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ECOSYSTEMS

Components and Controls of Water Flux in an Old-growth Douglas-fir–Western Hemlock Ecosystem

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ABSTRACT

We report measurements of rates of sap flow in dominant trees, changes in soil moisture, and evaporation from coarse woody debris in an old-growth Douglas-fir–western hemlock ecosystem at Wind River, Washington, USA, during dry periods in summer. The measurements are compared with eddy-covariance measurements of water-vapor fluxes above the forest (E_e) and at the forest floor (E_u) to examine the components of ecosystem water loss and the factors controlling them. Daily values of E_u were about 10% of E_e. Evaporation from coarse woody debris was only about 2% of E_e. Transpiration (E_t), estimated by scaling sap-flow measurements accounted for about 70% of (E_e–E_u); transpiration from subdominant trees may account for the remainder. The daily total change in soil moisture (E_s) in the top 30 cm was larger than the net change, probably because of hydraulic redistribution of soil water by roots. Observed differences between E_s and E_e were probably because roots also extract water from greater depth, and/or because the measuring systems sample at different spatial scales. The ratio of E_t to E_s decreased with decreasing soil water content, suggesting that partitioning in water use between understory and overstory changed during the season. The rate of soil drying exceeded E_e early in the day, probably because water vapor was being stored in canopy air space and condensed or adsorbed on tree stems, lichens, and mosses. The daily variation of E_e with vapor-pressure deficit showed strong hysteresis, most likely associated with transpiration of water stored in tree stems and branches.

Key words: sap flow; soil moisture; eddy covariance; transpiration; evaporation; condensation; hydraulic redistribution; hysteresis.

INTRODUCTION

The carbon exchange of ecosystems is strongly influenced by water status, including the effects of water stress on stomatal conductance, and the influence of moisture on heterotrophic and

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autotrophic respiration. To understand and model how the carbon budget of a forest ecosystem will respond to weather and climate, it is necessary to understand how soil water content is related to the hydrologic processes of precipitation, evaporation, transpiration, and drainage. The aims of this article are (a) to quantify the rate of water loss to the atmosphere from the old-growth Douglas-fir–western hemlock ecosystem at Wind River, Washington, USA [specifically, from measurements at the Canopy Crane Research Facility (WRCCRF)] in summer when precipitation and drainage were negligible, (b) to identify the magnitudes of the main components of the water loss, and (c) to explore how climate and other factors control these components. Shaw and colleagues (2004) described the ecological setting of the Wind River old-growth forest.

The water-vapor-flux density (E, mm h^{-1}) from forests to the atmosphere arises from several sources. In closed-canopy forests, when leaf-area indices (LAIs) exceed about 3–5, transpiration from the trees is the main component of E when the canopy is dry (Denmead 1984; Kelliher and others 1986, 1990; Baldocchi and Vogel 1996; Blanken and others 1997). Transpiration from understory shrubs and evaporation from the soil surface are usually small components of total ecosystem water flux because there is limited available energy at the forest floor to drive evaporation (Kelliher and others 1990; Blanken and others 1997). However, Baldocchi and Meyers (1991) showed that water-vapor fluxes from a forest floor depended on the frequency of large-scale turbulent eddies that coupled the air above and within the canopy, and on air pressure fluctuations that probably enhanced transfer of water vapor from litter and soil pores. The relative importance of turbulent eddies and air-pressure fluctuations in driving evaporation depended on whether the forest floor was wet or dry. It is therefore likely that the structure of a forest canopy and of forest-floor litter layers both influence the proportion of E that can be attributed to evaporation from soil and litter. Evaporation from other sources, such as coarse woody debris at the forest floor, standing dead wood, and bryophytes and lichens, has seldom been quantified in ecosystem water-balance studies, but could be significant in an old-growth ecosystem where the biomass of these components is relatively large compared to younger forests.

At the WRCCRF, there is typically very little precipitation from June to October (Shaw and others 2004), so soil moisture declines substantially through the summer. Plant water stress induced by the combination of dry soil and low humidity can significantly reduce photosynthesis in late summer (Winner and others 2004). Additionally, the high temperatures of foliage, branches, boles, and soil at this time may result in increased respiration. Consequently, net ecosystem carbon exchange (NEE) may be significantly reduced as water availability declines (Paw U and others 2004). Anthoni and colleagues (1999) found that NEE was substantially reduced as soils dried and air temperatures increased in summer in an old-growth ponderosa pine stand in central Oregon, about 80 miles from the WRCCRF, and showed data suggesting that the scale of reduction was likely to vary between years, depending on seasonal weather patterns.

The forest structure at the WRCCRF is complex (Parker and others 2004; Shaw and others 2004), with seven conifer and two angiosperm tree species in the 2.3-ha crane circle, large amounts of woody debris on the forest floor, and a diverse understory. The stand is dominated by a few large individuals of *Pseudotsuga menziesii* (Douglas-fir), 40–65 m high and up to 450 years old, which contribute about half of the wood volume of the stand and 33% of the foliage area. *Tsuga heterophylla* (western hemlock), which are more numerous but smaller, contribute the largest fraction of the foliage area (about 53%) (Parker and others 2004). Within the canopy are many smaller stems of *Thuja plicata* (western red cedar) and two species of *Abies* (fir). The understory contains numerous small *Acer circinatum* (vine maple) trees. Thomas and Winner (2000) estimated that the average total LAI in the crane circle was about 8.6, distributed vertically as 4.8 in the middle and upper canopy, 2.1 in the lower canopy, and 1.7 in the understory. They emphasized that the magnitude and vertical distribution of local LAI varied substantially as a function of the uppermost tree species present. Soils and drainage are also quite variable across the site, with forested wetlands lying about 500 m to the northeast of the crane, and a gradual upward slope to the west that typically has drier soils. This spatial heterogeneity in vegetation and soil properties presents a challenge in scaling up the components of latent heat flux, and this is further complicated by the different scales at which the fluxes are sampled by the measuring systems described later.

In this report, we analyze data collected from several soil moisture-monitoring sensors, sap-flow sensors in dominant Douglas-fir trees, moisture sensors in coarse woody debris, air temperature and humidity sensors at several heights in the canopy, and eddy-flux systems operated above the forest canopy and at the forest floor. To illustrate the dependence of component fluxes on environmental conditions, we selected four periods between September 1998 and September 1999 when there were contrasting weather and soil moisture conditions. The year 1998 was an El Niño period, warmer and drier than normal. By September 1998, soils were at their driest of all the analysis periods, and air temperature (T_{air}) and atmospheric vapor-pressure deficit (VPD) were both high; in contrast, temperatures and precipitation in 1999 were more typical of long-term means (Shaw and others 2004) so soil moisture was larger than for corresponding summer months in 1998.

