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How soil moisture mediates the influence of transpiration on streamflow at hourly to interannual scales in a forested catchment

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Abstract:

The water balance equation dictates that streamflow may be reduced by transpiration. Yet temporal disequilibrium weakens the relationship between transpiration and streamflow in many cases where inputs and outputs are unbalanced. We address two critical knowledge barriers in ecohydrology with respect to time, scale dependence and lags. Study objectives were to correlate components of the water balance equation at hourly to annual scales, quantify time lags, and simplify critical components of the water budget during wet and dry conditions. We tested interrelationships among precipitation, vapour pressure deficit, transpiration, soil moisture, and streamflow within the confines of a 60-hectare forested watershed in the western Cascades of Oregon. The Pacific Northwest is an ideal location to compare wet and dry seasons because of its Mediterranean climate. Soil moisture explained more than 80% of the variation in streamflow at all temporal scales investigated. Streamflow was most strongly coupled to soil moisture in the wet season because of gravitational drainage patterns; strong coupling of transpiration to vapour pressure deficit was dominant in the dry season and driven by low humidity. We observed progressively longer hourly time lags between soil moisture and streamflow in the dry season, which relates to an increasing soil moisture deficit that took an average of 48 days to refill after the onset of winter rains. We propose that transpiration drives seasonal patterns in soil moisture that relate to patterns in streamflow only after long time lags. In other words, soil moisture mediates the influence of transpiration on streamflow.

KEY WORDS diurnal variation; ecohydrology; scale dependence; sapflow; temporal patterns; time lags

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INTRODUCTION

The total water balance of a catchment can be represented as an equality between inputs (primarily precipitation), losses (evaporation, transpiration, and streamflow), and changes in storage. On an annual time step, if the net change in storage is zero, all precipitation must be partitioned between liquid and vapour fluxes out of the system. This simple analysis has led many researchers to use a 'black box' approach in accounting for annual water balance, where evaporation and transpiration are calculated as the difference between precipitation and streamflow (McDonnell, 2003). But at shorter time steps the relationships between these fluxes are much more complex due to spatial and temporal variations in water storage, resulting in temporal lags at multiple timescales between evaporative losses and streamflow. Soil moisture 'memory' caused by variations in water storage can even produce lags on coarse monthly timescales (Wu and Dickinson, 2004). From hourly to interannual scales, such imbalances due to seasonality in transpiration are not fully understood and can lead to partial or complete decoupling of vegetation from the hydrologic system (Katul *et al.*, 2007).

Several recent studies have shown relationships between streamflow and transpiration at hourly time steps with time lags of a few hours in forested watersheds during prolonged precipitation-free summer periods. In a young, rapidly growing Douglas-fir forest in the Pacific Northwest, Bond *et al.* (2002) and Barnard *et al.* (2010) observed strong coupling between hourly patterns in vegetation water use and streamflow at lags of 4–8 h during the summer dry period. Although the diel variability may represent a large fraction of dry-season streamflow, it represents only a small fraction of total transpiration in a basin. This is because dry-season transpiration over much of these watersheds involves water held at higher than gravitational potentials (Brooks *et al.*, 2010). However, this creates a paradox: if most of the vegetation in a watershed is decoupled from gravitational water feeding the stream during the dry season, and if some of the gravitational signal is distributed among varying hillslope flow pathways, and if much of the rest of the signal is absorbed by changes in soil moisture in the unsaturated zone, then why is the hourly transpiration signal so evident in the streamflow pattern?

Soil moisture and streamflow recession curves between storm events are clearly visible in many systems. The

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slopes of these curves are a function of antecedent moisture, saturated soil hydraulic conductivity, and evapotranspiration (ET) (Dunne and Leopold, 1978). Therefore, ET should and does play a primary role in soil and streamflow dynamics at the daily scale following storm events. However, the degree of coupling between vegetation and streamflow at the storm scale has been compromised by temporal disequilibrium. This has led researchers to conclude that the relative influence of vegetation on runoff responses at the watershed scale is systematically transformed or desensitized with increasing timescales (hourly to daily to interannual) (Farmer *et al*., 2003). Furthermore, time lags transfer or propagate from one timescale to the next, which effectively establishes a codependency among temporal scales (Ruddell and Kumar, 2009a).

In regions with Mediterranean climates characterized by distinct cool wet winters and hot dry summers, streamflow is foremost related to seasonal patterns in precipitation. At the onset of the dry season, streamflow declines as soil water storage is depleted by transpiration. This process continues through the dry season until the next wet season. At the onset of rain, the soil water deficit generated by summer transpiration must be refilled before streamflow recovers. Once soil water storage is refilled, precipitation patterns, not ET, should dominate streamflow during seasons when water is abundant in the soil because percolation driven by gravitational gradients is the dominant process (Barnard *et al*., 2010). Such wet periods typically correspond with high humidity, which suppresses transpiration.

Conversely, ET dynamics should be important during periods when precipitation inputs and atmospheric moisture are low; the system will be driven by strong vertical soil-plant-atmosphere gradients. Transpiration, rather than evaporation, should dominate ET during the dry season in closed-canopy forests. For example, transpiration may act as the dominant hydrologic process to accelerate stormflow recession curves over periods of a few days to weeks, leading to unique hydrologic behaviour in summer seasons (Hammond and Han, 2006). We expect steeper recession curves during periods of high transpiration. Once gravitational inputs to streams from the vadose zone are depleted, however, it follows that soils and streams could become weakly or entirely decoupled (Brooks *et al*., 2010). This effectively could sever connections between horizontal and vertical fluxes at certain times of year, meaning the impact of high transpiration on streams may not be immediately apparent.

