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Microhabitat comparisons of transpiration and photosynthesis in three subalpine conifers

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Differences in water and photosynthetic relations were compared for three codominant conifers (Engelmann spruce (*Picea engelmanii*), subalpine fir (*Abies lasiocarpa*), and lodgepole pine (*Pinus contorta*)) at microhabitats within a subalpine forest (central Rocky Mountains, U.S.A.) that were considered representative of different successional stages. Diurnal measurements of photosynthesis, leaf conductance, and transpiration were taken at microhabitats considered early-successional (open), intermediate (forest gap), and late-successional (forest understory) environments to evaluate possible influences of gas-exchange physiology in observed distributional and successional patterns. Pine had greater water-use efficiency (photosynthesis/transpiration) in early- versus late-successional environments, primarily as a result of a lower leaf conductance and transpiration. Photosynthetic performance was similar among all three species at each respective microhabitat and increased as the openness of the microhabitat increased. Greater water-use efficiency may significantly improve the growth of pine over spruce and fir on more open, drier sites at lower elevation. Higher transpiration in spruce and fir may limit these species to higher elevation sites, to understory sites at middle elevations, and to moister open sites at lower elevations (e.g., riparian sites).

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Les auteurs ont comparé les différences entre les relations eau–photosynthèse chez trois conifères co-dominants : *Picea engelmanii, Abies lasiocarpa* et *Pinus contorta* en microhabitats situés dans une forêt subalpine (centre des Montagnes Rocheuses, États-Unis) considérée représentative des différents stades de succession. Des mesures diurnes de la photosynthèse, de la conductance foliaire et de la transpiration furent prises sur les conifères dans les microhabitats de début de succession, de position intermédiaire et de fin de succession, en vue d'évaluer les influences possibles de la physiologie des échanges gazeux sur les patrons de distribution et de succession observés. Le pin avait une plus grande efficacité d'utilisation de l'eau (photosynthèse/transpiration) au début qu'à la fin de la succession, ce résultat étant dû surtout à une conductance et à une transpiration plus basses. Les gains photosynthétiques furent similaires chez les trois espèces dans chacun de leur microhabitat respectif, et ils ont augmenté avec le degré d'ouverture du microhabitat. L'efficacité plus grande de l'utilisation de l'eau peut améliorer significativement la croissance du pin par rapport à celle de l'épinette et du sapin dans les sites plus ouverts et plus secs de basse altitude. La transpiration plus grande de l'épinette et du sapin peut limiter ces espèces aux sites d'altitude plus élevée, aux sous-bois en altitude intermédiaire et aux sites plus humides dans les dépressions (example : rivages).

[Traduit par la revue]

Introduction

The subalpine forests of the central Rocky Mountains are largely dominated by Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), and lodgepole pine (*Pinus contorta* ssp. *latifolia* Engelm.) (Daubenmire 1943; Whipple and Dix 1979). Among these species, lodgepole pine has generally been viewed as early successional, regenerating only on open, disturbed microhabitats within preexisting lodgepole pine stands and climax spruce–fir stands below about 3200 m elevation. Because of the apparent dependence of lodgepole pine forests on fire for regeneration, pine is considered the dominant subclimax conifer within its geographical and elevational range in Colorado and southern Wyoming (Stahelin 1943). It has also been suggested that with complete protection from fire, lodgepole pine forests above approximately 2800 m elevation would be replaced by a spruce–fir climax forest (Billings 1969). These hypotheses have been supported recently by synecological work in the Medicine Bow Mountains (Romme and Knight 1981). However, lodgepole pine forests that appear to have persisted without fire have been located in Yellowstone National Park and Colorado (Moir 1969; Despain 1983).

Successional relationships among spruce, fir, and pine are most evident in transition, or seral, zones found between the lower elevation pine forests and the higher elevation spruce–fir stands (Moir 1969). Following disturbance in these areas, lodgepole pine will characteristically dominate the young forest for 50–100 years, with Engelmann spruce and subalpine fir becoming established in the understory after 80–90 years (Whipple and Dix 1979). Ultimately, spruce and fir can replace pine as forest dominants in 200–300 years (Oosting and Reid 1952; Billings 1969) unless more frequent fires occur. Thus, a successional system involving only three major conifer species is evident, particularly at midelevations.

