Comparison of soil moisture and meteorological controls on pine and spruce transpiration

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ABSTRACT

Transpiration is an important component of the water balance in the high elevation headwaters of semi-arid drainage basins. We compare the importance of soil moisture and meteorological controls on transpiration and quantify how these controls are different at a ponderosa pine site and a spruce site in the Jemez river drainage basin of northern New Mexico, a sub-basin of the Rio Grande. If only soil moisture controls fluctuations in transpiration, then simple hydrologic models focussed only on soil moisture limitations are reasonable for water balance studies. If meteorological controls are also critical, then more complex models are required.

We measured volumetric water content in the soil and sap velocity, and assumed that transpiration is proportional to sap velocity. Ponderosa sap velocity varies with root zone soil moisture. Nearly all of the scatter in the ponderosa sap velocity–soil moisture relationship can be predicted using a simple model of potential evapotranspiration (ET), which depends only on measured incident radiation and air temperature. Therefore, simple hydrologic models of ponderosa pine transpiration are warranted. In contrast, spruce sap velocity does not clearly covary with soil moisture. Including variations in potential evapotranspiration does not clarify the relationship between sap velocity and soil moisture. Likewise, variations in radiation, air temperature, and vapour pressure do not explain the observed fluctuations in sap velocity, at least according to the standard models and parameters for meteorological restrictions on transpiration. Both the simple and more complex models commonly used to predict transpiration are not adequate to model the water balance in the spruce forest studied here. Copyright © 2008 John Wiley & Sons, Ltd.

KEY WORDS   transpiration; soil moisture; evapotranspiration; meteorology

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INTRODUCTION AND MODELS OF TRANSPIRATION

In semi-arid drainage basins, most precipitation is returned to the atmosphere via evapotranspiration (ET). At low elevations, ET is roughly equal in magnitude to precipitation on timescales longer than seasons (Sala *et al.*, 1992; Reynolds *et al.*, 2000; Kurc and Small, 2004), so recharge of aquifers is minimal (Phillips, 1994). Although it is difficult to quantify, evaporation likely exceeds transpiration in these environments because rainstorms usually only wet the top ∼20 cm of the soil (Kurc and Small, 2004; Huxman *et al.*, 2005).

At higher elevations, the fraction of precipitation that is lost to ET is smaller, although it is still likely greater than half in most locations. Relative to transpiration, evaporation is reduced in higher elevation forest ecosystems. Forest canopies limit the net radiation at the soil surface and turbulent exchanges between the soil and the atmosphere. In addition, snowmelt and greater total precipitation yield wetting fronts that penetrate relatively deeply into the soil column, beyond the depth from which most evaporation occurs (Boulet *et al.*, 1997). Therefore, transpiration is an important component of the water balance in the high elevation headwaters of semi-arid drainage basins. Understanding this flux is critical to calculate and model the portion of precipitation that does flow to streams and aquifers, which is critical for water resources.

The magnitude and fluctuations of transpiration depend on soil moisture and texture, meteorological conditions, forest stand characteristics and dynamics, plant physiology, and a host of other factors. It is critical to identify inter-species differences in transpiration, including how transpiration responds to various factors. If substantial differences do exist, then changes in species composition (e.g. Allen and Breshears, 1998; Breshears *et al.*, 2005) would impact both transpiration and the other components of the water balance. In addition, it would be necessary to account for inter-species differences in hydrologic models, rather than the common approach of lumping similar species into a single plant type, such as 'needle-leaf evergreen' (e.g. Noilhan and Planton, 1989).

Soil moisture is the fundamental state variable in hydrologic studies of the land surface (Rodriguez–Iturbe *et al.*, 1999, 2001; and others). Soil moisture reflects the differences between inputs (precipitation) and outputs (ET, runoff, drainage) from the system. It both influences and is controlled by vegetation. Most hydrologic models are centred on soil moisture accounting (e.g. Simunek *et al.*, 1998; Chen and Dudhia, 2001; Feddes *et al.*, 2001;

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Guswa *et al.*, 2002). Therefore, accurately defining the relationships between soil moisture and fluxes from the soil, such as transpiration, is fundamental to hydrologic modelling. Coordinated field observations of soil moisture and various fluxes are required for this effort. Plant physiology–based studies of transpiration serve an equally important role in the improvement of hydrologic models. Observations of stomatal conductance and leaf water potential (e.g. Law *et al.*, 2001; McDowell *et al.*, this issue) provide a physical basis for the relationships that define the fluxes in hydrologic models.

