Effect of soil temperature on stem sap flow, shoot gas exchange and water potential of *Picea engelmannii* (Parry) during snowmelt

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Summary. The effect of cold soils on stem sap flow, shoot gas exchange and water potential of *Picea engelmannii* (Parry) was investigated during the snowmelt period in the Medicine Bow Mountains, Wyoming, USA. Shoot net photosynthetic rates were higher in young trees (1.5–1.8 m in height) growing in cold soils ($<3.5°$ C) associated with snowpack, than trees in warm soils until about 1500 h. Higher shoot photosynthetic rates of trees in cold soils continued after snow was removed and could not be completely explained by higher visible irradiance over highly reflective snow. Following soil warming higher photosynthetic rates were evident in these trees for five days. High nutrient availability associated with snowmelt may improve shoot nutrient status leading to higher gas-exchange rates during snowmelt. Shoot conductance to water vapor was higher in trees in cold soil until midday, when declining shoot conductance led to lower intercellular CO_2 concentrations. Midday through afternoon shoot water potentials of trees in cold soils were similar or higher than those of trees in warm soils and the lower afternoon shoot conductances in cold soils were not the result of lower bulk shoot water potentials. Decline in net photosynthesis of trees in cold soils at 1500 h paralleled increases in intercellular CO_2 concentrations, implying a nonstomatal limitation of photosynthesis. This scenario occurred consistently in mid-afternoon following higher morning and midday photosynthesis in cold soils, suggesting a carbohydrate feedback inhibition of photosynthesis. Diurnal patterns in stem sap flow of all trees (cold and warm soils) reflected patterns of shoot conductance, although changes in stem sap flow lagged 1–3 h behind shoot conductance apparently due to stem water storage. Total daily stem sap flow was similar in trees in cold and warm soils, although diel patterns differed. The morning surge and night-time drop in sap flow commenced 1–2 h earlier in trees in

cold soils. Overnight stem sap flow was lower in trees in cold soils, possibly due to higher resistance to root water uptake in cold soils, which may explain lower predawn shoot water potentials. However, midday shoot water potentials of trees in cold soils equalled or exceeded those of trees in warm soils. Higher resistance to root water uptake in *P. engelmannii* in cold soils was apparently overshadowed by transpirational forces and significant shoot water deficits did not develop.

Subalpine forests of the central Rocky Mountains are characterized by long, cold winters with over 70% of the annual precipitation occurring in the form of snow from October to May. This snowpack commonly persists into late June or early July and impedes soil warming (Day et al. 1989). In contrast, air temperatures rise rapidly through May and June leading to the suggestion that cold soils may limit photosynthesis and growth in subalpine conifers well after favorable air temperatures are attained (Smith 1985; DeLucia and Smith 1987; Day et al. 1989).

Reductions in leaf conductance to water vapor (g) and transpiration of trees in cold soils have generally been attributed to decreased water uptake resulting from decreased root permeability and increased water viscosity (Kramer 1940, 1942; Lopushinsky and Kaufmann 1984). Decreases in water uptake often lead to lower shoot or leaf water potentials (ψ) in conifers in cold soils (Kaufmann 1975; Kaufmann 1977; Lopushinsky and Kaufmann 1984). However, the magnitude of the reductions in ψ at low soil temperatures is often small and may be insufficient to cause lower g (Kaufmann 1975; Kaufmann 1977). It is not clear if reductions in water uptake under cold soils are an important constraint to physiological processes under field conditions.

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Other mechanisms may be responsible for lower gas-exchange rates under cold soils. Reductions in g (Teskey et al. 1983; Benzioni and Dunstone 1988) as well as apparent stomatal limitations to leaf or shoot net photosynthesis (A) (Day et al. 1989) have been observed without changes in bulk shoot ψ in cold soils. The mechanisms involved are unknown but may be associated with changes in xylem-water flux (Teskey et al. 1983) or hormonal messages from roots (Davies et al. 1986). In addition to stomatal responses, nonstomatal limitations of photosynthesis may develop in some conifers at low soil temperatures (Turner and Jarvis 1975; DeLucia 1986; Day et al. 1989), possibly through carbohydrate feedback inhibition of photosynthesis (DeLucia 1986).

The majority of studies addressing cold-soil effects on conifer gas exchange have been conducted under controlled environmental conditions. In some cases these experiments may overestimate the detrimental effects of cold soils in the field because unhardened or non-acclimated seedlings were used. Unhardened seedlings display larger reductions in gas exchange (Turner and Jarvis 1975) and xylem-water conductance (Teskey et al. 1984) under cold soils than seedlings emerging from winter dormancy. In addition, differences in environmental conditions used in laboratory experiments and those of naturally-growing trees are unavoidable. These considerations may be particularly important in subalpine forests of the central Rocky Mountains where environmental conditions change rapidly during the growing season and trees may spend much of this period in transitional states of breaking and entering dormancy (Smith et al. 1984; Smith 1985).

