

## Influence of cold soil and snowcover on photosynthesis and leaf conductance in two Rocky Mountain conifers

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**Summary.** The influence of cold soil and snowcover on photosynthesis and conductance of *Picea engelmannii* and *Pinus contorta* was investigated early in the growing season in the Medicine Bow Mountains, Wyoming, USA. Trees of both species growing in cold soil (<1°C) associated with snowpack had 25–40% lower leaf photosynthesis than trees in warm soils (>10°C). In cold soils leaf conductance of both species was lower, but more so in *Pinus*, leading to lower intercellular CO<sub>2</sub> concentrations and greater stomatal limitation of photosynthesis. Soil temperature had no effect on predawn and midday shoot water potentials of *Pinus* and *Picea* and lower photosynthesis and conductance did not appear to be a result of lower bulk shoot water potential. Predawn, as well as midday, water potentials of *Pinus* were consistently higher than *Picea* suggesting that *Pinus* may have deeper roots, although trenching experiments indicated young *Picea* trees have more extensive lateral root systems than similar sized *Pinus* trees. Young *Picea* trees (<2 m in height) in snowbanks were capable of utilizing warmer soil 4 m from their base. Under similar conditions *Pinus* in snowbanks had lower photosynthesis and conductance than controls and *Pinus* did not appear capable of utilizing warmer soils nearby. Under full sunlight, PPF reflected from the snow surface was 400–1400 μmol m<sup>-2</sup> s<sup>-1</sup> higher than from snow-free surfaces. This reflected light resulted in a 10%–20% increase in photosynthesis of *Picea*. The beneficial effect of reflected light was apparent whether or not photosynthesis was reduced by low soil temperatures.

**Key words:** Soil temperature – Photosynthesis – *Picea engelmannii* – *Pinus contorta* – Roots – Snow

Subalpine environments in the central Rocky Mountains pose severe abiotic limitations on carbon assimilation in plants. Low day-time air temperatures and freezing nights are common until early June and can limit photosynthesis in subalpine conifers (DeLucia and Smith 1987; DeLucia 1987). However, soil temperatures at root depths in the forest increase more slowly than air temperatures during the growing season and could be a persistent limitation

to photosynthesis in conifers well after favorable air temperatures are attained (Smith 1985; DeLucia and Smith 1987).

Low soil temperature can reduce root growth (Bowen 1970; Lopushinsky and Kaufmann 1984; Andersen et al. 1986) and nutrient absorption in conifers (Bowen 1970). In laboratory experiments, leaf conductance to water vapor (g) in conifers decreases as root temperature drops (Kramer 1942; Kaufmann 1977; Lopushinsky and Kaufmann 1984; Teskey et al. 1984), and in field experiments low g has been correlated with low soil temperature (Kaufmann 1975; Carter et al. 1988; Jurik et al. 1988). It has been suggested that increased water viscosity and decreased root permeability result in reduced root water uptake in cold soils (Kaufmann 1975; 1977; Running and Reid 1980; Kramer 1983). However, cold soils had variable effects on shoot or leaf water potential ( $\psi$ ) in these studies, and the mechanism responsible for lower g is not known.

Low soil temperature may also reduce net photosynthesis (A) (Babalola et al. 1968; Turner and Jarvis 1975; DeLucia 1986; DeLucia and Smith 1987) and shoot growth (Lopushinsky and Kaufmann 1984). Few investigators have examined mechanisms responsible for decreased A at low soil temperature. However, in growth chamber experiments Turner and Jarvis (1975) and DeLucia (1986) found reduced A of spruce seedlings in cold soils was caused primarily by non-stomatal limitations.

In this study we examined the response of A, g and  $\psi$  in Engelmann spruce (*Picea engelmannii* Parry) and lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.) to field manipulations of soil temperature. The interaction of soil temperature and snowcover on gas exchange was also investigated. *Picea engelmannii* and *Pinus contorta* are dominant components of subalpine forests in the central Rocky Mountains (Fowells 1965; Oosting and Reid 1952). Experiments were conducted early in the growing season following alleviation of day-time air temperature limitations to photosynthesis.

