

Air and soil temperature limitations on photosynthesis in Engelmann spruce during summer

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The relative importance of air and soil temperature as potential limitations to photosynthesis during summer was assessed in Engelmann spruce over its natural elevational range in southeastern Wyoming. Low photosynthetic rates measured at constant temperature, irradiance, and vapor pressure deficit were highly correlated with low minimum (night) air and soil temperature, but at different times during the early summer growth period. Substantial and irreversible reductions in photosynthesis occurred after exposure to night air temperatures of -4 to -5°C that occurred through mid-June. After middle to late June, decreased photosynthetic rates were correlated with low soil temperature. Correlation analyses indicated that subfreezing air temperature followed by an extended period of low soil temperature were the primary limitations to photosynthesis in early summer. Additional laboratory and field experiments corroborate these field observations.

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Les auteurs ont évalué l'importance relative de la température du sol et de l'air comme facteurs limites potentiels pour la photosynthèse au cours de l'été chez l'épinette d'Engelmann, dans l'intervalle d'altitude où se situe son habitat naturel dans le sud-est du Wyoming. Les taux photosynthétiques mesurés à des températures, des irradiances et des pressions de vapeur constantes montrent une forte corrélation avec de faibles températures du sol et de l'air (nuit), mais à des moments différents pendant les toutes premières périodes de croissance du début de l'été. On observe des réductions marquées et irréversibles de la photosynthèse après les expositions aux températures nocturnes de l'air de -4 à -5°C survenant jusqu'au milieu de juin. Après la période de la mi-juin à la fin juin, les diminutions des taux photosynthétiques sont corrélées avec les faibles température du sol. Les analyses de corrélation indiquent que les températures de l'air au dessous du point de congélation, suivies d'une longue période de température basse du sol, constituent la principale limite à la photosynthèse au début de l'été. D'autres expériences conduites sur le terrain et en laboratoire confirment ces observations de terrain.

[Traduit par la revue]

Introduction

Tree growth and productivity in subalpine forests are limited by the short period of time available annually for net carbon assimilation. Although the growing season for evergreen species is not well defined, the duration of the frost-free season in the subalpine forest (3048 m) of the central Rocky Mountains is often less than 60 days (Barry 1973). During this relatively short growing season, carbon assimilation in conifers can be further reduced for extended periods by low daytime air temperature, low soil temperature, the persistent effects of intermittent frost, and other factors (Tranquillini 1979). In years with little snow accumulation, the availability of water may become limiting in late summer.

Engelmann spruce (*Picea engelmannii* Parry) is a dominant component of the subalpine forest community in the Rocky Mountains of North America (Fowells 1965). Together with subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), spruce forms the "Subalpine Forest Climax" (Marr 1961). In the Medicine Bow Mountains of Wyoming the spruce–fir forest attains its greatest stature and importance between 2900 and 3200 m above sea level (Oosting and Reed 1952). However, the elevational distribution of spruce is considerably greater, extending from the lower (2590 m) to the upper (3530 m) elevational limits of tree growth.

Several important physical factors that may influence photosynthesis can change dramatically along the natural elevational range occupied by Engelmann spruce (Smith and Geller 1979). Many of these factors, including air and soil temperature, soil moisture, vapor pressure deficit, and irradiance, influence the seasonal pattern of stomatal opening (Kaufmann 1976, 1979a, 1979b, 1982a, 1982b; Smith et al. 1984; Smith 1985). Although it is well documented that most of these factors can directly or indirectly affect photosynthesis, little is currently known regarding the comparative importance of different environmental factors that can restrict photosynthesis at different times during the summer.

During early summer both cold air and soil temperature can curtail photosynthetic performance. Initially, low air temperature is the dominant limitation to photosynthesis followed by an extended period when soil temperature limitations may continue (Smith 1985). The purpose of this investigation was to characterize the seasonal pattern of photosynthesis in Engelmann spruce during early summer and to assess the relative importance of maximum and minimum air temperature and soil temperature as environmental limitations to photosynthesis.

Materials and methods

Three research sites were selected along an elevational transect on the east slope of the Medicine Bow Mountains of southeastern Wyoming ($41^{\circ}21' \text{N}$, $106^{\circ}13' \text{W}$). The sites chosen are representative of the habitats in which spruce occurs at each elevation and are located on gentle ($\leq 8\%$) south-facing slopes. The low elevation or Beaver

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Pond site is 2704 m above sea level. Lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.) is dominant, and spruce is restricted to a narrow band of trees between the lodgepole forest and adjacent sedge meadow. The forest cover at the middle elevation or Science Camp site (3048 m) is dominated by spruce and fir and represents the best development of the spruce-fir forest type in the Medicine Bow Mountains (Oosting and Reed 1952). The high elevation or Ribbon Forest site (3316 m) is just below treeline and represents the highest elevation in the Medicine Bow Mountains where spruce grows in an erect form and develops a closed canopy with only occasional flagging of tree tops. The three sites cover 612 m of elevation and encompass the elevational distribution over which Engelmann spruce forms a characteristic spruce or spruce-fir canopy.