Relatively little research has attempted to interpret these successional and distributional patterns by considering physiological differences among the three species (see Smith 1985*a* for a review of conifer ecophysiology in the central Rocky Mountains). In the region, most precipitation occurs during winter, and prolonged periods without rain may occur in summer following snowmelt runoff (Knight et al. 1985). Open areas generally accumulate less snowpack than forests, and surface soils in these areas may dry earlier in the summer than in the understory, particularly at lower elevations. In addition to potentially dry surface soils and intense solar radiation, increased water vapor diffusivity at high elevations may also

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contribute to water stress (Smith and Geller 1980). Pine is adept at establishing on exposed, dryer sites at lower elevation and has been categorized as more drought tolerant than either spruce or fir (Minore 1979). Also, pine may have a greater tolerance to the prolonged high irradiance on these sites (Ronco 1970). In contrast to pine, spruce and fir are limited to higher elevation sites, the forest understory, or riparian sites (Day 1963; Whipple and Dix 1979; Alexander 1984). Possibly as a result of interspecific differences in photosynthetic relations, spruce, and particularly fir, grow well in the low light of the forest understory, whereas pine is rare in densely shaded understories and is considered the least shade tolerant of the three species (Minore 1979). However, it has not been determined whether apparent differences in shade intolerance are due to limitations in photosynthetic performance.

Bazzaz (1979) attributed numerous physiological characteristics to species of a given successional status and also recognized that successional systems with constant physiognomies have received little study, especially with regard to ecophysiology. The purpose of the present study was to evaluate differences in the water and photosynthetic relations among Engelmann spruce, subalpine fir, and lodgepole pine in microenvironments representing different successional stages. The pine–spruce–fir forests of the central Rocky Mountains represent an ideal system for evaluating ecophysiological characteristics of codominant species within a forest successional system that has low species diversity and relatively constant physiognomy.

Materials and methods

Carbon dioxide and water vapor flux densities (*A* and *E*, respectively) were measured diurnally for each species over several days in a forest understory (late successional), a forest gap (intermediate), and an open area (early successional) in the Medicine Bow Mountains (41°21′ N, 106°10′ W). The forest understory and adjacent forest gap (approximately 250 m^2) sites were on nearly level ground in a relatively low elevation (2610 m) mixed spruce–fir–pine forest. An open (clear-cut) site with a slight southerly aspect was chosen at 3080 m, near the upper elevational limit of lodgepole pine forests. The open site was necessarily at a higher elevation than the gap and understory sites, since spruce and fir do not commonly regenerate along with pine on lower, drier, open sites. Three healthy (as indicated by general appearance and the presence of new shoot growth) saplings of each species (approximately 7–15 years old, 0.35–0.80 m in height) were chosen at each site for diurnal measurements.

Because of the variability of cloud patterns on a given day, particularly during afternoon (Young and Smith 1980; Knapp and Smith 1987), measurements had to be made over extended time periods to enable selection of representative days with ample sunshine. Also, cloud pattern variation from one day to the next made interspecific comparisons at each microsite difficult. Thus, our emphasis here is on intraspecific comparisons between microsites to evaluate the performance of each species at the three different successional stages, not differences between species at a particular microsite. Measurements were made from June 7 to 14 in the forest gap and June 19 to 29 in the understory. Generally, maximum air temperatures at sapling heights (2 m) of 18–22°C occurred by late June to early July at 2610 m elevation, but not until mid-July at the 3080-m elevation (G. A. Carter and W. K. Smith, unpublished data). Depending on the year, snowmelt near 3100 m may not be complete until late July or early August, and soil temperatures low enough to inhibit stomatal conductance may persist longer at these elevations (Running and Reid 1980; Kaufmann 1975; Smith et al. 1984; Smith 1985*b*; Delucia and Smith 1987; Carter et al. 1988). Thus, measurements were taken from August 23 to 29 (1983) at the higher elevation, open site (3080 m).