### Methods

Experiments were conducted in the Medicine Bow Mountains of southeastern Wyoming (41°21'N, 106°13'W) during 1988. In the first set of experiments the effects of soil temperature on gas exchange and water relations of naturally-growing small trees (<2 m in height) of *Pinus contorta*

and *Picea engelmannii* were investigated at a low and high elevation site. We had no a priori information on the root distribution of small trees of these species and the lateral distribution of functional roots of *Pinus* and *Picea* was determined by a series of soil trenching experiments. The effect of soil temperature on shoot gas exchange was also examined using potted *Picea* seedlings which enabled us to manipulate the temperature of the entire root system. Some of our results suggested that reflected light from snow surfaces could have beneficial effects on photosynthesis. To determine the contribution of reflected light from snow we measured the photosynthetic-light response of *Picea* shoots.

#### *Cold soil effects on gas exchange*

*Site 1.* In late May *Pinus* was studied at the low elevation (2591 m) site (i.e. site 1). This site was in an approximate 10 × 20 m gap in a mature *Pinus* stand. Snow covered approximately 50% of the gap at the beginning of the experiment on 22 May. Five trees (0.4 to 1.0 m in height) which had continuous snowcover for at least a 2-m radius from their bases were assigned to the cold-soil treatment, and five trees in snow-free areas of the gap were assigned to the warm-soil treatment. Soil temperatures at the surface of the mineral soil and at 5, 10, 20, 30, and 40 cm depths were measured adjacent to one tree in each treatment with copper-constantan thermocouples. Air temperatures were measured with shielded fine-wire thermocouples placed adjacent to the mid-canopy of each tree. Temperatures were measured every 5 s and summarized with a data logger (Campell Scientific 21-X). After two days at ambient soil temperatures, thermostatically-controlled heating mats (Propagation Mats, Pro-Grow Supply Corp.) were placed at the base of selected heat-treatment trees. The mats extended at least 1 m from the stems and were covered with 2-cm thick air-cell insulation. For the next three days soil temperature at 5-cm depth was maintained at 20°C for the heat-treatment trees and snow was maintained to a depth of 0.4 m and at least 4 m from the base of the cold-treatment trees.

During the five-day experiment, net photosynthesis (A) and transpiration were measured between 1000 and 1200 hours (MST) on two sun shoots (1–3 yr old needles) on each tree with a closed IR gas analysis system (LiCor Model LI-6200). The rate of CO<sub>2</sub> depletion inside the cuvette was measured over a 15-s interval after orienting the shoot normal to the solar beam and waiting for the depletion rate to approach steady-state. Measurements were typically initiated within 12 s of placing the stems in the cuvette. Cuvette CO<sub>2</sub> concentration at the beginning of each measurement was within 2 µl/l of ambient levels (350 µl/l) and did not decrease more than 25 µl/l during measurement. Relative humidity was maintained within 2% of ambient levels. A quantum sensor (LiCor Model 190S) attached to the cuvette was used to measure photosynthetic photon flux density (PPDF), and all measurements were made under full sunlight (PPFD ≥ 2000 µmol m<sup>-2</sup> s<sup>-1</sup>). Intercellular CO<sub>2</sub> concentration (c<sub>i</sub>) and leaf conductance to water vapor (g) were calculated from A and transpiration rate using the equations of von Caemmerer and Farquhar (1981). Gas-exchange calculations were made on a total needle surface area basis by correlating leaf dry weight to geometrically determined surface areas (Knapp and Smith 1981). Predawn and midday  $\psi$  were measured with a pressure

chamber (PMS Model 1000) on 25 and 27 May on one sun shoot of each tree. Water potential measurements were repeated on all trees on 15 July when soil and air temperatures appeared near optimal for growth at the site.

*Site 2.* A second experiment was conducted in a subalpine meadow along the edge of a mature *Picea/Abies lasiocarpa* stand (site 2). Young trees of *Pinus* and *Picea* were abundant along the forest edge and both species were investigated. This site was considerably higher in elevation (3033 m) than site 1 and was approximately 70% snowcovered on 16 June, one day before the experiment began. Two groups of young trees (0.5–2.0 m in height) were chosen for study. For the warm-soil treatment, snow was removed within 2 m of the bases of five trees of *Pinus* and *Picea*. Midday gas-exchange measurements were made the following six days. After the first measurements (17 June), clear plastic sheets were placed over the ground for a radius of 1 m from the base of each tree to further increase soil temperatures (Waggoner et al. 1960), as power was not available for heating pads. A second group of five trees of each species was selected on 16 June from an adjacent snowcovered area and served as the cold-soil controls. Snowcover was maintained 0.4 m deep for at least a 4-m radius from each tree during the experiment. From 17–22 June, midday gas-exchange data on sun shoots of *Pinus* and *Picea*, along with environmental data were collected as at site 1. Shoot water potential was measured on 20 and 22 June, and on 17 July when soil and air temperatures appeared near optimal at the site.

