STOMATAL CONDUCTANCE IN THREE CONIFER SPECIES AT DIFFERENT ELEVATIONS DURING SUMMER IN WYOMING

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Stomatal conductance in three conifer species at different elevations during summer in Wyoming

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Stomatal conductances to water vapor diffusion in Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), and lodgepole pine (*Pinus contorta* Engelm.) were compared to determine environmental influences on conductance at higher (3220 m) and lower (2860 m) elevations in the central Rocky Mountains. Measurements were taken on clear days, and soil water potentials remained at or greater than −0.1 MPa. Interspecific differences were small between spruce and fir at either site, but pine conductance was generally higher than spruce or fir at 2860 m. Daily maximum conductance in spruce and fir at 3220 m did not increase above 1.0 mm s^{-1} until daily minimum air temperature (early morning) increased to near 1 °C in early summer. Increases in maximum conductance above 2.0 mm s^{-1} occurred at both elevations when minimum air temperature rose above approximately 5 °C. At the lower elevation site, increases in maximum conductance during late July and mid-August appeared to depend strongly on soil temperature increasing above 7–8 °C. The persistence of cold soil temperatures in the highest elevations of the subalpine forest may serve to inhibit stomatal opening in spruce and fir in comparison to spruce, fir, and pine in lower elevation forests.

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La conductivité des stomates à la diffusion de la vapeur d'eau chez l'épinette engelmann (*Picea engelmannii* Parry ex Engelm.), le sapin subalpin (*Abies lasiocarpa* (Hook.) Nutt.) et le pin tordu (*Pinus contorta* Engelm.) a été comparée dans le but de déterminer les influences environnementales sur la conductivité à haute altitude (3220 m) et à basse altitude (2860 m) dans la partie centrale des montagnes Rocheuses. Les mesures ont été prises par temps clair, pendant que la capacité en eau du sol demeurait à au moins −0,1 MPa. Les différences interspécifiques étaient petites entre l'épinette et le sapin à l'un ou l'autre emplacement, mais la conductivité du pin était en général plus grande que celle de l'épinette ou du sapin à 2860 m d'altitude. La conductivité journalière maximale de l'épinette et du sapin à 3220 m n'a augmenté au-dessus de 1,0 mm s^{-1} que lorsque la température minimale journalière de l'air (au petit matin) eut elle-même augmenté à près de 1 °C au début de l'été. Des hausses de conductivité maximale au-dessus de 2,0 mm s^{-1} se sont produites aux deux altitudes lorsque la température minimale de l'air eut dépassé environ 5 °C. À l'emplacement de plus basse altitude, les hausses de conductivité maximale durant la fin de juillet et le milieu d'août ont semblé dépendre fortement des hausses de la température du sol au-dessus de 7–8 °C. La persistance de froides températures du sol aux plus hautes altitudes de la forêt subalpine pourrait servir d'inhibition à l'ouverture des stomates de l'épinette et du sapin par comparaison au comportement de l'épinette, du sapin et du pin dans les forêts de plus basse altitude.

[Traduit par la revue]

Introduction

Studies involving several conifer species have shown that stomatal conductance to water vapor diffusion varies with incident solar irradiance and the leaf to air humidity difference (Kaufmann 1982*a*) as well as vapor pressure deficit of the air (Fetcher 1976; Running 1980; Murphy and Ferrell 1982) and plant water status (Fetcher 1976; Kaufmann 1982*b*; Running 1980; Murphy and Ferrell 1982). Also, significant reductions in leaf conductance have been observed on days following near-freezing or subfreezing nights (Fahey 1979; Kaufmann 1982*b*; Smith et al. 1984; Delucia 1987; Delucia and Smith 1987). In view of these and other potential influences on conductance in conifers, Smith et al. (1984) and Smith (1985) proposed a conceptual model of interaction between environmental factors and stomatal opening in conifers of the central Rocky Mountains.

With increasing elevation, solar irradiance, leaf to air temperature differences, and the diffusivity of water vapor may increase, while air and soil temperatures may decrease, leading to a complex array of potential elevational effects on plant transpiration (Smith and Geller 1979). With these factors in mind, the purpose of the present study was to compare summer trends in stomatal conductance for two different elevational sites.