This hardening effect may explain the large variation in the response of Picea engelmannii to low soil temperatures. In growth chamber experiments on unhardened P. engelmannii seedlings, DeLucia (1986) found gas-exchange rates were reduced at root temperatures below 8° C. In contrast, Day et al. (1989) found higher gas-exchange rates in young P. engelmannii trees growing in snowbanks than adjacent warm soils. Although they provided evidence suggesting trees in snowbanks had roots extending into warm soil areas and may also benefit from visible radiance reflected from snowbanks, they were able to demonstrate reduced gas-exchange rates only when they chilled root systems of seedlings growing in warms soils (i.e. relatively unhardened). The importance of cold-soil limitations in P. engelmannii under field conditions is also confounded by findings of peak annual rates of stem sap flow in May which coincided with peak snowmelt and low soil temperatures (Swanson 1967).

In this study we address whether low soil temperatures reduce gas exchange of Picea engelmannii (Parry), a dominant component of subalpine forests in the central Rocky Mountains. In addition, we examined daily patterns of shoot ψ and stem sap flow in P. engelmannii to assess whether reduced root water uptake appears to be an important consideration under these conditions. Our experiment focused on naturally-growing trees during the snowmelt period in late spring and early summer, when day-time air temperatures are generally favorable for gas exchange in P. engelmannii but cold soils are still prevalent because of a persistent snowpack (DeLucia and Smith 1987; Day et al. 1989).

Materials and methods

Experiments were conducted on the edge of a subalpine meadow at 3530 m elevation in the Medicine Bow Mountains of southeastern Wyoming, USA. The experiment ran from 14 through 22 June, 1989. Five days prior to the experiment we removed all snow within 3 m of five young P. engelmannii trees (1.5–1.8 m in height) which served as the warm-soil treatment. The cold-soil treatment consisted of five similar-size P. engelmannii trees in an adjacent snowbank. During the first two days of the experiment snowcover extended at least 6 m from the base of these trees. A trench (down to parent material) around the snow insured that roots from these trees did not extend into warmer soil. At 1800 h on the second day of the experiment (15 June) all snow within 6 m of the cold-soil treatment trees was removed and at 1800 h on the following day clear plastic tarps were placed over the bare soil to facilitate warming.

Soil temperatures at 5, 10, 20, 30 and 40-cm depths were measured at three locations in each treatment with copper-constantan thermocouples. Air temperatures were measured with shielded fine-wire thermocouples at midcanopy in two trees of each treatment. Temperatures were measured every 5 s and summarized with a datalogger (Campbell Scientific 21-X).

Net photosynthesis (A) and transpiration of a sun shoot (1–3 y old needles) in the upper canopy of each tree were measured from about 800 to 1600 h (MST) each day with a closed IR gas-analysis system (LiCor Model LI-6200) following the procedure described by Day et al. (1989). The same shoot on each tree ($n = 5$) in a treatment were returned to at each sampling time throughout the day. All measurements were made under clear sky. Intercellular CO_2 concentration (c_i) and leaf conductance to water vapor (g) were calculated from A and transpiration rate using the equations of von Caemmerer and Farquhar (1981). Stem respiration may have caused an error in estimates of c_i, however, relative values can be used to compare treatments. Gas-exchange calculations were made on a total needle surface area basis by correlating leaf dry weights to geometrically determined surface areas.

The importance of reflected light from the snow surface on shoot gas exchange was also assessed. A black 0.5 m square tarp placed 0.5–1 m below shoots in the cold soil treatment enabled us to manipulate upward or reflected photosynthetic photon flux density (PPFD) to levels similar to those of shoots in the snow-free treatment. Photosynthetic photon flux density was measured with quantum sensors (LiCor Model 190S). After 8–10 min at the adjusted PPFD gas-exchange rates were remeasured. The combination of breezy conditions and evaporative cooling by the surrounding snowbank maintained needles within 1.5° C of their initial temperatures.

Water potential (ψ) was measured on one sun shoot in the upper canopy of each tree with a pressure chamber (PMS Model 1000) at regular intervals from predawn to about 1600 h. Shoots selected for measurement after dawn were in direct sunlight.