*Site 3 (potted seedlings).* An additional soil-temperature experiment was conducted with potted five year-old *Picea* seedlings which enabled us to manipulate the temperature of the entire root system. Plants were grown from seeds (White River National Forest, Colorado, seed zone 222) in pots (40 × 20 cm) in the understory of a *Pinus contorta* stand. The experiment was conducted in early July in a subalpine meadow (3219 m elevation) bordered by a mature *Picea/Abies* forest (site 3). Plants were moved to the site one week before the experiment began. Nine seedlings were randomly selected for the cold-root treatment and the pots were buried in a nearby snowbank with the top of the pots approximately 3 cm below the snow surface. An additional nine seedlings were placed in the adjacent snow-free meadow. Soil temperature in the pots (5-cm depth) and air temperature were measured as described previously. Midday gas-exchange measurements on one shoot of each seedling were made for 3 days beginning on 11 July, and predawn and midday  $\psi$  were measured on the last day of experiment. All seedlings were watered daily.

#### *Lateral root distributions*

There was a possibility that roots of naturally-growing trees extended past snowcovered areas into warmer soil. The lateral distribution of functional roots of naturally-growing young *Pinus* and *Picea* trees was examined by a series of soil-trenching treatments combined with corresponding  $\psi$  measurements. Ten isolated trees (<2 m in height) of each species were selected at site 2 in early August and midday  $\psi$  of one shoot on each tree was measured. Following the  $\psi$  measurements a circular 20-cm deep trench was dug on a 4-m radius from the bases of five trees of each species.

The remaining trees served as controls. A subsequent decrease in midday  $\psi$  in trenched trees relative to controls would indicate that functional roots had been severed and water uptake was reduced. After the sixth day, concentric trenches were dug on 2-m radii and  $\psi$  measurements continued for four days.

#### *Effect of visible light reflected from snow*

To assess the effect of visible radiation reflected by snow on shoot gas exchange, we covered the snow around each cold-root treatment seedling in the experiment at site 3 with a black tarp following gas-exchange measurements. After 2 min gas exchange was remeasured. To further examine the potential effect of reflected visible radiation from snow, we measured the photosynthetic-light response for sun shoots of young *Picea* trees. Three trees (1.5–2 m in height) at site 3 growing in a snow-free area of the meadow along with three nearby trees in a snowbank were selected. One horizontal sun shoot from each tree was exposed to different total PPFD (upward PPFD + downward PPFD) by use of a series of gray neutral-density screens in combination with either a black or reflective (aluminum-foil coated) tarp placed on the ground below a tree. Total PPFD was determined as the sum of PPFD measured simultaneously with one quantum sensor pointing up and the other pointing down. Gas exchange was measured after approximately 2 min at each total PPFD.

