SAP FLUX OF CO-OCCURRING SPECIES IN A WESTERN SUBALPINE FOREST DURING SEASONAL SOIL DROUGHT

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Abstract. Co-occurring species may utilize vastly different strategies to cope with limited water resources, particularly in areas subjected to predictable and recurring drought. While these physiological responses have commonly been measured at the leaf level, in small seedlings, and integrated in fluxes of whole stands or watersheds, sap flux measurements in large trees have become a useful tool for monitoring transpiration of individual canopies over long time periods. In this study, sap flux (Jₚ) was measured with constant heat sap flow gauges for co-occurring species which have been previously evaluated at the leaf level. Measurements were taken in a subalpine stand containing most of the dominant species of the central Rocky Mountains (Pinus contorta, Abies lasiocarpa, Populus tremuloides, and Pinus flexilis). Daily Jₚ values were parabolically related to daytime average atmospheric vapor pressure deficit (D) in all species, with a broad range of maximum Jₚ values occurring between 1.2 and 1.8 kPa. Populus tremuloides had the greatest increases in Jₚ with increasing D, while Pinus contorta showed the lowest Jₚ. A decrease in maximum Jₚ was observed for all species later in the season when soil moisture declined from 0.35 to 0.24 m³/m³ at 0–45 cm. Late-season Jₚ in A. lasiocarpa decreased 50% due to stomatal closure in response to the soil moisture deficit, regardless of daily D. In contrast, the Pinus species were sensitive to D, showing larger late-season reductions in Jₛ on high than on low D days. Populus tremuloides showed less sensitivity to soil moisture than the other species, with relatively high Jₛ continuing late into the season and intermediate change in the response of Jₛ to D with decreasing soil moisture. Stand-level estimates of transpiration by plots dominated by Pinus contorta and A. lasiocarpa (2.6 ± 0.6 mm/d) were found to be similar to plots dominated by Populus tremuloides (2.7 ± 0.6 mm/d) despite the nearly fourfold higher leaf area indices for the conifers.

Key words: Abies lasiocarpa; hydraulic conductance, whole plant; leaf water potential; Pinus contorta; Pinus flexilis; Populus tremuloides; sap flow; seasonal drought; subalpine forest; transpiration; water relations.

INTRODUCTION

The effects of water availability on species distribution and stand composition can be assessed by quantifying water use of co-occurring species in relation to atmospheric parameters. This approach is particularly suitable in areas where atmospheric demand commonly exceeds precipitation and soils are shallow. In the Medicine Bow Mountains of the Central Rockies, the subalpine zone generally receives 650–750 mm/yr of precipitation, about two-thirds of which are in the form of snow between October and May (Billings 1969, Fahney and Young 1984). During the summer season, thunderstorms of short duration may deliver small amounts of rain almost daily. However, a large proportion of seasonal soil moisture is delivered in spring snowmelt, so that many areas experience a general decline in moisture availability as the growing season progresses (Billings 1969). Areas where species of varying drought tolerance co-occur may be particularly useful in evaluating differences in water relations and may provide insight into the distributions of these species.

In the central Rocky Mountains, the primary fir species is Abies lasiocarpa (Hook.) Nutt., which occurs as a codominant with Picea engelmannii Parry from ~3000 m to the upper treeline at 3500 m (Oosting and Reed 1952, Billings 1969). Two pine species co-occur with fir to elevations of 3200 m: Pinus contorta Dougl., a pioneer species, and Pinus flexilis James, a species generally restricted to open areas or dry, south-facing slopes (Billings 1969, Knapp and Smith 1981, Burns and Honkala 1990, Smith and Knapp 1990). Clonal patches of Populus tremuloides Michx. are present in moister areas up to 3050 m (Billings 1969). Abies lasiocarpa, a late successional species (Oosting and Reed 1952), has been found to be more drought tolerant than the early successional Pinus contorta, which has shown greater declines in transpiration and conductance during drought stress (Lopushinsky 1969, Lopushinsky and Klock 1974, Carter and Smith 1988).
In contrast, *Populus tremuloides* appears to exhibit little stomatal control over water loss. This species has shown significant stomatal conductance at leaf water potential values as low as −6 MPa (Tobiassen and Kana 1974). During severe droughts *P. tremuloides* suffers substantial leaf senescence (Kozlowski 1976), shedding leaves which continue to have open stomata (Kaufmann 1982). Although *Pinus flexilis* is somewhat less studied, drought tolerant behavior may be expected in this species, as *P. flexilis* is restricted to dry, open sites (Billings 1969, Burns and Honkala 1990). In a season-long study of this species, McNaughton (1984) reported low stomatal conductance that remained constant as the season progressed.

