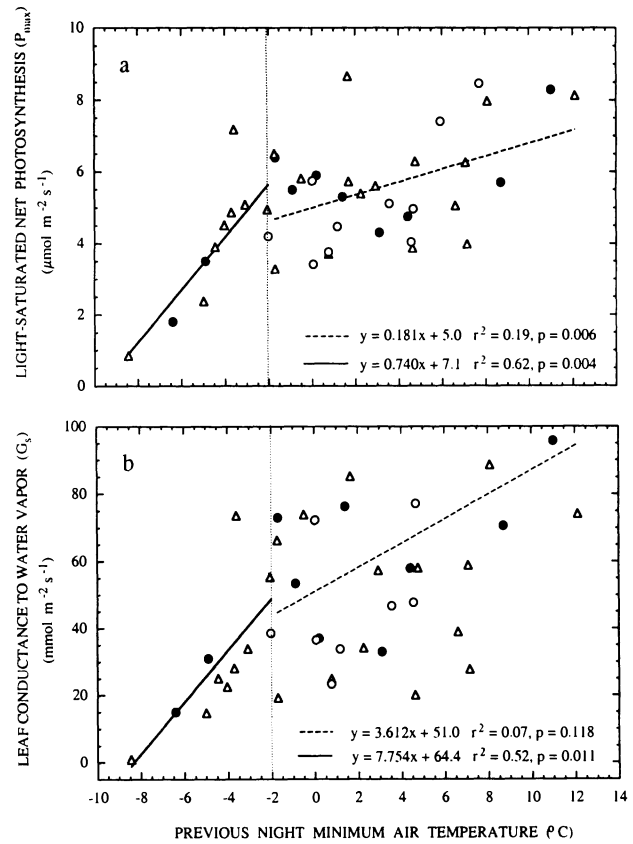
FIGURE 3. Previous night minimum temperature versus mid-day (a) P_{max} and (b) G_s during autumn (21 September–2 December). Measurements were taken in 1997 (solid circles), 1998 (open circles) or 1999 (open triangles). Each point represents the average of four measurements, one from each of four trees. Regression lines and equations indicate linear least-squares fits to the data. The lines at $-2\,°C$ indicate approximate thresholds for reduced P_{max} and G_s due to cold night temperatures.

For days with $T_{min} \leq -2°C$, only T_{min} significantly affected G_s, but on days with $T_{min} > -2°C$ only day of year and time of day affected G_s (Table 1).

The difference between hourly average sapwood and air temperatures was used to determine the temperature where freezing of sapwood occurred, because this is a possible cause for

TABLE 1

Stepwise multiple regression analysis of P_n and G_s during autumn 1999 (21 September–2 December)[a]

Temp range (°C)	Dep. var.	Indep. var.(s)	n	R^2	DF	Coefficient	SS	MS	t/F	p
$= -2$	P_n	T_{min}	11	0.62	1	0.74	19.2	19.2	**14.6**	0.004
$= -2$	G_s	T_{min}	11	0.52	1	7.75	2102	2102	**4.59**	0.011
> -2	P_n	Julian date	32	0.20	1	−0.041	—	—	−3.60	0.001
		Time (hours)	32	0.05	1	−0.367	—	—	−2.54	0.017
		T_{min}	32	0.19	1	0.137	—	—	2.51	0.018
		Full model	32	0.49	3	—	36.1	12.0	**9.02**	0.0002
> -2	G_s	Julian date	32	0.16	1	−1.44	—	—	−3.41	0.002
		Time (hours)	32	0.01	1	−12.8	—	—	−2.37	0.025
		Full model	32	0.28	2	—	25164	12582	**6.68**	0.004