The relative stem sap flow in four trees in each treatment was estimated by measuring the steady-state convective heat transfer from a probe inserted into the stem, following Cermak et al. (1973) and Granier (1987). Two aluminum probes (0.24 cm diameter by 2 cm length) were inserted into the sapwood, one above the other, 10 cm apart on the northwest side of each tree. The upper probe was 40 cm above the ground, but below any branches. The probes were slightly modified from Granier (1985). Both probes contained an inner stainless steel tube (0.11 cm diameter) which housed a fine-wire copper-constantan thermocouple junction at its mid-section. The thermocouples for each pair of probes were wired in opposition. The inner tube of the upper probe was wrapped with fine-wire constantan which was heated by applying a constant current of 100 mA. Insulation (aluminum-coated air cells) was

wrapped around the stem containing each pair of probes to reduce ambient temperature differences between probes. The temperature difference between the heated and unheated probes on each tree was an index of stem sap flow, and was determined by measuring the voltage output from each pair of thermocouples every 5 s with a datalogger.

Results

Soil temperature

Midday soil temperatures in the warm-soil treatment ranged from 12 to 18° C at the 10-cm depth and 4 to 7° C at the 40-cm depth during the experiment (Fig. 1 a). Soil temperatures in the cold-soil treatment ranged from 0 to 3.5° C at all depths (5–40 cm) during the first two days of the experiment. The day after snow removal (early evening 15 June), soil temperatures remained relatively low (<4° C at 5 cm to 1° C at 40 cm) until the plastic tarps were laid down at 1800 h. The nocturnal drop in soil temperature was relatively small after the tarps were in place and soils warmed quickly the following morning (17 June). From 17 June through the end of the experiment soil temperatures down to the 20-cm depth were similar in the treatments.
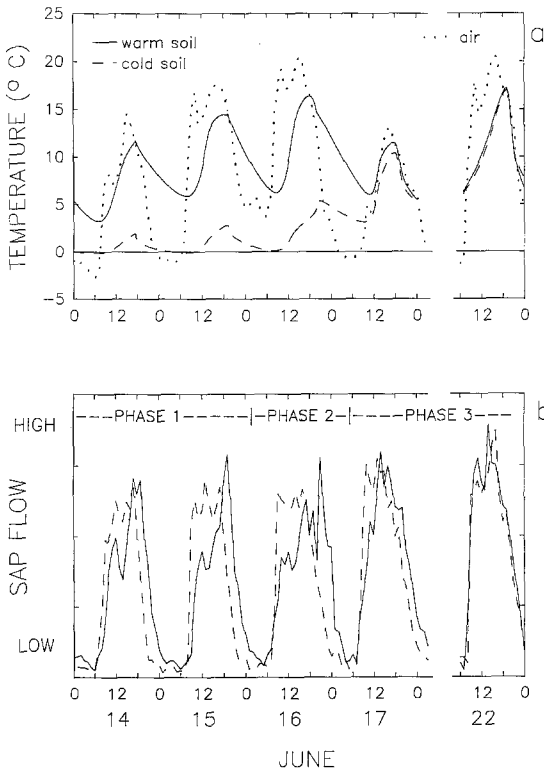

Fig. 1. Diel patterns of soil temperature at the 5-cm depth, air temperature (a) and relative stem sap flow (b) of a tree in the cold- and warm-soil treatment. Trees had equivalent sapwood areas at probe height. Patterns of other trees in each treatment were similar. Phases refer to environmental conditions in the cold-soil treatment: Phase 1, cold soil and snowcover; Phase 2, cold soil without snow-cover; Phase 3, warm soil (i.e., soil temperatures down to the 20 cm depth were similar to those in the warm-soil treatment)

Phases

We divided the experiment into three time periods or phases based on soil temperature and snowcover. *Phase 1* was the first two days of the experiment, when both cold soil and snowcover were maintained in the cold-soil treatment. This was followed by a transition period or *Phase 2* where soils remained cold but snow was absent. This phase lasted one day (16 June). *Phase 3* began on 17 June when most of the soil profile had warmed to temperatures similar to those in the warm-soil treatment.

Phase 1 (cold soil with snowcover)

Although the difference in temperature between the heated and unheated probe on each tree should be directly related to stem sap flow, detailed information on the thermal and conductive properties of stems is needed
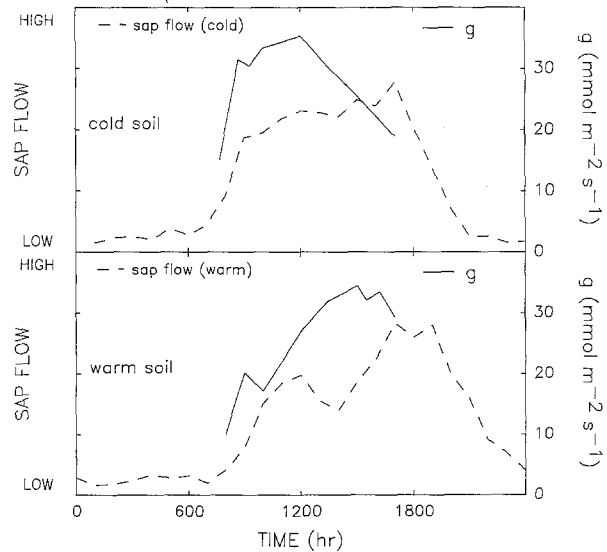