METHODS

Analysis Periods, Microclimate and Soil Moisture Data

Periods of 11–17 days were selected to capture a range of atmospheric and soil moisture conditions in summer. In 1999, the periods were 13–23 June (days 164–174), 15–31 July (days 196–212), and 7–17 September (days 250–260). To illustrate interannual variability, we also included 7–17 September 1998.

For each period, measurements of air temperature, relative humidity, net radiation, wind speed, and wind direction were taken as half-hour averages from archived data. A net radiometer was located above the crane jib, 85 m above the ground; other measurements describing above-canopy microclimate were taken on the crane tower at 68 m, just below the jib. Half-hour averages of air temperature, relative humidity, wind speed and direction within the canopy were also available at heights of 2, 12, 23, 40, and 57 m on the crane tower; the temperature and humidity profiles were used to derive profiles of dew-point temperature, VPD, and absolute humidity, and hence to estimate changes in the storage of water vapor in the canopy air space (see below). Soil moisture was taken as the mean from four sensors (see below). Soil temperature (used for corrections to soil moisture sensors) was measured at depths of 0, 5, 10, and 25 cm near the within-canopy microclimate profiles and at 15 cm adjacent to a soil moisture sensor. Figure 1 shows the daily mean above-canopy microclimate and soil moisture data for each period calculated from ensemble averages of half-hour data.

In June 1999, soils were still quite moist from winter and spring precipitation, air temperature and VPD were the lowest of the four periods, and net radiation was relatively variable because most days were partly cloudy. In July, there was less cloud, air temperature and VPD increased, and soil moisture declined, primarily because of evapotranspiration. By September 1999, soils were at their driest for the year, and radiation and air temperature were beginning to decline, but VPD remained large. For comparison, in September 1998, the soil was driest of all four periods, and temperature and VPD were slightly larger than values measured in September 1999.

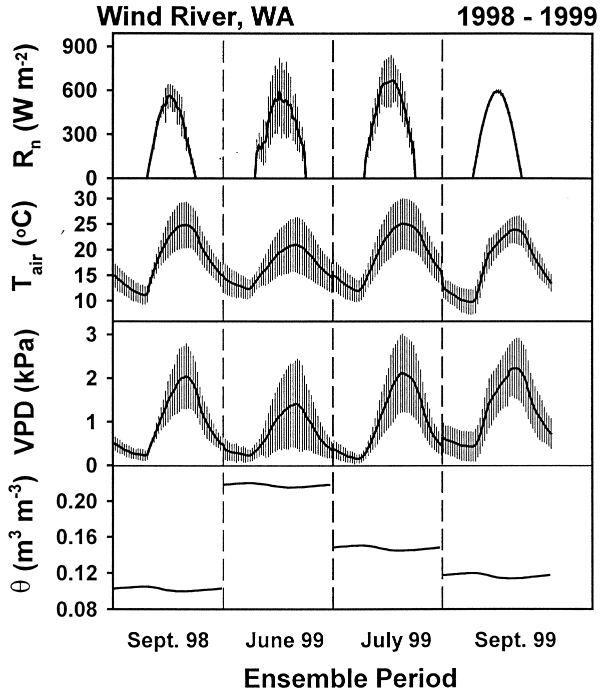

Figure 1. Daily variation in above-canopy microclimate and soil moisture for four analysis periods in 1998 and 1999, calculated from ensemble averages of half-hourly observations. R_n, net radiation; T_{air}, air temperature; VPD, vapor-pressure deficit; and θ, volumetric soil water content.

Data from each of the major component sources of water use (E) were analyzed (where available) to produce half-hour records for each day. To study mean diurnal cycles, we made ensemble averages of half-hour data for each of the periods to reduce variability and avoid occasional data gaps. We also calculated the mean daily values for each component by summing the half-hour periods.

Water-vapor Flux Above and Below the Canopy

To measure water-vapor (and carbon dioxide) exchange for the whole ecosystem and at the forest floor by micrometeorological methods, eddy-covariance systems were mounted at 70-m height on the crane tower, and at 3-m height 35 m west of the tower. Full details of the methods and corrections applied are provided by Paw U and colleagues (2004). The lower eddy-covariance system measured E_u, the transpiration from the understory below the sensors and evaporation from the soil, and the upper system measured the total ecosystem water-vapor flux from evaporation and transpiration, E_e.

The area over which eddy-covariance systems integrate fluxes (the *footprint*) depends on atmospheric stability, wind speed, and canopy structure (Schuepp and others 1990; Paw U and others 2004). For the 70-m sensors, the footprint probably extends less than 100 m upwind of the tower in unstable daytime conditions, but may exceed 1000 m (beyond the range of uniform forest conditions in some directions) in stable conditions at night. For the 3-m sensors, the footprint is often less than 30 m. Measurements were also affected by the structure of the crane tower when the wind direction was between 45° and 135°. In screening water-vapor-flux measurements at 70 m for this analysis, we rejected all flux data from the 45°–135° sector, but accepted data from all other directions because water-vapor fluxes are heavily weighted around noon, when footprints are small enough for fluxes to be characteristic of the old-growth forest. We accepted eddy-flux data measured at 3 m for all wind directions because of the small footprint at that height.

Soil Moisture

Soil Water Content Measurements. Estimates of temporal changes in volumetric soil water content (θ) were made using water-content reflectometers [WCRs (model CS615; Campbell Scientific, Logan, UT, USA)]. These instruments respond to the change in capacitance of soil, which is proportional to the dielectric constant, primarily a function of θ. Although the devices are reliable for assessing daily mean values of θ, there is debate over whether they, and similar devices, are useful for measuring changes in θ over shorter periods when temperature changes may influence the response (Paltineanu and Starr 1997; Seyfried and Murdock 2001). We discuss this further in the Results section.

Four WCR sensors were placed along a 30-m transect that spanned an area of closed canopy and a canopy gap close to the location where sap fluxes were monitored. The probes, 30 cm long, were installed vertically. Field comparisons with independent measurements of θ supported use of the manufacturer's calibration factors in WRCCRF soils. Small corrections for soil temperature variation were made using the manufacturer's algorithm applied to soil temperature data at 15 cm acquired concurrently. The resolution of each θ measurement is about 10^{-6} m^3 m^{-3}, enabling the accurate estimation of small temporal changes provided that temperature corrections can be made.