We can also expect different processes to dominate at short (hourly) and long (seasonal) timescales, which necessitates a language of temporal scales at which various processes are operating (Jones and Swanson, 2001). Dominant processes should imprint a signal that propagates from one temporal scale to the next (Ruddell and Kumar, 2009a). This is best illustrated by the sine wave of temperature driven by the earth's movements at daily, seasonal, and interannual timescales. Because temperature is strongly coupled to many metabolic processes, diurnal, seasonal, and interannual trends are strongly detected in the biota. Likewise, temperature drives daily and seasonal trends in vapour pressure deficit, the primary driver for ET.

This study addressed two critical knowledge barriers in ecohydrology with respect to time—scale dependence and lags—through the following three questions:

1. How much does transpiration affect streamflow variability at subdaily, daily, and seasonal timesteps?
2. Under what hydrologic conditions is transpiration most closely related to streamflow?
3. How long are time lags at each temporal scale?

We expanded upon the work by Bond *et al*. (2002) in an adjacent old-growth forest within a small, forested watershed in the Pacific Northwest. We provided a new focus on intermediate coupling between the stream and soil moisture patterns and between the soil and vegetation patterns, determined how time lags change over the course of the summer dry season, and quantified time lags to refill dry-season soil moisture storage deficits at the beginning of the wet season. The Pacific Northwest is an ideal location to compare wet and dry periods because of its maritime climate. The vast majority of precipitation occurs during the winter months; soils are wet, and evaporative demand is low. During summer months, water becomes limiting, surface soils dry out, evaporative demand is high, and streamflow declines sharply.

METHODS

Conceptual model

Water balance can be simply expressed as:

$$Q = P - ET - \Delta S - \Delta G \qquad (1)$$

where Q = streamflow, P = precipitation, ET = evapotranspiration, and ΔS and ΔG are changes in soil moisture and groundwater storage for a given time period t. Assuming no net changes in ΔG over long time periods of years to decades, this can be rewritten as:

$$Q_t = P_t - ET_t - \Delta S_t \qquad (2)$$

ET depends upon vapour pressure deficit (V) in time period t:

$$\mathrm{ET}_t = f(V_t) \qquad (3)$$

During periods when soil moisture is near saturation (i.e. gravitational potential exceeds matric potential), soil moisture drainage is directly proportional to precipitation inputs. This may occur, for example, throughout the wet season, or immediately after large winter precipitation events. Wet periods correspond with near-zero vapour pressure deficits, so ET tends to be relatively small. Therefore in wet periods, soil moisture changes may be very large relative to ET losses, and the water balance simplifies to:

$$Q_t = P_t - \Delta S_t \qquad (4)$$

Conversely, during periods when soil moisture is very low, drainage is slow because matrix potential often exceeds gravitational potential. This may occur, for example, throughout the dry season, even after small summer precipitation events, but not after large summer precipitation events. Dry periods correspond with large vapour pressure deficits, so ET tends to be maximized. Much of the dry season ET in forests, however, is transpiration (T) rather than evaporation. Therefore in dry periods, soil moisture changes may be very small relative to transpiration losses, and the water balance simplifies to:

$$Q_t = P_t - T_t \tag{5}$$

During dry periods with no precipitation (between storms in summer in the climate of the Pacific Northwest), Equation 5 predicts Q is inversely related to T. However, to account for delayed storage and release of water in the soil (i.e. time lags) during periods when $p = 0$, Equation 6 becomes:

$$Q_t = -T_{t-n} - \Delta S_{t-n} \tag{6}$$

or, given Equation 3,

$$Q_t = -V_{t-n} - \Delta S_{t-n} \tag{7}$$

where T_{t-n} and S_{t-n} are transpiration and soil moisture n time steps (hours or days) previous to t. We tested these relationships in Equations 2–7 with observations from hourly, daily, multi-day (following storm events), and seasonal time intervals.

Study area

This study was conducted in a 60-hectare small watershed (WS2) in the HJ Andrews Experimental Forest in the western Cascades of Oregon. The climate, vegetation, and geology of WS2 were described in Moore *et al.* (2004); vegetation consists of old-growth Douglas-fir/western hemlock forests (approximately 500 years since last disturbance). Many studies have utilized data from WS2 (Rothacher, 1970, 1973; Harr, 1981; Hicks *et al.*, 1991; Jones and Grant, 1996; Jones, 2000; Andreassian *et al.*, 2003). In June 2000, a 20×70 m^2 sap-flow study area for monitoring transpiration, soil moisture, and climatic variables within the forest canopy was established near the climate station (CS2met) on the ancestral alluvial fan below the stream gauge at WS2.

Data collection

Continuous streamflow discharge (Q, cm) records at 15-min resolution were obtained from WS2 for three water years (1 October 1999 until 30 September 2002) and daily Q data were obtained for 15 water years (1 October 1987, until 30 September 2002) (http://www.fsl.orst.edu/lter/). Discharge records were aggregated to mean values at hourly, daily, and stormflow recession timescales. WS2 is gauged with a trapezoidal flume, but starting in 1999 a v-notch plate was installed for June–October to measure low streamflow.

Stormflow recession times (R, h) were identified for a set of individual storm events between 1 October 1999, and 30 September 2002, using a programme developed by H. Hammond (see Jones and Grant, 1996; Jones, 2000 for descriptions). Storms were selected based on a 0·1-cfs (0·002832 cm) increase in unit area flow at 1-min temporal resolution. Storms ended when stream stage dropped to within 20% of the initial pre-storm stage height, or when the hydrograph trend increased again with new precipitation inputs.