Fig. 2. Comparison of diurnal patterns in stem sap flow and shoot conductance to water vapor of two trees with equivalent sapwood areas on 14 June
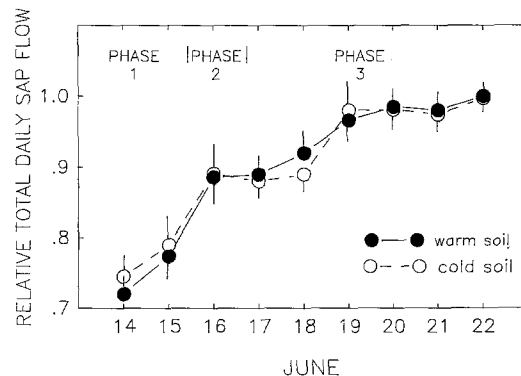

Fig. 3. Mean total daily stem sap flow of trees in the cold- and warm-soil treatment. Total daily sap flow of each tree was renormalized to its sap flow on 22 June when total sap flows in each treatment were similar. *Vertical lines* indicate 1 SE (*n*=4)

to calculate absolute sap flux density (Granier 1985, 1987). We lack this information and are unable to calculate absolute sap flux density. However, the selection of trees in each treatment with similar sapwood area and placement of probes at the same height enables a comparison of diurnal trends in sap flow between treatments.

During Phase 1 the morning surge, as well as night-time drop in sap flow occurred 1–2 h earlier in all cold-soil relative to warm-soil trees (Fig. 1b). Night-time stem sap flow was consistently lower in trees in cold soil. The differences in diurnal patterns of stem sap flow probably reflect different g (and transpiration) patterns, as sap flow apparently lagged 1–3 h behind parallel trends in g in each treatment (Fig. 2). To compare total daily sap flow between the trees in each treatment we summed hourly mean sap flow over 24 h periods. Because sap flow continues to decline after midnight (Fig. 1b), we used 0600 h as the beginning of each 24 h period. Daily sap flow of each tree was normalized to its sap flow on 22 June, when total sap flow in treatments were similar. Mean

normalized daily sap flow gradually increased in both treatments through the experiment (Fig. 3). Despite differences in diel sap flow patterns, normalized total daily sap flow was not significantly different between treatments through the experiment (t-test, $P > 0.05$).

In Phase 1 net photosynthetic rates of trees in cold soil were consistently higher than warm-soil trees until about 1500 h (Fig. 4). Leaf conductances of trees in cold soils were higher in the morning but dropped below levels in warm-soil trees by midday. Intercellular CO_2 concentrations of trees in cold soils declined from 1200 to 1500 h when c_i rose in conjunction with declining A. Trees in cold soil had lower predawn ψ but by midday ψ was similar to or higher than warm-soil trees (Fig. 4). Treatment differences in diurnal patterns of gas-exchange and ψ were similar on 15 June (not shown).

Although reflected irradiance was 300–1600 µmol $m^{-2} s^{-1}$ higher over snow than snow-free areas, needle temperatures in each treatment were within 2° C through Phase 1 (not shown). Higher visible irradiance from snow had a beneficial effect on gas-exchange; morning through midday A declined when reflected light from snow was removed with a black tarp (Fig. 4). Midday upward or reflected PPFD ranged from 30–60 µmol $m^{-2} s^{-1}$ over the black tarp which was similar to values over snow-free meadow (50–80 µmol $m^{-2} s^{-1}$). However, higher visible
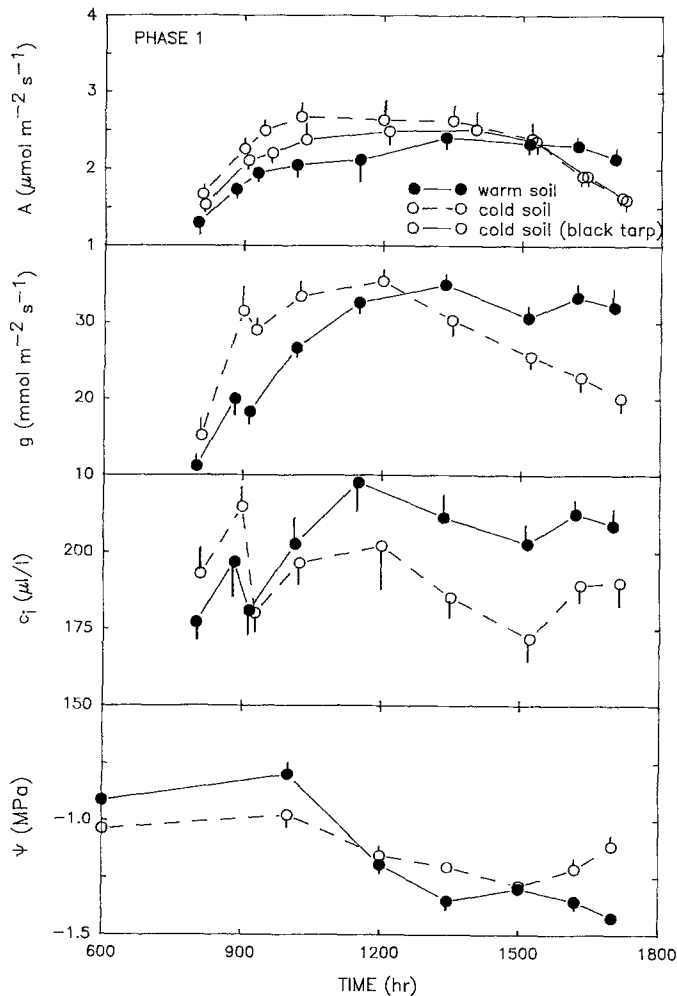