To scale the high temporal resolution measurements of θ to the plot scale, an array of 34 pairs of stainless steel waveguides was installed in the 2.3 ha crane circle for determination of θ by time-domain reflectometry (TDR). The SWC at each location was determined using a Trace time-domain-reflectometry system (model 6050XI; Soilmoisture Equipment, Santa Barbara, CA, USA) at 1- to 4-week intervals. The mean seasonal trend in θ determined with the spatially distributed probes closely matched the mean trend of the automated CS615 sensors.

Soil Moisture Data Analysis. During all four periods, the surface soils were relatively dry, and calculations using a soil hydrology model with appropriate values of soil physical properties (T. Link unpublished) indicate that no drainage from the 0- to 30-cm soil layer was likely to occur. We therefore assume that decreases in θ were caused by the water flux (E_s) from this soil layer to the atmosphere, either by root extraction and subsequent transpiration or by soil surface evaporation. No significant precipitation occurred during each of the four periods, so it is assumed that observed increases in θ resulted from upward transfer of water from deeper layers, by capillary rise and by hydraulic redistribution (Dawson 1993; Burgess and others 1998). The total daily water flux from the 0- to 30-cm soil layer was calculated from the difference between the maximum and minimum values of θ observed during a day. The net daily water flux is the difference between one daily maximum and the next. Mean half-hourly soil water fluxes were determined for each analysis period by numerically differentiating the soil moisture vs time relationship for each day, converting the values to mm h^{-1}, and computing the ensemble-averaged fluxes.

Overstory Transpiration

Sap-flux Measurements. Estimates of overstory transpiration from Douglas-fir were made by scaling sap-flux measurements, obtained using the heat-dissipation method (Granier 1985). Sap-flow sensors were 2 cm long, dissipated 200 mW thermal power into xylem, and were inserted into the hydroactive xylem at two depths (0–2 cm beneath cambium and 1.5–3.5 cm beneath cambium) to account for radial variation in sap-flux density. Depth of sapwood averaged 43 mm in the measured trees. There were 3–5 sensors installed about 4 m above the ground on each of six dominant Douglas-fir individuals for scaling to the plot level. Sap-flux density (J_S), in grams of water per second per unit sapwood area, was estimated by the empirical equation of Granier (1987). Further details of the sap-flux measurements made at this site are described by Phillips and colleagues (2002).

Scaling Considerations. Sap-flux measurements were restricted to Douglas-fir trees, which represent the largest trees and the greatest proportion of basal area (43%) at the WRCCRF site. However, scaling of sap fluxes from six large Douglas-fir individuals to the ecosystem level involves several potentially large sources of uncertainty, including (a) within-tree and between-tree variation in sap flux, (b) variation in sap flow among tree species, and (c) spatial variation in the distribution of trees of the dominant species at this site, which extends beyond the plot scale to the footprint of eddy-covariance measurements of E_e. In this study, we have directly considered only the first level of variation listed above for Douglas-fir. We indirectly assessed the second level of variation listed above by using supplemental sap-flow measurements taken during another period at this site for the most prominent other tree species in this site (western hemlock and western red cedar). In this study, we do not assess the third level of variation listed above. Although ecosystem-scaled sap-flux measurements in this study likely represent relative differences in ecosystem transpiration well throughout the season, caution is necessary in interpreting the absolute magnitude of these estimates in relation to eddy-covariance measurements of E_e.

Sap flux per unit ground area in Douglas-fir was estimated by multiplying sap flux per sapwood area by the sapwood area per unit ground area estimated for Douglas-fir in the 4-ha crane plot [4.56 $m^2\ ha^{-1}$ (depts.washington.edu/wrccrf/database.html)]. To estimate total overstory transpiration E_t, it was necessary to include estimates of sap flux in western hemlock and western red cedar, which comprise 31% and 20% of the stand basal area, respectively (compared to 43% for Douglas-fir). Supplemental sap-flux measurements were made at this site during the summer of 2000 from three large western hemlock trees, three large western red cedar trees, and three large Douglas-fir trees (A. Schauer unpublished data). Relationships between sap flow (in $kg\ m^{-2}\ day^{-1}$) of these species were

J_S (hemlock) = −47.7 + 0.353 J_S (Douglas-fir) $r^2 = 0.88$ and $P < 0.0001$

J_S (red cedar) = 1.12 J_S (Douglas-fir) $r^2 = 0.75$ and $P < 0.0001$

These relationships from 2000 were used with 1998 and 1999 sap-flow data from Douglas-fir to obtain sap-flux estimates for hemlock and red cedar in those years. To scale those estimates to unit ground area, sap fluxes in hemlock and red cedar were multiplied by the sapwood area per unit ground area ratios of 11.07 $m^2\ ha^{-1}$ and 1.42 $m^2\ ha^{-1}$ for hemlock and red cedar, respectively (depts.washington.edu/wrccrf/database.html). Additionally, we assumed that sap fluxes from *Abies amabilis* (sapwood area = 1.7 $m^2\ ha^{-1}$) and *Taxus brevifolia* (sapwood area = 0.98 $m^2\ ha^{-1}$) were similar to those of western hemlock.

Evaporation from Coarse Woody Debris

Harmon and colleagues (2004) describe how coarse woody-debris mass was sampled. All downed coarse woody detritus (greater than 0.1 m in diameter and more than 1.0 m long) and standing dead trees (greater than 0.1 m in diameter and more than 1.0 m high) were inventoried in a 4-ha area centered on the crane circle. Volumetric water contents of a subsample of downed coarse wood and standing dead trees were measured at approximately monthly intervals using time-domain reflectometry. The inventory and measurements enabled us to estimate the mass store of water. Monthly changes in water mass stored in each species and decay class were computed and converted to mm day^{-1} to match the other water fluxes reported in this article.

Water-vapor Exchange by Bryophytes and Lichens

The canopy contains about 1.3 tonnes (dry weight) ha^{-1} of lichens and probably a similar mass of bryophytes (Shaw and others 2004; B. McCune personal communication), which intercept precipitation and exchange water vapor with the air. When completely wet, lichens and bryophytes absorb about 6-10 times their dry weight of water (B. McCune personal communication). We discuss their possible role in adsorbing and desorbing water vapor later, when considering diurnal variation in fluxes.

RESULTS

Interpretation of Observed Changes in Volumetric Soil Water Content

Figure 2 shows the typical daily variation in θ that we observed during all periods. The decrease in θ in the first part of each day, and downward trend over the period, are consistent with water extraction by root uptake and soil surface evaporation. The increases in θ observed each night suggest that hydraulic redistribution was occurring, as reported by Brooks and colleagues (2002), who used a different type of soil moisture probe (Sentek PTY, Adelaide, Australia) at a site with 20-year-old Douglas-fir a few kilometers from the WRCCRF. Figure 2 indicates that the average total daily water flux from the 0- to 30-cm layer was about 2 mm (daily maximum–minimum θ range of 0.0065 m^3 m^{-3} applied over a depth of 0.30 m), and that the average net daily water flux was about 0.24 mm (a decline of about 0.0008 m^3 m^{-3} per day over a depth of 0.30 m). However, reports of temperature sensitivity in the CS615 soil moisture probes (Seyfried and Murdock 2001) raised concern over whether some of the apparent daily variation we observed in θ could have been caused by temperature variation in the soil layer or in the instrument electronics. We used results of other experiments to assess this concern.