At all sites, southerly oriented branches were chosen from midcanopy (20–40 cm above the ground) for physiological measurements. In the understory and gap sites during June, individual shoots (10–15 cm lengths) of previous-year growth were sealed into a transparent cuvette in as near-natural orientation as possible. In late August on the open site, current-year growth was measured, since gas-exchange characteristics of current-year growth for these species are similar to those of previous-year shoots by mid-August (G. A. Carter and W. K. Smith, unpublished data). Gas exchange was monitored using a standard open-flow system incorporating a CO_2 analyzer (Anarad model AR-411). Water vapor concentration inside the cuvette was monitored with a dew-point hygrometer (EG & G model 911) or fast-response humidity sensor (Vaisala humicap). Flow rates of air entering and exiting the cuvette (400–1000 mL min^{-1}) were monitored with a mass flow meter (Matheson model 8116-0152). The cuvette atmosphere was mixed at approximately 2.5 m s^{-1} wind speed with an internal fan. Average leaf temperature (T_l) for an individual shoot was determined by wrapping fine-wire (0.018 cm diam.) copper–constantan thermocouples around the midpoints of three needles near the center of the shoot. Cuvette air temperature (T_{air}) was determined with a fine-wire thermocouple shielded from direct sunlight and was maintained within −2 to +3°C of ambient air temperature, using the cuvette fan, by circulating cold water through a water jacket in the cuvette bottom and by filtering the incident sunlight through 10 cm of water. Atmospheric and cuvette pressure was monitored with an aneroid barometer.

Photosynthetic photon flux density (PPFD) was measured with a quantum sensor (LI-COR model 190SB) mounted horizontally on the cuvette. Net CO_2 uptake (*A*) was computed as a flux density (micromoles per metre squared per second) based on PPFD measured with the quantum sensor oriented in the same plane as the main axis of the measurement shoot. Light-compensation points for *A* were determined from diurnal field measurements of maximum solar PPFD when *A* was zero, or from experimental measurements using neutral-density filters. Sunlight levels at which photosynthesis became saturated were determined by recording the minimum PPFD at which the highest measured (maximum) *A* occurred. Total daily PPFD on a flat, horizontal surface was used as a measure of site openness as well as an approximation of differences in the light environment under which each sapling developed.

To compare physiological traits among all three species in greater detail and to monitor changes over a growing season, instantaneous *A* and *E* were measured under high sunlight (>1500 μmol m^{-2} s^{-1}) from July 3 to September 8, 1984, at an additional open site at 2865 m elevation. This site was approximately midway in elevation between the 3080- and 2610 m sites. At 2865 m, *A* and *E* for two saplings per species (previous-year shoots) were measured during midmorning (09:00–11:00), using a closed-flow CO_2 gas-exchange system (LI-COR, Inc. model LI-6000 portable photosynthesis system). Measurements were made during midmorning to avoid afternoon clouds and plant water stress and were taken approximately biweekly. All measurement saplings were approximately 10–15 years old and ranged from 0.9 to 1.5 m in height. Computations of *A*, *g*, and *E* were made as described by von Caemmerer and Farquhar (1981). Instantaneous *A* and *E* values were integrated over a day to give total daily estimates of carbon gain and water loss. Conversion from leaf conductance units of millimetres per second to molar flux density units (micromoles per metre squared per second) can be achieved by multiplying all *g* values by 38 to give a ±3% error over the ambient pressure and temperature range measured.

To estimate plant water stress, shoot xylem pressure potentials (ψ_p) were measured for detached shoots (immediately after excision), using a Scholander-type pressure chamber (PMS model 1000). Soil water potentials (ψ_s) and soil temperatures (T_s) at 15-cm depths were measured at three shaded locations during early morning (06:00–07:00), before T_s began to increase, with thermocouple psychrometer probes (Wescor, Inc.) and a microvoltmeter (Wescor model HR-33T). Total needle surface areas were determined using a glass bead coating technique (Thompson and Leyton 1971) and were used to compute *g*, *E*, and *A* as described in Carter and Smith (1985).