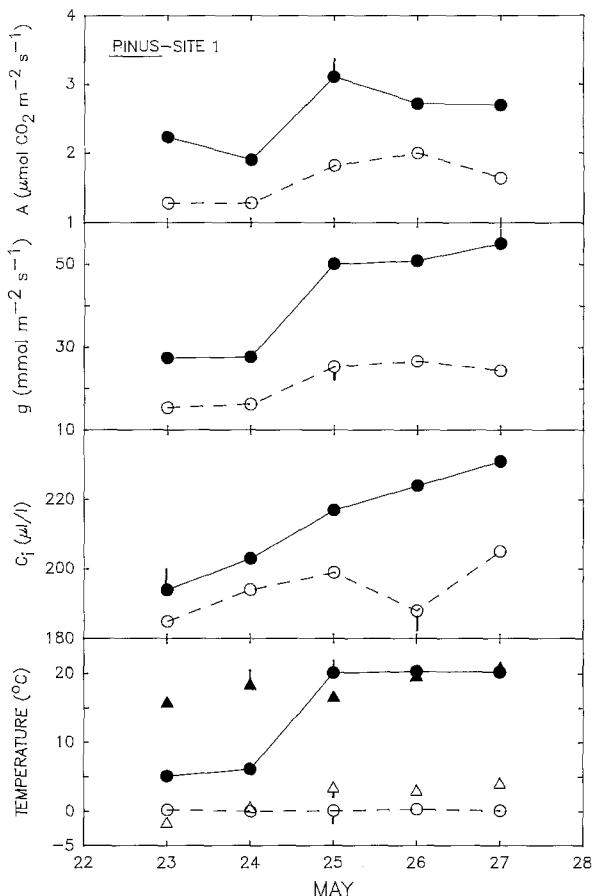
## Results

#### *Cold soil effects on gas exchange*

At the low elevation site 1, midday soil temperatures (5-cm depth) below the cold-soil trees were  $<1^\circ\text{C}$  (Fig. 1). Soils under snow showed little diurnal fluctuation and less than  $0.5^\circ\text{C}$  variation from depths of 5 to 40 cm. Midday soil temperature at 5-cm depth in the snow-free area of the gap was  $5\text{--}6^\circ\text{C}$  on 23 and 24 May, with diurnal variation of  $<1^\circ\text{C}$ . Temperatures at 40-cm depth ranged from  $3\text{--}4^\circ\text{C}$  for these dates. After soil heating commenced on the afternoon of 24 May soil temperature at 5 cm increased to  $20^\circ\text{C}$  within 10 h, and soil temperature at 40 cm was between  $11^\circ\text{C}$  and  $13^\circ\text{C}$  over the heating period.

Midday A and g for *Pinus* were approximately 30%–40% and 45%–60% lower, respectively, under the cold-soil treatment (Fig. 1). Soil heating caused a substantial increase in g on 25 May. A small increase in g was also observed for cold-soil plants on this date and may be associated with the increase in minimum air temperature above  $0^\circ\text{C}$ . Calculated  $c_i$  was higher in the warm-soil treatment throughout the experiment. Predawn and midday shoot  $\psi$  in each treatment were similar (Table 1;  $t$ -test,  $P > 0.05$ ). On July 15 soil temperatures throughout the site were  $>15^\circ\text{C}$  at 5-cm depth and predawn and midday  $\psi$  of all trees were significantly lower than May values (data for both treatments in May were combined for comparison with the July data;  $P < 0.05$ ).

In mid June the experiment was repeated at the higher elevation site 2 using clear plastic mulch on snow-free soils to warm soils under *Pinus* as well as *Picea*. Midday soil temperatures at 5-cm depth for the snow-free treatment were  $>9^\circ\text{C}$  for the first two days of the experiment (Fig. 2).



**Fig. 1.** Mean midday shoot net photosynthesis (A), conductance (g) and intercellular  $\text{CO}_2$  concentration ( $c_i$ ) of *Pinus* in snowcovered (○) and snow-free or heated areas (●) at site 1. Soil heating began after measurements on 24 May. Temperatures are soil temperature 5 cm under snowcovered (○) and snow-free or heated areas (●), and midday (▲) and minimum air temperatures (△). Vertical lines are largest SE

After the mulch was in place (late afternoon of 18 June) soil temperatures increased steadily to  $>16^\circ\text{C}$ .

