

Water use of interior Douglas-fir

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Abstract: Water use of individual Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) trees was measured in two plots at a forest site in southern British Columbia, Canada. Average daily early summer water use by trees with diameters of 7.5–70 cm varied from 1.8 to 166 L. Sap flux density (cm^3 water/ cm^2 sapwood per hour) was linearly related to shoot xylem pressure potential and was found to increase with increasing vapour pressure deficit (VPD) and short-wave irradiance (I), reaching maximum rates with $\text{VPD} > 0.6$ kPa and $I > 200$ $\text{W}\cdot\text{m}^{-2}$. Daily sap flux density varied among trees but was not related to tree diameter, so an average value of 1137.4 $\text{L}\cdot\text{m}^{-2}$ sapwood area was used to estimate average early summer stand transpiration for the two plots of 1.08 and 1.5 $\text{mm}\cdot\text{d}^{-1}$. A close curvilinear relationship ($r^2 = 0.85$) was found between stem cross-sectional area increment and sapwood area. The relationship was only slightly better ($r^2 = 0.89$) between area increment and early summer individual tree water use. Stand volume growth for 1988–1998 for the two plots was 36 – 47 $\text{m}^3\cdot\text{ha}^{-1}$. Stem volume relative growth rate over this 10-year period is estimated at 0.027 and 0.029 $\text{m}^3\cdot\text{m}^{-3}\cdot\text{a}^{-1}$.

Résumé : La consommation d'eau par des tiges individuelles de douglas (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) a été mesurée dans deux parcelles situées en forêt dans le sud de la Colombie-Britannique, au Canada. La quantité moyenne d'eau consommée quotidiennement au début de l'été, par des arbres dont le diamètre avait 7,5 à 70 cm, variait de 1,8 à 166 L. La densité du flux de sève (cm^3 d'eau/ cm^2 de bois d'aubier par heure) était linéairement reliée à la pression potentielle du xylème dans les pousses et augmentait avec une augmentation du déficit de pression de vapeur (DPV) et un rayonnement de courte longueur d'onde (I), atteignant un taux maximum pour $\text{DPV} > 0.6$ kPa et $I > 200$ $\text{W}\cdot\text{m}^{-2}$. La densité quotidienne du flux de sève variait selon les arbres mais n'était pas reliée au diamètre d'un arbre de telle sorte qu'une valeur moyenne de $1137,4$ $\text{L}\cdot\text{m}^{-2}$ de surface de bois d'aubier a été utilisée pour estimer la transpiration du peuplement au début de l'été dans les deux parcelles à $1,08$ et $1,5$ $\text{mm}\cdot\text{d}^{-1}$. Il existe une relation curviligne étroite ($r^2 = 0,85$) entre l'accroissement de la surface transversale de la tige et la surface de bois d'aubier. La relation entre l'accroissement de la surface et la consommation d'eau par un arbre au début de l'été était seulement légèrement meilleure ($r^2 = 0,89$). De 1988 à 1998, la croissance en volume du peuplement dans les deux parcelles a été de 36 – 47 $\text{m}^3\cdot\text{ha}^{-1}$. Le taux relatif de croissance en volume de la tige au cours de cette période de 10 ans a été estimé à $0,027$ et $0,029$ $\text{m}^3\cdot\text{m}^{-3}\cdot\text{a}^{-1}$.

[Traduit par la Rédaction]

Introduction

The dry interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) forests of western Canada have historically been a source of large trees used by the lumber industry for high-quality structural wood products. Many of these forests were logged earlier in the century by selective harvesting of the larger, more valuable trees. This logging history, coupled with fire protection and widespread cattle grazing has resulted in present forest stands, which consist of trees that are of uneven ages and sizes. Typically, the stands have an overstory of irregularly spaced larger trees (>25 cm diameter) and an understory of often-clumped smaller trees. Although germinates are often profuse, survival and growth of young naturally established or planted seedlings is often precluded by intense competition with pine grass (*Calamagrostis rubescens* (Buckl.)). Considerable spatial and temporal variability in soil moisture occurs resulting from a number of factors including site topography and aspect, depth and coarse fragment content of soil, spatial

distribution of root systems of large trees, precipitation interception by large overstory as well as by dense clumps of understory trees, leaf area density of pine grass, and amount and type of coarse woody debris.

Although significant timber volumes have been removed from these dry interior Douglas-fir forests, it remains unclear what levels and form of forest harvesting can be sustained. As a result, large areas of dry interior Douglas-fir forests are presently not included in the annual allowable cut determinations for British Columbia's southern interior. Significant economic benefit will be realized by determining what levels and form of harvesting are sustainable for these forests. The productivity and spatial distribution of trees in these stands is affected to a large extent by moisture availability. It seems reasonable then to suppose that a quantitative understanding of the water use by the three main vegetation types in these dry interior Douglas-fir stands (large overstory trees; smaller understory trees; pine grass) is an important step in understanding the biological processes which contribute to the spatial structure and productivity (wood production) of these sites.

Measurement of water use by individual trees is well documented (Kaufmann and Kelliher 1991; Kostner et al. 1998b; Percy et al. 1991; Smith and Allen 1996) and now routine. For larger trees, the flow of sap is most commonly

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measured by heat tagging. There are two general approaches, heat pulse velocity (HPV) and thermal dissipation (TD). In HPV methods, a pulse of heat is injected into the xylem and the velocity of its travel to a point further along in the direction of flow is used to estimate sap flow velocity. TD approaches involve continuous heating of the xylem. Granier (1985, 1987) developed a TD method utilizing a pair of needle heater-sensors that are inserted into the sapwood. Constant power is applied to the heated sensor and the recorded temperature difference between the two sensors has been found to be related to sap flow by a universal relationship (see Kostner et al. 1998b; Pearcy et al. 1991). Granier's methods have been applied in a wide range of tree species (Anfodillo et al. 1998; Diawara et al. 1991; Goulden and Field 1994; Kostner et al. 1998a; Loustau et al. 1996, 1998; Lu 1997; Oren et al. 1998; Phillips et al. 1997; Teixeira Filho et al. 1998; Tournebize and Boistard 1998). Comparisons have been made among various sap flow methods, and the results have generally been found to be similar (Granier et al. 1996; Hall et al. 1998; Hogg et al. 1997; Kostner et al. 1998b; Tournebize and Boistard 1998).

The specific objective of this study was to measure the water use of individual Douglas-fir trees in an uneven-aged dry interior Douglas-fir forest using Granier type TD sap flux density probes. The study reported here is part of larger study aimed at developing means to predict the sustainable yield of complex forest stands.

Methods

Study area

A 6-ha research site representative of dry uneven-aged interior Douglas-fir forests was located at Pothole Creek (49°54'N, 120°36'W; elevation, 1300 m) which is about 25 km southeast of Merritt, B.C. A dry continental climate provides annual precipitation of about 400–500 mm with most occurring in fall, winter, and early summer as remnants of Pacific frontal storms reach into the southern interior. Winter snow packs are typically 35–60 cm, with snowmelt complete by mid-April. Precipitation in May–June usually results in soil moisture near field capacity from mid-May through mid-June. Convective storms during the summer provide periodic summer precipitation events of variable intensity. A period of mid- to late-summer drought is expected each year. The site has been classified as being of the Thompson Dry Cool Interior Douglas-fir (IDFdK1) biogeoclimatic subzone (Lloyd et al. 1990). The soils at the research site are 50–70 cm deep Orthic Dystric Brunisols often with a substantial amount of coarse fragments. The site was partially logged in 1966, and the present stand structure consists of an overstory of fairly widely spaced larger Douglas-fir, an understory of smaller Douglas-fir often in clumps, and pine grass dominated openings.