In this study, we evaluated seasonal patterns of water use in these species at the canopy level, as well as the mechanisms underlying contrasting responses to seasonal drought. From previous information based on leaf-level measurements, we hypothesized that drought tolerance, defined as sustained sap flux during dry, late-season conditions, would follow a pattern of *Populus tremuloides > Pinus flexilis > Abies lasiocarpa > Pinus contorta*. To test this, sap flux was recorded during the growing season in stems of mature individuals for each species in a mixed species stand in the Medicine Bow National Forest, Wyoming, USA, consisting of *A. lasiocarpa, Pinus contorta,* and *Populus tremuloides,* with *Pinus flexilis* individuals at the forest edge. Unlike previous information gathered with short-term, leaf-level measurements on these species, the use of sap flow gauges permitted continuous, season-long measurements on a large portion of the canopy of each individual. Species-level sap flow data were then scaled to the stand level with sapwood area estimates to compare differences in transpiration between plots varying in species composition.

**Materials and Methods**

**Study site.**—The site was a mixed species forest located on an east-facing slope at 2750 m elevation in the Medicine Bow Mountains of southeastern Wyoming, USA (41°21′ N, 106°10′ W). The soil at the site was an inceptisol with weakly developed horizons at <10% slope. The forest contained mature individuals of *Pinus contorta, Abies lasiocarpa,* and *Populus tremuloides,* and was adjacent to an open field with *Pinus flexilis* occurring along the forest edge. Measurements were replicated in five individuals of each species located within a 40 m diameter area. Measured individuals ranged from 5 to 20 m in height and from 9 to 42 cm in diameter.

Density within the stand was homogeneous. Therefore, the competition experienced by each individual was estimated by establishing 3 m radius plots around each monitored tree. The species and diameter at breast height of each individual taller than 1.3 m within these plots was recorded.

**Atmospheric and soil moisture measurements.**—A temperature and relative humidity probe (Vaisala HMP 35C, Campbell Scientific, Logan, Utah, USA) was placed within the study plot at two-thirds mean canopy height of the stand. In addition, five point measurements of soil moisture variables were located throughout the site. Each point contained a standard rain gauge to estimate throughfall precipitation (PD) and a pair of steel rods for time domain reflectometry (TDR) measurements at 0–30 cm and 0–45 cm depths to estimate volumetric water content (θ). One measurement point contained a theta soil moisture probe (Delta-T Devices, Cambridge, UK) located at 20–25 cm for continuous measurements. Soil water content and PD data were collected approximately twice weekly with a cable tester (1502B, Tektronix, Beaverton, Oregon, USA) for θ. Microclimate and theta probe data were logged on a DL2 datalogger (Delta-T Devices) which sampled at 30-s intervals and averaged every 30 min continuously.

**Sap flux measurements.—**The 20 monitored trees contained constant heat sap flow gauges constructed after Granier (1987). The Granier-type sensors consisted of a copper-constantan thermojunction inserted 1 cm into a 2 cm long, 2 mm diameter stainless steel probe. Two probes were inserted radially into the stem at breast height, with one spaced ~5 cm above the other. The upper probe was equipped with a constantan heater supplied with a constant power source. The two thermojunctions were coupled and the temperature difference between the two probes was recorded to obtain the sap flux (Jzł, in grams per second square meter), as derived empirically (Granier 1987):

\[
J_{zł} = 119 \left( \frac{\Delta T_r}{\Delta T} - 1 \right)^{1/2}
\]

where \(\Delta T\) is the temperature difference between the heated and unheated probes, and \(\Delta T_r\) is the baseline temperature difference under zero flow conditions.