Soil moisture (S, m^3 m^{-3}) was represented by integrated volumetric water content of the top 0·30 m of the soil. Hourly measurements were obtained from four water content reflectometer sensors located within 100 m of the stream (Model CS615, Campbell Scientific, Logan, UT, USA) between August 2000 and November 2000, and April 2001 and September 2002. Our expectation was that soil moisture in the top 0·30 m would vary more than it would in deeper soil layers, despite roots extending to greater depths. Hourly measurements based on 10-s recordings were averaged over the four soil moisture sensors. Storm-scale analyses incorporated the initial S averaged on the day prior to the beginning of a storm event.

Transpiration (T, mm) was determined from thermal dissipation sap-flow sensors (Granier, 1987) monitored in the two dominant species, Douglas-fir and western hemlock (three overstory individuals each), within the sap-flow study area between June 2000 and 20 July 2002, as described in Moore *et al.* (2004). The data were upscaled to represent total T of woody species within the riparian area of WS2 at hourly and daily intervals. To represent T during stormflow recessions only, an index of potential T (ranging from 0 to 100 mm) on the day of the stormflow peak was generated based on smoothed transpiration of 18-year-old Douglas-fir trees at a nearby site (Moore, 2003).

Hourly vapour pressure deficit (V, mbar) at 67 m above the canopy was derived from temperature and humidity measurements (Vaisala HMP35C, Campbell Scientific, Logan, UT) between September 2000 and September 2002. Twenty-four-hour mean values represented the daily scale. During stormflow recessions, measurements were averaged between the peak and ending time of the storms.

Precipitation (P, mm) was recorded from the WS2 climate station located within the study area using a standard 8-in. (20·3 cm) National Weather Service gauge at 15-min intervals (totalled from 5-min resolution data) between October 1989 and September 2002 (http://www.fsl.orst.edu/lter/). At the storm scale, P is represented by the total amount of precipitation from the onset of the rise in the hydrograph to the end of the stormflow recession.

Data analysis

Data from each timescale were first tested for normality and transformed as needed to normalize. Q required log transformation at the hourly and daily scales, but not for storms. After the necessary transformations, Q was normally distributed at all three scales. S did not require transformation at any scale. S was normally distributed at the hourly scale but bimodally distributed at the daily scale, with a sharp peak at low values corresponding to summer and a broad peak at higher values corresponding to winter. T required log transformation at the hourly and storm scales, but not the daily scale. T was bimodally distributed at the daily scale, with a sharp peak at very low values corresponding to the wet season and moist summer days, and a broad peak at higher values corresponding to typically dry summer days. V required log transformation at all three scales. After log transformation, the frequency of low V was higher at the hourly scale because dew point is reached each night during the vast majority of days of the year, regardless of how high V became during midday. Transformed V was bimodally distributed at the daily scale such that on an annual basis the air was generally very dry or very moist, but rarely in between. This was only the case after log transformation; nontransformed V was highly skewed towards low values (data not shown).

After meeting the normality assumption, hourly and daily data next were corrected for autocorrelation (lack of independence). To account for autocorrelation at the daily scale, the dataset was reduced to one in 7 days by selecting every seventh day starting at day 1. Analyses at the hourly scale were restricted to lag correlations because of strong autocorrelation. Storm data were assumed to be independent because of the selection procedure described above.

Generalized least squares (simple and multiple regression) models were fitted to daily and storm-scale data grouped by season, wet or dry. At the hourly and daily scales, the response variable for simple regression was Q and the independent variables were P, S, T, and V (Equations 2 and 3). At the storm scale, the response variable for simple regression was R and the independent variables were P before and during recessions, P intensity, antecedent S, potential T, and average V during recessions. Simple regression models were evaluated based on goodness of fit determined from the highest significant r^2-values.

Equations 6 and 7 were tested using lag correlation models. For hourly data, lag cross-correlations were calculated for multi-day periods in early and late August of 2000; June, July, August, and September of 2001; and June 2002. Periods were determined by the existence of overlapping records of Q, S, T, and V. Periods interrupted by precipitation were excluded. Lag correlations (Pearson's r) were tested between all six possible pairs: Q versus S, Q versus T, Q versus V, S versus T, S versus V, and T versus V. p-values denoted the significance of slope estimates for the relationships. Models were evaluated based on goodness of fit determined from the highest significant ($p < 0{\cdot}05$) Pearson's r-values for lag correlations.

Longer time lags (weeks to months) between the onset of wet-season precipitation, which occurs annually in this region beginning around October 1, and streamflow responses were used to represent the time required to refill soil moisture storage deficits created by summer transpiration (Equation 6). This was approximated for 15 water years by testing the linear relationship between daily cumulative P and daily cumulative Q after reaching steady-state conditions ($P > 500$ mm). The x-intercept represents a proxy for $\Delta S_{t-\mathrm{Oct}\ 1}$ for the period beginning October 1 provided ET was low relative to $\Delta S_{t-\mathrm{Oct}\ 1}$; measured T from this study and estimated E from nearby old-growth Douglas fir forests (Link *et al*., 2004; Pypker *et al*., 2005) were used to approximate ET. The corresponding date t when cumulative $P = \Delta S_{t-\mathrm{Oct}\ 1}$ was determined for each water year from 1987 until 2001. Time lags to refill summer soil moisture deficits were represented in days. Given the arbitrary start date of October 1, we assume the mean lag time over 15 years to be a close approximation of actual lags in WS2. Studies have shown that annual T is relatively conserved over a range of wet and dry years (Oishi *et al*., 2010).