Continuous measurements of air temperature and relative humidity and periodic measurements of soil temperature, soil moisture, and snow cover were made at each site during the summers of 1984 and 1985. Air temperature and relative humidity were measured with hygrothermographs placed in weather shelters at about one third of canopy height. The hygrothermographs were calibrated *in situ* every other week. Atmospheric vapor pressure deficit (VPD) was calculated from air temperature and relative humidity at the time of the daily maximum air temperature. Soil moisture was measured gravimetrically (dried at 105°C to constant mass) at weekly intervals. Three 40-g samples were collected at each site at a 15-cm depth. The percentage soil moisture at -1.5 MPa was calculated for each site using a pressure plate. Diurnal measurements of soil temperature were made under the forest canopy every 2 weeks with copper-constantan thermocouples buried at 5, 10, 20 and 30 cm during the summer of 1984. In 1985, maximum soil temperatures were measured between 14:00 and 15:00 (solar time) each week.

Photosynthetic measurements were made on excised shoots in a humidity- and temperature-controlled cuvette with an IR gas analyzer (ADC Series 225) in an open system. Different gas exchange systems were used in 1984 and 1985. In 1984, measurements were made with ambient air pumped from above the forest canopy and, although humidity was controlled in the cuvette, transpiration was not measured. In 1985, the air was mixed to 21% O₂ and 0.035% CO₂ from bottled gas using mass flow valves (Tylan) and transpiration was measured. Gas exchange measurements were made under standard conditions of saturating photosynthetically active irradiance (1200 μmol s⁻¹ m⁻²), 20°C air temperature, and 1 kPa VPD. One-year-old needles on fully exposed branches were used for all gas exchange measurements. One branch from the south side of the crown at midcanopy height from each of three trees per site was removed before dawn. Entire branches were excised and then recut under water 5 dm from the initial cut. All laboratory measurements on excised shoots were made under the same conditions as described above.

Separate experiments were conducted to examine the effect of shoot removal on the gas exchange properties of spruce. In one case, shoots were excised as described above and then resuspended in their original position with the cut ends immersed in water. Leaf conductance to water vapor and transpiration were measured on the cut shoots and on neighboring attached shoots for a period of 24 h with a LiCOR 1600 steady-state porometer. Leaf conductance remained between 0.60 and 0.92 mm s⁻¹ from 10:30 to 17:00 (solar time) and was not significantly different in cut and attached shoots. Furthermore, gas exchange measurements of CO₂ uptake in detached shoots were quite similar (± 18%) to values for adjacent attached shoots using a LiCOR portable photosynthesis system (W. K. Smith, unpublished).

Gas exchange parameters for individual shoots were calculated on a total leaf area basis (Carter and Smith 1985). The inability to measure transpiration during 1984 precluded correcting the photosynthetic calculations for interdiffusional effects of water vapor (von Caemmerer and Farquhar 1981). This can cause as much as 5% overestimate of photosynthetic rate in spruce. The necessary data were collected and corrections applied to the 1985 measurements.

Photosynthesis was measured biweekly on tissue collected at the three sites from June to September in 1984 and weekly in 1985. The net photosynthesis - temperature response (10 to 30°C, VPD = 1 kPa) and

response to subfreezing air temperatures were measured during early, middle, and late summer in 1985.

The effect of subfreezing air temperatures on photosynthesis was measured on shoots collected from each site. After making an initial measurement at the time of collection branch sections with the cut ends immersed in water were inserted into a refrigerated box and exposed to -5°C for 2 h. Photosynthesis was then remeasured after a 30-min recovery period at room temperature. The proximal end of the shoot passed through an opening in the wall of the refrigerator so that the water reservoir could be maintained at room temperature. Air inside the box was mixed with a high-velocity fan.

The effect of a "hard freeze" (-5.0°C) or a "light freeze" (-2.5°C) on various gas exchange parameters, including apparent quantum yield and photosynthetic efficiency, was also examined. Apparent quantum yield was computed as the slope of the linear portion of the photosynthetic light response curve. Photosynthetic efficiency is the ratio of net photosynthesis to the internal or substomatal CO₂ concentration (C_i) and is a measure of photosynthetic utilization of internal CO₂ (Sasek et al. 1985). Measurements were made before the freezing treatments and after 30 min and 24 h of recovery on shoots collected in mid-August from the Science Camp site.