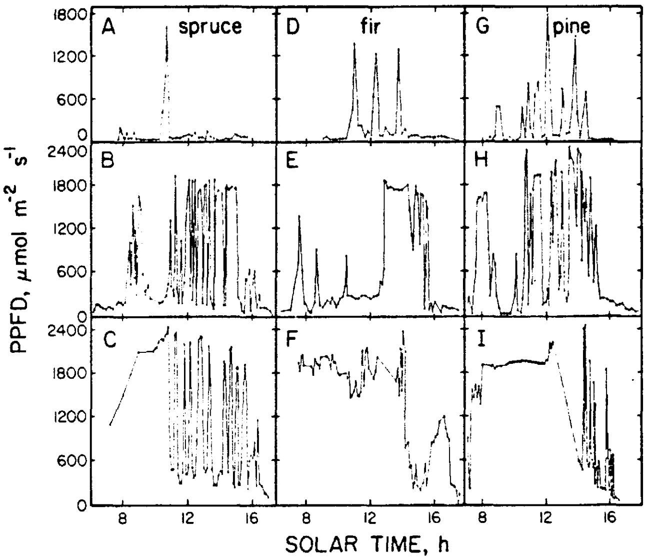

FIG. 1. Photosynthetic photon flux density (PPFD) versus solar time in *P. engelmanii* (A, B, C), *A. lasiocarpa* (D, E, F), and *P. contorta* ssp. *latifolia* (G, H, I) at the forest understory site (A, D, G), forest gap (B, E, H), and open site (C, F, I). Data were chosen as representative based on 5- to 9-day sampling periods (see text for further explanation).

Results

Frequent precipitation occurred in late June and July, 1983, and ψ_s at 15-cm depths remained near zero (> -0.10 MPa) at the understory and forest gap sites throughout the study period. Early morning T_s ranged from 10.0 to 14.0°C. Minimum ψ_s for the study period occurred at the open site in late August and ranged from -0.2 to -0.6 MPa, while T_s was 11.0–13.3°C.

Light environments for the most cloud-free measurement days were used to quantify the openness of the environment to which each sapling was acclimated (Fig. 1). Instantaneous measurements of PPFD in the understory were generally low (<300 μmol m^{-2} s^{-1}) as a result of shading by overstory trees, except during sun-patch occurrence, when maximum PPFD approached 1800 μmol m^{-2} s^{-1} (Figs. 1A, 1D, 1G). Total clear-day photon densities (integrated PPFD) adjacent to each sapling at the understory site were 3.6, 5.5, and 7.4 mol m^{-2} measured adjacent to the spruce, fir, and pine, respectively. In the forest gap, where overstory trees shaded the saplings only during early morning and late afternoon, maximum PPFD approached 2400 μmol m^{-2} s^{-1} and daily integrated photon densities were 22.5, 19.4, and 25.7 mol m^{-2} for the sampled spruce, fir, and pine saplings, respectively (Figs. 1B, 1E, 1H). Maximum PPFD at the open site (3080 m) was often near 2500 μmol m^{-2} s^{-1} (Figs. 1C, 1F, 1I), and total daily irradiance was over twice that measured in the forest gap (52.6, 50.0, and 52.6 mol m^{-2} for the spruce, fir, and pine, respectively).

The leaf-to-air vapor pressure differences (*D*) were similar among sites and species and ranged from approximately 0.5 to 1.0 kPa early and late in the day and from 2 to 3 kPA during midday. The primary exception to this was during later afternoon sun patches for gap spruce, when *D* values of greater than 4.0 kPa occurred for a short time as a result of very still air conditions and elevated leaf temperatures. Measured needle and air temperatures of natural shoots taken periodically throughout measurement days indicated that *D* values for shoots inside the cuvette were always within -26 to $+32\%$ of natural shoot values.

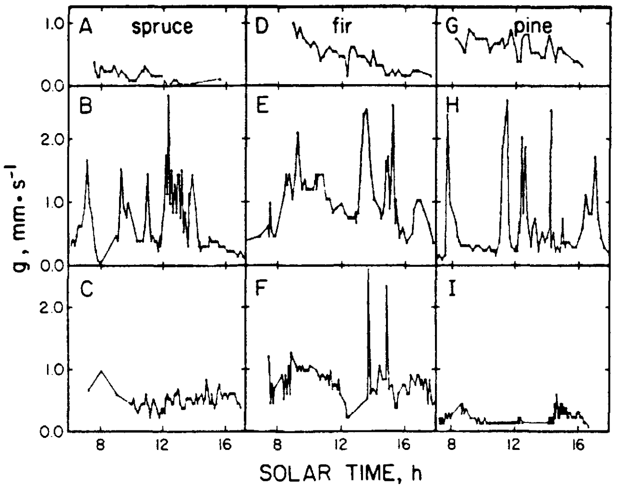

FIG. 2. Leaf conductance to water vapor (*g*) versus solar time. See Fig. 1 caption for label key.