Multiple regression models entailed sequential (forwards) addition of independent variables in the order S, T, V, and P using a manual procedure. Final multiple regression models were selected for each time period using a sequential F-test procedure (Ramsey and Schafer, 1997). In this test, for each variable not already included in the model, an F-statistic was calculated to test whether it significantly improved the model. The final models included only the variables whose coefficients were significant ($p < 0{\cdot}05$).

RESULTS

Distinct seasonal patterns in S, Q, V, and T are shown in Figure 1, where S and Q are closely coupled and approximately inversely related to V and T, which are also tightly coupled at seasonal timescales. Average Q declined steadily from January and reached a minimum in October (Figure 2a). Monthly Q did not vary much during the summer, but was highly variable during the fall. Minimum S occurred 1 month earlier than minimum Q (Figure 2b). Annual patterns in T (Figure 2c) resembled annual patterns in temperature and solar radiation. The highest variability in T occurred in the spring (April) and early fall (September). Sporadic cool, moist days in the summer greatly reduced T, producing low outliers. V was closely related to T, although maximum T occurred in July while maximum V did not occur until August (Figure 2d). T declined between July and September while V was fairly constant, corresponding to the sharp reduction in soil moisture during these months. Therefore, at the daily timescale, daily Q appears to be positively related to P and S and negatively related to T and V.

At the hourly scale, strong diel variation in V, T, S, and Q was observed for some periods (Figure 3). P, V, T, and

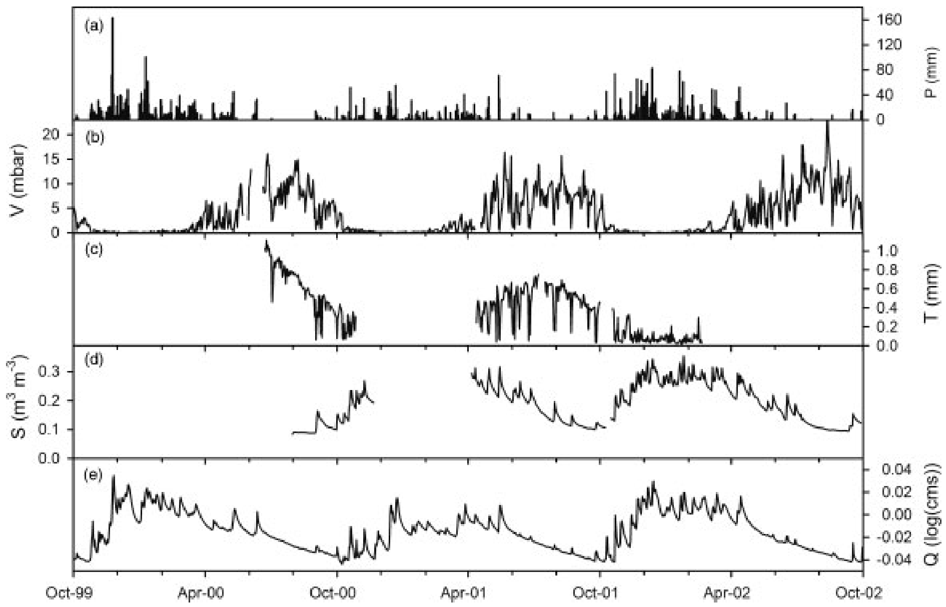

Figure 1. Temporal variation in water fluxes through a small, forested watershed for water years 2000, 2001, and 2002 at the daily scale. (a) Daily total precipitation (P, mm); (b) daily average vapour pressure deficit (V, mbar) measured at the nearby primary climate station; (c) daily total transpiration (T, mm); (d) daily average soil moisture (S, m^3 m^{-3}); and (e) log-transformed daily average streamflow (Q, log(cm))