The water use of 8 individual trees was measured in 1997 in plot A and on 26 trees in 1998 in plot B (Table 1). The plots are representative of the larger 6-ha study area and the forest type in general. The size distribution of trees in the two plots (Fig. 1) shows that the stands consist of a few larger trees and numerous smaller trees, particularly in plot B.

Water use

The sap flux density ($\text{cm}^3 \text{ water/cm}^2 \text{ sapwood per hour}$) of individual Douglas-fir trees was measured using methods described by Granier (1985, 1987) and sensors (TDP-30) manufactured by Dynamax Co., Houston, Tex. These sensors consist of a pair of 30 mm $\times$ 1.2 mm probes, which are inserted into the sapwood. The

probes are installed in a vertical line about 40 mm apart. As older Douglas-fir trees have thick bark, it was necessary to remove the outermost bark over a small area so that the probes can reach into the sapwood. To minimize external thermal gradients, the tree trunks with installed probes were wrapped with layers of poly-foam and reflective bubble wrap. The upper probe contains a heater (ca. 50 Ω) and a thermocouple, while the lower probe contains only a thermocouple. Constant voltage (3 V) is applied to the heater, which results in a temperature difference (dT) between the upper and lower thermocouples. The magnitude of this temperature difference is affected by the sap flow such that maximum dT occurs when no flow is occurring. For a range of tree species, including Douglas-fir, Granier (1985, 1987) reported an empirical relationship between sap flux density ($\text{cm}^3 \cdot \text{cm}^{-2} \cdot \text{h}^{-1}$) and dT , which was used as follows:

$$\text{sap flux density} = 42.8 \{[(dT) - 1]^{1.231}\}$$

where dT is the temperature difference ($^{\circ}\text{C}$) between the two probes, determined every 30 s with the averages of each 10-min period used for calculation, and dM is the maximum temperature difference between the two probes when there is zero sap flow (for calculation purposes, for each 24-h period this is the maximum 10-min mean dT). An array of 32 sensors powered by 12-V batteries were monitored at 30-s intervals using a data logger and multiplexer (CR10x and AMP416, Campbell Scientific, Edmonton Alta.). Data was recorded as 10-min mean sap flux density for later analysis. Data from all sensors was assessed graphically to check that sap flux densities fell within reasonable bounds and daily patterns were consistent among sensors. In 1997, measurements were made on eight trees in plot A on 48 days between May 30 (day 150) and September 25 (day 268). In 1998, measurements were made on 26 trees in plot B on 23 days between June 4 (day 155) and September 4 (day 247). For trees with diameters >20 cm, 1.5–2.0 m above ground level a sensor was installed at each of the four cardinal azimuths (N, S, E, W). For trees with diameters <20 cm, sensors 0.5–1.5 m aboveground were used only on the N and S sides of each tree.

Water use by individual trees varies substantially among trees and between days. To optimize the amount of data that can be collected with 32 sensors and to provide water use data for a greater number of trees over a several-day measurement period a "roving sensor" method was used (Vertessy et al. 1995). By this method, some sensors remained in a small (<15 cm) or large (>25 cm) "reference tree" for the entire measurement period, while most of the sensors were moved between trees so measurements for most trees were available for only parts of the total measurement period. Over 2- or 3-day periods, the linear relationships between the 10-min mean sap flux density measurements for each measurement tree and an appropriate reference tree were found to be highly significant ($r^2 = 0.84\text{--}0.99$). These relationships were used to generate data for days when sensors were not present in the measurement trees. This method has the effect of creating data for all trees over the entire measurement period and thus minimizing the confounding that occurs by not measuring all trees on the same days.

Individual tree daily sap flow (L) was calculated as the product of the mean (of two or four sensors) daily sap flux density ($L \cdot \text{m}^2$) and the sapwood cross-sectional area (m^2) of each tree. Daily sap flux density is the daily integral of the 10-min sap flux densities. Sapwood area was determined from measurements of tree diameter at the point of sensor installation and measurement of bark and sapwood thickness made on two increment cores taken from each tree.

Plant moisture stress

At intervals from mid-day on June 11 until mid-day June 12, 1998, small midcrown branches were removed from six sap flow

Table 1. Stem diameter, sap wood area, stem cross-sectional area increments and average early summer (May 30 – June 29) water use of Douglas-fir trees at Pothole Creek in 1997 (Plot A) and 1998 (Plot B).

Tree No.	Diameter (cm)	Sapwood area (m ² , ×10 ⁻³)	10-year area increment (m ² , ×10 ⁻³)	Early summer sap flow (L·d ⁻¹)		Early summer sap flux density (L·m ⁻² ·d ⁻¹)	
				Mean	SD	Mean	SD
Plot A (1997)							
1012	8.3	3.20	3.23	4.45	1.21	1387.3	378.8
1000	10.2	3.14	4.51	6.49	2.39	2062.9	760.1
1005	10.2	5.45	5.40	11.38	3.84	2087.1	703.3
863	14	9.25	8.96	7.21	2.48	779.6	267.8
1026	25.2	17.53	13.41	33.32	13.38	1900.8	763.2
834	32	19.24	7.38	22.16	5.50	1151.5	285.7
658	34.1	32.04	12.36	33.62	11.91	1049.1	371.6
1007	35.7	39.06	21.74	57.28	18.97	1466.5	485.7
Plot B (1998)							
18	7.5	2.87	2.56	2.18	0.89	760.3	311.2
21	8.1	3.05	2.97	1.81	0.78	592.0	254.2
24	9.25	4.31	4.02	4.73	1.74	1097.7	403.5
22	9.3	3.73	4.41	4.29	1.76	1150.2	472.4
17	10.35	4.70	5.24	5.72	2.18	1216.5	463.1
19	11	5.03	4.93	3.94	1.52	783.6	301.5
23	11.1	5.03	4.54	4.10	1.57	815.4	311.7
20	12.8	6.68	7.04	6.44	2.40	964.1	359.7
25	15.9	11.00	9.35	9.40	3.20	854.2	291.2
26	17.9	12.71	13.28	15.66	5.25	1232.1	413.2
4	20.8	17.08	6.60	12.02	4.65	703.7	272.4
6	25.05	16.75	7.85	12.43	4.37	742.0	260.6
16	31.45	24.74	9.55	28.05	11.62	1133.7	469.7
8	32.65	31.73	12.46	35.01	11.49	1103.5	362.3
7	32.75	33.38	16.32	54.24	19.35	1624.9	579.8
9	33.2	23.41	10.74	16.36	5.85	698.9	249.8
3	33.55	31.73	13.08	30.92	11.15	974.5	351.4
15	34	29.51	16.06	53.37	18.52	1808.6	627.7
5	34.3	32.46	14.74	40.59	12.72	1250.4	391.9
13	34.35	43.72	21.55	47.17	17.35	1078.9	397.0
12	34.45	29.58	14.77	38.71	15.27	1308.9	516.4
2	34.9	33.62	18.95	52.42	16.68	1559.1	496.1
14	35.85	25.39	13.96	39.10	15.43	1539.8	607.8
1	36.35	34.37	10.91	39.03	14.38	1135.6	418.3
10	36.9	35.81	9.71	41.22	14.43	1151.2	402.9
11	70	93.10	32.96	166.08	56.96	1783.8	611.8

Note: In 1997, reference trees were Nos. 1000 and 1007. In 1998, reference trees were Nos. 1 and 17.

measurement trees using pole pruners. Shoot xylem pressure potential was measured using a pressure chamber (model 600, PMS Corp., Corvallis, Oreg.) within 1 min of sampling.