As a general measure of sapling water stress, ψ_p values were compared among sites and species. The mean daily minimum in ψ_p was not statistically different (ANOVA, $p > 0.05$) between sites or species. The lowest ψ_p of -1.7 MPa occurred in spruce at the forest gap, and the greatest ψ_p measured was -0.3 MPa for the understory fir during early morning.

Considerable short-term variation in *g* in response to variable sunlight occurred for all three species (Fig. 2). In general, spruce *g* appeared to increase somewhat as the exposure of the microhabitat to sunlight increased, while *g* in fir remained relatively constant, and pine had a substantial decline in *g* from the understory and gap to the open site. In the understory, leaf conductances (*g*) were usually greatest in the morning (0.4, 1.0, and 0.9 mm s^{-1} for spruce, fir, and pine, respectively) and gradually decreased through the day (Figs. 2A, 2D, 2G). At the forest gap site, *g* fluctuated more sporadically during the day for all species, and maximum *g* values were over 2.0 mm s^{-1} in all three species (Figs. 2B, 2E, 2H). At the open site, *g*, fluctuated less and maximum *g* tended to be lower for all species than in the gap, especially in pine (Figs. 2C, 2F, 2I).

From the understory to the open microhabitat, maximum *A* values increased for each of the three species from about 1.0–1.5 to over 4 μmol m^{-2} s^{-1}, respectively (Fig. 3). However, in the forest gap, *A* increased significantly in the spruce and fir, while pine *A* appeared relatively unchanged. As a result, the pine had the greatest increase in *A* from gap to open sites (from about 1.0 to over 4.0 μmol m^{-2} s^{-1} Figs. 3H, 3I).

In all three species, intraspecific comparisons of light saturation points for photosynthesis (minimum PPFD at maximum *A*) were similar between understory and gap environments but were much greater in the open (Table 1). In the understory, the mean PPFD required for saturation was considerably lower for spruce (149 μmol m^{-2} s^{-1}) and fir (163 μmol m^{-2} s^{-1}) than for pine (686 μmol m^{-2} s^{-1}). At the gap site, light saturation was lowest in spruce (417 μmol m^{-2} s^{-1}), followed by fir (460 μmol m^{-2} s^{-1}) and, again, was substantially greater for the pine (1139 μmol m^{-2} s^{-1}). In the open environment, light-saturated *A* occurred at approximately 1800 to 2100 μmol m^{-2} s^{-1} for all three species (Table 1).

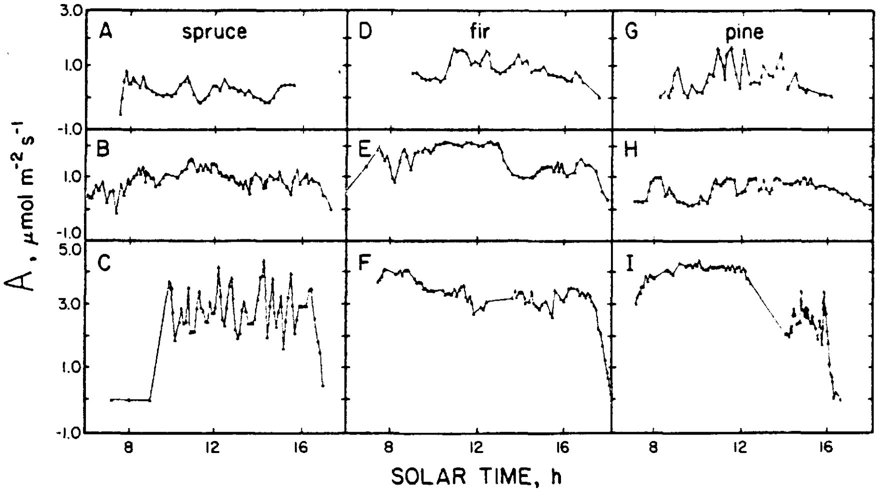

FIG. 3. Net photosynthesis (A) versus solar time. See Fig. 1 caption for label key.