Modelling transpiration and root water uptake is difficult given the complexity of hydroecological interactions (Sperry, 2000; Guswa *et al.*, 2002; Lai and Katul, 2000). In the simplest approach, transpiration varies between 0 and a maximum possible value, T_{max}, according to soil moisture in the root zone (Rodriguez–Iturbe *et al.*, 1999, 2001; and others).

$$T = F_{soil} T_{max} \tag{1}$$

where the fractional reduction in transpiration due to soil moisture, F_{soil}, is

$$
\begin{aligned}
&F_{soil} = 0\cdot0, \text{ for } \theta \leq \theta_{wilt} \\
&F_{soil} = \left(\frac{\theta^* - \theta}{\theta^* - \theta_{wilt}} \right), \text{ for } \theta_{wilt} < \theta < \theta^* \\
&F_{soil} = 1\cdot0, \text{ for } \theta \geq \theta^*
\end{aligned}
\tag{2}
$$

θ is volumetric water content in the soil, θ_{wilt} is the water content at which transpiration ceases, and θ^* is the water content above which transpiration is not limited by soil water stress. F_{soil} may also be expressed as a function of soil water potential instead of volumetric soil moisture. The dependence on soil moisture may be a function of a single root zone value or integrated over multiple soil layers (Guswa *et al.*, 2002). In some cases, transpiration and evaporation are lumped together in a single ET term.

The lack of dependence on meteorological forcing in Equation (1) is intended to represent the 'growing season', where T_{max} is appropriate for optimal conditions for plants. The next level of complexity includes the dependence of transpiration on potential evapotranspiration (PET) (Mahfouf *et al.*, 1996; Simunek *et al.*, 1998; Feddes *et al.*, 2001; and others).

$$T = F_{soil} PET \tag{3}$$

This approach allows the investigation of seasonal changes in transpiration (e.g. Small, 2005). A problem with this approach is that some formulations of PET are data intensive and models of PET are not always consistent with the ecosystem being studied (Shuttleworth, 1993).

The next level of complexity allows for limitations by different meteorological variables, including light, vapour pressure, and temperature, in addition to the constraints from soil moisture. The functional relationship and associated parameters are consistent with observational studies, typically of leaf-level fluxes (e.g. Jarvis,

1976; McDowell *et al.*, this issue). This approach has been taken in numerous studies. The details of how it has been implemented vary widely. Our description here is based on Chen and Dudhia (2001) and references cited therein. Their model was designed to simulate fluxes of water and energy at the land surface for hydrologic and climate models. In the absence of water evaporating from the interception reservoir, the transpiration flux from the vegetated portion of the landscape is

$$T = B_c PET \tag{4}$$

where B_c is a term that encompasses canopy resistance, an aerodynamic exchange coefficient, and the slope of the saturation vapour pressure curve. The canopy resistance term, R_c, is a function of soil moisture and meteorological variables

$$R_c = \frac{R_{cmin}}{LAI F_{soil} F_{temp} F_{vp} F_{rad}} \tag{5}$$

The soil reduction term is described in Equation (2). The other three terms represent the effects of non-optimal values of air temperature, vapour pressure, and solar radiation. They are described in more detail below in the methods section. The formulation in Equation (5) is based on the assumption that the net effect of suboptimal meteorological conditions and soil moisture is multiplicative. The term B_c varies as $1/R_c$. Therefore, T varies as

$$T \propto F_{soil} F_{temp} F_{vp} F_{rad} PET \tag{6}$$

In this paper, our goal is to compare the relative importance of soil moisture and meteorological controls on transpiration and how they vary between two forest ecosystems. We combine the three meteorological restrictions on transpiration into a single term, F_{met}, equal to $F_{temp} F_{vp} F_{rad}$. This allows a direct comparison of the soil moisture and meteorological controls as

$$T \propto F_{soil} F_{met} PET \tag{7}$$

There are numerous reasons why the approach outlined in Equations (5)–(7) are simplifications. For example, the same parameter values are often used for species of the same life form, for example, needle-leaf trees (e.g., Chen and Dudhia, 2001). However, ponderosa pine and spruce exhibit different sensitivities to vapour pressure deficit (McDowell *et al.*, this issue). The formulation of F_{soil} does not account for the ability of plants to compensate for only part of the roots being in dry soil (Guswa *et al.*, 2002). Recently, it has been shown that the interaction between limitations of different meteorological variables and soil moisture may be critical (Emanuel *et al.*, 2007). For example, as relative humidity decreases, the effective θ_{wilt} (or water potential equivalent) decreases.