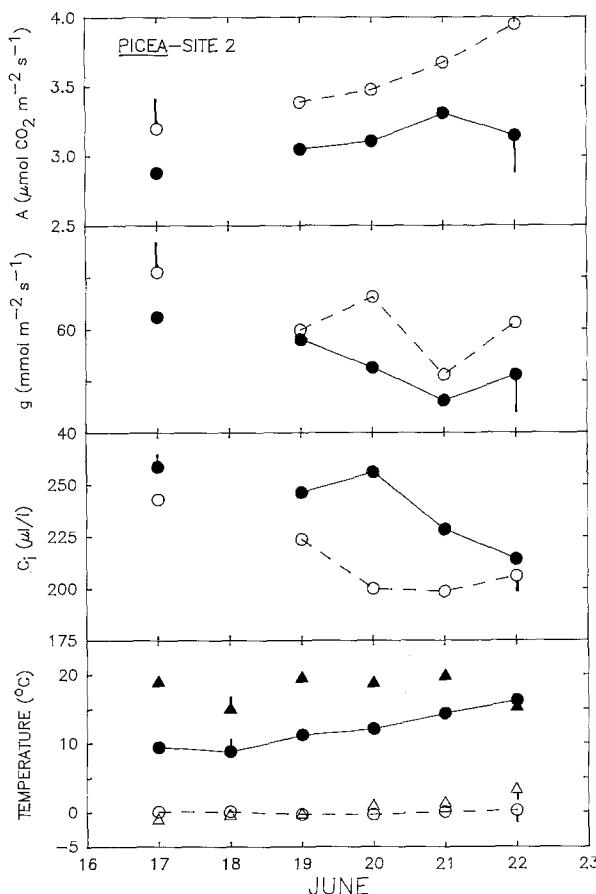
The effects of soil temperature on gas exchange of *Pinus* at this site were similar to those at site 1 and are not shown. In contrast, A was 12%–22% higher in *Picea* under the cold-soil treatment (Fig. 2). There was a steady increase in A over the course of the experiment in both treatments which coincided with increasing minimum air temperatures. Midday g was consistently higher and  $c_i$  was lower in the cold-soil *Picea* (Fig. 2).

There were no significant differences in predawn or midday  $\psi$  between treatments in either species (Table 1;  $P > 0.05$ ). On July 17 soil temperature at the 5-cm depth was  $>12^\circ\text{C}$  throughout the site and predawn and midday  $\psi$  in both species were significantly lower than on 20 June, but not 22 June. Comparing species, predawn and midday  $\psi$  of *Picea* were significantly lower than *Pinus* on all dates tested ( $P < 0.05$ ).

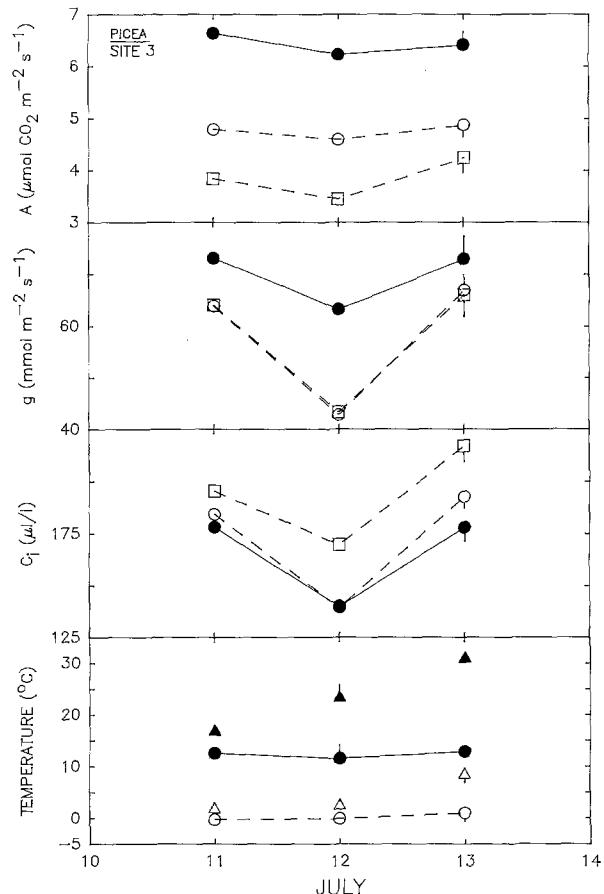
At site 3 soil temperatures for potted seedlings placed in a snowbank were  $<1^\circ\text{C}$  while soil temperatures in the warm-soil group were  $>10^\circ\text{C}$  (Fig. 3). Midday A and g of cold-soil *Picea* were reduced by 25%–30% and 10%–32%, respectively, relative to warm-soil seedlings. Intercellular  $\text{CO}_2$  concentrations, as well as predawn and midday  $\psi$  (Table 1), were similar in *Picea* in the two treatments.