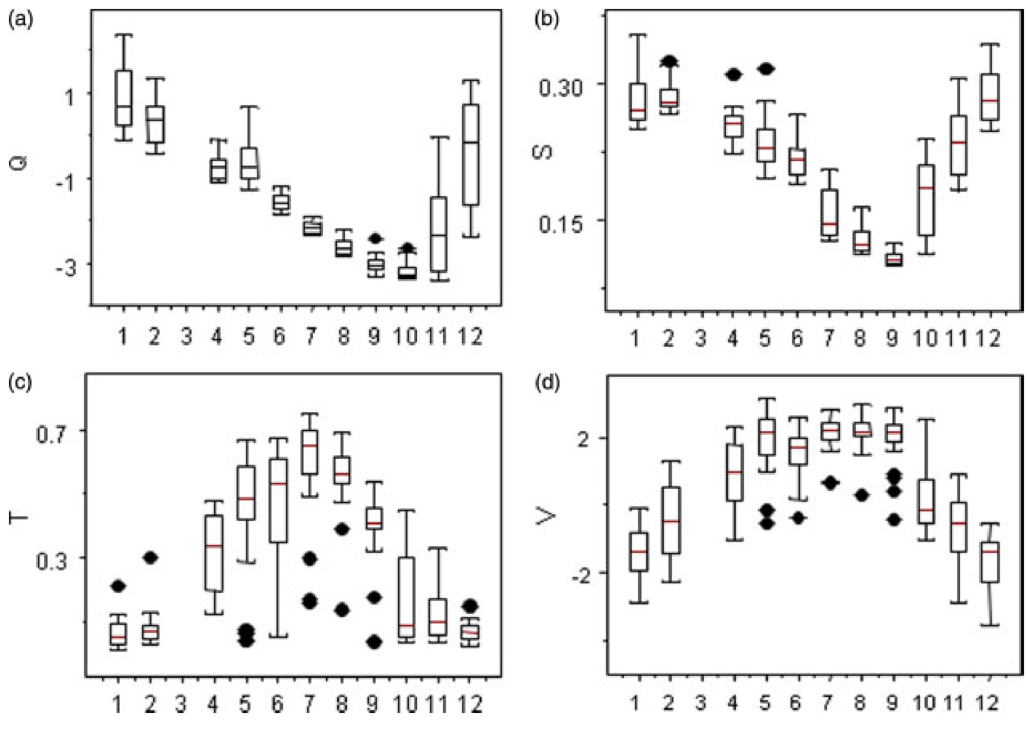

Figure 2. Temporal variation in water fluxes through a small, forested watershed by month of year for the period 13 April 2001 to 30 September 2002. Box plots indicate monthly mean values, box areas include one standard deviation from the mean, whiskers include two standard deviations from the mean, and outliers are indicated when present by closed circles for (a) log-transformed streamflow (Q); (b) soil moisture (S); (c) transpiration (T); and (d) natural log-transformed vapour pressure deficit (V). Month 1 = January

S varied most at the shortest timescales, while patterns in Q were most variable at the daily scale (Figure 4a). In general, variance of $P > V > T >$ S however, depends in part on the form in which data are expressed.

Variance in P was greatest in the spring and fall (Figure 4b), corresponding to transition periods between the wet and dry season; variance in P was lowest in the winter, corresponding to many days of steady wet-season rainfall. The lowest variability in Q, T, and V occurred in the dry summer months; in contrast, the lowest variability in S occurred in the wet winter and spring. The seasonal pattern of variance in Q was particularly dynamic, with a sharp increase in the fall when storms produced a 'flashy' response in the stream, followed by a sharp, progressive decrease in the winter and summer as saturated soils or lack of precipitation or both delivered a more steady supply of water to the stream, i.e. as daily ΔS approaches zero. These steady-state conditions allowed for the estimation of seasonal lags between P and Q indicative of ΔS in transition between the dry and wet season (Equation 6).

Correlations between variables for an entire annual time period indicates most of the variation in daily and hourly Q was explained by S rather than T. Q was closely positively related to S at the daily and hourly timescales ($r^2 = 0{\cdot}81$ and $0{\cdot}82$, respectively), but less so at the storm scale ($r^2 = 0{\cdot}29$). Q was weakly positively related to P at daily, hourly, and storm timescales ($r^2 = 0{\cdot}07$, $0{\cdot}12$, and $0{\cdot}09$, respectively). Q was weakly negatively related to T and V at daily scales ($r^2 = 0{\cdot}27$ and $0{\cdot}27$, respectively). At the hourly and storm scales, the negative relationship between Q and T was even weaker ($r^2 = 0{\cdot}10$ and $0{\cdot}12$, respectively). Finally, at the hourly and storm scales, no relationship was found between Q and V.

We also found little correlation between Q and T (Equation 6) or V (Equation 7) in the dry summer season, possibly because of delayed storage and release of water in the soil. However, the duration of lags at the hourly timescale and how they change through the dry season are shown in Figure 5. At hourly timescales in June, July, August, and September of 2001 Q responded positively to S, and T responded positively to V, but other variables were only weakly related except in August 2000 when S responded to negatively T and V. Q was strongly positively related to S at lags that extended from 1 to 7 h as the dry season progressed, while T was strongly positively related to V at lags of less than 1 h throughout the dry season. Q was weakly negatively related to T and V at lags of 4–12 h, if at all. S was weakly negatively correlated with T and V at lags of 2–4 h in June, July, and September, and strongly negatively correlated with T at lags of 3–4 h in August 2000. At the storm scale, Q trends also differed between the dry and wet seasons. Stormflow receded significantly faster in the dry season than in the wet season ($p < 0{\cdot}05$, Figure 6). There was considerable variation in slopes of these recessions.

To investigate seasonal time lags in the system caused by delayed storage and release of water in the soil, we capitalized on the steady-state conditions of soil moisture storage in the mid-to-late wet season described above, which produced a highly conserved relationship between cumulative P and cumulative Q over 15 years with varying P (Figure 7). We observed a time lag of $47{\cdot}7 \pm 4{\cdot}2$ days between the onset of winter precipitation and the refilling of soil water deficits from the summer dry season. From Equation 6, this time frame amounted