In the central Rocky Mountains of southeastern Wyoming, the subalpine forest ranges from approximately 2700 m elevation to timberline at about 3400 m and is dominated by Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), and lodgepole pine (*Pinus contorta* Engelm.) (Oosting and Reid 1952). Lodgepole pine, however, does not occur frequently in the highest elevations of the subalpine forest above approximately 3000 m (Billings 1969). The present study compared conductances for spruce and fir on a site above the elevational range of lodgepole pine, and for all three species on a lower elevation site.

Methods

Two study sites were chosen to be representative of conifer stands within the higher and lower elevation subalpine forest of the central Rocky Mountains. Both sites were located in the Medicine Bow Mountains of southeastern Wyoming, approximately 12 km west of Centennial (41°15′ N, 106°15′ W). The lower elevation study site (2860 m) was a mixed stand of mature lodgepole pine,

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Engelmann spruce, and subalpine fir. Trees selected for study were located on a slight southeasterly facing slope. The higher elevation site (3220 m) was a mature stand of Engelmann spruce and subalpine fir located on level ground about 5 km from the lower elevation site.

On both sites, continuous measurements of air temperature (T_a) and relative humidity were made using hygrothermographs in weather shelters placed at mid-canopy height. These data were used to compute the atmospheric vapor pressure deficit (VPD) (List 1951). Subsurface soil temperatures (T_s) and water potentials (Ψ_s) were measured at two locations on each site using soil thermocouple psychrometers (Wescor model PT-10). At each location, psychrometers were buried in the major rooting zone at 10- and 40-cm depths (Fahey 1979) during early summer while 1-2 m of snow still covered the ground. On the 3220 m site, three representative trees each of spruce and fir were chosen for study. At 2860 m, two representative trees of spruce, fir, and pine were chosen.

Stomatal conductances (g_s) were measured approximately biweekly, or more often early in the summer, from late May through mid-August 1982 on clear days. Xylem pressure potentials (Ψ_X) were determined with a pressure chamber (PMS model 1000) on four mid-canopy shoot tips of spruce, fir, and pine that were excised during early morning (approximately 07:00 solar time). Due to small needle sizes, Ψ_X was measured on shoot tips of spruce and fir. Pine needles were sufficiently large to enable Ψ_X determinations on individual needle fascicles. Needle Ψ_X in lodgepole pine have been reported to be similar to Ψ_X of the associated shoot (Ritchie and Hinckley 1971). Conductances were determined from approximately 07:00 to 19:00 using a field-calibrated transient diffusion porometer that incorporated a mixing fan (Kaufmann and Eckard 1977). The wind speed inside the porometer chamber increased shoot boundary layer conductance to an estimated 50 mm s^{-1} (Smith 1980). Due to this high boundary layer conductance, porometry essentially determined stomatal conductance. To estimate average conductances for each species, small branch tips were taken from north, south, east, and west aspects of the trees at mid-canopy height using clippers on an extension pole. Current-year growth, if present, was quickly removed, all cut surfaces were coated with petroleum jelly, and 1-year-old needles were immediately sealed into the porometer chamber. Transit time necessary for a given humidity increase to occur in the chamber was then recorded. Each determination required less than 20 s. Similar to the findings of Delucia and Smith (1987) for spruce, we found no decrease in conductance of excised shoots in comparison with adjacent attached shoots over the brief measurement period.

Total needle surface areas inside the porometer were determined by correlating leaf dry weight to geometrically determined surface areas. This method provided a ± 11% error when compared with the glass-bead coating technique of Thompson and Leyton (1971). Conductances were corrected for atmospheric pressure effects on water vapor diffusivity (Smith and Geller 1979).

Results

During 1982, a heavy winter snowpack persisted until mid-June at 2860 m and early August at 3220 m. Also, summer precipitation (June–August) was 28% above normal for a 12-year period according to U.S. Forest Service records from a nearby weather station (Little Brooklyn Lake, Medicine Bow Mountains). As a result, soil water potentials measured at 10 and 40 cm were never less than −0.1 MPa on either site (May 29–August 18).

Maximum and minimum T_a increased steadily from late May through mid-August at both elevations, although the lower site warmed to maximum nearly 3 weeks earlier (Figs. 1A, 1B). Minimum T_a was consistently above freezing after June 20 at 2860 m and June 23 at 3220 m. The maximum VPD increased until early August at the higher elevation site and until early July at the lower elevation site (Figs. 1C, 1D). Also, the maximum VPD measured during the study period was almost 30% greater at the lower versus higher elevation (2.4 kPa vs. 1.8 kPa). On both study sites, the VPD that coincided with daily maximum conductances remained low and nearly constant during the summer (Figs. 1C, 1D).