[a] For $T_{min} > -2$, R^2 values for individual variables are for the variable in a single-factor regression, as opposed to the R^2 for the multivariate model given below. t-statistics and P values are given for single variables in multivariate models; F-statistics (in bold) are for complete single-factor or multivariate models. Dep. var. is dependent variable; Indep. var. is independent variable.
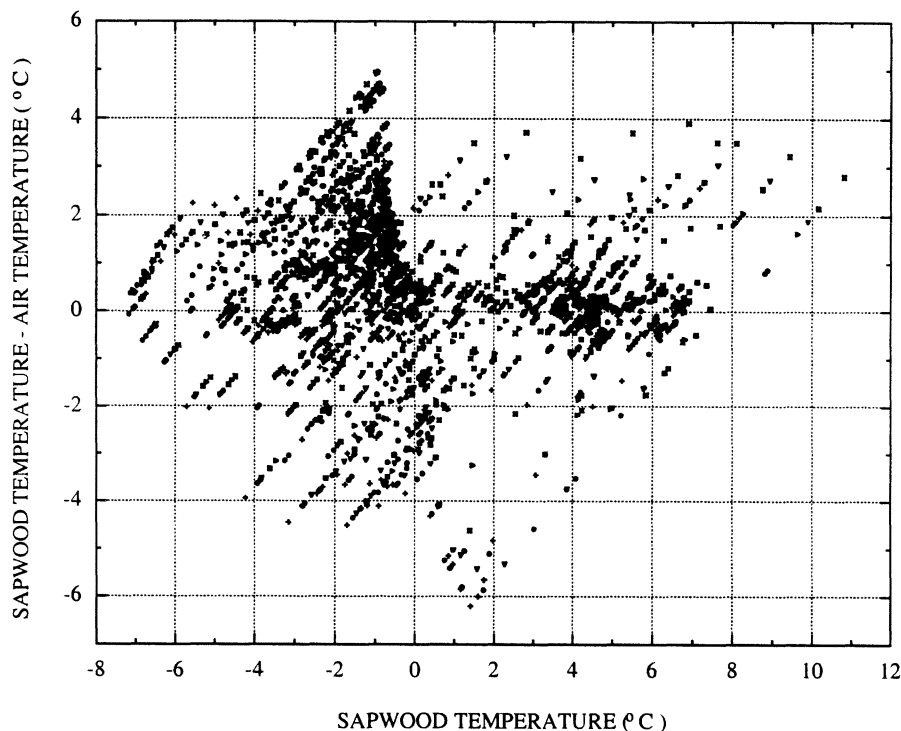
FIGURE 4. Hourly average sapwood temperature in seven middle canopy branches versus sapwood temperature—air temperature during 17 d (8 November to 25 November 1997). Branches were 6 to 8 cm in diameter where sapwood temperature was measured. The peak at $-1°C$ can be explained by freezing and thawing of xylem water.

reduced G_s and P_{max}. In mid-November 1997, sapwood temperature minus air temperature showed a peak at a sapwood temperature of $-1°C$ (Fig. 4). During heating and cooling, sapwood probably stayed at this temperature until freezing or melting was complete.

PHOTOSYNTHESIS AND LEAF CONDUCTANCE IN WINTER (15 DECEMBER–20 MARCH)

Photosynthesis was measured after nights when T_{min} ranged from -6 to $7°C$, but only one T_{min} was above $0°C$. Because of this and the small number of measurements, no statistically significant relationships were evident. However, all P_{max} values in winter were low, reaching only 2.4 μmol m^{-2} s^{-1} even after a T_{min} of $7°C$ (Fig. 5a) on 18 March. This suggests that during winter, P_{max} is limited by more than the previous night temperature alone. Stepwise multiple regression was used to test the effect of average minimum temperature for 1 to 7 d preceding winter measurements. Average T_{min} for the full week preceding a P_{max} measurement explained the largest amount of variation ($R^2 = 0.46$) and was the only value with a statistically significant effect on P_{max} ($P = 0.04$). In contrast, only the T_{min} just prior to a measurement affected G_s ($R^2 = 0.36$, $P = 0.05$).

## EFFECT OF MINIMUM TEMPERATURE ON ESTIMATED NET ECOSYSTEM CARBON EXCHANGE (NEE)

From December through March, estimated NEE was very sensitive to average T_{min} of the two previous days in the range from -5 to $2°C$, in which there was a shift in daily estimated NEE from about -1 g C m^{-2} d^{-1} (carbon loss) to between 1 and 4 g m^{-2} d^{-1} (carbon uptake). From -5 to $2°C$, average T_{min} on the day of an NEE estimate and on the previous day explained only about 43% of the variation, but was highly significant statistically (Fig. 6). For all days in December through March, stepwise multiple regression showed that among all environmental variables measured, this T_{min} value and daylength were the best predictors of NEE ($P < 0.001$ and $P = 0.01$, respectively).