TABLE 1. Summary of some physiological characteristics for *Picea engelmanii* (S), *Abies lasiocarpa* (F), and *Pinus contorta* (P) at late-successional (understory), intermediate (forest gap), and early-successional (open area) microsites

		Microhabitat		
Parameter	Species	Understory	Gap	Open
g (mm s^{-1})	S	0.4±0.4	2.7±0.7	1.0±0.3
	F	1.0±0.3	2.6±0.4	2.6±0.8
	P	0.9±0.4	2.6±0.6	0.6±0.4
E (mmol m^{-2} s^{-1})	S	0.57±0.19	1.28±0.41	0.90±0.33
	F	0.63±0.26	1.10±0.40	0.88±0.25
	P	0.67±0.22	0.52±0.17	0.46±0.09
A (μmol m^{-2} s^{-1})	S	1.1±0.4	1.6±0.5	4.2±0.9
	F	1.5±0.6	2.1±0.5	4.0±1.4
	P	1.5±0.4	1.4±0.5	4.4±1.3
WUE ($A/E \times 10^4$)	S	19	13	46
	F	24	19	45
	P	22	27	96
Light saturation	S	149(136–181)*a*	417(316–508)*c*	1933(1886–2105)*e*
	F	163(124–216)*a*	460(288–639)*c*	1891(1791–2070)*e*
	P	686(614–822)*b*	1139(912–1311)*d*	2061(1870–2147)*e*
Light compensation	S	34(19–44)*a*	49(33–84)*b*	44(34–62)*b*
	F	36(26–43)*a*	37(19–46)*a*	69(64–84)*d*
	P	29(16–39)*a*	52(36–61)*b*	87(79–141)*c*

NOTE: Values for leaf conductance to water vapor (g), transpiration flux density (E), and net photosynthetic CO_2 uptake (A) are mean maximums obtained under saturating sunlight (PPFD > 1500 μmol m^{-2} s^{-1}) for one shoot of two or three saplings of each species at each site over 5–9 sampling days. Values of light saturation and compensation points for net photosynthesis are given as means with ranges in parentheses. Plus and minus values are standard error. Values followed by a letter are not significantly different at α = 0.05 (ANOVA).

Light compensation points for photosynthesis (greatest PPFD when A equaled zero) generally increased with the openness of the microsite. Mean compensation points were low (<36 μmol m^{-2} s^{-1}) and similar among species in the understory (Table 1). In the forest gap, compensation values were slightly higher (37–52 μmol m^{-2} s^{-1}) but, again, relatively similar among the three species. Pine in the open had the highest mean compensation point (87 μmol m^{-2} s^{-1}), followed by fir (69 μmol m^{-2} s^{-1}), while virtually no change occurred for spruce relative to the gap site (Table 1).

Mean daily leaf conductance (g_{day}) was determined by averaging the continuous leaf conductance in Fig. 2 over all clear days from 09:00 to 16:30. Figure 4 compares g_{day} with the integrated PPFD measured at each of the three microhabitats. Spruce and fir g_{day} was greatest at the gap and open sites, while pine g_{day} decreased markedly at the open site (Fig. 4A). Total daily transpiration (E_{day}) in the pine also decreased with increasing openness of the environment, whereas E_{day} in spruce and fir increased from the shaded to more open microhabitat (Fig. 4B).