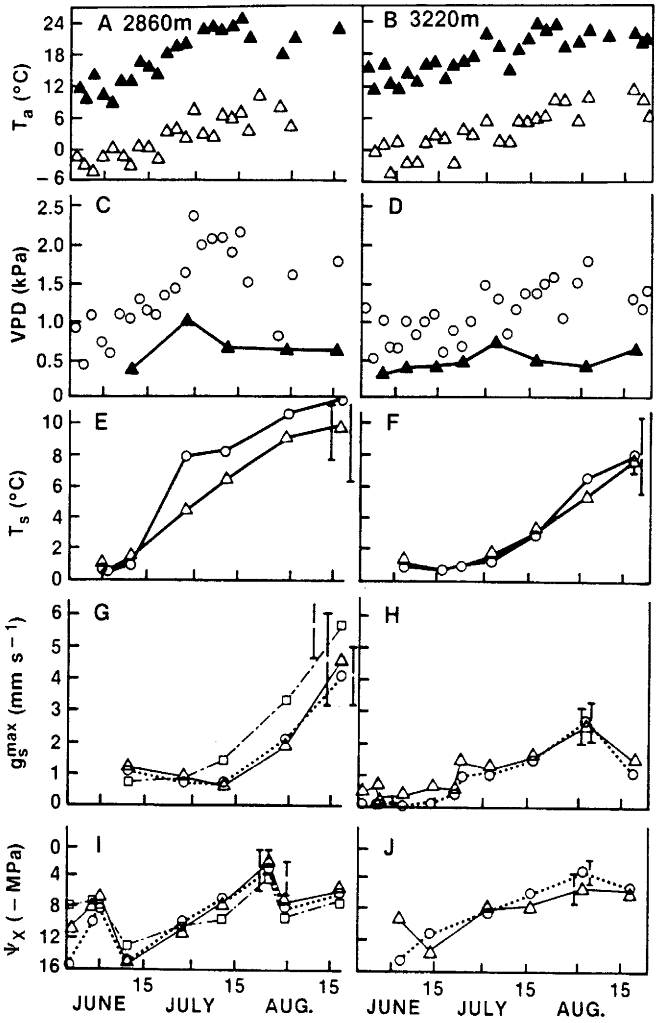

FIG. 1. Environmental and physiological data for conifers at two elevations in the Medicine Bow Mountains, Wyoming, during summer 1982. Represented are 3-day minimum (△) and maximum (▲) air temperatures (A, B); 3-day maximum vapor pressure deficits of the air (○) or VPD during the measurement of daily maximum leaf conductance (▲) (C, D); average soil temperatures ($n = 2$) at 10- (○) and 40-cm depths (△) (E, F); daily maximum leaf conductance for lodgepole pine (□), Engelmann spruce (△), and subalpine fir (○) (G, H), and early morning (07:00) xylem pressure potentials (I, J). For conductances and pressure potentials, n = 8 per species at 2860 m and n = 12 per species at 3220 m. Bars indicate maximum 95% confidence intervals.

Soil temperatures at both elevations increased steadily over the summer (Figs. 1E, 1F). Maximum $T_s \pm$ SE at 10- and 40-cm depths were 11.5 ± 0.4 and 9.5 ± 0.2°C, respectively, at the lower elevation site, and 7.8 ± 0.2 and 7.5 ± 0.1°C, respectively, at the higher elevation site. Greater differences between the 10- and 40-cm T_s occurred at the lower site compared with the higher site.

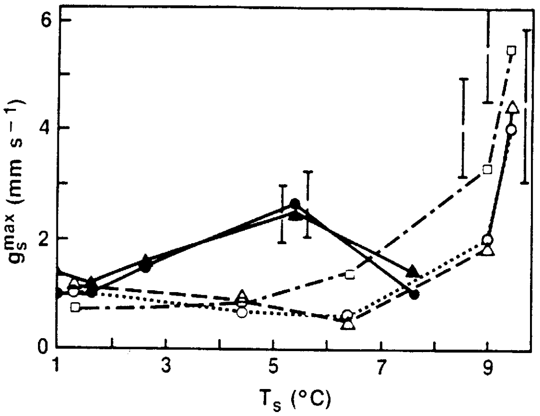

FIG. 2. Daily maximum stomatal conductance vs. soil temperature at 40-cm depth for the 2860 m (open symbols) and 3220 m (solid symbols) elevations. Conductances are for Engelmann spruce (△,▲), subalpine fir (○, ●), and lodgepole pine (□). Bars represent maximum 95 percent confidence intervals.