The effect of low night air temperature and low root temperature on net photosynthesis in spruce was evaluated *in situ* during mid-June 1985. Three groups of trees growing in an open meadow (3055 m) within a 50-m radius of one another were selected. The soil immediately surrounding these trees was entirely snow free, partially covered, or completely covered with snow. Soil temperatures were measured under each snow-cover treatment with thermistors buried at 5, 15, and 25 cm, and maximum and minimum air temperature (shielded thermistor) was recorded hourly with a Campbell CR-21 micrologger. Net photosynthesis was measured on one fully exposed shoot on the south side of each of five trees per treatment. A LiCOR 6000 portable photosynthesis system was used to measure net photosynthesis in the field under ambient air temperature, relative humidity, and CO₂ concentration and saturating photosynthetically active irradiances (≥ 1200 μmol s⁻¹ m⁻²). The depletion of CO₂ and increase in relative humidity in the cuvette during a measurement were generally less than 10 μL L⁻¹ and 3%, respectively. Needle temperatures inside the cuvette were within 1°C of air temperature. Measurements were made between 10:00 and 11:00 (solar time) from June to July. By the end of the experiment the snow had melted and soil temperatures were increasing. Soil moisture was at or above field capacity for the duration of the experiment.

Results

Mean maximum air temperature increased steadily until about July 1 at each site and was inversely related to elevation (Figs. 1A and 2A). Maximum air temperatures were generally 5 to 10°C warmer at the Beaver Pond site (2704 m) than at the Ribbon Forest site (3316 m) corresponding to a relatively dry adiabatic lapse rate of 1°C 100 m⁻¹. In contrast, minimum night air temperature increased with greater elevation and was often 2 to 5°C warmer at the Ribbon Forest than at the lower elevation sites. Freezing nights were common through June and reoccurred in early (1985) to late (1984) August (Figs. 1B and 2B).

The percentage of days per 2-week interval with minimum temperatures less than or equal to 0°C (Fig. 3A) or -5.0°C (Fig. 3B) was determined from climatic data collected by the Wyoming Water Research Institute (Laramie, Wyoming). The data consisted of 8- to 9-year records compiled for three sites of comparable elevations (± 132 m) to the sites chosen for this study. The lowest frequency of freezing temperatures occurred in middle to late July and began to increase sharply by the 1st week in September (Fig. 3A). During late summer, mid-July through August, the frequency of freezing nights was 10 to 12% at the lowest elevation site and 0 to 5% at higher elevations. No

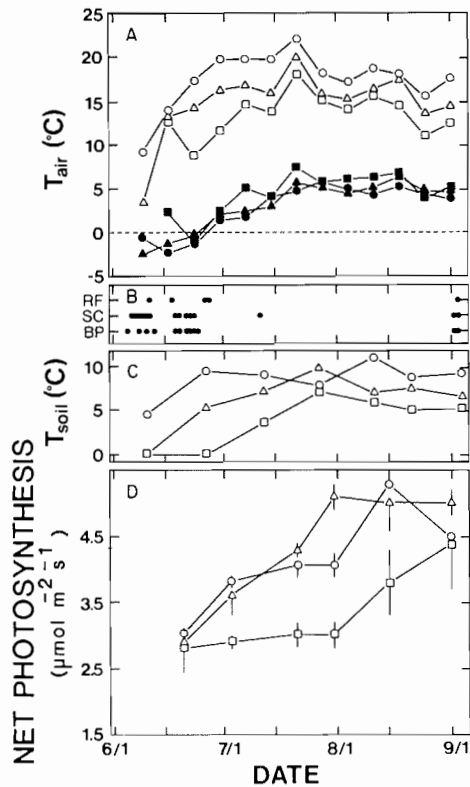


FIG. 1. The seasonal pattern of air temperature (A), soil temperature (C), and photosynthesis measured under constant environmental conditions (D) for Engelmann spruce during the summer of 1984. The occurrence of night temperatures of 0°C or below is shown in B. ●, ○, Beaver Pond (BP, 2704 m); ▲, △, Science Camp (SC, 3048 m); ■, □, Ribbon Forest (RF, 3316 m). The mean maximum and minimum air temperatures are indicated by the open and closed symbols, respectively (A). Error bars are ± 1 SD.

hard freezes (−5.0°C or below) have been recorded during this period in the past 8 years (Fig. 3B).

The seasonal increase in subsurface soil temperature (10 cm) was considerably slower than air temperatures. Maximum soil temperatures under the forest canopy were typically between 5 and 11°C depending on the site and did not occur until middle to late July (Figs. 1C and 2C). Atmospheric vapor pressure deficit was strongly correlated with air temperature and was inversely related to elevation (data not shown). The greatest vapor pressure deficits occurred in midsummer and were typically between 1.0 and 2.55 kPa at the highest and lowest elevation sites, respectively. With the exception of 2 weeks in early July (1984) at the Beaver Pond site, soil moisture (15 cm) remained above −1.5 MPa at all sites and predawn xylem water potentials were generally above −1.8 MPa.