Total daily carbon gain (A_{day}) was also determined by integrating the A curves from 09:00 to 16:30 over all clear days. All species had general increases in A_{day} from the understory to open sites, although pine A_{day} remained relatively unchanged between the understory and gap sites (Fig. 4C). A large increase in A from the gap to the open site occurred for all three species. Mean daily WUE ($A_{\text{day}}/E_{\text{day}}$) was similar for all three species and relatively low at the understory and gap sites com-

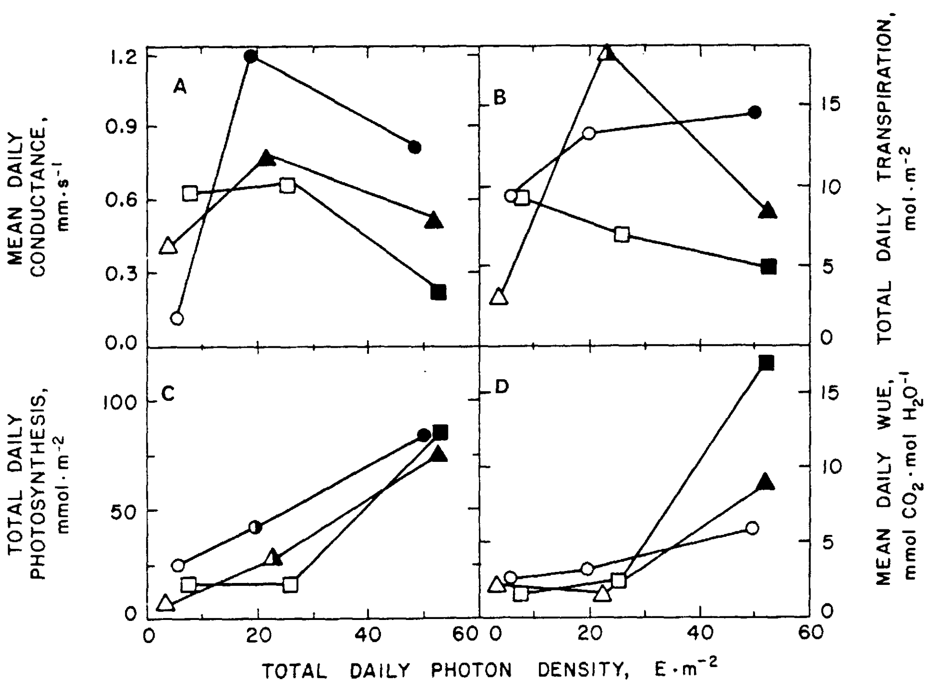

FIG. 4. (A) Mean daily leaf conductance (09:00 – 16:30) versus total daily photosynthetic photon density (measured at the understory, gap, and open sites) for *P. engelmannii* (△, ▲), *A. lasiocarpa* (○, ●), and *P. contorta* ssp. *latifolia* (□, ■). Each point represents means from relatively cloud-free days for each species and microsite location. Solid symbols indicate where intraspecific differences occurred for the indicated microsite compared with the other two sites, using analysis of variance tests ($\alpha = 0.05$). (B) Total daily transpiration (0:900 – 16:30) versus total daily photosynthetic photon density. (C) Total daily photosynthesis (09:00 – 16:30) versus total daily photosynthetic photon density. (D) Mean daily (09:00 – 16:30) water-use efficiency (WUE) versus total daily photosynthetic photon density. WUE was computed by dividing total carbon gain in Fig. 4C by total water loss in Fig. 4B.

pared with the open site, especially for the pine (Fig. 4D). At the open site, daily WUE in the pine (18) increased over 8-fold above gap values and was about 2-fold greater than computed for the spruce (9) and nearly 3-fold greater than the fir (6).

Discussion

Soil temperatures during all measurement periods remained sufficiently high to prevent apparent temperature inhibition of g (Kaufmann 1975; Running and Reid 1980; Teskey et al. 1984; Smith 1985*b*; Delucia and Smith 1987; Carter et al. 1988). Also, relatively high ψ_s (> -0.7 MPa) appeared to provide nonlimiting soil moisture conditions for all saplings during the study period. Several researchers have reported that ψ_p effects on g in conifers do not become significant until ψ_p decreases to less than about -1.5 MPa (Lopushinsky 1969; Watts and Neilson 1978; Kaufmann 1976; Beadle et al. 1978, 1981; Running 1980*a*). Thus, low T_s or ψ_p did not appear to be strongly influencing stomatal behavior at any of the three microsites during the study period.