Environmental measurements

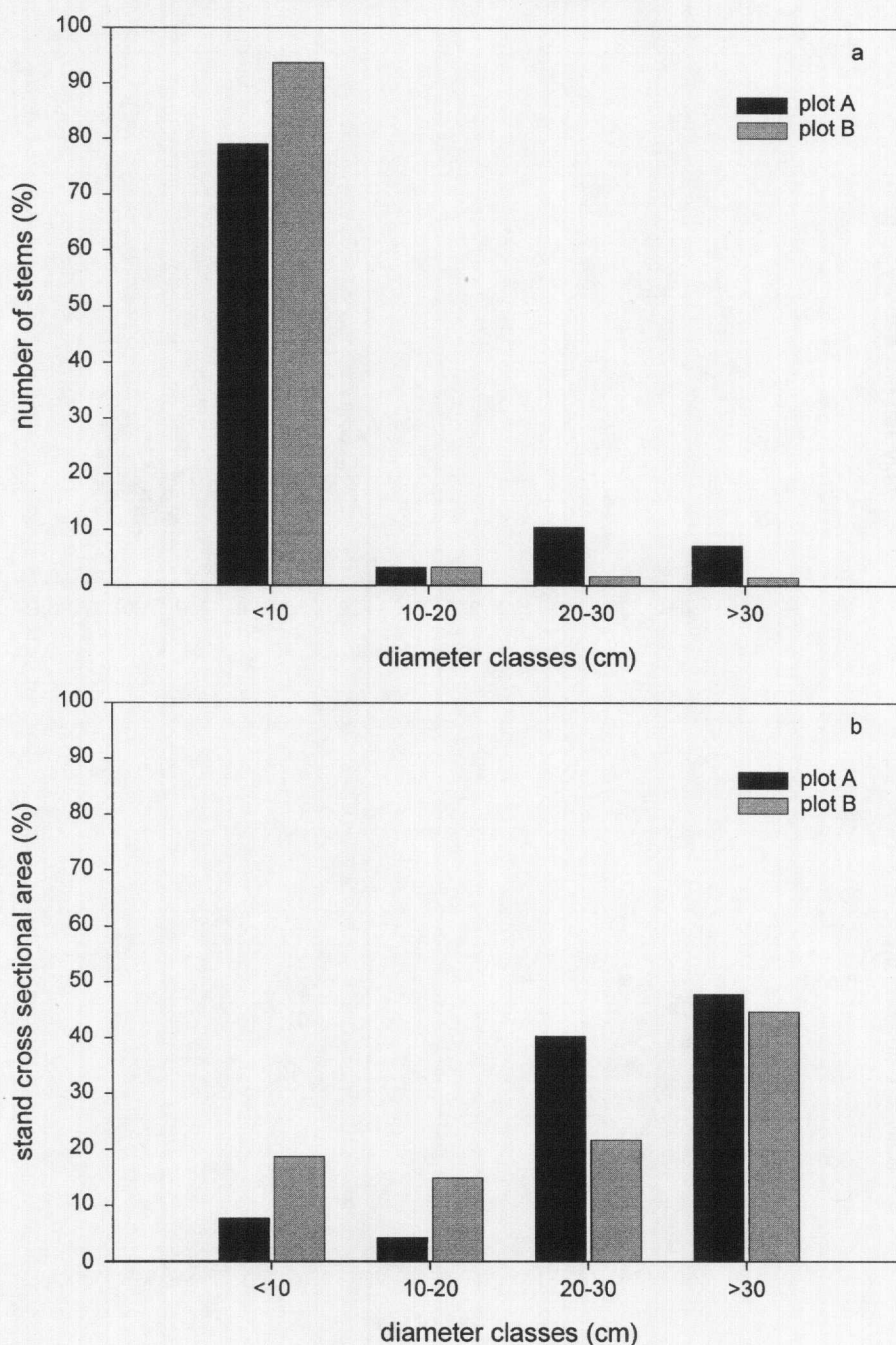
Above-canopy light (short-wave irradiance), air temperature, and relative humidity were measured at 5-s intervals at a large nearby clearcut. The light sensor was a LI-COR LI-200SA pyranometer sensor (LI-COR, Inc., Lincoln, Neb.), while temperature and relative humidity were measured with a Campbell Scientific HMP-35 sensor. The data was recorded as 5-min mean values using a data logger (Campbell Scientific CR-10).

Tree measurements

Diameters of all trees in the two plots were measured by diame-

ter tape. As well, tree heights of all trees in plot A were measured using an electronic surveying device (Criterion model 400, Laser Technology Inc., Englewood, Colo.) for larger trees or height poles and rulers for smaller trees. For the sap flow measurement trees the stem diameters were measured using large calipers as the average of two measurements made at right angles at the point where sensors were installed. From each sap flow measurement tree, two increment cores (taken at right angles) were removed. In the field, the sapwood thickness for each increment core was measured as the translucent portion of xylem. Bark thickness for each increment core was also recorded. Increment cores were wrapped in plastic and frozen stored until with aid of a dissecting microscope the thickness of the previous 10 years growth was measured. From these measurements outside bark cross-sectional area, sapwood area, and area increment for the previous 10 years for each sap flow measurement tree were calculated (Table 1). Individual tree

Fig. 1. Douglas-fir diameter and stand cross sectional area distribution at Pothole Creek.



volume was calculated using a B.C. Ministry of Forests Douglas-fir volume equation:

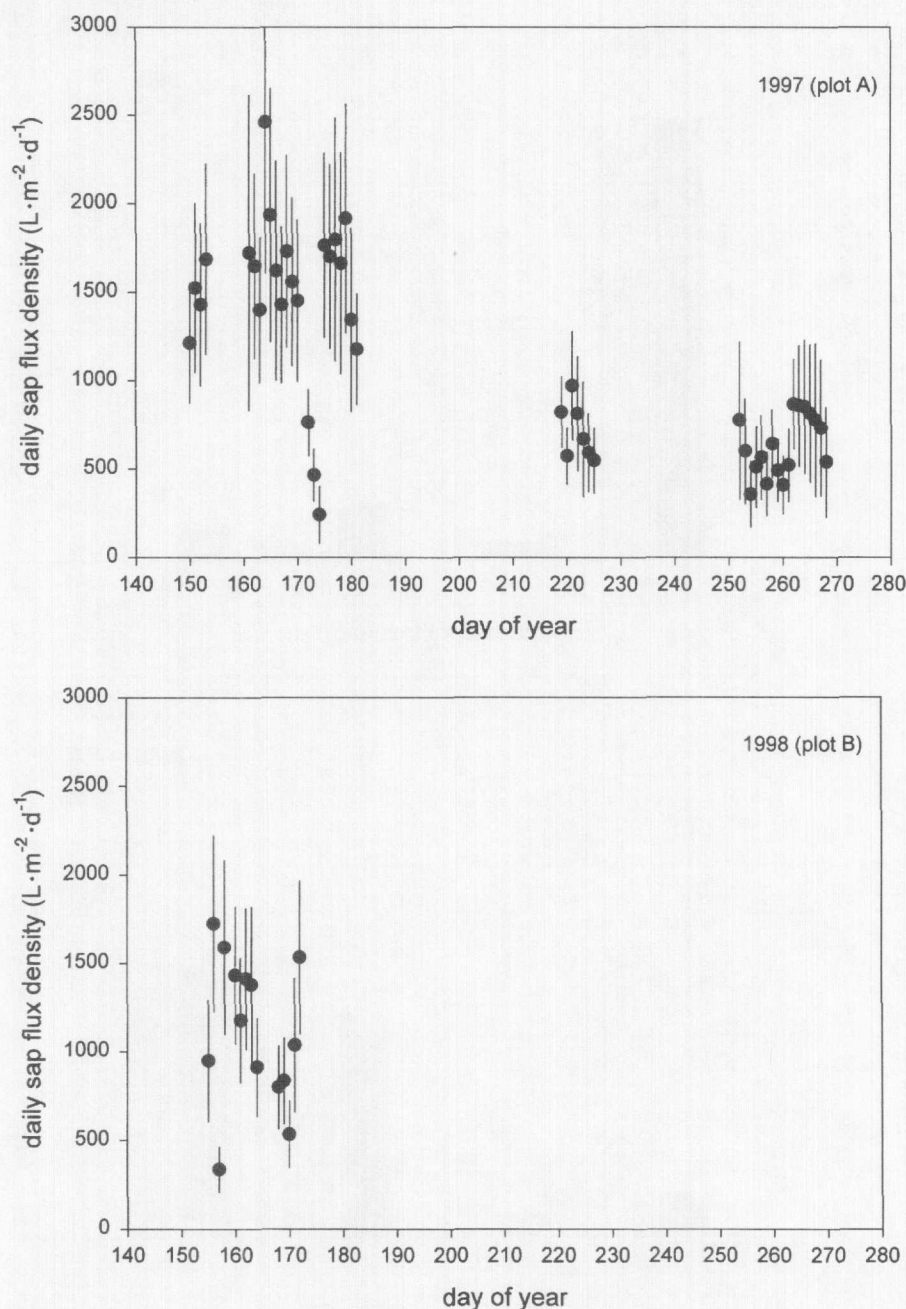
$$\log_{10} \text{ volume} = -4.348375 + [1.692440 \log_{10} \text{ diameter}] \\ + [1.181970 \log_{10} \text{ height}]$$

Individual tree volume and outside bark cross-sectional area for trees in plot A were found to be related by linear regression (volume = $7.178 \times \text{area} - 0.011$, $r^2 = 0.98$, $n = 148$). This relationship was used to estimate tree volumes where height measurements were not available.

Estimates of stand water use

Mean daily early summer stand water use ($\text{mm} = \text{L} \cdot \text{m}^{-2}$) was estimated as the sum (L) of the calculated individual tree water use for each tree in plots A or B divided by the area of each plot, 900 and 2500 m^2 , respectively. For trees with diameter >10 cm, individual tree daily water use (L) was calculated as the product of the overall mean early summer daily sap flux density ($1137.4 \text{ L} \cdot \text{m}^{-2}$) for days 150–181 in 1997 and days 155–172 in 1998 and the individual tree sapwood area. Sapwood areas for all trees in plots A and B were calculated from a regression equation developed from 33 measurement trees (sapwood area = $0.0024 + 0.315 \times \text{outside bark cross-sectional area}$, $r^2 = 0.92$). Daily water use for small trees (<7.5 cm diameter) were not measured in this study. Based on

Fig. 2. Daily sap flux density in 1997 and 1998 for Douglas-fir at Pothole Creek. Each point is the mean ($\pm$ SD) for 8 or 26 trees in plot A or B (day of year 152 is June 1).



measured data for the smallest trees, daily water use for trees with diameter <2.5, 2.5–7.5, and 7.6–10 cm are extrapolated to be 0.5, 2, and 4 L per tree, respectively.

Results

Individual tree water use

Mean daily sap flux density varied from day to day in 1997 and 1998 with the early summer values generally greater than the late summer and early fall measurements (Fig. 2). A prolonged drought (early July to mid-September in 1998) resulted in very low and possibly erroneous sap

flux densities in late summer; thus, only the early summer data for 1998 is shown. It is uncertain if higher early summer (May 30 – June 29) sap flux densities for 1997 ($1485 L \cdot m^{-2} \cdot d^{-1}$) compared with 1998 ($1117 L \cdot m^{-2} \cdot d^{-1}$) reflect true differences among the different trees being measured in the 2 years or are a confounding of different soil moisture availability and weather patterns in the 2 years. In early summer, mean sap flux density varied between trees of different sizes (Fig. 3) with no clear effect of size.

Because of their larger sapwood areas, daily water use (L) of larger trees in early summer was substantially greater than for smaller trees (Fig. 4). Among larger trees (30–35 cm

Fig. 3. Daily early summer sap flux density of 1997 (solid circles) and 1998 (open circles) sap flow trees. Each point is the mean ($\pm$ SD) for 24 (1997) or 11 days (1998).

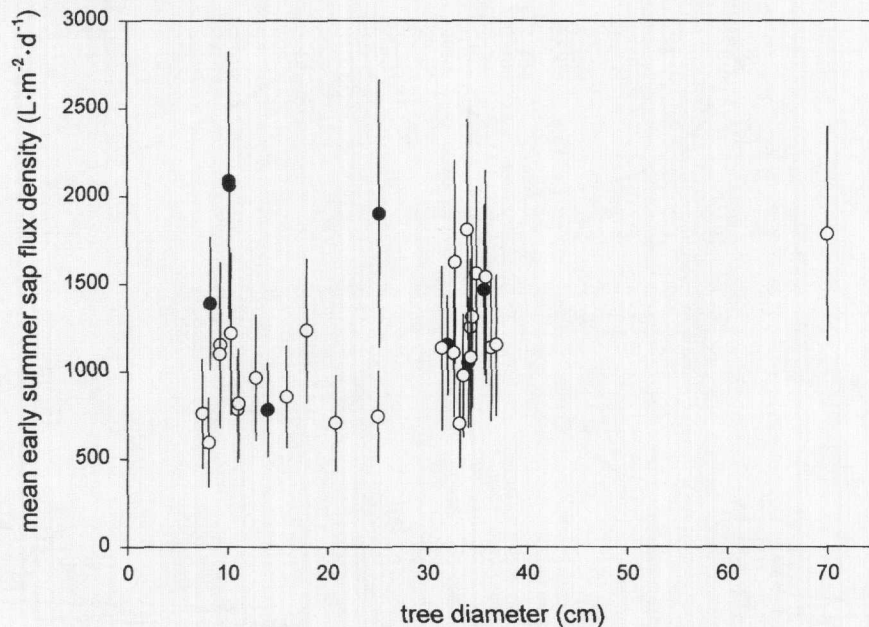
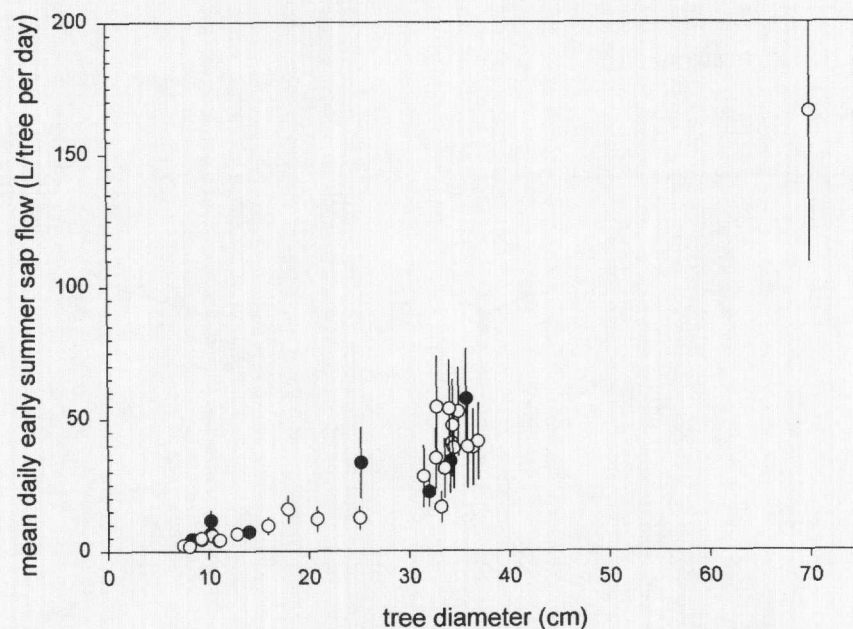


Fig. 4. Daily early summer sap flow for 1997 (solid circles) and 1998 (open circles) sap flow trees. Each point is the mean ($\pm$ SD) for 24 (1997) or 11 days (1998).