Sap flow data were sampled at 30-s intervals with the same datalogger (Delta-T Devices) as the microclimate measurements, and averaged every 30 min. Data were collected from 16 June to 25 August 1996.

**Leaf water potential.**—Every 2–3 wk, predawn (0430) and midday (~1200) leaf water potential (Ψpd and Ψr, respectively) were measured for the five trees of each conifer species with a Scholander-type pressure chamber (PMS Instrument, Corvallis, Oregon, USA), for a total of four measurement times throughout the growing season. One fascicle was taken from the same branch at each period. For *A. lasiocarpa* and *Pinus flexilis,* samples were taken from the individuals containing sap flow sensors. For *P. contorta,* branches were low enough to allow Ψ measurements to be taken on two trees containing sap flow sensors; three other trees were chosen for equal sample size. Branches were not accessible on the *Populus tremuloides* individuals, so that Ψpd only was measured on five *P. tremuloides* saplings. Given the clonal nature of *P. tremuloides,* we
assumed that $\Psi_{P_{C_0}}$ values of saplings approximated those of mature individuals before dawn, whereas this assumption could not be made for midday conditions. For the first measurement period, samples were taken from bagged branches on two of five individuals of each species, but no differences were found between bagged and unbagged leaves (ANOVA, $P > 0.05$), so that subsequent measurements were performed on unbagged foliage. Leaf-level water potential measurements were combined with whole-tree sap flux estimates to calculate whole plant hydraulic conductance ($L$, in grams per megapascal second square meter) after Loutau and Granier (1993):

$$L = J_i/(\Psi_i - \Psi_{P_{C_0}}).$$  

**Stand transpiration.**—In order to calculate stand transpiration from sap flux data, estimates of the active sapwood area ($A_S$) for each species were obtained from increment cores taken between the two sap flow sensors at the conclusion of the study. The depth to active sapwood was visually determined by the wood translucency. A relationship between diameter and sapwood area in 3 m radius plots established around each individual equipped with sap flow gauges in the stand interior (i.e., *Pinus flexilis* plots were excluded). For *P. contorta*, which often appeared to contain active sapwood far beyond sensor length, rates of $J_S$ at depth were scaled according to the radial measurements of Mark and Crews (1973; see also Phillips et al. 1996). Of the 20 subplots, five were dominated by *Populus tremuloides* (>70% of total $A_S$), four were dominated by *A. lasiocarpa* and *Pinus contorta* (>70% combined of total $A_S$), and six contained nearly equal proportions of the two groups (<70% of total $A_S$ for each group). Transpiration of each species was then scaled to the stand level:

$$E_{Ci} = J_{Si} \times [A_{Si}/A_{Gi}]$$  

where $E_{Ci}$ is the transpiration of species $i$, $J_{Si}$ is the sap flux of species $i$, and $A_{Si}/A_{Gi}$ is the sapwood to ground area ratio of species $i$.

Total transpiration of each species was then combined to obtain estimates of total stand transpiration ($E_C$) and its variability for each plot type following Oren et al. (1998).

**Statistical analyses.**—Species differences in the response of $J_S$ to $D$ early (June) and late (late August) in the season were tested with $F$ tests comparing a null model of $J_S$ and $D$ without species effects and an alternative model with species added as a nominal variable. Differences in $\Psi_t$, $\Psi_{P_{C_0}}$, and $L$ values during the four measurement periods were analyzed with a two-way, nested ANOVA with measurement period as a repeated measure (proc GLM, SAS software: SAS Institute 1985). All statistical analyses were conducted with SAS software (SAS Institute, 1985).