Fig. 4. Diurnal patterns in mean shoot gas exchange and water potential of trees in cold soils with snowcover and warm soils on 14 June (Phase 1). *Black tarp* in upper graph refers to rates after a black tarp was placed below shoots to manipulate upward or reflected PPFD over the snowbank to levels similar to those over snow-free meadow. *Vertical lines* indicate SE ($n = 5$)
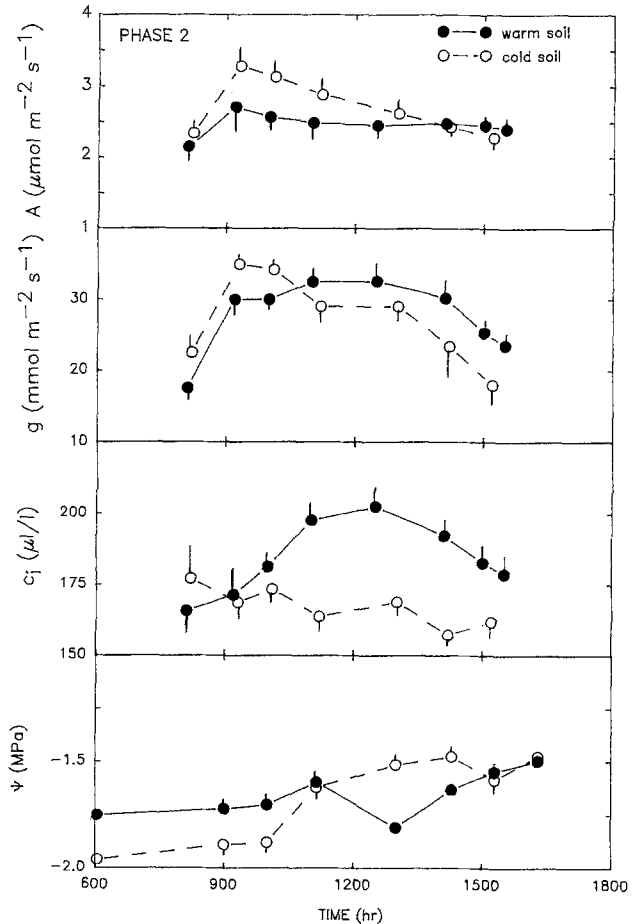

Fig. 5. Diurnal patterns in mean shoot gas exchange and water potential of trees in cold soils without snowcover and warm soils on 16 June (Phase 2). *Vertical lines* indicate SE ($n = 5$)
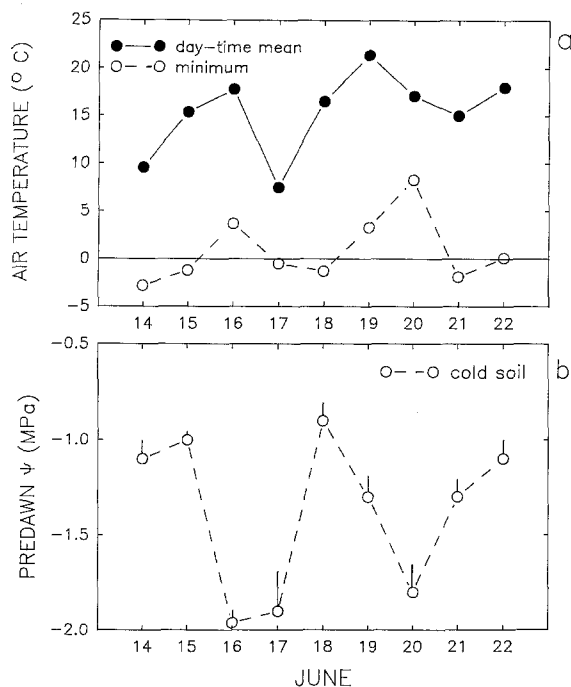
Fig. 6. Air temperatures (**a**) and mean predawn shoot water potentials (**b**) of trees in cold soils during the experiment. Day-time mean air temperature was mean air temperature at mid-canopy height from 800–1800 h. Minimum air temperature was the minimum overnight temperature preceding each diurnal period. *Vertical lines* indicate SE $(n=5)$