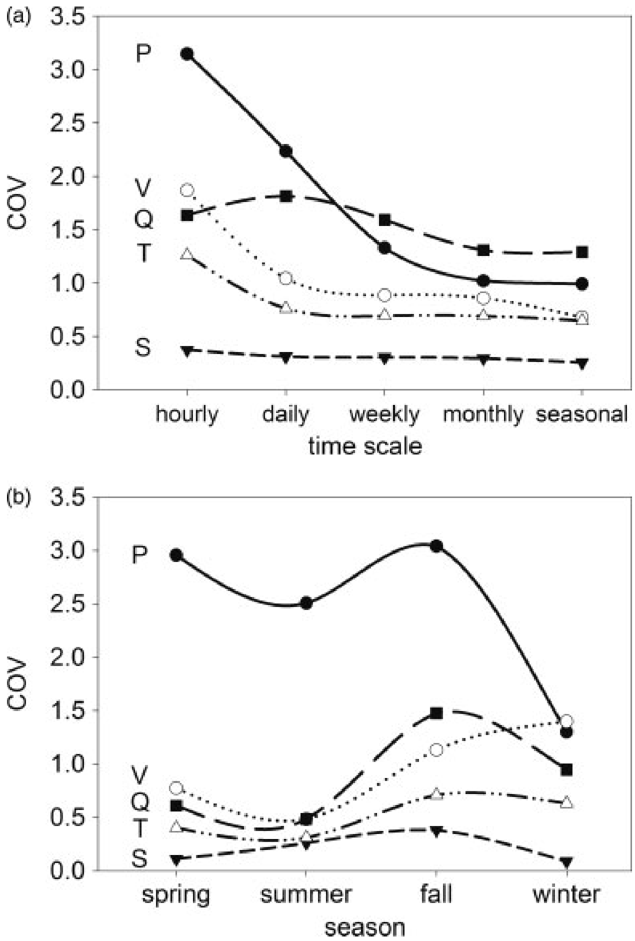

Figure 4. (a) Coefficient of variation by time interval for precipitation (closed circles, solid lines), vapour pressure deficit (open circles, dotted lines), soil moisture (closed inverted triangles, dashed lines), transpiration (open triangles, dash/dot lines), and streamflow (closed squares, long dashed lines) at hourly, daily, weekly, monthly, and seasonal timescales between 1 August 2000 and 30 September 2002 (hourly transpiration only between June and November 2000). (b) Coefficient of variation by season for variables at the daily timescale during the spring (April–May), summer (June–August), fall (September–November), and winter (December–February) based on daily mean values between 13 April 2001 and 1 June 2002

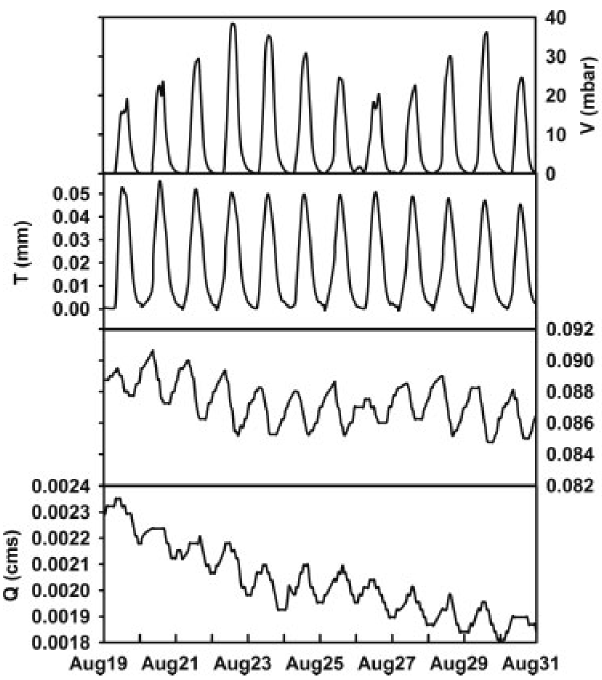

Figure 3. Temporal variation in water fluxes through a small, forested watershed for the period 19–31 August 2000 at the hourly scale. (a) Hourly average vapour pressure deficit (V, mbar) measured at the nearby primary climate station; (b) hourly total transpiration (T, mm); (c) hourly soil moisture (S, $m^3\ m^{-3}$); and (d) hourly total streamflow (Q, cm)

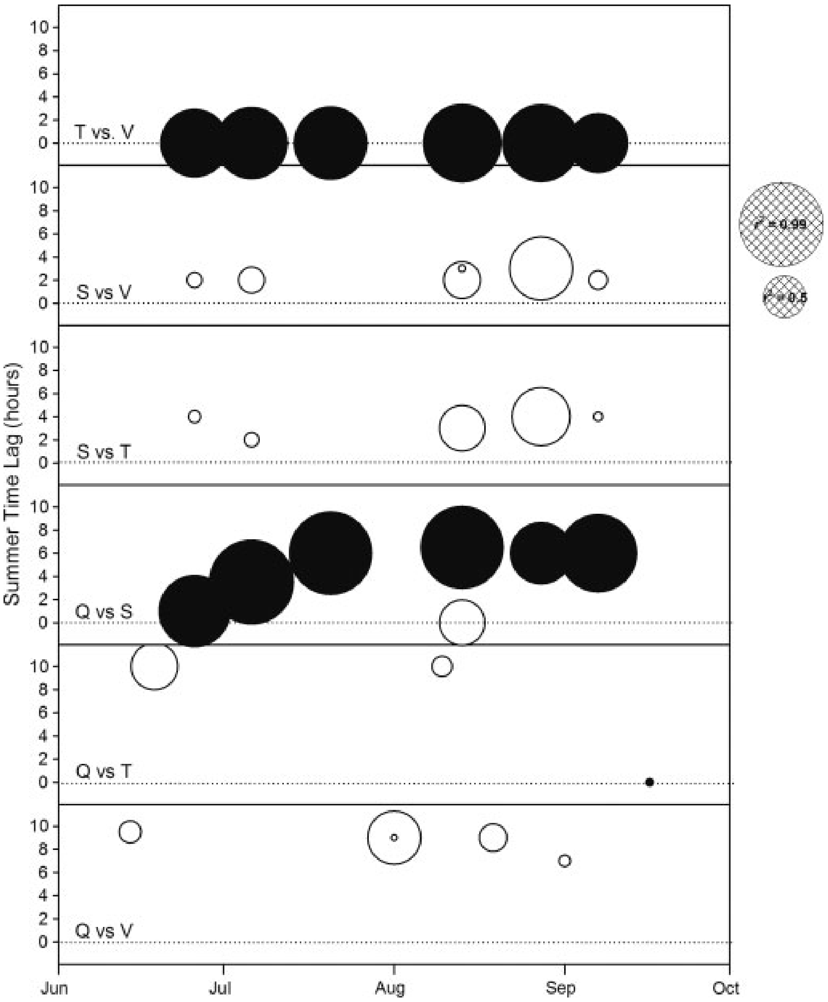

Figure 5. Hourly time lags between all possible pairs of variables for a period of 6–23 days between rain events during June, July, August, and September. Black represents positive Pearson's correlations; white represents negative correlations ($p < 0{\cdot}05$). The circle diameter size increases proportionally with the strength of the correlation. Pearson's $r = 0{\cdot}99$ and $0{\cdot}5$ are illustrated on the right margin

to 277 ± 17 mm of the annual storage losses over the 15-year study period. Because ET continues into the wet season, albeit at minimal rates, we did not consider this amount equal to annual ET.