**Table 1.** Predawn and midday shoot  $\psi$  of *Pinus* and *Picea* in warm and cold soils. Measurements were repeated after alleviation of any temperature limitation at site 1 (15 July) and site 2 (17 July). Results for these dates are for all trees (both previous treatments). Values are means (1 SE). There were no significant differences in predawn or midday  $\psi$  between soil treatments within a species ( $P > 0.05$ ). At site 2 predawn and midday  $\psi$  of *Pinus* were significantly higher than *Picea* on all dates ( $P < 0.05$ )

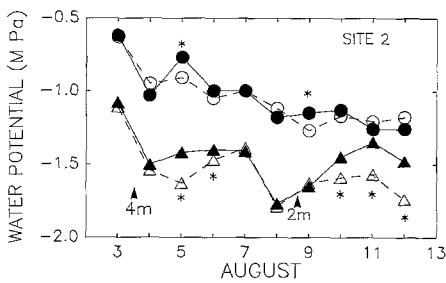
Site	Date	Time	<i>Pinus</i>		<i>Picea</i>	
			Warm	Cold	Warm	Cold
1	25 May	Predawn	-0.24 (0.03)	-0.31 (0.05)		
		Midday	-0.68 (0.10)	-0.64 (0.08)		
	27 May	Predawn	-0.22 (0.03)	-0.29 (0.04)		
		Midday	-0.68 (0.04)	-0.60 (0.06)		
2	15 July	Predawn		-0.54 (0.05)		
		Midday		-1.20 (0.13)		
	20 June	Predawn	-0.31 (0.05)	-0.33 (0.08)	-0.50 (0.06)	-0.50 (0.06)
		Midday	-1.06 (0.13)	-1.00 (0.14)	-1.43 (0.13)	-1.46 (0.11)
3	22 June	Predawn	-0.40 (0.05)	-0.42 (0.06)	-0.62 (0.06)	-0.61 (0.08)
		Midday	-1.24 (0.12)	-1.23 (0.10)	-1.60 (0.12)	-1.69 (0.10)
	17 July	Predawn		-0.59 (0.03)		-0.80 (0.05)
		Midday		-1.31 (0.10)		-1.74 (0.08)
3	13 July	Predawn			-0.47 (0.03)	-0.41 (0.02)
		Midday			-1.19 (0.11)	-1.10 (0.08)



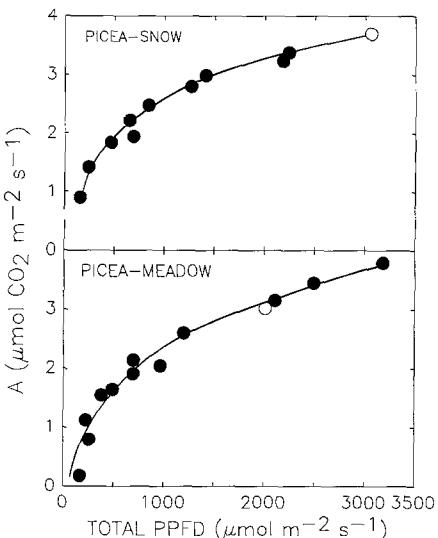
**Fig. 2.** Mean midday shoot net photosynthesis, conductance and intercellular  $\text{CO}_2$  concentration of *Picea* in snowcovered (○) and snow-free or heated areas (●) at site 2. Heating was with clear plastic mulch placed over snow-free areas after measurements on 17 June. Rain prevented gas-exchange measurements on 18 June. Temperatures are the same as in Fig. 1. Vertical lines are largest SE



**Fig. 3.** Mean midday shoot net photosynthesis, conductance and intercellular  $\text{CO}_2$  concentration of potted *Picea* seedlings placed in snow (□) or snow-free meadow (●) at site 3. Gas exchange was remeasured after a black tarp was placed under snow seedlings (□). Temperatures are the same as in Fig. 1. Vertical lines are largest SE



**Fig. 4.** Mean midday shoot water potentials of trenched (○) and control (●) *Pinus*, and trenched (△) and control (▲) *Picea* at site 2. Trenches were dug 4 and 2 m from tree bases in late-afternoon 3 and 8 August, respectively. Asterisks denote treatment was significantly lower than control mean (paired *t*-test,  $P < 0.05$ )