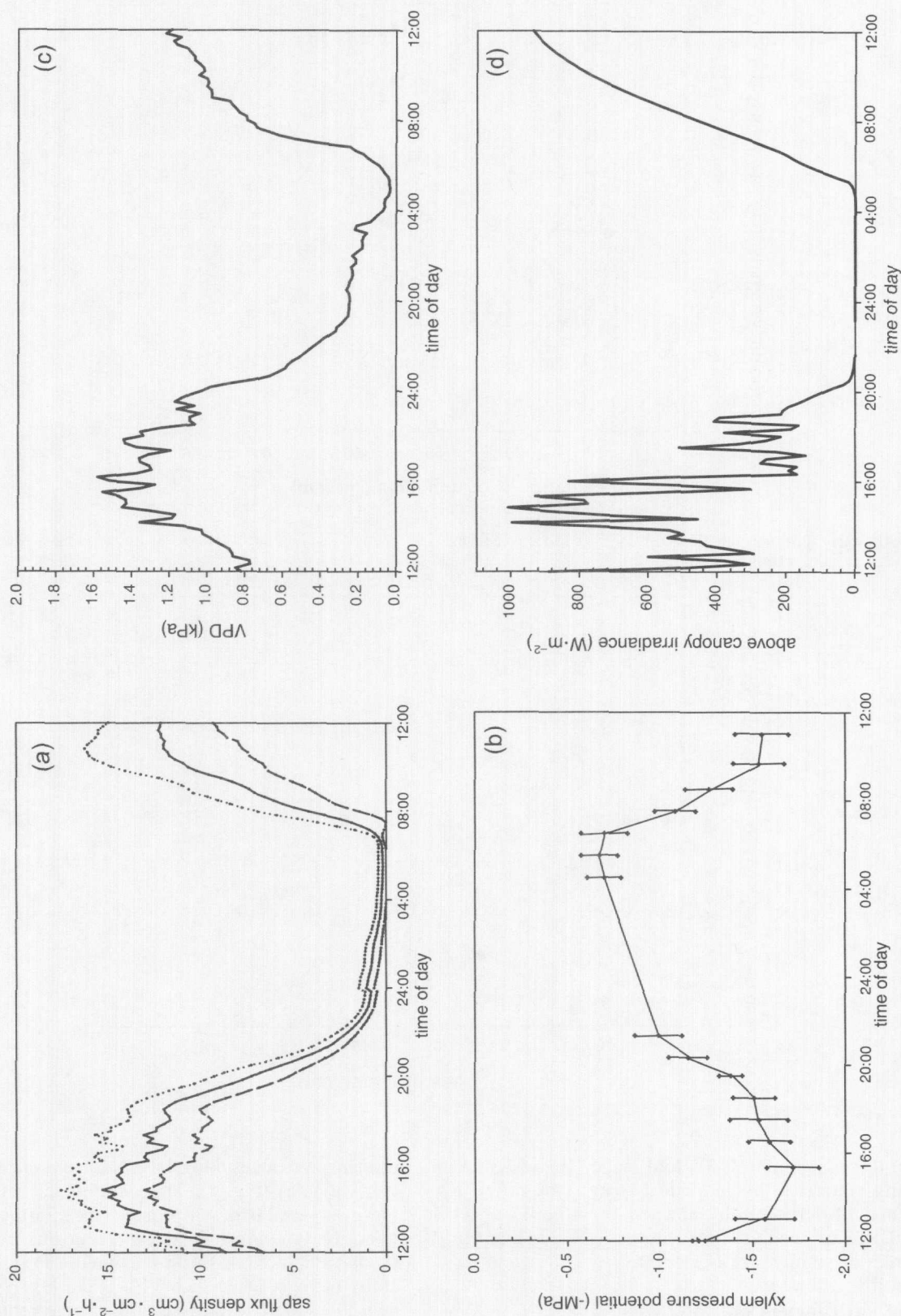
diameter) there is an almost 3.5-fold range (16.4–57.3 L) in mean daily water use by individual trees. This difference reflects both differences in sapwood cross-sectional area ($0.0192\text{--}0.0437\text{ m}^2$) and sap flux density ($700\text{--}1800\text{ L}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) among trees of similar size (Table 1).

Effects of environment on water use

From mid-day June 11 to mid-day June 12 (days 162 and 163), sap flux density and xylem pressure potential of three large and three smaller trees followed very closely the same

diurnal pattern resulting in a close correlation between the two variables (Fig. 5). The slope of the relationship is the mean sapwood hydraulic conductance for the six Douglas-fir trees, $14.34\text{ cm}^3\cdot\text{cm}^{-2}\cdot\text{h}^{-1}\cdot\text{MPa}^{-1}$. Sap flux density increased as air VPD increased with maximum sap flux densities generally being reached with VPD $> 0.6\text{ kPa}$ (Fig. 5). Sap flux density similarly increased with increasing irradiance; however, the relationship is confounded by a time lag such that, for similar but declining irradiance levels, afternoon sap flux densities are greater than for morning values (Fig. 5). Sap

Fig. 5. Mean ($\pm$ SD) sap flux density (a) and mean ($\pm$ SD) shoot xylem pressure potential (b) for six Douglas-fir trees at Pothole Creek from mid-day June 11 to mid-day June 12. VPD (c) and above canopy irradiance (d) for the same period. Real-time relationship between mean sap flux density and shoot xylem pressure potential (e), VPD (f), and irradiance (g).