Here, we use measurements of sap velocity as a proxy for transpiration. We compare how sap velocity varies with soil moisture and meteorological conditions at two

forested sites in the Jemez river drainage basin of northern New Mexico, a sub-basin of the Rio Grande. Compared to the entire range of vegetation that exists in semi-arid drainage basins, such as the Rio Grande basin, the dominant trees at these sites are rather similar. Both are needle-leaf evergreen trees, and therefore are often represented identically in hydrologic models (e.g. Noilhan and Planton, 1989). In this paper, we evaluate whether or not it is reasonable to lump these two different forested ecosystems into a single type in hydrologic models. We compare the importance of soil moisture and meteorological controls on transpiration, and quantify how these controls are different between the two forest ecosystems. If soil moisture controls dominate transpiration, then simple models focussed only on soil moisture limitations are reasonable for water balance studies. In this case, soil moisture alone (Equation (1)) or soil moisture and PET should be sufficient to estimate transpiration. If meteorological controls are critical, then more complex models, for example, Equations (4)–(6), with sufficient meteorological data inputs are necessary for water balance applications. In this case, it is also critical to assess whether or not different parameters are needed for relatively similar ecosystems.

SITE DESCRIPTIONS

Here, we use data from two sites that are located within the Valles Caldera National Preserve. The lower site, at 2200 m elevation, is dominated by ponderosa pine (*Pinus ponderosa*). The higher site, at 2500 m elevation, is dominated by spruce (*Picea engelmanii*). The sites are relatively similar with regard to various ecosystem properties. Soil texture at the spruce site is a sandy loam. The soil is a bit finer at the ponderosa site, falling along the boundary of the loam and sandy loam texture classes. Although soil texture is similar, the geomorphological contexts of the soils differ. The soil at the spruce site is roughly 150 cm deep, overlying the volcanic rock parent material. The soil at the ponderosa site overlies relatively deep (>10 m) alluvial material. The depth to groundwater in the alluvial fill is roughly 5 m and varies both seasonally and from year to year. The surface slope is gentle at both sites, varying from flat to several degrees.

Details of the tree density and dimensions are described in McDowell *et al.* (this issue). At both sites, the tree canopy covers ~70% of the area. The leaf area index (LAI) is 2·47 at the pine site and 3·43 at the spruce site. The intervening areas are covered primarily by grasses. At the ponderosa site, there are also some scrub oaks in the understory. We measured root distributions at both sites, in pits dug beneath the tree canopy and the intervening open areas (Figure 1). At the spruce site, nearly all of the roots are in the top 1 m of the soil, although some fine roots were observed down to the soil–bedrock interface at ~1·5 m. At the ponderosa site, fine roots (<1 mm diameter) were observed all the way to the bottom of the pits at 2·5 m. No tap roots were observed in the ponderosa root pits.

METHODS

Soil moisture

We measured volumetric water content using Campbell Scientific water content reflectometers (WCRs). The
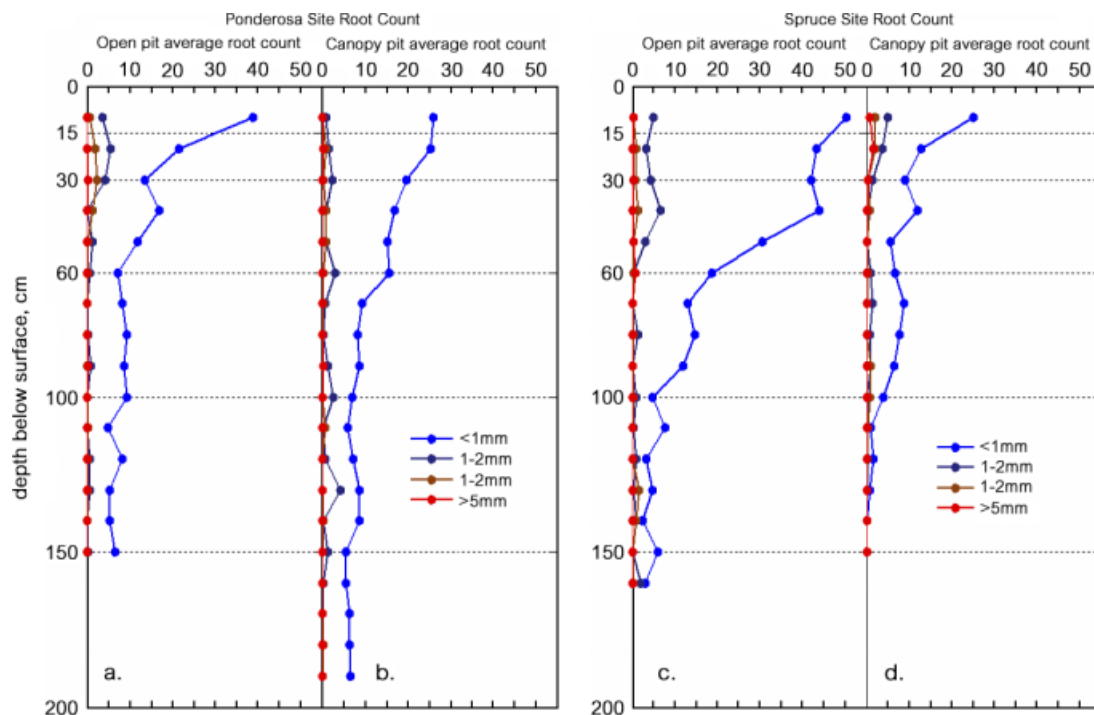