Variation in soil temperature at the mean depth of the probes (15 cm) does not appear to cause significant errors. Using the temperature sensitivity reported by Seyfried and Murdock (2001), and the observed WRCCRF soil temperature at 15 cm, the influence of soil temperature on the daily variation of θ was less than 0.0003 m^3 m^{-3}, about 5% of the typical variation we observed. From studies with the sensors in air, Seyfried and Murdock (2001) reported a temperature sensitivity of about −0.0004 m^3 m^{-3}°C^{-1}, which they interpreted as the sensitivity of the electronics of the devices. By changing the temperature of the aboveground electronics on CS615 sensors inserted vertically in a Pacific Northwest forest soil when θ was about 0.1, Moore found a temperature sensitivity for the electronics of about −0.0002 m^3 m^{-3}°C^{-1} (G. Moore, Department of Forest Science, Oregon State University, personal communication). Using the mean of these two sensitivities, with typical daily variations in air temperature close to the soil surface at the WRCCRF, indicated that our estimated typical daily total water use of about 2 mm may overestimate the true value by 40%–60%. The phase of the variation in θ was not changed by the simulated temperature effect. Errors in the net daily water use (maximum on one day to maximum on the next) are much smaller because temperatures at those times would be similar. Because of the many uncertainties in these estimates (for example, temperature of the electronics compared to air temperature, influence of soil properties, and moisture content on the sensitivity), we have not attempted to correct the data in the following analysis, but comment on the uncertainty throughout the text.

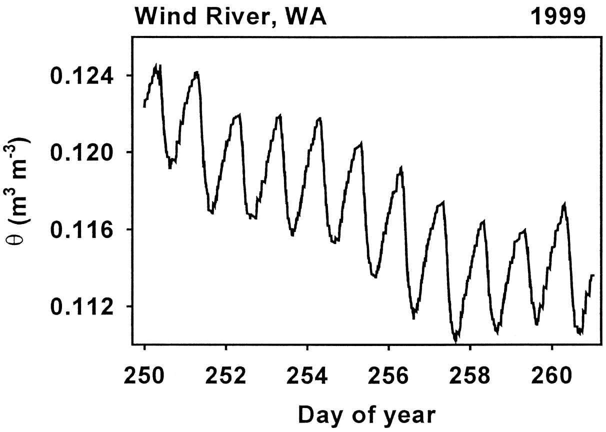

Figure 2. Change of soil moisture in the 0- to 30-cm layer with time in July 1999.

Daily Components of Water Fluxes

Table 1 shows the daily mean water flux from each of the main components for each period. Eddy-flux data were available only for June and July 1999, and evaporation from coarse woody debris was assessed only in June, July, and September 1999. In June and July, the ecosystem lost about 2.3 mm water per day (E_e, eddy flux above the canopy). Daily understory water flux, E_u (eddy flux below the canopy), was about 10% of E_e. Daily evaporation from coarse woody debris was only about 2% of E_e. Transpiration E_t, derived by scaling the sap-flow measurements, accounted for about 73% and 76% of E_e–E_u in June and July, respectively. Variation of sap flux within trees was high, with an average coefficient of variation of 50.5% (range, 17.8%–78%). Variation among trees (where sap fluxes were averaged within trees) was almost as high, with a coefficient of variation of 46.5% for the entire time series. There was no relationship between average sap flux in trees and tree diameter ($r^2 = 0.04$ and $P = 0.71$) within the size range of the six trees used in this study. Variation among days was much less, with coefficients of variation of about 10% for each of the four ensemble periods (Table 1).

Table 1. Daily Mean Water-flux Components (mm d^{-1}) and Standard Deviations (in Parentheses) for the Four Analysis Periods

	Ensemble Period			
Component	9/98	6/99	7/99	9/99
Ecosystem flux, E_e	ND	2.38 (0.55)	2.26 (0.73)	ND
Soil flux, E_s	1.66 (0.33)	1.71 (0.39)	1.97 (0.37)	1.98 (0.31)
Sap flux, E_t	0.96 (0.10, 0.52)	1.54 (0.34, 0.82)	1.39 (0.18, 0.60)	0.94 (0.10, 0.33)
Understory flux, E_u	ND	0.26 (0.11)	0.21 (0.10)	ND
Coarse woody-debris flux	ND	0.03 (0.01)	0.07 (0.01)	-0.01 (0.002)

Ensemble periods 9/98, 7–17 September 1998; 6/99, 13–23 June 1999; 7/99, 15–31 July 1999, and 9/99, 7–17 September 1999.
Standard deviations are derived from variation among days, except for sap flux, which shows both variation between days and variation among trees, respectively. ND, no data available.

The mean soil moisture content in the 0- to 30-cm layer declined from about 0.22 to 0.14 m^3 m^{-3} through June and July, corresponding to a net loss of about 0.4 mm day^{-1}. But Table 1 shows that the total change in soil moisture in the 0- to 30-cm layer, E_s, was about 1.9 mm day^{-1}, 73% and 88%, respectively, of the total ecosystem water flux, E_e. This fraction may be somewhat overestimated, but it indicates that hydraulic redistribution allows this layer of soil to supply much more of the evaporative flux than its mean moisture content suggests. Transpiration E_t was 93% and 71%, respectively, of soil flux, E_s, in June and July. E_t was a much smaller fraction of E_s in the two September periods [58% (1998) and 47% (1999)].

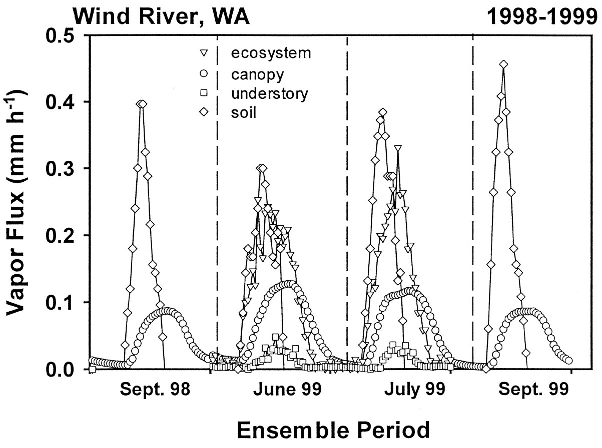

Figure 3. Ensemble-averaged diurnal variation in water fluxes for 1998 and 1999 data.