**Fig. 5.** Typical photosynthetic-light response curves of sun shoots on *Picea* trees in a snowbank and adjacent meadow. Total PPFD refers to upward plus downward PPFD. Open circles denote ambient conditions at each area. Lines were fitted by eye

#### Lateral root distributions

A trenching experiment was used to determine the lateral extent of functional roots for small trees of *Picea* and *Pinus* at site 2. On 5 August, two days after digging trenches 4 m from the bases, a significant decrease in midday  $\psi$  was evident for *Picea* and *Pinus* (Fig. 4; paired *t*-test,  $P < 0.05$ ). This effect was also significant for *Picea* on 6 August. On the afternoon of 8 August trees were trenched 2 m from their base. The following day there was a significant decrease in  $\psi$  of *Pinus* (Fig. 4). By 10 August  $\psi$  of trenched *Pinus* had recovered to control values and remained similar for the remainder of the experiment. The  $\psi$  of *Picea* was still significantly lower in trenched individuals from 10 August through the end of the monitoring period.

#### Effect of visible light reflected from snow

Eliminating reflected light from snow resulted in a 10%–22% decrease in  $A$  for *Picea* at site 3 (Fig. 3). Typical photosynthetic-light response curves for trees ( $< 2$  m height) growing in a snow-free area and an adjacent snowbank are shown in Fig. 5. Air temperatures adjacent to the shoots were between 20° and 24° C during the gas-exchange measurements and foliage temperatures were

within 1.5° C of air temperature. Reflected light from snow or a reflective tarp had no effect on foliage temperature or  $g$  but caused a 10%–20% increase in  $A$ . Leaf conductance generally was constant, while  $c_i$  decreased with increasing total PPFD in all cases (not shown). At a given total PPFD,  $A$  was similar between treatments suggesting that trees growing in the snowbank had roots extending into snow-free areas (about 1 m away).

#### Discussion

Previous field studies have correlated low conifer gas-exchange rates with low soil temperature (see introduction). In this study artificial soil heating increased  $A$  and  $g$  of conifers originally growing in cold soils. The mechanism causing lower  $A$  under low soil temperature was different in *Pinus* and *Picea*. In cold soil  $c_i$  of *Pinus* was lower than in heated controls (Fig. 1) indicating a stomatal limitation to  $A$  (Farquhar and Sharkey 1982). Stomatal conductance of *Picea* was also lower in cold soil, but in contrast to *Pinus* there was no difference in  $c_i$  between treatments (Fig. 3). This implies some non-stomatal limitation of  $A$  in *Picea* under cold soil conditions. Non-stomatal limitations of  $A$  at low soil temperatures have also been found in growth chamber experiments with *Picea engelmannii* (DeLucia 1986) and *P. sitchensis* (Turner and Jarvis 1975). At low root temperatures soluble carbohydrates and starch accumulate in *Picea* shoots (DeLucia 1986) and may cause feedback inhibition of  $A$  (Herold 1980).

Water uptake and shoot  $\psi$  of conifers are sometimes reduced at low soil temperatures (see introduction). However, we found midday shoot  $\psi$  was similar between soil treatments and  $\psi$  was always lower in July than during cold-soil experiments (Table 1). Thus, lower  $g$  in cold soils in our study did not appear due to decreased bulk shoot  $\psi$ . There is increasing evidence that stomata may not respond to changes in bulk shoot  $\psi$  (Ashton and Lawlor 1979; Coutts 1980; Bates and Hall 1981; Schulze 1986; Turner 1986) but may respond to signals from roots experiencing drought (Blackman and Davies 1985; Davies et al. 1986) or changing soil temperatures (Kuppers et al. 1982).