**RESULTS**

**Sap flux.**—Sap flux was strongly influenced by soil moisture during the study period. Diurnal patterns of $J_S$ in early July and mid-August showed a reduction in August, although $D$ remained constant (Fig. 1). There were no seasonal trends in temperature, relative humidity, or $D$ (Fig. 2). However, a general decline in soil moisture availability was apparent (Fig. 2) resulting in a seasonal reduction in $J_S$ in all species (Fig. 3). On average, $J_S$ was lower in *Pinus contorta* than the other species ($P < 0.05$), although the seasonal decline was similar to the other conifers. In *Populus tremuloides*, an early season increase in $J_S$ was apparent in June (Fig. 3) which was not related to trends in $D$ and minimum nighttime temperature ($P > 0.05$). Tree size and sapwood area density within a 3 m radius (i.e., competition) did not account for variability in $J_S$ within or among species ($P > 0.05$). Therefore, interactions between tree size and $J_S$ were not considered in calculating the variability in stand transpiration, such that the variance equation given by Oren et al. (1998) may be simplified to

$$\sigma^2 E_{Ci} = (J_{Si}^2)(A_{Si}/A_{Gi}) - (J_{Si})^2 \times (A_{Si}/A_{Gi})^2$$  

where brackets indicate the mean and $i$ designates species $i$.

The relationships between $J_S$ and $D$ followed three distinct patterns. In the early part of the season (16–25 June), $D$ was relatively constant at ~0.35 m/s^2 (Fig. 2). During this period, $J_S$ and $D$ were curvilinearly related; $J_S$ was highest for all species at 1.5–1.7 kPa,
and decreased thereafter (Fig. 4). Later in the season (26 June–14 August), as $\theta$ began to decline more rapidly (Fig. 2), the variability in $D$, particularly at lower values, was insufficient to separate the effect of $D$ from that of $\theta$ on $J_s$ ($P > 0.05$). However, in the last several weeks of the study period (15–25 August), $\theta$ stabilized at ~0.24 m$^3$/m$^3$ and a relationship between $D$ and $J_s$ was found for Pinus contorta, A. lasiocarpa, and Populus tremuloides ($P < 0.05$). At this time, similar values of $D$ were associated with much lower values of $J_s$ than during the early period of high soil moisture availability (Fig. 3).

No differences were found between the responses of $J_s$ to $D$ in A. lasiocarpa and Pinus flexilis ($P > 0.05$); however, all other models were significantly different, with the largest increases in $J_s$ in response to $D$ in Populus tremuloides, and the smallest increases in Pinus contorta ($P < 0.05$, Fig. 5). Models of late-August $J_s$ for all species were found to be different ($P < 0.05$). These predictions were divided by June predictions for each species to calculate the percent reduction in $J_s$ at a given $D$ as a result of soil moisture depletion (Fig. 5). Sap flux decreased similarly for the two pine species, with large late-season reductions in $J_s$ on high $D$ days. Populus tremuloides, which began the season with the highest fluxes, showed the lowest percent reductions, ranging from 36–45%. In contrast, A. lasiocarpa maintained fairly constant late-season reductions of ~50% even on high $D$ days.

Linear regression models of $J_s$ vs. $\theta$, excluding the days of lowest and highest $D$, had different intercepts ($P < 0.05$), but similar slopes ($P > 0.05$) for all species.

Water potential and hydraulic conductance.—$\Psi_{pd}$ was lowest in Pinus flexilis ($P < 0.05$) on 24 June (Fig. 5).
Fig. 4. Daily sap flux ($J_s$) in relation to volumetric soil moisture content ($\theta$) and vapor pressure deficit ($D$). On the left, regression lines are given for the relationship between $J_s$ and $\theta$ during the study period ($P < 0.05$). Three periods during the season are differentiated; symbol shading represents the same sample period on the right and left. From 16 June to 25 June, $\theta$ appeared relatively constant at 0.35 m$^3$/m$^3$ (filled symbols). During this period a second-order polynomial was found to describe the relationship between $J_s$ and $D$ ($P < 0.05$). For *Populus tremuloides*, the first five days of the season were excluded from the relationship due to early-season increases in $J_s$ (see Fig. 3). From 26 June to 14 August (shaded symbols), $\theta$ rapidly decreased with small variations in $D$, such that no relationships were found in all species ($P > 0.05$). In the remaining portion of the season (open symbols), $\theta$ appeared to stabilize at $\sim$0.25 m$^3$/m$^3$, and a second-order polynomial was again fitted to $J_s$ vs. $D$ ($P < 0.05$ for all species except *Pinus flexilis*).