Because of differences in the gas exchange systems and calculations employed (see Materials and methods) in 1984 versus 1985 some variation in absolute values of photosynthesis can be expected. However, seasonal and elevational comparisons for each summer should not reflect these limitations. Photosynthesis at all three sites increased gradually over the first two-thirds of the summer and reached the highest values in mid-August, 1984 (Fig. 1D). Maximum photosynthesis was attained approximately 2 to 4 weeks earlier during the summer of 1985 and decreased slightly during August (Fig. 2D). Although there were no direct relationships between maximum

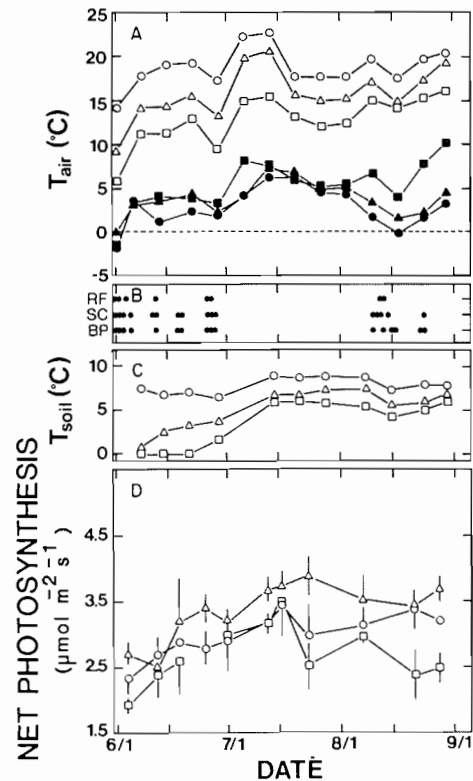


FIG. 2. The seasonal pattern of air temperature (A), soil temperature (C), and photosynthesis measured under constant environmental conditions (D) for Engelmann spruce during the summer of 1985. The occurrence of night temperatures of 0°C or below is shown in B. Symbols as in Fig. 1.

photosynthesis and elevation, values were generally lower at the Ribbon Forest site than at either of the two lower elevation sites.

The coefficient of determination (r^2) for independent comparisons of photosynthesis measured under laboratory conditions with maximum and minimum air temperature and soil temperature are shown in Table 1. Mean maximum air temperature for the 3 days prior to gas exchange measurements accounted for a very low percentage of the seasonal variation in photosynthesis at any elevation. Photosynthesis at the Science Camp site was strongly correlated with mean minimum air temperature for the previous three nights in 1984 and 1985. A similar relationship was observed for minimum air temperature during the previous night for tissue collected at the Beaver Pond site in 1984. A highly significant relationship was observed between photosynthesis and soil temperature at the Beaver Pond and Science Camp site for both years.

The photosynthetic temperature optimum for shoots collected in early, middle, and late summer (1985) was between 19 and 22°C for tissue collected at the Beaver Pond site, and between 16 and 18°C for tissue collected at the two higher elevation sites (Fig. 4). The temperature responses became broader as the summer progressed. By August, photosynthetic values were within 90% of the maximum values between 10 and 25°C. The temperature optimum was consistently higher than the mean maximum air temperature for the 3 days prior to the measurements and there was little evidence for acclimation to seasonal changes in air temperature at a given elevation.

The sensitivity to a hard freeze (−5.0°C) changed seasonally and was related to the initial photosynthetic rate in shoots collected at the Science Camp ($r^2 = 0.76, p \leq 0.05$) and Beaver