Diurnal Variation in Components of Water Fluxes

Figure 3 shows the ensemble-averaged diurnal fluxes for each of the periods. There was a pronounced lag in the flux, E_t, derived from sap flow in relation to the other fluxes, and a smaller lag between the ecosystem eddy flux, E_e, and the soil water depletion flux, E_s. In June, ecosystem flux, E_e, peaked close to noon and was relatively symmetrical around noon; in July, E_e peaked at about 1400 and declined rapidly in the afternoon. Soil water flux, E_s, increased rapidly in the morning, apparently exceeding E_e between about 0600 and 1000 PDT in each period. E_s declined more rapidly than E_e after noon. The understory flux was approximately symmetrical around noon in June and July and was larger in June when soils were moister.

Controls of Water Flux

Vapor-pressure deficit (VPD) is expected to be the most important atmospheric variable influencing ecosystem water use at Wind River when radiation is not limiting. Consequently, on most days the variation in ecosystem water flux, E_e, showed a strong influence of VPD. However, there were occasional days throughout the summer when E_e was small despite large VPD, because radiation was a limiting factor. Figure 4 shows the ensemble average variation of E_e with VPD in July 1999 between 0630 and 1830 PDT. Hours of the day are marked in Figure 4. The VPD increased steadily from 0630 until about 1400, and then remained almost constant until 1800. E_e increased approximately linearly with VPD up to a VPD of about 0.75 kPa, and then increased more slowly until about 1300 when VPD was almost 2 kPa. After 1300, E_e declined substantially. The tendency for E_e to level off at large VPD has been reported for many conifer forests (Price and Black 1990; Jarvis and others 1997; Anthoni and others 1999) and is usually an indication of stomatal closure as evaporative demand increases. The decline in E_e with time while

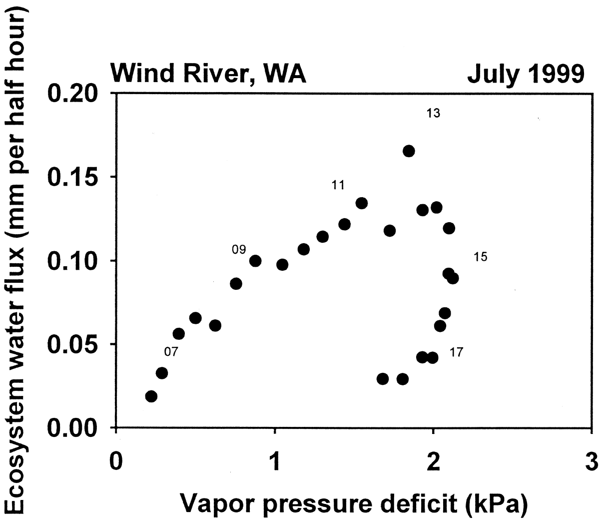

Figure 4. Relationship between ecosystem water flux, E_e, and vapor pressure deficit, July 1999.

VPD remained large and constant (Figure 4) may indicate increasing stomatal closure as water potential declined in the large trees of this ecosystem.

To quantify the controls of water use, we used observed values of E_e, E_t, and VPD to calculate ecosystem conductance (g_e) and canopy (transpirational) conductance (g_t) from the Penman–Monteith equation, assuming that the canopy was well coupled to the atmosphere (Monteith and Unsworth 1990). With this assumption, conductance g (mm s^{-1}) is given by

$$g = 10^3 \lambda E \gamma / 3.6 \rho c_p D \qquad (1)$$

where λ is the latent heat of vaporization of water (J kg^{-1}), E is water flux (mm h^{-1}), γ is the psychrometer constant (J kPa^{-1}), ρc_p is the volumetric heat capacity of air (J m^{-3} K^{-1}), and D is the atmospheric VPD (kPa). We note that the use of our sap-flow data in this computation was only for comparing magnitudes and did not correct for any lag and storage effects that alter the timing of transpiration from that of stem water uptake (see later).

Figure 5A shows the estimated diurnal variation of g_e and g_t for June and July 1999. In each period, g_e increased rapidly in the early part of the morning and then declined steadily through the day. The canopy conductance g_t also rose rapidly, with a lag that is associated with transpiration from stored water, and then declined through the daylight hours only slightly in June but more in July.

Figure 5B shows the variation with time of daily mean canopy conductance G_t, calculated using daily values of E_t and daily mean VPD. Values of G_t were lowest in the two September periods and were rather variable, but larger, in June and July. Plotting G_t versus θ (not shown) revealed that daily mean G_t varied between about 2 and 8 mm s^{-1} when θ was greater than about 0.15 m^3 m^{-3}, but was consistently less than 2.5 mm s^{-1} at lower values of θ.

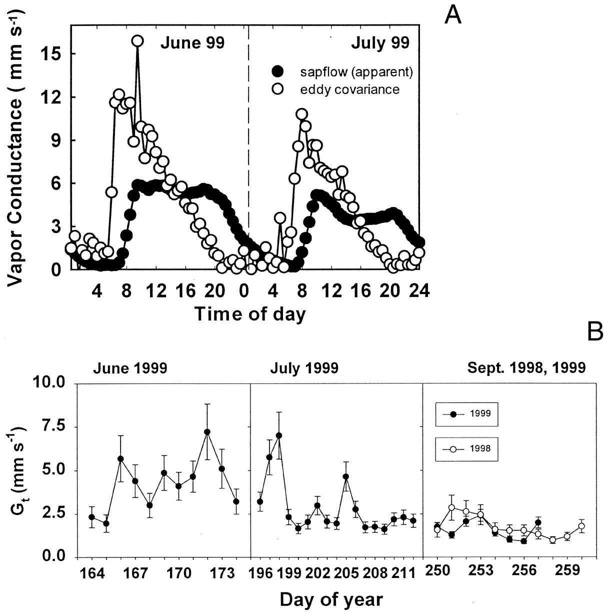

Figure 5. A: Ensemble-averaged diurnal variation in ecosystem conductance (g_e) and apparent canopy conductance (g_t) in June and July 1999. *Apparent* indicates that the canopy conductances are calculated from sap flow measured at the base of trees and are uncorrected for time lags between sap flow and transpiration. **B:** Variation of daily mean canopy conductance (G_t) with time in June, July, and September. Values were calculated using daily total sap flux and daily mean vapor-pressure deficit.