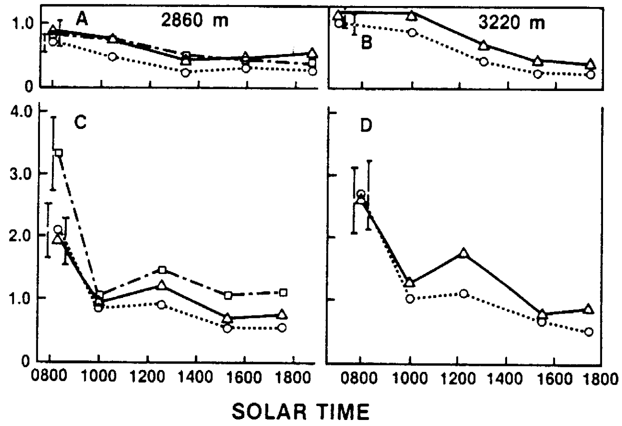

FIG. 3. Representative diurnal trends in leaf conductance early (A, June 28; B, July 3) and late (C, July 31; D, August 3) in the study period at 2860 m and 3220 m. For the higher and lower elevation sites, n = 12 and 8, respectively, for lodgepole pine (□), Engelmann spruce (△), and subalpine fir (○). Bars indicate maximum 95 percent confidence intervals.

Maximum conductance during a given day (g_s^{max}) increased at both elevations over the summer after the onset of nonfreezing nights (minimum T_a above 1°C) (Figs. 1G, 1H). Increases in g_s^{max} for spruce and fir were gradual at the higher elevation site, with the exception of a large increase in g_s^{max} following the beginning of consistently nonfreezing nights (June 23). During the period when nights were below freezing at 3220 m, g_s^{max} in spruce averaged 0.5 mm s^{-1}, while fir g_s^{max} remained near 0. At the lower elevation site, g_s^{max} increased to greater values by mid-August than on the higher site, and lodgepole pine maintained high g_s^{max} throughout the summer compared with spruce and fir. The greatest g_s^{max} occurred on August 18 at 2860 m and on August 2 at 3220 m.

Early morning Ψ_X generally increased over the summer at both elevations, although pronounced decreases occurred in early June and late July at 2860 m (Figs. 1I, 1J). Interspecific differences in Ψ_X were usually small except during late May at 2860 m and early June at 3220 m. At the lower elevation, Ψ_X in lodgepole pine were generally greater than in spruce and fir until late June. After June, Ψ_X in pine was slightly less than in spruce and fir. Spruce Ψ_X was generally less than fir at the higher elevation site.

Maximum g_s was below 2.0 mm s^{-1} at both sites until minimum T_a rose above 5°C. In contrast, the variation in g_s^{max} with T_s differed considerably between the higher and lower elevation sites. At the lower site, g_s^{max} increased greatly as T_s increased above approximately 7°C (Fig. 2). On the higher site, however, an increase in T_s from approximately 5-8°C corresponded to a decreased g_s^{max}. Regression analyses indicated that on the lower elevation site, approximately 80% of the variation in g_s^{max} over the summer could be explained by T_s at the 40-cm depth regardless of conifer species. On the higher site, where T_s remained colder for a longer period due to the persistent snowpack, g_s^{max} was not well correlated with T_s. Instead, g_s^{max} was best related to VPD, which accounted for approximately 30 and 55% of the variability in g_s^{max} for spruce and fir, respectively. In general, neither T_a at the time of g_s measurement nor early morning Ψ_X appeared closely correlated to g_s^{max} on either site.