The final models from sequential multiple regressions also highlighted the importance of soil moisture compared to T and V for explaining Q. When considering all seasons, S explained 85 and 27% of the variation at daily and storm scales, respectively. A 5% increase in daily S was associated with a doubling of daily Q, holding all else constant ($Q = -2{\cdot}07 + 6{\cdot}04 \times S + 0{\cdot}004 \times P$, $F = 10{\cdot}60$, $p < 0{\cdot}05$). Soil moisture was also most important in predicting stormflow recessions throughout the year. A 5% increase in initial S was associated with a 30% increase in median recession time during the entire year ($R = 0{\cdot}77 + 2{\cdot}37 \times S$, $p < 0{\cdot}05$). Another indication of the importance of S in explaining Q was that the antecedent precipitation index greatly improved the model fits at the daily scale, with the best fit at a k-value of 0·9. In contrast, the addition of T, V, or P into the daily or storm-scale multiple regression model improved the model fit by less than 1%. During summer only, however, T explained 10 and 51% of the variation at daily

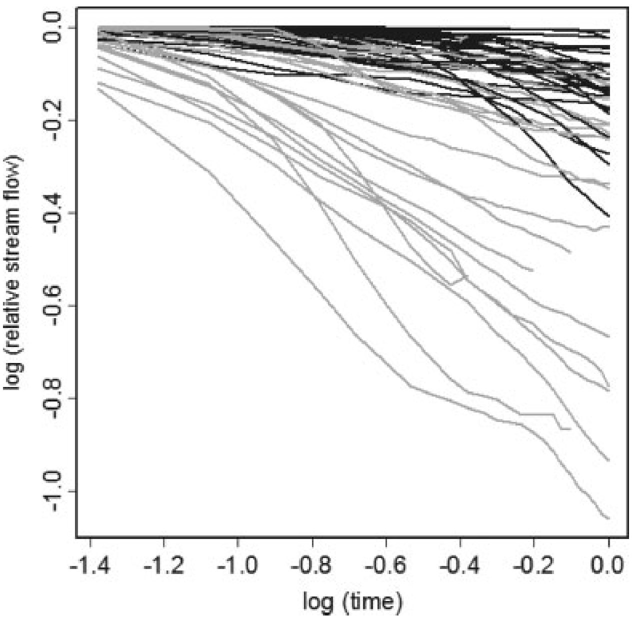

Figure 6. Relative streamflow recession during the first day after the peak for two time periods, wet season (black solid lines, December–March) and dry season (grey dotted lines, June–October)

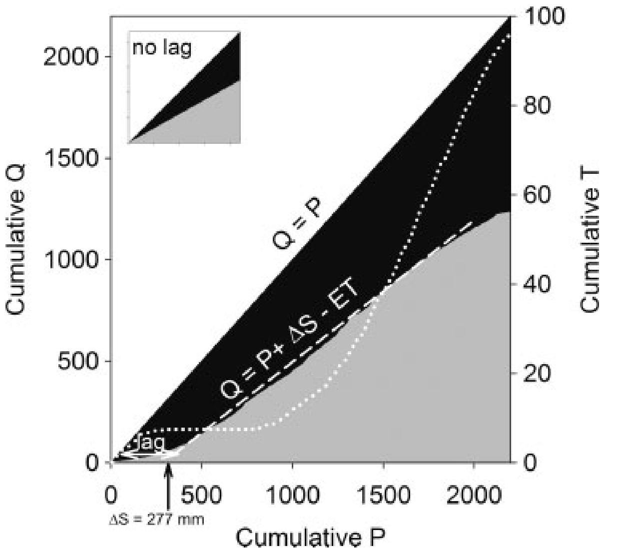

Figure 7. The relationship between cumulative streamflow (Q, mm) and cumulative precipitation (P, mm) averaged for 15 years (shaded grey area) beginning on October 1. This relationship becomes linear during steady-state conditions after a lag period when soil water deficits are refilled. Without a lag, cumulative Q should increase proportionally to cumulative P beginning on October 1 (figure inset). Because ET can disrupt steady-state conditions between P and Q, cumulative transpiration (T, mm) for 1 October 2000 to 30 September 2001 is also shown (dotted line). In the early fall, most P (up to 277 mm) is partitioned into ΔS with only 7·4 mm partitioned to T (dotted line) and an estimated 55 mm partitioned into E (from Link *et al.*, 2004; Pypker *et al.*, 2005). After soil water deficits are refilled, most P is partitioned to Q. This trend continues until T again becomes a major component of the water balance in the springtime

and storm scales, respectively, in addition to the 51 and 7% explained by S alone.

DISCUSSION

This study showed that, as expected, the coupling between vegetation and the atmosphere, and between soil moisture and streamflow, persist in a conifer forest watershed throughout a water year. For most of the year, soil moisture tension is so low compared to vapour pressure and sap-flow gradients that streamflow responds only to soil moisture. Streamflow was more closely related to soil moisture than to transpiration or vapour pressure deficit at every timescale investigated. Precipitation directly contributed to increased soil moisture. Stronger correlations between streamflow and precipitation would be expected in systems with significant overland flow. Streamflow and vegetation water use were weakly related at hourly, daily, and storm scales during the dry season, and unrelated during the wet season.