6), suggesting lower water availability at the forest edge early in the growing season. By 25 August, $\Psi_{PD}$ of *P. contorta* and *P. flexilis* decreased to similar values measured for *A. lasiocarpa* and *Populus tremuloides* (Fig. 6). Thus, *Pinus contorta* showed the greatest seasonal decline in $\Psi_{PD}$ as compared to the other species. $\Psi$, decreased during the season for all species ($P < 0.05$), but remained higher in *A. lasiocarpa* than the *Pinus* species in August ($P < 0.05$). *P. flexilis* showed the highest values of $L$ in June and July ($P < 0.05$, Fig. 6), followed by a decline in $L$ for August. On 25 August, $L$ of *P. flexilis* was similar to *A. lasiocarpa* ($P > 0.05$), as $L$ had remained unchanged throughout the study.

*Stand transpiration.*—Sap flow gauge length did not exceed sapwood depth in any species (Table 1). The highest basal area was found in the pine–fir plots, while aspen plots showed the highest density (Table 2, $P < 0.05$). Mean diameters and $A_s/A_0$ were similar in all types (Table 2, $P > 0.05$). Transpiration rates during the study period were estimated to be $2.6 \pm 0.6$ mm/d (mean $\pm 1$ SE) for aspen, $2.7 \pm 0.6$ mm/d for pine–fir, and $1.7 \pm 0.4$ mm/d for the mixed plots, with errors calculated after Eq. 4. Transpiration in the aspen and pine–fir plots showed similar responses to $D$, while the mixed plots appeared to attain a lower maximum $E_c$ (Fig. 7).

The mean cumulative $E_c$ during the study period for all composition types was 168.4 $\pm$ 2.9 mm. Stand evapotranspiration was independently estimated as the reduction in soil moisture during the study measured from the 0–45 cm depth with time domain reflectometry TDR, $(49.5 \pm 11.2$ mm), plus the total throughfall precipitation ($P_T$, $72.1 \pm 7.1$ mm). Soil moisture depletion from the 0–30 cm depth was considerably more variable due to precipitation inputs such that the decline for all measurement points could not be distinguished from zero (data not shown). Thus, $E_c$ from this layer approximately equals $P_T$, assuming zero drainage and lateral flow. In addition, evapotranspiration estimated by $P_T$ plus soil moisture depletion at 0–45 cm is equivalent to actual evapotranspiration assuming that rooting depth does not exceed 45 cm. Drainage below 45 cm was negligible, as evidenced from the nearly continuous decrease in soil moisture content at the 20–25 cm depth, and soil moisture content remained well below the saturation values of 0.4 m$^3$/m$^3$, despite frequent rain events. However, the assumptions of lateral flow and insignificant rooting density below 45 cm may be incorrect. Therefore, evapotranspiration estimated by this method was designated $E_c'$. This estimate was lower than $E_c$ calculated from sap flow, suggesting additional sources of water from below 45 cm or from lateral flow. To evaluate temporal patterns in transpiration, separate water balances were calculated for the beginning (17 June–12 July), middle (16 July–5 August) and end (8 August–25 August) of the study. These results indicate that $E_c'$ estimated from $\theta$ and $P_T$ significantly underestimated $E_c$ scaled from sap flux only in the latter portion of the study (Table 3, $P < 0.05$).
The species in this study displayed fairly similar reductions in $J_s$ during the growing season (Fig. 3). However, absolute rates of water use varied by species. In addition, physiological mechanisms underlying drought responses to seasonal reductions in soil moisture were also species dependent. Changes in stomatal responses to $D$, reductions in midday $\Psi_s$, and reductions in $L$ occurred to varying degrees in the four species.