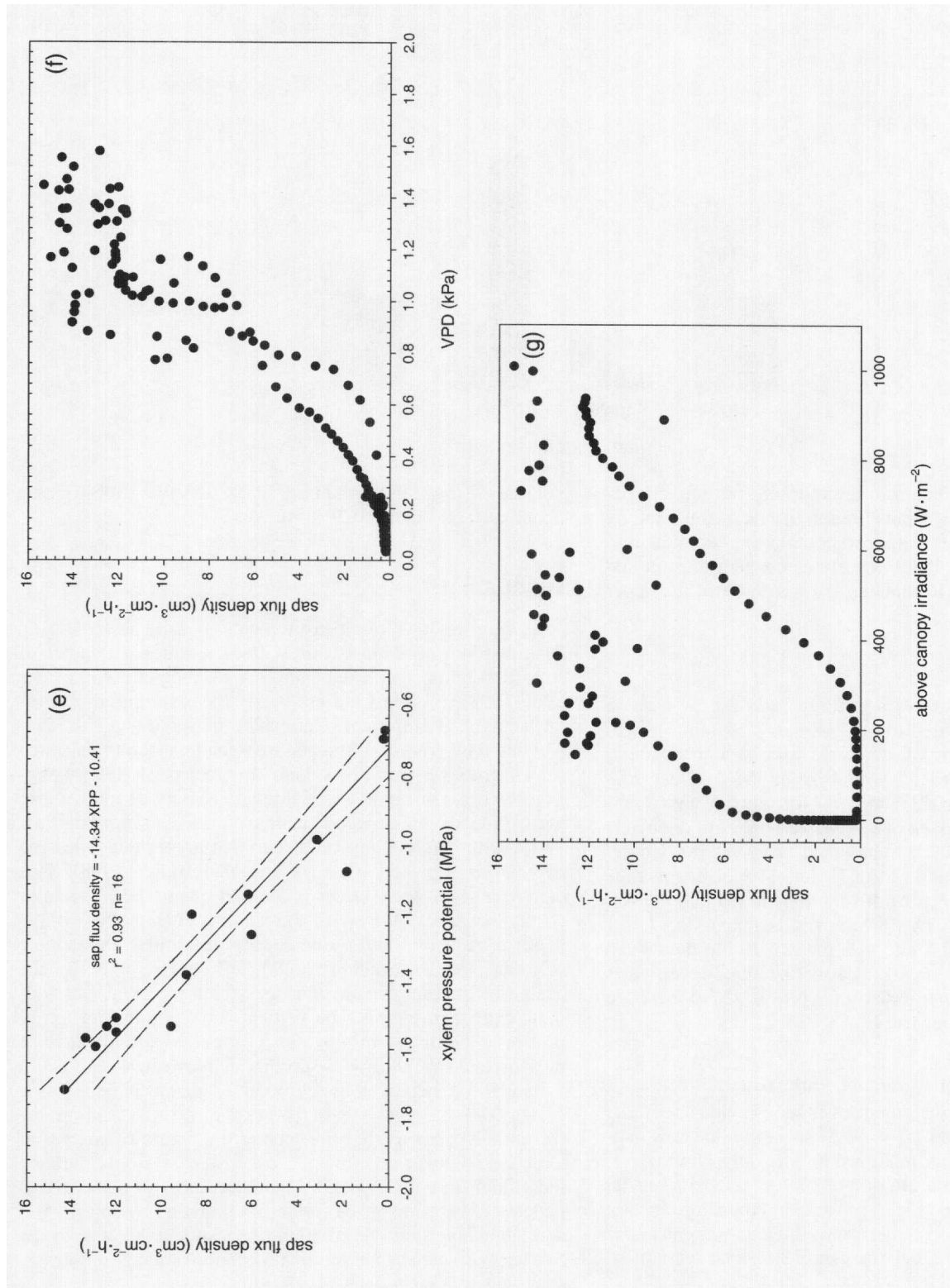
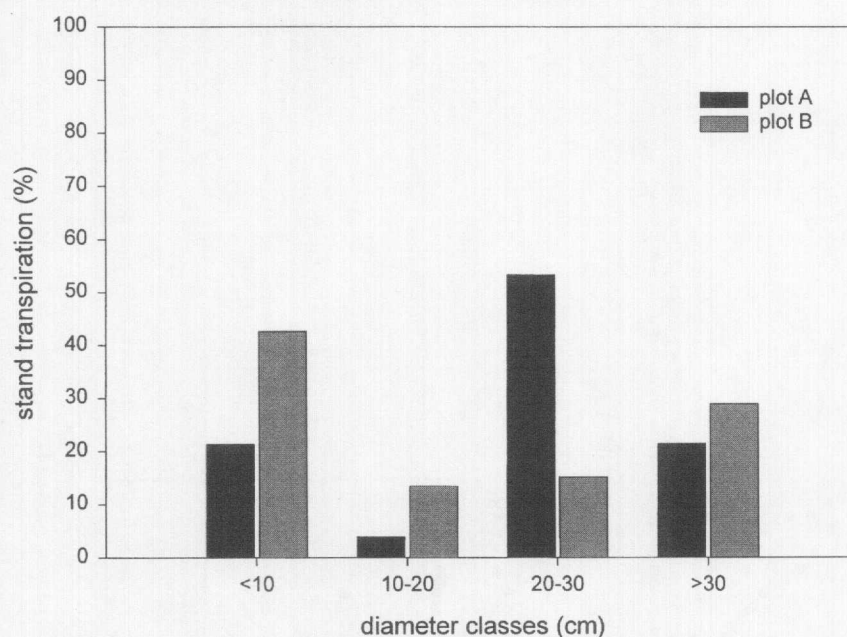


Fig. 6. Relative stand water use by diameter class for Douglas-fir at Pothole Creek.

flux density is slow to begin in the morning presumably because of early morning transpiration needs being met by stored water. Likewise, sap flow continues after dark into the evening so long as there is sufficient xylem tension and available soil moisture to replenish stored water in the upper crown.

Stand water use

Current early summer average daily water use by trees in plots A and B is estimated to be 1.08 and 1.59 mm, respectively. The distribution of this use among four diameter classes (Fig. 6) suggests that water use by the smallest trees (<10 cm diameter) was 21 and 42% for plots A and B, respectively. The two classes of larger trees (>20 cm diameter) representing 88 and 66% of the stand cross-sectional basal area (Fig. 1) are estimated to use 75 and 44% of the average daily stand water use (Fig. 6). It should be noted that the water use for small trees was arbitrarily assigned (0.5 L for <2.5 cm; 2 L for 2.5–7.5 cm; 4 L for 7.5–10 cm diameter); thus, if these assumptions are in error the stand-level water use would be in error, particularly for plot B where there are large numbers of smaller trees.

Relationships between water use and growth

Individual tree area increment over the previous 10 years was very closely related ($r^2 = 0.85$) to individual tree sapwood area (Fig. 7). This relationship was only slightly improved ($r^2 = 0.89$) when area increment is related to mean early summer sap flow (Fig. 7). These relationships are not linear so that relative to smaller trees, the area increments of larger trees are not as great for using the same amount of water.

Stand volume for plots A and B is estimated to have been 116 and 139 $\text{m}^3\cdot\text{ha}^{-1}$ in 1988 and 152 and 186 $\text{m}^3\cdot\text{ha}^{-1}$ in 1998, respectively. Over the 10-year period (1988–1998) the stem volume annual relative growth rate ($\text{RGR} = [\log_e(1998$