irradiance did not fully account for higher gas-exchange rates over snow since A remained higher than rates in warm-soil trees.

Phase 2 (*cold soil without snowcover*)

Differences in diel sap flow patterns between treatments were still evident when soils were cold but snow was absent (Fig. 1b). In this period, morning through midday gas-exchange rates remained higher in the cold-soil treatment (Fig. 5). Differences in ψ between treatments were also similar to those in Phase 1 with trees in cold soil having lower predawn but higher afternoon ψ than trees in warm soil. Diurnal patterns of ψ in trees in cold soil were unusual in that ψ was relatively low at predawn and increased through mid-afternoon (Fig. 5). A comparison of ψ and air temperature (Fig. 6) suggests that low predawn ψ was correlated with high air temperatures the preceding day. For example, low predawn ψ on 16 and 17 June followed relatively warm day-time mean air temperatures on 15 and 16 June (Fig. 6). Similarly, low predawn ψ on 20 June followed high day-time air temperatures on 19 June.

Phase 3 (*warm soil*)

At the beginning of Phase 3 (17 June) treatment differences in diel stem sap flow patterns remained unchanged. These differences gradually declined through Phase 3 and were no longer apparent on 22 June, five days after soil warming (Fig. 1b). No immediate effects of soil
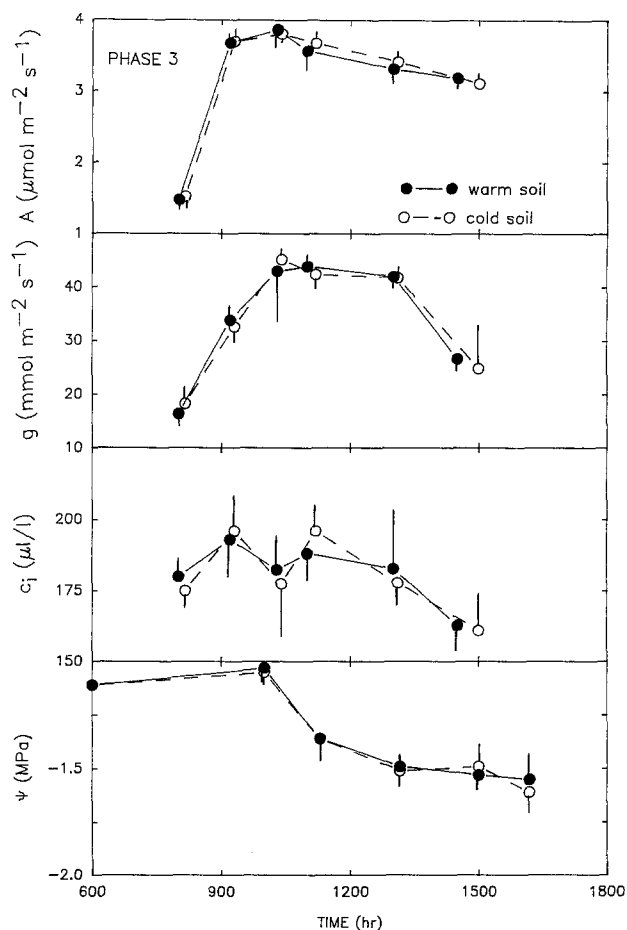

Fig. 7. Diurnal patterns in mean shoot gas exchange and water potential of trees on 22 June (Phase 3), 5 days after soils in the cold-soil treatment had warmed to temperatures similar to those in the warm-soil treatment. *Vertical lines* indicate SE $(n=5)$

warming were observed in trees in the cold-soil treatment and differences in A, g, c_i and ψ between treatments remained similar to those found in Phases 1 and 2. As was the case with stem sap flow patterns, the differences in gas exchange and ψ between treatments gradually declined through Phase 2 and on 22 June diurnal patterns were similar between treatments (Fig. 7).