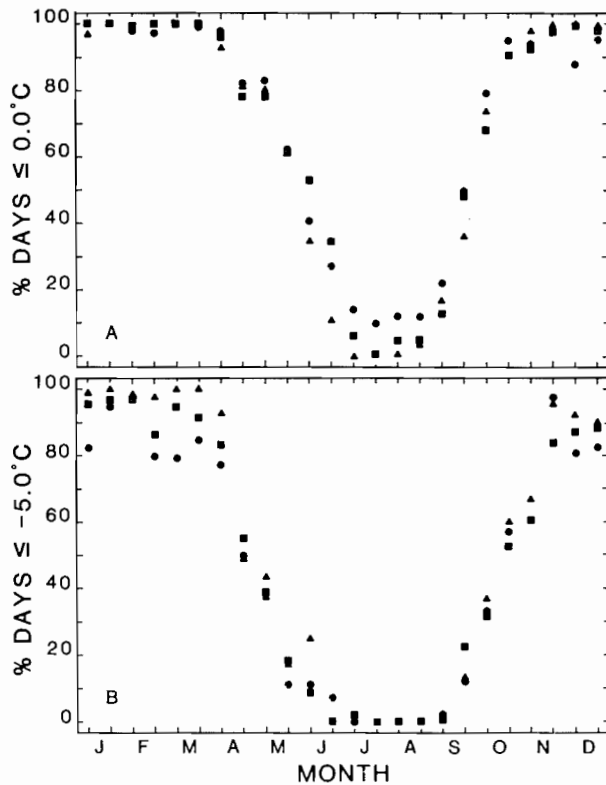


FIG. 3. The frequency of days with minimum temperatures (A) $\leq 0.0^{\circ}\text{C}$ and (B) $\leq -5.0^{\circ}\text{C}$ at 2572 m (●), 3030 m (▲), and 3273 m (■). The data were collected from 1976 to 1984 using hygrothermographs in standard instrument shelters by the Wyoming Water Research Institute, Laramie, Wyoming. The frequency of freezing nights was calculated on a biweekly basis.

TABLE 1. Coefficients of determination (r^2) for linear regressions of photosynthesis in Engelmann spruce measured under laboratory conditions versus several environmental factors: T_{max} , mean maximum air temperature for the previous 3 days; T_{min} , mean minimum air temperature for the previous 3 nights; $T_{\text{min}1}$, minimum air temperature for the previous night; T_{soil} , maximum soil temperature at 10-cm depth

Site	Year	T_{max}	T_{min}	$T_{\text{min}1}$	T_{soil}
Beaver Pond	1984	0.04	0.64*	0.76***	0.77***
	1985	0.26	0.11	0.10	0.49***
Science Camp	1984	0.06	0.77***	0.14	0.85****
	1985	0.30*	0.66****	0.26	0.78****
Ribbon Forest	1984	0.18	0.10	0.03	0.20
	1985	0.28*	0.10	0.34*	0.25

NOTE: An F -test was used to test the significance of the slope of each regression. Significance levels: *, 0.100; ***, 0.025; ****, 0.010.

Pond ($r^2 = 0.83$, $p \leq 0.05$) sites (Fig. 5). A similar trend was observed at the Ribbon Forest site. In early June, exposure to -5.0°C for 2 h resulted in a 25 to 35% reduction in photosynthetic values when the shoots were remeasured at the prefreeze conditions. As photosynthetic rates increased during the summer the freezing treatment caused an 80 to 90% reduction in shoots from the Science Camp and Beaver Pond sites.

The effect of a 2-h exposure to -2.5 or -5.0°C on various gas exchange parameters was compared on shoots collected from the Science Camp site in mid-August (Table 2). A light freeze (-2.5°C) had no statistically significant ($p \leq 0.05$) effect on photosynthesis or conductance measured after a 30-min or

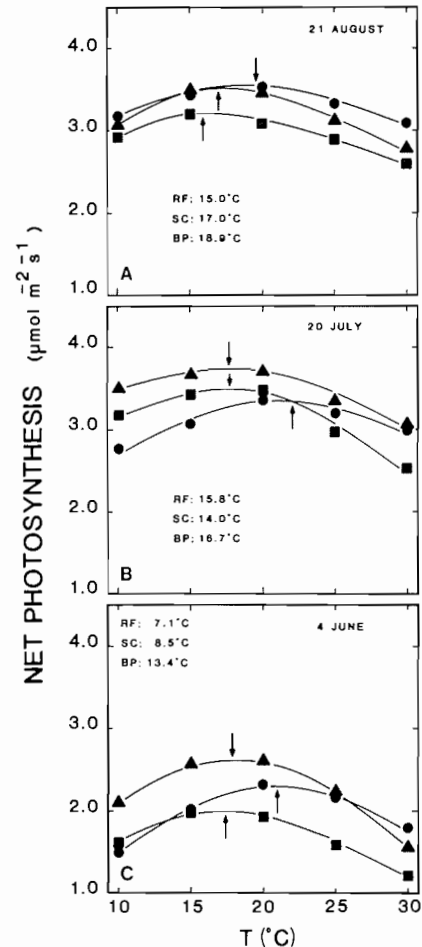


FIG. 4. The response of photosynthesis to air temperature at the Beaver Pond, 2704 m (BP, ●); Science Camp, 3048 m (SC, ▲); and Ribbon Forest, 3316 m (RF, ■). Each point is a mean of three independent measurements. The curves were fitted by hand and the temperature optima are indicated with arrows. The date and mean maximum temperature at each site for the 3 days prior to the measurement is shown in each panel. Needle temperatures were $\pm 1.0^{\circ}\text{C}$ of air temperature inside of the gas exchange cuvette.