At the daily and storm scales, vegetation water use and streamflow were most strongly correlated at the beginning of the dry season when streamflow was high and stormflow recession times were long. Some amount of transpiration may have contributed to steeper stormflow recession slopes during the summer (Figure 6). However, this trend could also result from a smaller effective contributing area for summer storms compared to winter storms, so that the winter storm recession is delayed by continued inputs from upslope.

Correlations between transpiration and streamflow declined progressively as soil water was depleted. This finding is consistent with findings from a nearby watershed, WS10 (Brooks *et al.*, 2010), where isotopic water signatures indicate that transpired water is decoupled from streamflow in the summer. We infer that trees were not using significant amounts of water from the saturated zone beyond the early dry season.

While most trees were dependent upon vadose water during the summer, some trees near the stream may have accessed groundwater. At the hourly scale, streamflow in this study (WS2) was negatively correlated with vegetation water use only for short periods in the summer, driven by daily water withdrawals from the soil by vegetation that was translated to the stream at lags of about 10 h. This finding is also consistent with the inference made by Bond *et al.* (2002) for the adjacent watershed (WS1) that trees rooted in the stream channel influenced summer diurnal patterns in streamflow. It is likely that trees near the stream channel have access to the saturated zone during these periods while upslope counterparts do not.

Despite these similarities, this study provides some novel information about diverse relationships of needleleaf forest vegetation to streamflow during dry summer conditions typical of Mediterranean climates. In this site (WS2), transpiration was less strongly coupled to streamflow than transpiration from a young forest in an adjacent watershed (WS1) over the same time period (Bond *et al.* 2002). Old-growth Douglas-fir trees in this study had lower transpiration rates than the vigorously growing young Douglas-fir and alder trees in the adjacent watershed (Moore *et al.*, 2004). Also, the trees in this study were rooted on a terrace a couple of metres above the stream channel, whereas trees studied by Moore *et al.* (2004) were rooted in lower hillslopes and riparian zones. This suggests that the strength of coupling between transpiration, soil moisture, and streamflow probably depends on forest age and type (deciduous *vs* evergreen). Generally speaking, coupling between streamflow and soil moisture is greatest at high soil moisture content (Ali *et al.*, 2010). Indeed, we can expect for humid forests patterns are driven by strong horizontal fluxes for much of the year. By contrast, semi-arid rangelands might be decoupled for much of the year because of strong vertical fluxes in ET and low soil moisture (Western *et al.*, 2004). Our study adds new insights by showing how forests in the Pacific Northwest switch back and forth between wet and dry seasons. Previously, this behaviour has only been described for rangelands (James and Roulet, 2007). Dry summers with high transpiration may result in a decoupling of hillslope surface soil moisture and streamflow when soil moisture tension precludes gravitational draining. In a nearby watershed (WS10), isotopic signatures of plant and soil water were not related to those of streamwater, suggesting that plant and soil water are decoupled from streamwater (Brooks *et al.*, 2010). Such a decoupling would be expected to result in correlations between transpiration rates and soil moisture, and no relationships between transpiration or soil moisture and stream discharge. In contrast, this study found weak or no correlations of transpiration to hourly soil moisture or discharge, but strong cross-correlations with lags of 0–6 h between hourly soil moisture content and discharge data. Further work is needed to determine whether these differences reflect fundamental differences between the study watersheds.

Large soil moisture deficits from summer transpiration were a major factor influencing streamflow well into the wet season (Figure 7). We presented a new strategy to estimate storage deficits and associated time required to refill those deficits without direct estimates of ET or ΔS. Our findings confirmed that knowledge of the ΔS term in the water balance equation is critical for models of streamflow. Lags of 48 days would undoubtedly create difficulties closing the water balance during certain time periods at any timescale.

An estimated 277 mm of fall precipitation was used to fill soil moisture storage deficits created during the summer dry season. Because fall ET was low (measured T amounted to only 7·4 mm during this period and interception losses were an estimated 55 mm (Link *et al*., 2004; Pypker *et al*., 2005)), this novel approach provides a robust estimation of long-term ΔS (Equation 4). As has been previously suggested, threshold responses in streamflow may occur once deficits are filled (Tromp-van Meerveld and McDonnell, 2006b; Teuling *et al*., 2010). Others have inferred ΔS in mountainous catchments directly from streamflow: 150 mm in Switzerland (Teuling *et al*., 2010) and 55 mm in Georgia (Tromp-van Meerveld and McDonnell, 2006a). We could not use measured ΔS from volumetric soil moisture sensors to verify our estimate because measurements were only to depths of 30 cm. We excluded additional measurements taken to 90 cm from our analysis because of insufficient data; however, the 90-cm values followed the same temporal trends as data from the 30-cm sensors. Deep soil moisture was likely an important source for late-summer transpiration.

An important consideration when working with data at different temporal scales is that variability changes with scale (Figure 4a). More variability occurs at shorter timescales for transpiration, vapour pressure, and discharge, but not for soil moisture. Highly variable properties at a given timescale are likely to appear in fitted statistical models (assuming the correct lag is built in). The best overall fits were obtained using the hourly lag corrections, which used the most variable data. Given the likelihood that lags propagate systematically from short to long timescales (Ruddell and Kumar, 2009a,b), the next step is to investigate how temporal signals of transpiration in streamflow transfer between timescales. Ecohydrologists are only beginning to gain a mechanistic understanding of the linkages between streamflow and vegetation water use. Much more work is needed to find unifying principles in temporal dynamics of small watersheds that apply to landscapes with different land cover types, vegetation age and structure (Moore *et al*., 2004), and climates.

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