Ratios of leaf-to-sapwood area have been found to vary from 0.1–0.2 m$^2$/cm$^2$ for *Pinus contorta* and *Populus tremuloides* to 0.8 m$^2$/cm$^2$ for *Abies lasiocarpa* (Kaufmann and Troendle 1981, Waring et al. 1982).

**TABLE 1.** To scale sap-flux measurements to the stand level in a subalpine conifer stand in the Medicine Bow National Forest, Wyoming, USA, depths to heartwood ($D_h$; means ± 1 se, measured in centimeters) were determined from increment cores of the measurement trees.

<table>
<thead>
<tr>
<th>Species</th>
<th>$D_h$</th>
<th>Intercept</th>
<th>Slope</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Pinus contorta</em></td>
<td>5.8 ± 0.9</td>
<td>−246.0</td>
<td>26.0</td>
<td>0.99</td>
</tr>
<tr>
<td><em>Pinus flexilis</em></td>
<td>3.9 ± 0.6</td>
<td>−194.0</td>
<td>20.4</td>
<td>0.97</td>
</tr>
<tr>
<td><em>Abies lasiocarpa</em></td>
<td>2.2 ± 0.3</td>
<td>7.5</td>
<td>0.6</td>
<td>0.67</td>
</tr>
<tr>
<td><em>Populus tremuloides</em></td>
<td>4.6 ± 0.6</td>
<td>−146.0</td>
<td>20.1</td>
<td>0.97</td>
</tr>
</tbody>
</table>

Note: Least-square regression coefficients used to predict sapwood area ($A_s$), as measured from $D_h$ from outside bark diameter at 1.3 m (dbh) are also given.

**DISCUSSION**

Fig. 5. (A) Predicted values from models of sap flux ($J_s$) vs. vapor pressure deficit ($D$) early and late in the season (filled and open circles, respectively), as given for the dates in Fig. 4. One curve is shown for the early season *Abies lasiocarpa* and *Pinus flexilis* predictions, as there was no difference between models ($P > 0.05$). (B) Reduction in $J_s$ (1 – the ratio between late and early season models for each species) as an indicator of soil moisture effects.

Table 1. To scale sap-flux measurements to the stand level in a subalpine conifer stand in the Medicine Bow National Forest, Wyoming, USA, depths to heartwood ($D_h$; means ± 1 se, measured in centimeters) were determined from increment cores of the measurement trees.
Thus, $J_s$ values recorded here correspond to high rates of sap flux per unit leaf area for *P. tremuloides* and very low values for *A. lasiocarpa*, with intermediate rates for the two *Pinus* species. This ranking roughly corresponds to the shade tolerance of these species, generally increasing from *Populus tremuloides* to *A. lasiocarpa*. Similar patterns have been found for measurements of stomatal conductance of these species (Smith et al. 1984, Carter and Smith 1988, Abrams and Mostoller 1995).

In all four species, $J_s$ was inhibited at a mean daily $D > 1.8$ kPa (Fig. 4). This pattern may be associated with rapid morning reductions in soil moisture near roots, a result of high transpiration rates (Pataki et al. 1998). However, the parabolic response of $J_s$ to $D$ was confounded in our study by seasonal changes in bulk soil moisture. We found that a multivariate model incorporating both $\theta$ and $D$ could not accurately predict changes in $J_s$ over the whole season for these data ($P > 0.05$). Rather, separate relationships between $J_s$ and $D$ were apparent at high and low $\theta$ (Fig. 4). This has been a common finding in studies of *Pinus contorta* (Fetcher 1976, Running 1980, Graham and Running 1984), indicative of a complex and nonlinear effect of $\theta$ on stomatal sensitivity to $D$.