DISCUSSION

Scaling and Spatial Considerations

In comparing water fluxes derived from different independent sets of measurements, we have made several assumptions that require further testing in more detailed analyses. Both the sap-flow and the soil moisture measurements were made at the local scale. The eddy-flux measurements record fluxes originating over much larger (and variable) source areas (the *footprints* of the observing systems). Although we have some confidence from noncontinuous, site-scale observations that the soil moisture measurements used here are representative of the larger spatial scale in the crane circle, we have no comparable data to support the representativeness of the sap flow.

The method we used in scaling from sap flow in dominant Douglas-fir trees to estimate transpiration per unit ground area involved the key assumption that sap flow in the other conifer species responded to environmental and physiological factors during 1999 in the same way as in dominant Douglas-fir trees. Partial support for this assumption comes from the linear relationships between sap flux in Douglas-fir and both western hemlock and red cedar during supplemental sap-flux measurements made during the 2000 growing season. Although we are unable at present to test the assumption rigorously in this forest, the ratios $E_t/(E_e-E_u)$ that we observed in June and July (0.73 and 0.68, respectively) are well within the ranges found in other studies that showed the possibility for appreciable variation in the components of evapotranspiration partitioning (Oren and others 1998; Black and Kelliher 1989). For example, our estimates for $E_t/(E_e-E_u)$ are similar to the fraction 0.69 found in a young loblolly pine forest (Oren and others 1998). Hogg and colleagues (1997) used a similar method to scale sap-flow measurements in a closed-canopy aspen forest with a hazel understory and found good agreement between E_t and above-canopy minus above-understory eddy-flux observations.

Daily Components of Water Flux

The mean ecosystem water flux to the atmosphere E_e was about 2.3 mm d^{-1} in June and July 1999, whereas soil moisture declined from about 0.22 to 0.14 m^3 m^{-3}. Tan and colleagues (1978) concluded that this range of soil moisture was probably unlikely to generate water stress that would cause a decline in stomatal conductance of Douglas-fir, at least in young stands. Figure 5B shows that the canopy conductance based on sap-flow measurements in dominant trees in the WRCCRF canopy began to decline during July, but this did not seem to reduce ecosystem water use significantly (Table 1). This may be because other, unmeasured, components of ecosystem transpiration increased over this period.

Mean values of E_e reported here are comparable to June–July values reported by Kelliher and colleagues (1986) for a younger (31 year) Douglas-fir forest on Vancouver Island with a combined (canopy and understory) LAI of about 9, comparable with the Wind River old-growth forest. Our mean values of E_e are also similar to values reported by Baldocchi and Vogel (1997) for jack pine in Saskatchewan, Amiro and Wuschke (1987) for jack pine in central Canada, and Fitzjarrald and Moore (1994) for a boreal spruce–lichen woodland. Below-canopy eddy flux, E_u, was about 10% of E_e, similar to values reported by Black and Kelliher (1989) and Kelliher and colleagues (1990). For comparison with peak values of daily water use by conifers reviewed by Kelliher and coworkers (1993) (4.5–4.8 mm d^{-1}), we estimated maximum daily E_e by adding 2 standard deviations to our ensemble mean daily E_e values. Our estimate of maximum E_e, about 3.6 mm d^{-1} for June and July, is less than Kelliher's figures but slightly larger than maximum E_e values reported by Jarvis and colleagues (1997) for boreal black spruce forest (up to 3.2 mm d^{-1} in July).

Daily apparent total soil water-use E_s from the 0- to 30-cm layer was 73% and 88% of E_e in June and July (1.7 and 2.0 mm day^{-1}, respectively; that is, about 113 mm over the 2 months). Water extracted from greater depth by deeper roots probably accounts for the difference. The value of E_s may be overestimated by the instruments we used, but is still likely to be considerably larger than the net rate of soil water decline in the 0- to 30-cm layer over this period. The measured soil water content in the layer at the beginning of June was 0.19 m^3 m^{-3}, corresponding to 57 mm water being held, and was 0.14 m^3 m^{-3} (42 mm) at the end of July—a net decline of only 15 mm, or 0.25 mm day^{-1}. The difference between net and total water use in the 0- to 30-cm layer is most likely a consequence of hydraulic redistribution, by which deep-rooted trees lift water from deep moist soil and release it at night in drier soil layers. Brooks and colleagues (2002), working in a 20-year-old Douglas-fir stand at Wind River, concluded that about 40% of the water used daily from the 20- to 60-cm soil layer was replaced by nocturnal redistribution in August. Our data for the old-growth Douglas-fir forest suggest that a larger percentage of the total water use from near surface soil layers comes from hydraulic redistribution. This may be because the old trees access deeper, moister soil, and because the old-growth site is in a lower-lying wetter location than the young stand.

It is also possible that the eddy-flux system measured evapotranspiration from a source area that was moister than the more localized soil moisture and sap-flow sampling. Throughout June and July 1999, wind directions were commonly from the sector 0°–180° from about midnight until about 1000 to 1100 PDT. Land to the east of the eddy-flux site is moister than to the west. Although above-canopy eddy fluxes when the wind was in the sector 45°–135° were excluded from our analysis, it is possible that, on many mornings when the wind had an acceptable easterly component, E_e

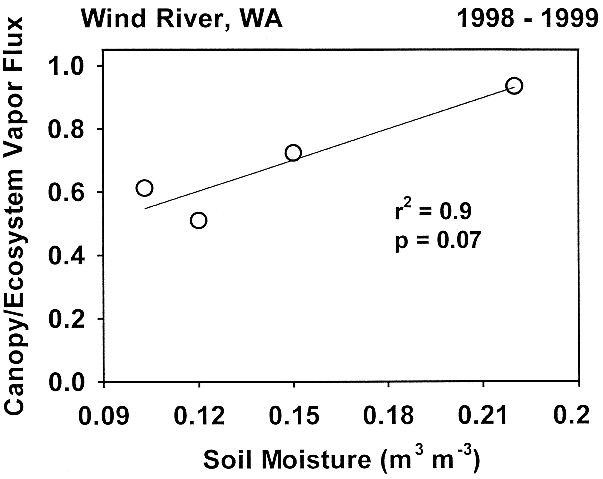

Figure 6. Ratio of overstory water flux, E_t, to total soil moisture flux, E_s, as a function of mean soil moisture content for 1998 and 1999 data.

measured by the eddy-flux system exceeded the local evapotranspiration that was responsible for measured soil water depletion and observed sap flow.