Discussion

Net photosynthesis and g of *P. engelmannii* growing in cold soils ($< 3.5°$ C) were similar or in some cases higher than rates of trees in warm soils. While several studies have demonstrated cold-soil reductions in gas-exchange rates (see Introduction), some studies have found gas exchange to be quite insensitive to cold soils. Turner and Jarvis (1975) did not observe reductions in A or transpiration of *P. sitchensis* until soil temperatures dropped below 1° C, and Linder (1973) found no reduction in *P. abies* and *Pinus sylvestris* until soil temperature declined below 3° C. Similarly, Anderson and McNaughton (1973) did not find reductions in gas-exchange rates under cold soils in a diverse group of vascular plants.

The discrepancy between previous findings of reduced gas exchange in cold soils and our results for *P. engelmannii* may partially stem from the use of unhardened seedlings in previous studies. Gas exchange and xylem-water conductance of unhardened seedlings are much more sensitive to low soil temperatures than hardened seedlings (see Introduction), which may explain why DeLucia (1986) found gas exchange to be reduced in unhardened *P. engelmannii* seedlings at soil temperatures of 8° C. This hardening effect may also explain why we have only been able to demonstrate lower gas-exchange rates of *P. engelmannii* under cold soils in the field when we have chilled root systems of potted seedlings previously growing in warm soils (Day et al. 1989). This hardening effect does not explain why lower gas-exchange rates of naturally-growing *P. engelmannii* are sometimes correlated with low soil temperatures associated with late-spring snowbanks (DeLucia and Smith 1987). In our cold-soil treatment soil temperatures under snowbanks rose to 3.5° C (at the 5-cm depth) in late afternoon. Similar diurnal patterns of soil temperature under snowbanks have been documented by other researchers (Merritt 1984; Pikul et al. 1989). Soil temperatures under snowbanks in the previous study (DeLucia and Smith 1987) may have remained closer to 0° C which may explain why lower gas-exchange rates were observed.

Our observation of higher gas-exchange rates in *P. engelmannii* growing in cold soils is consistent with a previous study of trees growing in snowbanks and adjacent warm-soil areas (Day et al. 1989). We suggested higher gas-exchange rates in *P. engelmannii* in cold soil resulted from (1) an extensive lateral root system of young *P. engelmannii* (<2 m in height) which extended >4 m from tree bases (snowbanks extended 4 m from tree bases), and (2) the beneficial effect of increased visible radiance from highly reflective snow. Subsequent experiments in this former study showed the potential importance of these factors. In the present study we have demonstrated that these factors can not completely account for higher gas-exchange rates of *P. engelmannii* growing in cold soil during the snowmelt period. A trench around the snowbank in the cold-soil treatment insured roots did not extend into warm-soil areas. Higher visible irradiance did have a beneficial effect on assimilation rates, but did not fully account for higher A in the cold-soil treatment (Fig. 4). In addition, snow was absent during Phase 2 but trees in cold soil still had higher gas-exchange rates (Fig. 5).

Higher gas-exchange rates in *P. engelmannii* in cold soils in early summer may result from enhanced shoot nutrient status due to higher nutrient availability in the soil solution during snowmelt. Melting of the deep snowpack that develops in subalpine forests of the central Rocky Mountains results in a rapid flush of water and dissolved nutrients (Fahey 1977; Knight et al. 1985), and it has been suggested that uptake of nutrients (particularly N and K) by conifers (and/or microbes) during snowmelt may explain why nutrient concentrations in run-off are lower than in snowpack (Fahey 1977). This scenario appears feasible as considerable conifer root growth can

occur under snow, especially during snowmelt (Grier et al. 1982; Hinckley et al. 1985). Furthermore, root ion absorption can be relatively insensitive to cold soils in species native to cold-soil regimes (Chapin and Bloom 1976; Chapin et al. 1986). This possible nutrient stimulation of photosynthesis was no longer apparent five days after snow removal. In the warm-soil treatment snow was removed 6 days prior to the experiment which could explain why gas-exchange rates of warm-soil trees were lower than trees still in snowbanks.

As expected, diurnal patterns of sap flow were correlated with g (and probably transpiration) in both treatments (Fig. 2). The 1–3 h lag between g and sap flow is common and reflects capacitance due to upper-stem water storage (Kramer 1983); morning transpiration initially depletes water from upper portions of the stem before enough tension develops in the xylem sap to initiate lower-stem flow and absorption through roots. Conifers may be particularly prone to these lags because the specific conductivity (to water flow) of their conducting systems is only 15–30% of those of deciduous broadleaf trees (Hüber 1956; Kramer 1983).

The morning surge and night-time decline in stem sap flow commenced 1–2 h earlier in cold-soil trees (Fig. 1b). These differences in diel patterns of sap flow between treatments probably reflect different g and transpiration patterns; the morning rise and afternoon decline in g occurred earlier in trees in cold soils (Figs. 2, 4 and 5). During Phase 3, differences in sap-flow patterns between the treatments gradually declined and were no longer apparent on 22 June (Fig. 1b), the same day similar gas-exchange patterns were observed in the treatments (Fig. 7).