24-h recovery period. A hard freeze (-5.0°C) caused substantial and irreversible reductions in photosynthesis, stomatal conductance, apparent quantum yield, and photosynthetic efficiency (photosynthetic capacity/internal CO_2 concentration).

The effect of low root and shoot temperature on net photosynthesis in spruce measured *in situ* is shown in Figs. 6 and 7. Composite photosynthesis-temperature response curves indicate a temperature optimum between 15 and 17°C (Fig. 6A). Night temperatures between 6 and -2°C had little effect on net photosynthesis on the following day (Fig. 6B). Exposure to -4°C , however, caused a substantial and persistent decrease in net photosynthesis. Photosynthetic rates following two nights with temperatures of -4°C or below (June 27 and 28) are indicated by 27 (Fig. 6B). Photosynthesis remained depressed on June 30 (Fig. 6B, 30) despite warmer night temperatures. Manipulation of soil temperature in the field produced a significant correlation between soil temperature (at 15 cm) and net photosynthesis ($r^2 = 0.59$, $p \leq 0.001$) (Fig. 7).

Discussion

Photosynthesis in spruce increased gradually during the summer, attaining maximum values in late July (1985) to mid-August (1984). Low photosynthetic rates early in the

TABLE 2. The effect of a hard (-5.0°C) or a light (-2.5°C) freeze on various gas exchange parameters in Engelmann spruce

	Photosynthetic rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Stomatal conductance ($\text{mmol m}^{-2} \text{s}^{-1}$)	C_i (μLL^{-1})	Apparent quantum yield ($\mu\text{mol CO}_2 \cdot \mu\text{mol PAR}) \times 10^{-3}$	Photosynthetic efficiency ($\text{mol CO}_2 \text{ fixed} \cdot \text{m}^{-2} \cdot \text{s}^{-1}) /$ ($\text{mol } C_i \cdot \text{L}^{-1}$)
Light freeze (-2.5°C)					
Prefreeze	3.41 ± 0.33	35.0 ± 2.7	169 ± 8	7.40 ± 1.58	0.45 ± 0.07
0.5 h	3.01 ± 0.45	26.7 ± 7.1	142 ± 25	6.12 ± 0.89	0.48 ± 0.08
24 h	3.12 ± 0.29	30.0 ± 10.8	159 ± 59	6.92 ± 1.32	0.51 ± 0.24
Hard freeze (-5.0°C)					
Prefreeze	3.13 ± 0.32^{ab}	32.5 ± 6.2^{ab}	162 ± 12	7.29 ± 1.12^{ab}	0.43 ± 0.05^{ab}
0.5 h	0.72 ± 0.43^a	8.7 ± 5.4^a	180 ± 71	3.94 ± 0.47^a	0.10 ± 0.05^a
24 h	0.99 ± 0.55^b	14.0 ± 7.6^b	207 ± 46	4.89 ± 0.91^b	0.11 ± 0.09^b

NOTE: The mean values (± 1 SEM) were compared using a one-way ANOVA and the HSD multiple range test. Values followed by the same letter are different at the 0.05 level.

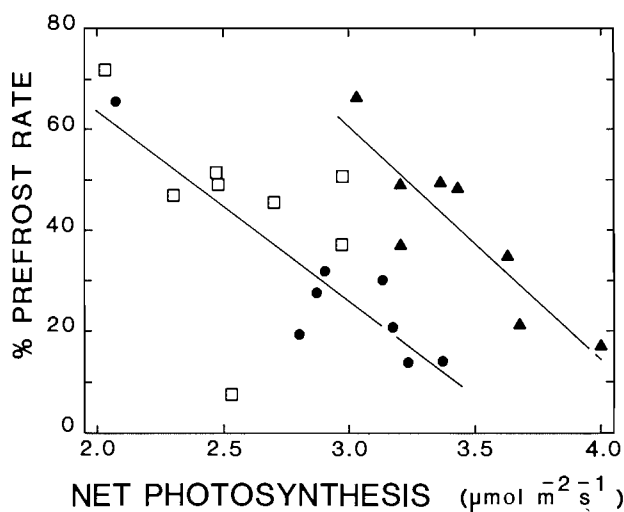


FIG. 5. The percentage of the initial photosynthetic rate in spruce after exposure to a hard freeze (-5.0°C) as a function of the prefrost rate for tissue collected from the Beaver Pond (2704 m, ●), Science Camp (3048 m, ▲), and Ribbon Forest (3316 m, □) sites. Measurements were made in June, July, and August 1985. Each point is a mean of three independent measurements.

season and at high elevations are often attributed to low daytime air temperatures (Pisek 1960; Tranquillini 1979; Oquist 1983). In the case of Engelmann spruce, low maximum air temperature did not appear to be a primary limitation to photosynthesis (Table 1). Even though mean maximum air temperatures are generally below optimum for photosynthesis, the possibility of an air-temperature limitation to photosynthesis is greatly reduced by the frequent occurrence of needle over air temperature, especially in exposed sun shoots with highly clustered needle arrangements (Smith and Carter 1987).