Despite recognition of the importance of photoinhibition at high irradiances and low temperatures (Oquist 1983; Powles 1984), we found that under full sunlight the reflected light from snow led to a 10%–20% increase in  $A$  of *Picea* (Fig. 5), even when  $A$  was initially reduced by cold soil (Fig. 3). This range of increase would account for differences in  $A$  of *Picea* growing over snow and bare areas at site 2 where roots of the former were probably utilizing warmer soil nearby (Fig. 2). Increased  $A$  at high irradiances was not a temperature response since we found no trends in foliage or air temperatures over the range of PPFD used. In sun shoots of other conifers  $A$  continued to increase at high irradiance and showed no sign of saturation (Beadle et al. 1985; Watts et al. 1976). We measured typical midday reflected PPFD at 1.5 m above snow and snow-free meadow at site 3. Under moderate to full sunlight (incoming PPFD 1500–2100  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) reflected PPFD ranged from 500–1500  $\mu\text{mol m}^{-2} \text{s}^{-1}$  over snow but only 50–80  $\mu\text{mol m}^{-2} \text{s}^{-1}$  over meadow. These values are consistent with much higher visible albedo of snow than vegetation (Rosenberg et al. 1983). Higher levels of diffuse radiation from snow could also reduce mutual shading of the

tightly-packed needles on sun shoots of *Picea* (Szawiawski and Wierzbicki 1978; Carter and Smith 1985). In the relatively open *Picea/Abies* forests of the central Rocky Mountains the light reflected off snow could have a significant effect on whole-tree carbon gain.

Gas-exchange rates of *Pinus* in snowbanks were always lower than that of controls. In contrast, *Picea* was apparently capable of utilizing warm soils over 4 m from its base (Fig. 2), and gas-exchange rates were lower only when we insured that the complete root system was chilled by using potted seedlings buried in snow (Fig. 3). Although root growth is often reduced in cold soils, major periods of conifer root growth can occur under snow, especially during snowmelt (Grier et al. 1981; Hinckley et al. 1985). The effect of trenching indicated that a substantial proportion of the actively absorbing roots of young *Pinus* and *Picea* trees occur over 4 m from their bases (Fig. 4). In *Abies amabilis* shoot  $\psi$  did not decline until over 50% of its root system was severed (Teskey et al. 1985; Hinckley et al. 1985). Trenching had a larger and longer-lasting effect on shoot  $\psi$  of *Picea* than on *Pinus*, and *Picea* probably had a higher proportion of its functional root system in warmer soil outside snowbanks. *Pinus* consistently had higher pre-dawn (and midday)  $\psi$  than *Picea* (Table 1 and Fig. 4) suggesting that *Pinus* has deeper functional roots than *Picea*. Knapp and Smith (1981) also found  $\psi$  was greater in *Pinus* than *Picea*.

A major difficulty in defining causative factors in field experiments is the inability to control several potentially interacting environmental factors. This study was conducted during a period of rapidly changing environmental conditions. In addition to low soil temperatures, freezing night-time air temperatures can reduce gas exchange in *Pinus* and *Picea* (Smith et al. 1984; DeLucia 1987; DeLucia and Smith 1987; Carter et al. 1988). At site 1, g of *Pinus* in both treatment groups increased on 25 May, coinciding with the rise in minimum overnight air temperature above 0°C (Fig. 1). The increase was twice as large in *Pinus* in warm soil and implies that soil heating on this date also had a role in increased g. Midday air temperatures were not limiting based on the photosynthetic temperature optima of *Pinus* (Smith and Carter 1988) and *Picea* (DeLucia and Smith 1987).

The apparent differences in root distribution between *Pinus* and *Picea* may partially explain the different elevational distribution of these species. From 1 June through 1 September we monitored soil temperatures (5–40 cm depth) at six sites along an elevational gradient (2951 to 3300 m). The four sites below 3000 m elevation were in *Pinus contorta* stands while the two higher sites were in *Picea engelmannii/Abies lasiocarpa* stands, which is typical of the elevational distribution of these species in the central Rocky Mountains (Billings 1969; Oosting and Reid 1952). Previous studies have consistently found A and/or g in these species to decrease at root temperatures <8°C (Kaufmann 1975; Running and Reid 1980; DeLucia 1986; DeLucia and Smith 1987; Carter et al. 1988). Soil temperatures in *Pinus* sites (<3000 m elevation) were never <8°C from June through August. The deeper roots of *Pinus* would promote water extraction at more xeric, lower elevations where soil temperatures do not appear particularly limiting. In contrast, soil temperatures in *Picea/Abies* sites remained <8°C until late June (3080 m) to mid July (3300 m elevation). The extensive lateral root system of *Picea* may be

better suited to a persistent mosaic of cold and warm soils at these higher elevations.

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