When estimates of leaf-to-sapwood area ratios taken from Waring et al. (1982) are applied to sapwood area-based calculations of $L$ (Fig. 6), values fall within the range of $L$ reported for the subalpine *Picea abies* (Lu et al. 1996). In the early part of the study, *Pinus flexilis* exhibited the most negative $\Psi_{rd}$ most likely as a result of its proximity to the stand edge. By the end of the study, however, $\Psi_{rd}$ of *P. contorta* was similar to *P. flexilis* (Fig. 6). This pattern suggests shallow rooting in the *Pinus* species, such that they were more affected by depletion of moisture near the surface as the season progressed.

Stomatal conductance in *A. lasiocarpa* and *P. contorta* has shown a strong correlation with seasonal declines in soil moisture and $\Psi_{rd}$ (Fetcher 1976, Running 1980, Fahey and Young 1984, Graham and Running 1984). In this study, late-season reductions in $J_s$ varied with daily $D$ for both *Pinus* species (Fig. 5) and may be associated with shallow rooting in these species. As soil moisture is exhausted on high $D$ days, hydraulically or chemically mediated feedbacks in stomatal closure may occur under dry conditions (Pataki et al. 1998, Sperry et al. 1998). For both *Pinus* species, $\Psi_{rd}$ fell to low values (≤−2 MPa) by the end of the study, resulting in declines in $L$ (Fig. 6). *P. contorta* and *P. flexilis* exhibited sustained late season $J_s$ and greater drought tolerance than *A. lasiocarpa*. When soil moisture decreased to <0.25 m$^3$/m$^3$, the *Pinus* species maintained relatively high transpiration at low $D$ (≤1.5 kPa, Fig. 5).

*Abies lasiocarpa* showed large late-season reductions in transpiration that were unrelated to $D$ (Fig. 5). This pattern is indicative of a seasonal increase in stomatal control over water loss. $\Psi_{rd}$ in *A. lasiocarpa* remained high (≥−2 MPa) near the end of the study period (Fig. 6), suggesting that stomatal closure oc-
Table 3. To evaluate components of local water balance in comparison to canopy transpiration estimated from stand flux ($E_C$) in a subalpine conifer stand in the Medicine Bow National Forest, Wyoming, USA, mean daily soil moisture depletion (SMD) and throughfall precipitation ($P_T$) are given for three periods.

<table>
<thead>
<tr>
<th>Sample period</th>
<th>$n$</th>
<th>SMD</th>
<th>$P_T$</th>
<th>$E_C^i$</th>
<th>$E_C$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>17 June–12 July</td>
<td>26</td>
<td>0.82 ± 0.6</td>
<td>1.16 ± 0.1</td>
<td>1.98 ± 0.6</td>
<td>2.57 ± 0.2</td>
<td>&gt;0.10</td>
</tr>
<tr>
<td>16 July–5 August</td>
<td>21</td>
<td>0.53 ± 0.8</td>
<td>1.57 ± 0.1</td>
<td>2.10 ± 0.8</td>
<td>2.31 ± 0.2</td>
<td>&gt;0.10</td>
</tr>
<tr>
<td>8 August–25 August</td>
<td>18</td>
<td>0.44 ± 0.1</td>
<td>0.48 ± 0.1</td>
<td>0.92 ± 0.1</td>
<td>1.73 ± 0.2</td>
<td>&lt;0.10</td>
</tr>
</tbody>
</table>

Notes: Evapotranspiration ($E_C^i$) is estimated as the sum of SMD and $P_T$. All data are means ± 1 se, in millimeters. $P$ values are given for a Student’s $t$ test of the difference between $E_C^i$ and $E_C$.

occurred to prevent cavitation and decreases in L. Constant $L$ was, in fact, maintained throughout the study (Fig. 6). This may be a necessary adaptation given the high vulnerability to cavitation previously reported for *A. lasiocarpa*, necessitating maintenance of high $\Psi_L$ (Sperry et al. 1994).