Discussion

In autumn, eastern hemlock is similar to six Rocky Mountain conifers in which leaf conductance to water vapor in autumn was strongly affected by T_{min}, but only when it was below freezing (Smith et al., 1984). Similar to Smith et al., I found that G_s and P_{max} showed a declining trend in autumn (Fig. 2b), but with great variation around the temporal trend. G_s and P_{max} varied greatly after $T_{min} \leq -2°C$ and there was no significant effect of T_{min} on G_s (Fig. 3a, b). The great variation in gas exchange can be attributed to differences in leaf temperature, time of day, and atmospheric vapor pressure deficit at the time of measurements. I have found these factors to be significant in predictive models for leaf conductance and photosynthesis in eastern hemlock, except during winter. Effects of low temperatures prior to the previous night may also explain some of the variation in P_{max} during autumn.

In contrast to the weak effects of $T_{min} \leq -2°C$, steeply declining P_{max} and G_s in the range of T_{min} from about $-2°C$ to $-8°C$ (Fig. 3a, b) suggest that freezing of either xylem water or extracellular water in needles plays a direct role in inhibiting stomatal opening. Freezing of xylem water is a more likely cause, in view of the evidence that xylem water in eastern hemlock freezes at $-1°C$ (Fig. 4). Tranquillini and Holzer (1958) found that freezing of extracellular water in *Picea abies* foliage occurs a few degrees below $0°C$, while DeHayes (1992) and Perkins and Adams (1995) reported that in red spruce needles extracellular freezing occurred at $-6°C$ and $-4°C$, respectively.

There have been few measurements of photosynthesis in winter under natural conditions. Schaberg et al. (1995) found that P_{max} in red spruce saplings in northern Vermont reached a maximum of 1 to 2 μmol m^{-2} s^{-1} during winter. Figure 5a shows that winter P_{max} in eastern hemlock was generally under 2 μmol m^{-2} s^{-1} if T_{min} was below $0°C$. Unfortunately, there have been no dramatic winter thaws during this study, so there is no data for $T_{min} > 0°C$, except for one measurement near the very end of winter (18 March—the highest P_{max} value in Fig. 5a). A stronger relationship between P_{max} and average T_{min} for the previous
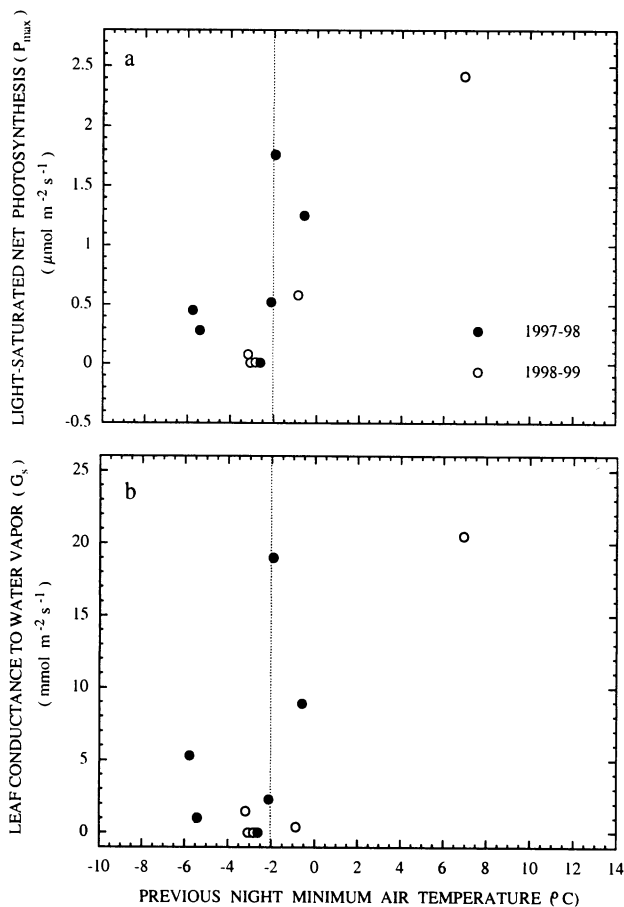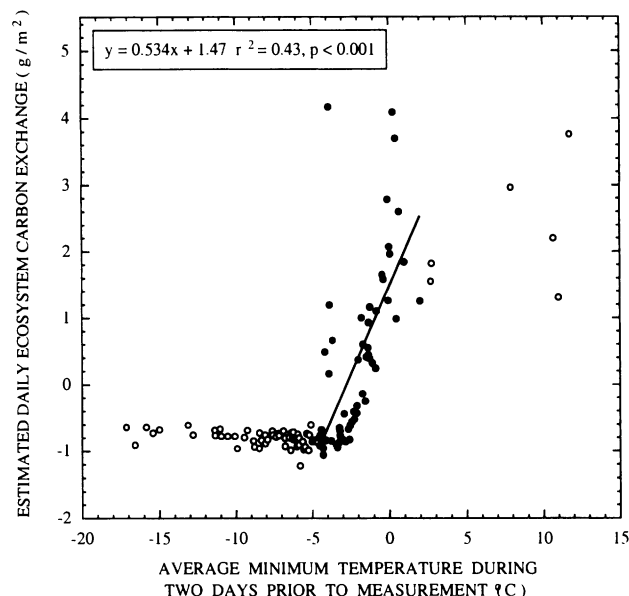
FIGURE 5. Previous night minimum temperature versus midday (a) P_{max} and (b) G_s during winter (15 December to 21 March). Each point represents the average of four shoots, one from each of four trees. The lines at $-2°C$ indicate the approximate temperature at which P_{max} and G_s begin to decline due to cold night temperatures in autumn.