As expected, daily transpiration estimated by scaling sap-flow measurements on large trees (E_t) was smaller than the soil water depletion flux, E_s; understory flux, E_u, measured in June and July partially accounts for the difference (Table 1). During the dry September periods, E_t was a substantially smaller fraction of E_s than in June and July. Figure 6 suggests that the ratio E_t/E_s was related to soil moisture content in the 0- to 30-cm layer. Thus, a shift in partitioning of total E_e from the overstory to understory components may have occurred as soils dried. A reduced overstory transpiration component when soil moisture was low (Figure 6) would be consistent with a greater water stress on tall trees because of possible hydraulic limitations (Yoder and others 1994; Ryan and Yoder 1997). Increased understory transpiration when soil moisture was low would be consistent with hydraulic lift by large trees making water available to shallower rooting trees with canopies above the lower eddy-covariance instrumentation (and consequently not influencing E_u) (Dawson 1996).

The soil flux, E_s, was relatively constant compared to E_t, as indicated by comparing the coefficients of variation (9.5% versus 38%, respectively) over the four ensemble periods. This constancy in E_s while E_t varies is consistent with the hypothesis of total forest water use as a conservative hydrologic process (Roberts 1983).

Our estimate of the transpired water flux, E_t, was only 73% and 68% of E_e–E_u in June and July, respectively. Evaporation from coarse woody debris was a small component and does not account for the difference. The discrepancy is likely to be because our assumptions in scaling from sap flow in dominant Douglas-fir trees to estimate ecosystem transpiration are not valid, because E_e over the footprint of the flux tower is larger than the local E_e, and/or because the understory eddy-flux system that measured E_u sampled a ground area that had smaller water-vapor fluxes than the average understory contributing to the above-canopy footprint. If an unidentified source of additional transpiration was the entire source of the discrepancy between E_t and (E_e - E_u), that source would need to be 0.46 mm day^{-1} in June and 0.42 mm day^{-1} in July. It is possible that subdominant trees, above the level of the understory eddy-flux system or beyond its footprint, but not included in the scaled sap-flow estimates, might provide this missing source.

Diurnal Variation of Water Fluxes

The time lag between E_e and E_t shown in Figure 3 is most likely an indication of the contribution to transpiration in the early part of the day from water stored in tree stems and branches above the level of the sap-flow probes. Estimates of the aboveground amount of stored water in conifer stands are about 0.5 mm (Schulze and others 1985; Diawara and others 1991; Cienciala and others 1994). Once this storage is used up, a steady state is reached where sap-flow balances transpiration. At the end of the day, sap flow measured at the base of trees exceeded E_e (Figure 3), indicating that the storage reservoirs were being replenished. Hogg and colleagues (1997) found that sap flow measured at about 1.3 m on trees in a boreal aspen forest lagged ecosystem water flux measured by eddy covariance. They estimated that the lag was equivalent to about 1 h of midday transpiration (about 0.33 mm). (T. Hinckley personal communication) measured sap flow near the base and at 51 m on the stem of a dominant Douglas-fir tree at the WRCCRF. With no correction for time lags, the correlation (r^2) between measurements at the base and at 51 m was 0.84. The best correlation between the two sets of measurements (r^2 = 0.96) was when the lag between the upper and lower sap flows was assumed to be 1 h. An additional lag is likely between the top of the stem and the foliage. Schulze and colleagues (1985) reported that this time lag was about 2–3 h in *Larix* and *Picea* trees;

there may be high interspecific variability in such lags, so Schulze's value should not be taken as directly applicable here.

In the ensemble-averaged data of Figure 3, E_e increased more slowly than did E_s in the early part of the day. The understory eddy flux, E_u, increased even more slowly. We are unable to explain the variation of E_s with time. Estimates of the effects of air temperature on instrument electronics reduced the magnitude of the flux but did not alter the phase. A possible explanation of the early increase in E_s is that water vapor transpired from subdominant trees above the 3-m eddy-flux instruments accumulated in the canopy air space in this period, condensed on tree stems and other objects with large thermal inertia [as observed and modeled by Monteith and Butler (1979)], and/or was adsorbed by lichens and bryophytes. Temperature profiles in the canopy indicate that the air was usually strongly stably stratified from about 0300 to 1000, and again from about 1600 to 2000 PDT. Using the temperature and humidity measurements at seven levels in the canopy, we calculated the rate of water-vapor storage in the canopy air space. Between about 0530 and 0900, water vapor accumulated in the canopy air space at about 0.02 mm h^{-1}, presumably from transpiration and evaporation, but insufficient to account for the discrepancy of about 0.10 mm h^{-1} in Figure 3. However, the temperature and humidity data also suggest that adsorption and condensation may occur on elements in the canopy. Figure 7 shows the variation of air temperature T_a and dew-point temperature T_d at 10 m for a typical period of days in July 1999. Similar patterns were observed at 2 and 20 m. From about 0530 to 0900 on many days, T_a was within about 1°C of T_d. From about 0700 to 0900, T_d increased at about 2.0°C h^{-1}, while air temperature increased more rapidly. However, the surface temperature of objects with large thermal inertia, such as tree stems, would not increase as quickly and may have fallen below dew-point temperature during this time, in which case condensation would occur on the stems. Exploratory calculations, using a numerical model of heat flow in a tree stem (Monteith and Unsworth 1990), indicated that condensation would have often occurred on lower stems of large trees between 0800 and 1000 daily in June and July 1999. It is also possible that the substantial amounts of mosses and lichens in the canopy also adsorb moisture during periods of high humidity.

Together, water-vapor storage in the canopy air space, condensation on stems, and adsorption by mosses and lichens may explain the observed differences early in the day in timing between soil drying and ecosystem evapotranspiration in Figure 3.

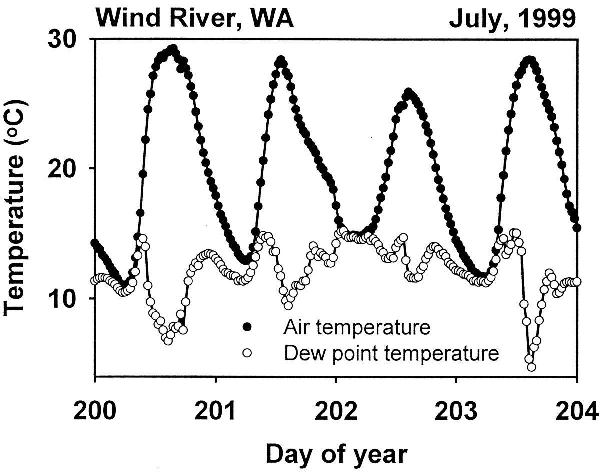

Figure 7. Variation of air temperature and dew-point temperature with time at 10 m above the soil surface, July 1999.