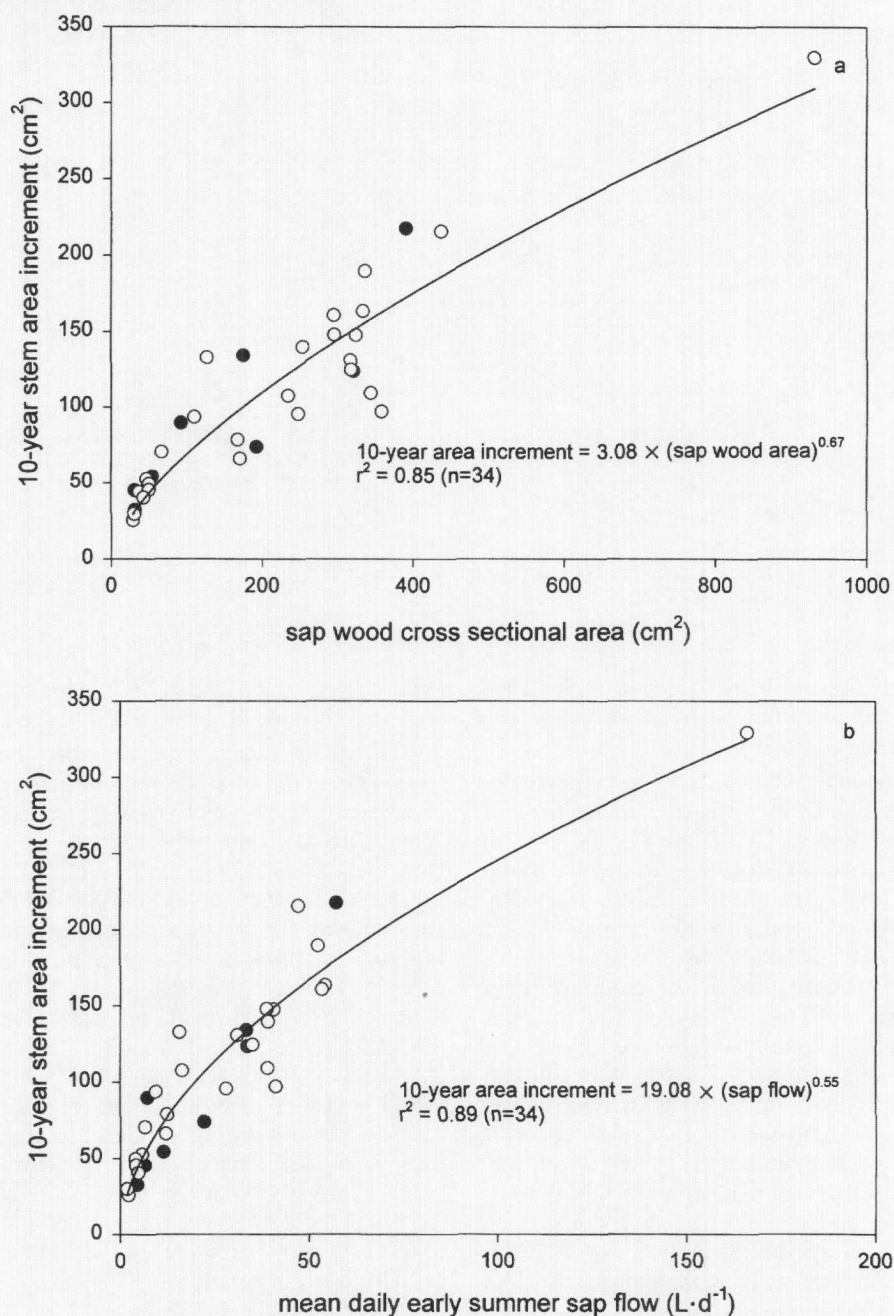
volume) – $\log_e(1988 \text{ volume})]/10$ for the two plots is estimated at 0.027 and 0.029 $\text{m}^3\cdot\text{m}^{-3}\cdot\text{ha}^{-1}$.

Discussion

Scaling up sap flow measurements to daily water use by an individual or stand of forest trees requires a number of steps that introduce various amounts of uncertainty (Kostner et al. 1998b). While I did not verify the assumption of a robust universal empirical relationship between sap flux density and temperature difference between heated and unheated sensor probes, reports by others (Kostner et al. 1998b) suggest the relationship is applicable to a variety of tree species with quite different wood anatomy and density. Sap flow varies with depth of sapwood such that higher rates are seen in younger sapwood (Cermak and Nadezhkina 1998). This can be a source of error, particularly with HPV systems (Hatton et al. 1995). With the Granier TD probes, if the depth of sapwood and probe length are similar, this source of radial spatial variation should be better sampled by the design of the temperature sensors, which integrate measurement over their length. The vertical and azimuth location of probes in the tree stem provides a further potential source of measurement variability as sap flux density often varies with azimuth and height above ground or distance below live crown (Herzog et al. 1998). The extent of this variation differs among trees, perhaps reflecting the nature of spatial interaction between crowns and root systems among individuals in a forest stand. The universality of these spatial patterns is expected to be further confounded by spiral grain and lateral sap flow. Installation of sensors at the base of the live crown seems to minimize variation among sensors in some cases (Lousteau et al. 1998).

Estimation of whole tree sap flow using the Granier TD method requires that an estimate of sapwood basal area be made. From increment cores, the sapwood depth in Douglas-fir is easily distinguished from the nonconducting heartwood

Fig. 7. Ten-year stem cross sectional area increment versus sapwood area (a) and mean early summer sap flow (b) for 8 trees in plot A (solid circles) and 26 trees in plot B (open circles).

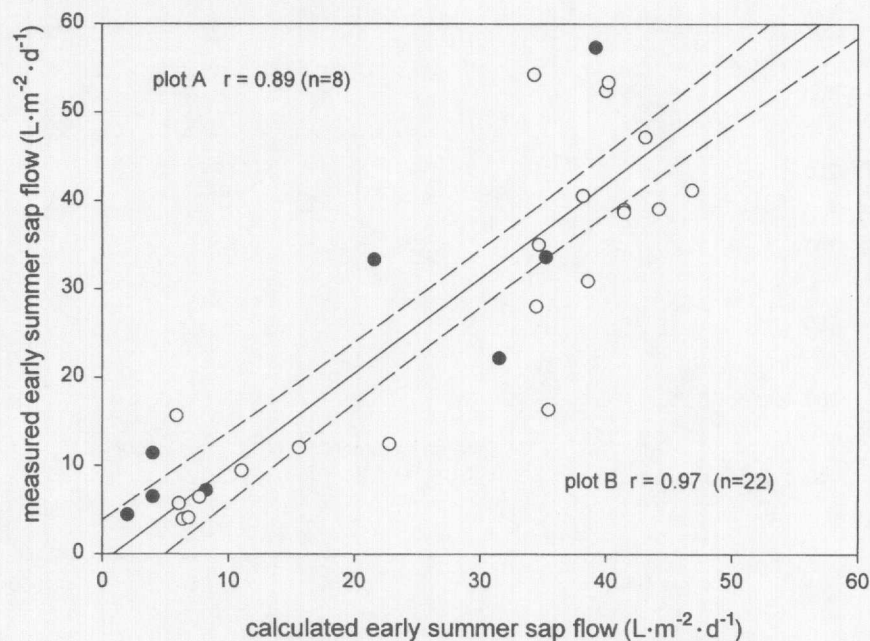


as the translucent outermost portion of the core. Estimation of tree sapwood area from increment cores is prone to some degree of error depending on the asymmetry of the sapwood and the trunk, particularly closer to the ground. The alternative of cutting down the trees to provide a more accurate sapwood area estimate compromises the nondestructive nature of the measurements.

As with other studies (Anfodillo et al. 1998; Becker et al. 1997; Cohen et al. 1985; Hogg and Hurdle 1997; Lopushinsky 1986; Martin et al. 1997; Zhang et al. 1997), I found short-term sap flux density to be closely related to the principal environmental variables driving transpiration, VPD, and irradiance. Daily estimates of individual tree and stand

transpiration derived by scaling leaf level porometer measurements of stomatal conductance using the Penman-Monteith model (Cienciala et al. 1992, 1998; Dye and Olbrich 1993; Gouldin and Field 1994; Granier 1985, 1987; Granier and Loustau 1994; Granier et al. 1996; Teixeira Filho et al. 1998) or by direct measurement of above canopy water vapour fluxes (Cienciala et al. 1997; Diawara et al. 1991; Hogg et al. 1997; Loustau et al. 1996; Oren et al. 1998) are usually in close agreement with stand transpiration estimates made by scaling individual tree sap fluxes. The 1- to 2-h lag in sap flow I observed is consistent with observations made by others (Hogg et al. 1997; Martin et al. 1997; Phillips et al. 1997). I have assumed that, at least in early

Fig. 8. Simple linear correlations between measured and calculated mean daily sap flow for trees in plot A (solid circles) and plot B (open circles). The 95% confidence intervals are shown.



summer, the daily depletion of stored water is replenished each evening; this I believe is a reasonable assumption as a zero sap flux period occurred each evening.