FIGURE 6. Previous night minimum air temperature (T_{min}) versus daily estimated net carbon exchange for the old-growth hemlock forest ecosystem (NEE) from December 1997 through March 1998. NEE is expressed per square meter of ground surface and was calculated by an ecosystem carbon exchange model incorporating continuous data on air, wood, and soil temperatures and photosynthetically active radiation throughout the canopy, in addition to T_{min}. Filled symbols are for minimum air temperatures of -5 to $2°C$, for which the regression line was plotted. Positive numbers indicate carbon storage in the forest.

week than for the previous day during winter (see Results) suggests that the foliage is more deeply dormant at this time than in autumn.

P_{max} on days with T_{min} near $0°C$ was markedly lower in winter than in autumn (Fig. 5a versus Fig. 3a). This was probably a result of cumulative inhibition of conductance and P_{max} from prolonged exposure to temperatures well below $0°C$, which was not released by a single milder night. After prolonged exposure to cold, changes in chloroplast structure of conifers have been observed (Senser et al., 1975), which limit photosynthesis until they are reversed by a sufficiently long period of warm temperatures. Conifer shoots can increase P_{max} to near-summertime values within a few days when exposed to continually higher temperatures (near $20°C$) and a plentiful water supply (Hadley et al., 1993; Schaberg et al., 1996). However, such rapid recovery of photosynthetic potential is unlikely under field conditions, where a free water supply is not available and night temperatures are cold enough to greatly reduce metabolic activity.

Photooxidative damage to eastern hemlock may occur during prolonged periods of sunny weather with little or no photosynthetic electron transport, as has been reported for other conifers (Öquist, 1983). South-facing upper canopy shoots on one of the four trees I sampled showed a brownish discoloration by mid-winter and had no measurable photosynthesis after relatively mild nights, even though with less sun-exposed shoots included, the average of all four trees was 1 to 2 μmol m^{-2} s^{-1}

(Fig. 5a). Repair of photooxidative damage may occur more slowly during thaw periods compared to the reversal of temperature-induced stomatal closure.

Inhibition of photosynthesis after very cold nights has obvious implications for the influence of climate change on cold-season carbon uptake by eastern hemlock forests. In fall, an increased frequency of near or above-freezing night minimums and a reduced frequency of minimum temperatures below $-2°C$ would clearly increase photosynthesis, based on the data shown in Figure 3a. In winter, there would also be increased photosynthesis with milder nights, but it is uncertain how large this effect would be. The highest P_{max} measured in winter was still quite low, about 2.5 μmol m^{-2} s^{-1} (Fig. 5a), but no winter thaws with repeated above-freezing nighttime minimums occurred at a time when we were able to measure photosynthesis. In fact, neither the winter of 1997–98 or 1998–99 had any major thaw periods. These winters were fairly mild but night temperatures were consistently below freezing, except on a few isolated dates (Fig. 1). Weather similar to mid-January 1995, when nighttime minimums were above $4°C$ for four consecutive nights (data from the NOAA weather station at Harvard Forest) will be necessary to test the effect of a major winter thaw.