Fritschen and Doraiswamy (1973) concluded that dew formed on a 28-m Douglas-fir tree growing in a weighing lysimeter in a naturally regenerated stand. Their data suggested that the source of the moisture was the atmosphere above the forest. In contrast, our data suggest a redistribution of water extracted from the soil. In neither case, however, can we exclude the possibility that water vapor advected horizontally (for example, in cold-air drainage) is responsible for the humidity changes at the local scale.

Figure 3 also indicates that the soil water flux declined to zero in the afternoon, and Figure 2 shows that the soil layer apparently began to moisten. Although we cannot entirely exclude the possibility that an unidentified interaction with temperature caused these observations, there are possible biological and physical explanations that should be investigated. For example, water uptake by the large trees may shift to deeper layers of soil. Additional measurements of soil and root water potential, and of directional sap flow in roots (Brooks and others 2002), as well as continuous soil moisture profile measurements with more accurate instruments, would help to identify whether there are potential gradients that favor rewetting of the upper soil layers over this period.

Controls of Water Flux

Maximum values of ecosystem conductance were similar to those reported from many other forest

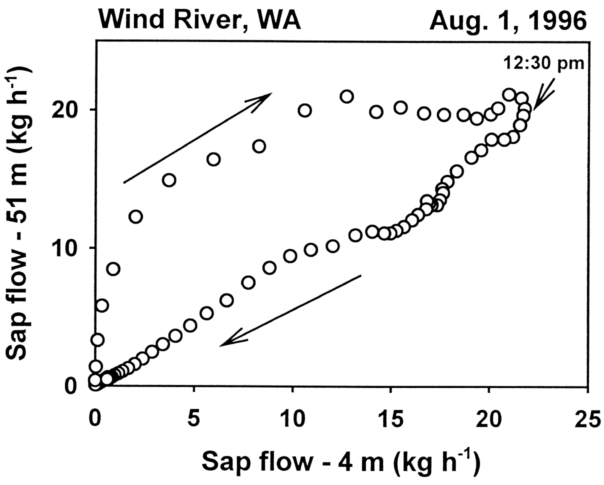

Figure 8. Relationship between sap-flow rates near the top of a dominant Douglas-fir tree and near the bottom of the tree for 1 August 1996. Data adapted from Cermak and others (in review).

studies [for example, as reviewed by Kelliher and others (1993)]. We mentioned earlier that the decline in E_e with time while VPD remained large and constant in Figure 4 may indicate increasing stomatal closure as water potential declined in the large trees of this ecosystem. Consistent with this interpretation is the decline in soil water extraction E_s over this interval (Figure 3), perhaps indicating that moisture in the surface layers had been depleted and could not be replenished sufficiently rapidly by upward transport from deeper, moister layers.

The E_e values presented in Figure 4 represent the integration of sources of water vapor occurring throughout the canopy and subcanopy volume. The role that water storage in the overstory trees plays in this E_e /VPD relationship can be assessed with sap-flow sensors located in the bottoms and tops of trees. A typical diurnal hysteresis relationship between sap flux at the base and near the top of a 60-m-tall Douglas-fir tree at the WRCCRF is shown in Figure 8 [data adapted from Cermak and others (in review)]. Flux near the crown top began earlier in the morning than flux in the base. A transition between the use of stored water versus that supplied from the soil occurred at around 1200–1300, close to the time in which E_e showed the substantial decline in Figure 4. Thus, some of the pattern shown in Figure 4 may be related to the diurnal pattern of internal water use by the overstory trees and its control on diurnal stomatal closure (Goldstein and others 1998).

The decline in maximum ecosystem conductance from June to July may indicate that soil moisture stress was beginning to influence maximum stomatal opening. The substantial decline in g_e during the afternoons in each period occurred because E_e declined as VPD stayed relatively constant; possible reasons were discussed above.

CONCLUSIONS

Our analysis suggests that, for the periods studied here, the ecosystem flux of water vapor from the WRCCRF ecosystem to the atmosphere can be attributed mainly (65%–70%) to transpiration from the dominant trees. Fluxes from the understory and woody detritus below 3 m were only about 10% of the total. Fluxes from subdominant trees above 3 m may have accounted for the remainder. There is evidence that the ratio of overstory–understory water flux depended on soil moisture. Daily net changes in soil moisture in the top 30 cm, though uncertain, were much smaller than the daily ecosystem flux. Hydraulic redistribution allowed the total water flux from this layer to be substantially larger than the net flux. It is not clear to what extent differences between E_e and E_s were because of the different spatial scales of the two measurements or because moisture from greater depths also contributes to the ecosystem flux. Moisture storage and condensation in the canopy may have been significant in delaying the transfer of water from the canopy to the atmosphere on many mornings. Ecosystem water-vapor flux was strongly influenced by VPD, as would be expected for this strongly coupled forest system. The principal control of ecosystem water-vapor flux, E_e, appears to have been exerted by stomatal responses influencing the canopy conductance. As VPD exceeded about 0.75 kPa, canopy conductance decreased, reducing the rate of increase of E_e with VPD. At a large VPD (more than 2 kPa), E_e declined with time, probably because of stomatal closure associated with limitations imposed by root water uptake.

It may seem surprising that the tall stature and old-growth structure of the forest at the WRCCRF did not result in substantially different rates of water use than those reported for a Douglas-fir forest with similar leaf area but only about 14 m high (Kelliher and others 1986). This may reflect the conservative nature of forest evapotranspiration (Roberts 1983), but is also a likely consequence of the dry summer periods on which we have focused. In such periods, stomatal control of transpiration is strong in young and old forest systems, and differences between the stomatal responses of young and old trees may be masked by feedback between trees and the atmosphere. It is likely that annual water use would show much larger differences with age, particularly because of the increased importance of interception of precipitation on foliage, stems, mosses and lichens in the old-growth forest, and the rapid evaporation of intercepted water from the aerodynamically rough surface of the tall old-growth forest.

By drawing together information from several independent studies at the WRCCRF, we have explored how different components of the ecosystem contribute to its total water use. The influence we have shown of VPD and soil moisture on ecosystem conductance has important implications for carbon exchange. Our analysis identifies several aspects where further investigations are needed to test hypotheses and quantify fluxes. More detailed analysis of the footprints of the eddy-flux systems above and below the canopy, in combination with better understanding of advection of water vapor, will help in interpreting diurnal patterns of E_e and E_u. Studies of soil moisture changes at greater depths, calculations of soil drainage by using validated physical models, and investigations of hydraulic redistribution will improve our understanding of seasonal and diurnal cycles in soil moisture. Further research on sap flow in roots, tree stems, and branches of overstory and understory trees will help quantify how the dynamics of water storage in plant tissue influence transpiration and stomatal control.

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