In cold soils increased water viscosity and decreased root permeability may limit water uptake in conifers (see Introduction). These factors could contribute to the lower overnight sap flow we observed in trees in cold soils (Fig. 1b). This would explain our present, as well as previous findings (Day et al. 1989), of lower predawn ψ in *P. engelmannii* in cold soils. Although cold soils may reduce overnight root water uptake, increased resistance to water uptake in cold soils does not appear to be an important factor once day-time transpiration begins. We observed higher morning stem sap flow in trees in cold soils (Fig. 1b) and by midday their shoot ψ was similar to or higher than those of trees in warm soils (Fig. 4 and 5). Since total daily sap flow was similar in trees in cold and warm soils (Fig. 3) the lower overnight water uptake in cold soils may have been offset by higher day-time water uptake which resulted from higher g and transpiration rates in cold soils. That cold soil failed to significantly reduce water uptake is supported by observations of peak annual stem sap flow in *P. engelmannii* in May, coinciding with cold soils and peak snowmelt (Swanson 1967). The water absorption capacity of conifer root systems can be considerably larger than needed for foliar water loss under non-water stress conditions (Teskey et al. 1985) and when combined with saturated soils during snowmelt may facilitate adequate root water uptake and maintenance of shoot water status in cold soils.

Diurnal patterns of ψ in both treatments were atypical in that ψ increased from predawn through mid-morning (June 14, Fig. 4) or even mid-afternoon (June 16, Fig. 5). While the rise in shoot ψ until mid-morning is understandable because of stem capacitance (Jarvis 1981), the very low predawn ψ and general increase of ψ through the day on 16 June is unusual. Smith et al. (1984) observed similar diurnal patterns of ψ in several conifers, including *P. engelmannii*, in cold soils following freezing nights in autumn. After comparing the minimum overnight air temperature with the following predawn ψ it appears low predawn ψ was not correlated with low night-time air temperatures (Fig. 6). This is not surprising since minimum air temperatures during our experiment were much higher than those encountered by Smith et al. (1984). In our study reductions in ψ appeared to follow warm days (Fig. 6). Higher water loss on these warm days (due to a likely increase in leaf-to-air vapor pressure deficit) combined with reduced overnight water uptake in cold soils would impede recovery of shoot ψ by the following morning.

Although afternoon g was lower in trees in cold soils (Figs. 4 and 5), ψ was similar to or higher than that of warm-soil trees; thus, lower g was not due to lower bulk shoot ψ. Other researchers have observed cold-soil induced declines in g which occurred independently of changes in bulk shoot ψ (Teskey et al. 1983; Benzioni and Dunstone 1988; Day et al. 1989). These reductions in g may be initiated by changes in xylem-water flux (Teskey et al. 1983) or hormonal signals from roots (Davies et al. 1986). Despite lower g in trees in cold soils, A was higher over most of the day. When A declined below rates in warm-soil trees at about 1500 h a parallel increase in c_i was observed, implying a nonstomatal limitation to photosynthesis. This scenario occurred consistently in mid afternoon following higher A in trees in cold soils suggesting a carbohydrate feedback inhibition of A (Herold 1980). During the late snowmelt period subalpine conifers may be particularly prone to carbohydrate feedback inhibition because of the combination of cold soils, favorable air temperatures and long daylight period. After chilling roots of *P. engelmannii*, DeLucia (1986) also observed a nonstomatal limitation of A, as well as parallel increases in starch content of needles and stems. Increases in leaf and stem carbohydrate concentrations (Davis and Lingle 1961; Smakman and Hofstra 1982) and reductions in translocation of photoassimilates from leaves (Hartt 1965; Hurewitz and Janes 1983) have been reported in several other species at low soil temperatures.

Despite our present findings, low soil temperatures may limit A and growth of many species in colder climates. More environmental information such as springtime soil temperatures below snowpack, as well as data on photosynthetic capacity during this period are needed before the relative importance of various abiotic factors can be determined in subalpine forests. Although gas exchange in *P. engelmannii* appeared quite tolerant of soil temperatures between 0 and 3.5° C during this experiment, A and g of the lower-elevation *Pinus contorta* are reduced about 35 and 50%, respectively, under

similar conditions (Day et al. 1989). These differences are not surprising as previous researchers have found cold-soil sensitivity varies considerably among species, with greater sensitivity in species from warmer soil regimes (Kramer 1940, 1942; Kaufmann 1975). The lack of any inhibitory effect of cold soils on gas exchange in *P. engelmannii* during late stages of the snowmelt period could result in a significant carbon gain because of generally favorable air temperatures, ample soil moisture, and possible nutrient flushes during this period.

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