The pattern of photosynthesis early in the season was significantly correlated with minimum (night) temperatures. The reduction in photosynthesis caused by a hard freeze (-5.0°C) was proportional to the initial photosynthetic rate (Fig. 5). In early June, the freezing treatment caused a 25 to 35% reduction in photosynthesis. By middle summer, when photosynthetic rates approached the highest seasonal level, a hard freeze caused 80 to 90% inhibition. This indicates that metabolic changes necessary to attain high assimilation rates also increase the sensitivity to frost. Several studies have demonstrated that metabolic changes associated with frost hardening, particularly changes in the lipid composition of

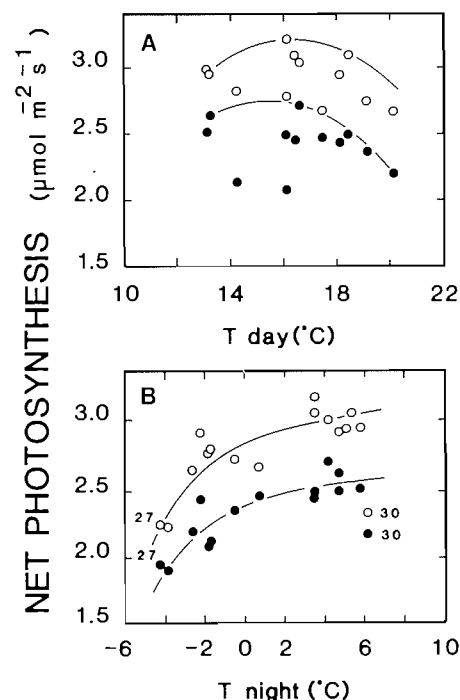


FIG. 6. The photosynthetic response of Engelmann spruce trees *in situ* to air temperature at the time of measurement (A) and to minimum air temperature for the previous night (B). Measurements of trees in warm and cool soil are shown with open and closed circles, respectively. Each point is a mean of five independent measurements. The curves in A were fitted by hand to the maximum rates. A least-squares regression was used for photosynthesis vs. minimum air temperature (B). For warm-soil trees (○): photosynthesis = $2.36 + 0.31 (\ln \text{ air temperature})$; $r^2 = 0.78$, $p \leq 0.001$. For cool-soil trees (●): photosynthesis = $1.95 + 0.27 (\ln \text{ air temperature})$; $r^2 = 0.80$, $p \leq 0.001$. A hard freeze occurred on June 27 and 28. Photosynthetic rates on the days immediately following the freeze and after 2 days with above-freezing nights are indicated by 27 and 30, respectively. Photosynthesis remained depressed 3 days after the initial hard freeze and measurements made at this time (30 June) were not included in the regressions.

membranes, result in reduced rates of electron transport and photosynthesis (Sensor and Beck 1978, 1977; see Oquist 1983 for review).

In addition to strongly inhibiting photosynthesis and stomatal conductance, exposure to a hard freeze caused a substantial and irreversible reduction in apparent quantum yield and photosynthetic efficiency (Table 2). Photosynthetic efficiency (photosyn-

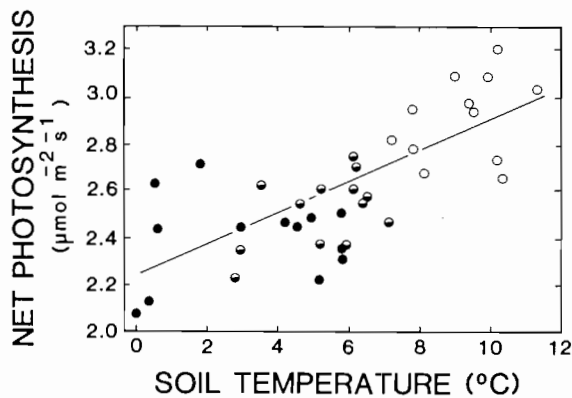


FIG. 7. The photosynthetic response of Engelmann spruce trees *in situ* to soil temperature (at a 15-cm depth) at the time of measurement. Each point is the mean of five independent measurements. ○, snow-free soil; ◐, partially covered; ●, completely snow-covered soil. Photosynthesis = $2.26 + 0.07(\text{soil temperature})$; $r^2 = 0.59$, $p \ll 0.001$.