Even with fairly low predicted winter photosynthesis, nighttime minimum temperature variation in the range of -5 to $2°C$ had a strong effect on estimated ecosystem carbon uptake (Fig. 6). T_{min} explained only about 40% of variation in NEE within this temperature range (Fig. 6), but this is not surprising considering that all forms of respiration in the ecosystem were controlled by current air, wood or soil temperature rather than by T_{min}. Furthermore, the temperatures of soil and large tree boles, where most respiration occurs, are highly buffered from changes in air temperature.

The ecosystem model which I developed showed that total

photosynthesis during the months of December through March accounted for about 10% of the annual total. While this may seem a fairly minor amount, it precedes the initiation of new shoot growth, and could provide a significant carbon source for that process. Schaberg et al. (2000) found that winter photosynthesis in red spruce contributed to a buildup of carbohydrates in foliage and twigs and this may also occur in eastern hemlock. If climatic warming increases the number of winter thaw periods and stimulates winter photosynthesis in hemlock there is clearly a potential for more winter carbohydrate storage and perhaps increased foliage or wood production in the subsequent growing season.

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Appendix
Model of Hemlock Forest Carbon Exchange for the Months of December 1997 through March 1998

The model calculates net ecosystem carbon exchange (NEE) as the difference between net photosynthesis (P_n) and the sum of foliage respiration (R_f), wood respiration (R_w), and soil respiration (R_s):

$$NEE = P_n - (R_f + R_w + R_s)$$

In the models, PFD = photosynthetic photon flux density at leaf surface, TIME = time of day in hours, G_s(mod) = a model estimate of leaf conductance, $T_{min}(2)$ = average minimum air temperature of two previous days, T_{air} = air temperature, T_{sw} = sapwood temperature, T_s = soil temperature at 10 cm depth. Models were derived by stepwise multiple regression of all measured environmental parameters, with testing of all possible interactions. P_n and R_f were calculated on a leaf area basis for current year foliage, with small reductions in maximum P_n and R_f with needle aging ($\sim$ 10% per year). P_n and R_f were then calculated for each foliage age class and multiplied by the leaf area index (LAI) in each age class and canopy layer to convert to a ground area basis. Total LAI was 3.5. R_w was calculated per unit volume of sapwood and converted to a ground area basis. R_s was calculated on a ground area basis.

Model of hemlock forest carbon exchange for the months of December 1997 through March 1998

Period	Process	Canopy layer	Model
December–February	Photosynthesis	Upper	$P_n = [1.7 + 0.42*T_{min}(2)]*[-0.56 + 0.082*\ln(\text{PFD})]$
December–February	Photosynthesis	Lower	$P_n = 1.3 + [0.88*T_{min}(2)] + [0.22*\ln(\text{PFD})]$
March	Photosynthesis	Upper	$P_n = [-1.7*T_{min}(2)] + [0.51*\ln(\text{PFD})] + [0.017*G_s(\text{mod})] + [0.13*T_{min}(2)*\ln(\text{PFD})]$
March	Photosynthesis	Lower	$P_n = -0.96 -[0.00086*\text{TIME}] + [0.22*T_{min}(2)] -[0.62*T_{air}] + [0.79*\ln(\text{PFD})] + [0.019*\text{TIME}*T_{min}(2)] + [0.039*T_{min}(2)*\ln(\text{PFD})]$
December–March	Foliage respiration (night)	Upper	$R_f = 0.267*10^{0.031*\text{Tair}}$
December–March	Foliage respiration (night)	Lower	$R_f = 0.210*10^{0.025*\text{Tair}}$
December–March	Wood respiration	Upper	$R_w = 0.920*10^{0.047*\text{Tsw}}$
December–March	Wood respiration	Middle	$R_w = 0.560*10^{0.028*\text{Tsw}}$
December–March	Wood respiration	Lower	$R_w = 0.413*10^{0.037*\text{Tsw}}$
December–March	Wood respiration	Bole	$R_w = 0.106*10^{0.036*\text{Tsw}}$
December–March	Soil respiration	—	$R_s = 12.306*10^{0.087*\text{Ts}}$

$P_n = [1.7 + 0.42*T_{min}(2)]*[-0.56 + 0.082*\ln(\text{PFD})]$