Dramatic differences in representative daily g_s patterns occurred between early and late summer measurements (Fig. 3). Diurnal changes in g_s during early summer were similar at the higher and lower elevation sites (Figs. 3A, 3B). Conductances of all species were generally greatest between 07:00 and 08:00, decreasing gradually until about 18:00. Diurnal g_s in lodgepole pine and Engelmann spruce at the lower elevation site were consistently higher than for subalpine fir. Spruce g_s was also consistently greater than fir g_s at 3220 m. Later in the summer, g_s was substantially greater at both sites with considerably more diurnal variation (Figs. 3C, 3D). Again g_s was greatest for all species at both elevations early in the day. Midday g_s at both elevations was slightly higher in fir and markedly higher in pine or spruce than midmorning values. At 2860 m, g_s in pine were typically higher than for spruce and fir throughout the day. Early morning g_s in spruce and fir were similar, although spruce g_s was greater during the remainder of the day. Regression analysis suggested that VPD was most important in influencing diurnal changes in g_s on both sites, though r^2 values in these relationships were less than 0.4.

Discussion

Due to the persistent snowpack and high summer precipitation, our results may represent an unusual growth season for this area of the central Rocky Mountains in that soil moisture remained exceptionally high ($\Psi_s > -0.1$ MPa). Also, because measurements were taken on clear days, light limitations on stomatal behavior were minimal. Thus, our results concerning the water relations of these conifer species growing at two different elevations do not include soil drying that may occur during summer (Young and Smith 1980; Fahey and Young 1984; Smith 1985) or the potentially strong influences of frequent cloud cover (Young and Smith 1983). However, high soil moisture enabled the present interpretation of potential T_s effects on g_s independently of possible soil moisture effects or moisture and temperature interactive effects on g_s. Furthermore, high soil moisture probably accounted for the low variability in T_s at a given depth on either site. Greater differences between T_s at 10 cm. vs 40 cm at the lower as compared with higher elevation site were probably due to the earlier snowmelt and warming of surface soils at the lower site.

Our results suggest that summer variations in g_s^{max} were most closely related to T_s on the lower elevation site and to VPD on the higher elevation site. A possible explanation for this difference between elevations may be that at 40-cm depth, T_s at 3220 m was never greater than 7.5°C, but rose to 9.5°C at 2860 m. Kaufmann (1975) reported that root resistance to water uptake in young Engelmann spruce became significant below a T_s of 7.5°C, and Running and Reid (1980) reported a similar threshold for lodgepole pine. Recently, Delucia (1986) found g_s and photosynthesis to decrease sharply in potted spruce seedlings at a T_s below 8°C, and Delucia and Smith (1987) associated summer increases in photosynthesis with increasing T_s under field conditions in the Medicine Bow Mountains. Our data may reflect this phenomenon, since a large increase in g_s^{max} on the lower elevation site correlated well with increases in T_s above 7-8°C. Also, Running and Reid (1980) observed these T_s effects to be significant mainly when soil moisture was not limiting, as in the present study. The poor relationship between T_s and g_s^{max} on the higher elevation site may have been due to T_s remaining below the apparent threshold of 7-8°C for most of the study period. A dependence of g_s^{max} on T_s in the present study is supported to some degree by the concurrent increases in Ψ_X with T_s as the summer progressed. Teskey et al. (1984) found conductance of water through fir seedlings to increase with increasing root temperatures. Thus, increasing Ψ_X may have indicated greater trunk recharge rates with increasing root conductance to water uptake. Greater Ψ_X later in the summer then might have contributed to the increased g_s^{max} and its high correlation with T_s. However, other processes which may be influenced by T_s, such as photosynthate source to sink transfer and nutrient uptake, might also provide mechanisms by which T_s influences g_s (Delucia 1986).

Several investigations have suggested that g_s is limited during early summer or late fall by low air or soil temperatures (Fahey 1979; Kaufmann 1982*b*; Smith et al. 1984; Teskey et al. 1984; Delucia and Smith 1987). The results presented here indicate that maximum g_s and diurnal fluctuation in g_s were limited by low T_a early in the summer at both elevations. Our data along with the results of other investigators and the interactive model of Smith et al. (1984) and Smith (1985) lead us to suggest that increases in g_s^{max} to greater than approximately 0.5 mm s^{-1} depend on minimum T_a rising above freezing in late spring, and that decreases in g_s^{max} to this level in the fall are due to freezing T_a. However, between these periods and given optimal light and soil moisture conditions, g_s^{max} in spruce, fir, and pine may be limited by T_s until it increases above 7-8°C. In the highest elevation spruce-fir forests of the central Rocky Mountains, T_s may remain at or below this level for the majority of the short growing season. Thus, stomatal conductances in both spruce and fir in these forests may seldom reach the greater values that may occur more commonly at lower elevations.

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