thesis/ C_i) reflects the ability of the photosynthetic apparatus to utilize internal CO_2 (Sasek et al. 1985). The freezing-induced reduction in photosynthetic efficiency indicates that carbon assimilation was limited primarily by high internal resistances despite the parallel decline in stomatal conductance. An increase in internal resistance to the diffusion of CO_2 in response to low air temperature has been observed in other woody species (Nielson et al. 1972; Bauer et al. 1985). Night temperatures of 4°C and below cause a decrease in the slope and maximum value of the photosynthesis vs. C_i curve for *Coffea arabica*, indicating that high internal or biochemical resistance and not stomatal resistance is primarily responsible for the decrease in photosynthesis (Bauer et al. 1985). In some cases the decline in stomatal conductance following exposure to low temperatures may be enhanced by the increase in C_i resulting from photosynthetic inhibition (Drake and Raschke 1974; Raschke 1975).

Exposure to a light freeze (-2.5°C) caused a slight and reversible reduction in photosynthesis and stomatal conductance (Table 2). These measurements were made in mid-August and presumably reflect a near maximum response to freezing. Although the effect of 0°C was not examined, it can be inferred from the minimal response to -2.5°C that exposure to warmer night temperatures would have had little or no effect on gas exchange parameters in spruce. A slight decrease in net photosynthesis measured *in situ* was observed the day after a -1 to -3°C night, although substantial inhibition was not evident until after a -4°C night (Fig. 6B). In species of tropical and subtropical origin, night temperatures as high as 10°C can cause irreversible reductions in photosynthesis and stomatal conductance (Lyons 1973; Levitt 1980). An irreversible reduction of photosynthesis in Engelmann spruce did not occur until -4 to -5°C , which is when water in unhardened needles typically freezes (Tranquillini and Holzer 1958).

The interaction of several environmental factors may govern the seasonal pattern of photosynthesis in spruce, though the relative importance of different factors can be expected to change temporally and with elevation (Smith 1985). At the beginning and end of the summer growth period the high frequency of freezing nights (Fig. 3) and low daytime air temperatures could substantially reduce photosynthesis in spruce. Furthermore, freezing nights may pose a greater limitation to

photosynthesis at low elevations during this time of year. Minimum daily temperature was lower and the frequency of freezing nights greater at the Beaver Pond (2074 m) than at the Ribbon Forest (3304 m) site (Figs. 1A, 1B, 2A, 2B). During July and August the number of days with night temperatures of 0°C or below was approximately 1 in 10 at the low elevation site and 1 in 20 or fewer at the two higher sites (Fig. 3A), suggesting that intermittent freezing nights may pose a greater limitation to photosynthesis at lower elevations during summer. Cold air drainage from higher elevations can explain the greater frequency of freezing nights at low elevations (Kaufmann 1984). The occurrence of hard freeze conditions (-5.0°C) associated with an irreversible inhibition of photosynthesis was negligible from early July through mid-September at all elevations. However, air temperature data potentially underestimate the frequency of inhibitory needle temperatures because a substantial depression in temperature below air temperature can occur as a result of radiative cooling, particularly at high elevations (Smith and Geller 1980; Hadley and Smith 1986). Cannell (1985) found that the foliage of unhardened *Picea sitchensis* is damaged by exposure to needle temperatures below -5.0°C , which often occurs when air temperature decreases to only -2.5°C .

Photosynthesis at the two lower sites was positively correlated with soil temperature and minimum (night) air temperature (Table 1). Moreover, net photosynthesis measured *in situ* showed a significant correlation with these parameters (Figs. 6B and 7). Several studies have established a relationship between rooting zone temperature and stomatal conductance in conifers (Teskey et al. 1983, 1984; Running and Reid 1980), including Engelmann spruce (Kaufmann 1979a). The decrease in conductance becomes pronounced at soil temperatures below 10°C as a result of increased root resistance to water flux (Kramer 1942; Kaufmann 1979a). Low soil temperature also inhibits photosynthesis (Lawrence and Oechel 1983; Tranquillini 1979); however, the mechanism of this inhibition is complex and may not be related to stomatal closure. Using potted spruce seedlings, DeLucia (1986) observed a parallel decrease in net photosynthesis and stomatal conductance in response to root chilling. Internal CO_2 concentration remained high, however, suggesting that photosynthesis was not under a stomatal limitation. Indirect effects of low soil temperature on photosynthesis may include decreased nutrient uptake, decreased hormone production in the roots, and alteration of carbohydrate source-sink relationships (Nielson 1974; DeLucia 1986). After the cessation of freezing nights, low soil temperature appears to be the primary limitation to photosynthesis in spruce and may continue to limit photosynthesis for the entire summer at higher elevations.

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