Scaling up from individual tree sap flows to estimates of stand level water use without measuring the actual flow of every tree requires that some scalar of tree size be used in conjunction with the distribution of that scalar in the stand (Hatton et al. 1995; Vertessy et al. 1995). Tree leaf area, stem diameter, and sapwood basal area are commonly used scalars. Tree leaf area is a useful scalar when comparisons or applications to stand level transpiration are required. Stem diameter is the easiest scalar to use, while sapwood area has perhaps the most compelling functional rationale for use as a scalar. I developed a relationship between stem diameter and sapwood area which was used to estimate individual tree sapwood area from stem diameter. In my study as with Kostner et al. (1998a) and Lousteau et al. (1996), there was no apparent effect of tree size (diameter) on sap flux density (Fig. 3); thus, on scaling up sap flow from individual trees to the stand level, the average daily sap flow for all trees >10 cm diameter was calculated as the simple product of the mean early summer daily sap flux density ($1137.4 L \cdot m^{-2}$ sapwood) and the sum of the individual tree sapwood areas. A comparison of calculated daily sap flow and measured daily sap flow for the 34 sap flow trees (Fig. 8) suggests that the individual tree estimates are fairly close ($r = 0.89$ and 0.97) to measured water use. As the stand water use estimates are simple sums of the individual tree estimates, these estimates should have similar relative accuracy. For smaller trees (<10 cm), data existed for only several in the 7–9 cm diameter size, and from these the daily sap flow (L) was arbitrarily assigned. Although this size class only constitutes 7.7–18.7% (Fig. 1) of the stand basal area, for small trees (compared with large trees) a larger portion of that basal area will be sapwood (Sellin 1991), and thus, small trees might be expected to use a significant amount of transpired

water (I estimate 21.3–42.6%; Fig. 6). Future study should examine in greater detail the water use by the small trees.

Growth of plants increases with the amount water they use. This is the basis for the concept of water-use efficiency (Landsberg 1986). For trees, water use efficiency measurements are not commonly made using whole plants (Livingston and Black 1988; Smit and van den Driessche 1992). However, because of well-established relationships based on instantaneous gas-exchange measurements of net carbon assimilation and water transpiration it is a widely accepted ecophysiological principle (Jones 1983). At the stand scale, linkages have been made between stand growth and evaporation (Le Maitre and Versfeld 1997). In this study, very close relationships have been found between individual tree basal area increment and stem cross sectional area or mean daily water use during the early summer (Fig. 7). Trees that use more water have greater growth. This relationship is consistent with a number of factors. First, the amount of water used by a tree is a function of the tree leaf area. Secondly, for trees growing under similar conditions, there is usually a linear relationship between leaf area and sapwood area; for example, for Douglas-fir ratios of 0.4–0.6 m^2 projected leaf area/ cm^2 sapwood basal area have been reported (Bartelink 1996; Brix and Mitchell 1983; St. Clair 1993). Thirdly, stem growth is a residual function of whole tree net carbon assimilation; larger amounts of stem increment growth will occur in trees with more foliage (= larger crowns). Thus, trees with larger crowns will have greater sapwood areas and will be expected to use more water and have greater stem increment growth.

For the Pothole Creek site, mean daily early summer water use by the trees appears to be between 1 and 1.5 mm. This is about 20–30% of the $5 mm \cdot d^{-1}$ maximum (soil water not limiting) potential evapotranspiration (ET) predicted by the Turc equation ($ET = [(I/41.868) + 50] \times [0.0137/(T + 15)]$; Ciencila et al. 1997) with mean daily short-wave irradiance

(I) and temperature (T) of 30 000 kJ and 15°C, respectively. Kelliher et al. (1997) reported that, on nice days in mid-July, a fairly sparse (LAI = projected leaf area/ground area = 1.5) Siberian larch (*Larix sibirica* Lebed.) forest used about 1.9 mm of water, with about 50% of this use by understory. Recently, Anthoni et al. (1999) reported average midsummer water use by a dry open-canopied (LAI = 1.6) ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) forest to be about 1.6 to 1.7 mm·d⁻¹. For a grass-covered forest clearcut at a site similar to Pothole Creek, Adams et al. (1991) reported daily evapotranspiration averaged 80% of the equilibrium evapotranspiration rate with measured values as high as 4.1 mm. Considering the open nature of the stand at Pothole Creek, water use by the grass and direct evaporation from bare ground could be expected to account for significant soil moisture depletion. The exact magnitude of this understory water use is presently unknown, however.

Stem increment cores taken to determine sapwood area show that, for many trees in the years following logging, there was an increase in the width of the annual growth rings. This increased growth increment would be expected if more water became available to each tree following logging. Future growth of the trees at the study site will result in an increase of stand sapwood area and presumably a proportional increase in the leaf area supported. The relationship between stem cross-sectional area increment and water use will begin to change as the growth increments diminish because of a shorter growing season with possibly greater moisture stress. Presently, assuming a leaf area/sapwood area ratio of 0.4 m²·cm⁻², the stand LAI is between 3 and 4. If LAI were to increase to 5, there is potential for stand water use to increase 25–30%. This increased tree water use will presumably be at the expense of grass water use as less light becomes available for grass growth and transpiration. For Douglas-fir, Granier (1987) showed that daily sap flow was not limited by soil water when the relative extractable water (REW) was greater than 0.4. Assuming a rooting depth of 60 cm and growth to be possible when soil moisture content is in the 10 to 25% range (REW > 0.3), the pothole site should have about 90 mm of potential growing season evapotranspiration.

For the two plots at Pothole Creek, the mean annual stem volume relative growth rate for the period 1988–1998 is estimated at 0.027–0.029 m³·m⁻³·ha⁻¹. This volume growth rate (2.7–2.9 m³·ha⁻¹·a⁻¹ for a stand with volume of 100 m³·ha⁻¹) is slightly less than the average volume growth (3.3 m³·ha⁻¹·a⁻¹) that Bonner et al. (1991) report for 92 interior Douglas-fir permanent sample plots having an average stand volume of 94 m³·ha⁻¹. The effect on forest productivity of various stand level silvicultural and harvesting treatments is usually assessed by making measurements of tree diameter and height. For dry interior forests, the very slow growth of trees means that a period of 5–10 years must elapse between subsequent measurements so that the incremental growth of trees is greater than the measurement error associated with repeated measurement using standard practices. This delay in obtaining useful information could be shortened by making individual tree water use measurements on trees in the different treatments, and inferring from the treatment effects on water use what the probable future growth effects might be.

A relationship between water use and tree growth is currently implicit in forest yield modelling and uneven age silvicultural management. The TASS model (Mitchell 1975) upon which many forest stand yield predictions in British Columbia are based, has its central assumption that there are functionally based relationship between the crown volume (a surrogate for leaf area) and stem growth of individual trees. Recently, O'Hara (1998) has advocated that silvicultural management of uneven-aged forests be based less on maintenance of certain diameter distributions and more on allocating growing space among size classes based on leaf area (sapwood area). As leaf area is a principal determinate of water use at both tree and stand level, uneven-aged stand management becomes then a matter of water management, both in total amount used by the stand (= site productivity) and the relative amount used by individuals (= competition).

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