With decreasing g and E in the progression from shaded to open environments, pine saplings may have an advantage over spruce or fir in early-successional environments as a result of lower E and greater WUE (Fig. 4), especially if the open sites are characteristically warmer and dryer. The greater water consumption by the spruce and fir may contribute to restricting these species to shade locations where moisture may be more abundant. Similarly, Lopushinsky (1969) and Lopushinsky and Klock (1974) suggested that the stomata of lodgepole pine seedlings closed more readily with increasing moisture stress than for Engelmann spruce. Knapp and Smith (1981) also found g in lodgepole pine saplings to be lower than for subalpine fir, while Smith et al. (1984) reported greater g in mature spruce and fir trees than for pine late in the growth season when ψ_p appeared to be strongly influencing g. However, Sperry (1936), Kaufmann (1982), and Carter et al. (1988) measured a greater g in mature lodgepole pine than for mature spruce or fir. Several additional studies reporting lower g or E in pine than spruce or fir have measured only young seedlings or saplings (Lopushinsky and Klock 1974; Knapp and Smith 1981, 1982; present results). Thus, pine g may be lower in younger, smaller trees (such as measured here) than in older, larger individuals, possibly because of factors associated with improved water storage or uptake in larger trees (Lassen and Okkonen 1969; Running 1980*b*).

All three species appeared to express significant acclimational capabilities in physiological responses according to microhabitat exposure (Table 1). At the open site, g values were much less variable than at the understory and gap sites. For lodgepole pine, g was particularly low and constant at the open site. This change in stomatal response could be associated with the higher irradiance levels and (or) somewhat less variability in daily insolation patterns compared with the understory and gap microhabitats. The greater changes in g and A, and the light compensation and light saturation points that occurred for lodgepole pine between microsites are characteristics associated with early-successional species (Bazzaz 1979). However, the relatively similar, saturating PPFD levels for all three species at the open site suggest capabilities in all three species for photosynthetic acclimation to high insolation levels. Given that pine grew in a slightly higher irradiance microenvironment than fir (Fig. 4), the photosynthetic "shade tolerance" of pine roughly equalled that of the spruce and fir and, thus, represents a late-successional characteristic. This result is similar to the observation that the photosynthetic responses to light in lodgepole pine were similar to those of Engelmann spruce (Bates 1935; Carter and Smith 1985).

Bennett and Rook (1978) found greater survival for a *P. radiata* clone that reduced transpiration in comparison with another, even though the clone having higher transpiration exhibited the higher WUE. In contrast, lodgepole pine in the present study had somewhat similar gains in photosynthesis in all three microhabitats but a much greater increase in WUE as a result of a substantial reduction in transpiration moving from the shaded understory to the open (Fig. 4). This combination would seem highly adaptive for a plant occupying more open and, possibly, dryer sites. It is interesting that all three species had substantial increases in photosynthesis at the open site without corresponding increases in *g*. In fact a marked reduction in *g* occurred for pine.

Kaufmann (1985) estimated stand-level WUE of lodgepole pine to be almost twice that estimated for Engelmann spruce and subalpine fir over a 120-year period. This difference was attributed to lower transpiration of pine forests due to lower leaf-area indices, coupled with probable lower photosynthesis in shaded portions of spruce and fir canopies. However, our results suggest that pine also has greater WUE than spruce or fir over the short term and on a per unit leaf area basis.

In the subalpine forests of the central Rocky Mountains, the physiognomy of the dominant vegetation may be very similar on early- versus late-successional sites (i.e., pine versus spruce–fir forests). Furthermore, understory sites are usually much less shaded than other forest understories such as temperate deciduous or tropical forests (Young and Smith 1980). Thus, a lesser physiological difference among plants acclimated to understory versus open environments might be expected for these subalpine forests than, for example, conifer forests of the eastern United States, where regeneration may involve severe biotic competition for light, moisture, and nutrients (e.g., Carter et al. 1984). However, distribution patterns among pine versus spruce and fir are distinctive, and synecologically, pine is frequently early successional in comparison with spruce and fir. Our results suggest that on exposed, early-successional sites, young pine trees may be capable of a carbon gain equivalent to that in spruce and fir, but with substantially more efficient water use. Data from the present study, however, do not suggest an explanation for the scarcity of lodgepole pine at higher elevations or the lower frequency of pine saplings in understory microhabitats through the subalpine forest.

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