*Populus tremuloides* showed the smallest seasonal reductions in transpiration, suggesting a lack of stomatal control (Fig. 5). Although $L$ in *P. tremuloides* was not evaluated here, this species has shown evidence of osmotic adjustment (Abrams 1988), as well as relatively high stomatal conductances late in the season (Kaufmann 1982) and at low $\Psi_L$ (Tobiessen and Kana 1974). In this study, daily $J_s$ increased with increasing $D$ throughout the season (Fig. 4). As *P. tremuloides* may be only moderately vulnerable to cavitation, with 50% loss of conductivity at $\sim$2 to $\sim$3 MPa (Sperry et al. 1991), a reduction in $L$ probably occurred as late-season $J_s$ continued, albeit at lower rates (Figs. 3, 4). Notably, when variations in daily $D$ were not considered, all species showed similar declines in $J_s$ with reductions in $D$ (Fig. 4).

*Populus tremuloides* also showed a departure from patterns of $J_s$ found in the conifer species early in the season (Fig. 3). Sap flux consistently increased during this period, perhaps due to early season leaf expansion, as leaf production has been found to persist in *P. tremuloides* well into the growing season (Tyree et al. 1978). In addition, year-to-year variability in refilling of winter-embolized vessels has been shown to affect whole plant $L$ in this species (Sperry and Sullivan 1992, Sperry et al. 1994, Hacke and Sauter 1995).

Stand-level responses.—Relationships between stand-level transpiration ($E_C$) and $D$ showed similar responses for aspen- and pine–fir-dominated plots (Fig. 7). Although leaf area index (LAI) in pine–fir plots was higher than in aspen plots (Table 2), this difference was offset by higher $J_s$ in aspen (Figs. 1 and 3). Thus, mean seasonal $E_C$ for both forest types were not different (2.6 and 2.7 mm/d, respectively). Knight et al. (1981) reported similar values (3.3 and 3.4 mm/d) using a potometer method in two *Pinus contorta* stands with a seven-fold difference in density and a 29% difference in biomass. Our maximum $E_C$ values on high $D$ days in the early moist part of the season were similar (Fig. 7).

Transpiration of the aspen–pine–fir plots showed lower $E_C$ than the aspen and pine–fir types (Fig. 7). Understory transpiration, which was not included in these estimates, has been found to be $\sim$5% of overstory transpiration in western conifer stands, where understory vegetation may be sparse, and 25–40% of overstory transpiration of aspen stands (Kaufmann 1985). The open, low-density aspen–pine–fir plots in this study may have promoted higher proportions of understory transpiration, consistent with the suggestion of Roberts (1983) that over- and understory transpiration values may balance to yield similar values of total transpiration in stands of varying species composition.

Lateral flow from spring snow melt may have provided additional inputs of water (0.6 mm/d by difference, Table 3) from upper elevations in the early part of the season (Knight et al. 1985). In the driest portion of the season, average $E_C^i$ was 47% lower than the mean $E_C$ (Table 2) and water uptake by canopy species may have occurred from below 45 cm (0.8 mm/d). Water uptake may shift to lower horizons during dry periods following the retreating front of available soil moisture (Rambal 1984, Meyer et al. 1988, Stogsdill et al. 1992, Bréda et al. 1995). Our data indicate that water uptake became more concentrated at depths below 45 cm as water availability became limiting in upper horizons, although the effect may have been species dependent, as $\Psi_{rd}$ data suggested shallow rooting in *P. contorta* and *P. flexilis* (Fig. 6).

The occurrence of these four species in the central Rocky Mountains reflects, in part, the spatial variation in the availability of soil moisture and atmospheric demand as well as physiological differences among species. Estimating stand transpiration provided useful information on stand-level patterns of water use under moist, early summer and dry, late summer conditions. In addition, continuous measurements of sap flux augmented intermittent physiological data collected at smaller scales of measurements to provide a greater understanding of whole-tree water use for the species in this stand.

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