Figure 1. Root distributions at the ponderosa and spruce sites. Roots were counted in 10-cm wide profiles, repeated three times in each soil pit. The average from the three profiles is plotted. The root count was tallied for four different size classes (by radius).

WCR measurement scheme is based on the time-domain reflectometry approach (Topp *et al.*, 1980). We did not calibrate the probes for the soils at the research site. However, the soils at both the sites are similar in texture to the soils used in the factory calibration (Figure 1). In addition, no adjustments were made for temperature.

At both sites, we installed identical WCR arrays in the 20×20 m areas that included the trees measured for sap velocity. In June 2005, we installed WCRs in three pits at each site. Probes were installed horizontally at 5, 15, 30, and 60 cm depth, for a total of 12 measurements at each site. The pits were subsequently backfilled. The locations of the pits were chosen to correspond to areas (1) beneath tree canopies, (2) in between canopies, and (3) at the intersection between the two areas. Data were recorded hourly. We calculated a single volumetric water content value to represent the soil moisture state of the root zone, θ_{rz}, by calculating a weighted average of the probes over the depth interval 0–60 cm. Roots were observed much deeper than 60 cm (Figure 1), so θ_{rz} is only an approximation for soil moisture throughout the root zone. Because of power, datalogger, and site access problems, the records from these probes are not continuous and do not always coincide with periods with continuous sap flow measurements. This problem was more serious at the spruce site: soil moisture data was recorded for parts of 2005 and 2006, while sap velocity was recorded for later portions of 2006 and 2007.

To fill in the gaps in the spruce soil moisture time series, we used measurements from a site within 1 km of the spruce site at a slightly higher elevation ($\sim$100 m), referred to here as Redondo Saddle. Vegetation around Redondo Saddle is similar to the spruce site, although the meteorological station is centred in a clearing. Therefore, the Redondo Saddle soil moisture record is most similar to the between-canopy measurements from the spruce site. There were only three probes installed at Redondo Saddle: horizontally at 10 and 40 cm, and vertically from 0 to 30 cm. The latter probe is intended to provide an average soil moisture value for the top 30 cm of the soil. We calculated θ_{rz} at this site by averaging the 0–30 and 40 cm probes, weighted for their respective depths. Values were similar when using all three probes. The root zone soil moisture from Redondo Saddle provides a good proxy for the variability and magnitude of soil moisture

at the spruce site, as seen during a 120 day period during the summer of 2005 (Figure 2). A similar correspondence exists during a shorter period of 2007 (not shown). We use the Redondo Saddle time series θ_{rz} for most of the comparisons at the spruce site, but also show the spruce data when it exists.

Sap velocity

We recorded sap velocity measurements using the thermal dissipation method (Granier, 1985, 1987; Barbour *et al.*, 2005). We assume that transpiration is proportional to sap velocity, enabling us to use the measured fluctuations in sap velocity as a gauge for fluctuations in transpiration. Given this assumption, significant seasonal variations in conducting sapwood area would introduce uncertainty into our analysis. At both sites, eight trees were selected for measurement over an area of $\sim$30 m by $\sim$30 m. Two TDP-30 thermal dissipation probes manufactured by Dynamax, Inc. (Houston, Texas) were installed on the north and south sides of each tree $\sim$1·6 m above ground level. Trunk diameters at this height ranged from 18·5 to 44·5 cm at the ponderosa site and from 13 to 43 cm at the spruce site. After installation, the tree trunks were tightly wrapped in reflective bubble wrap to insulate the probes from air temperature and insolation changes. Each probe consisted of two 3·0 cm long needles. The needles were installed into two holes drilled in the tree trunk, with one 4·0 cm directly above the other and the upper needle heated to well above ambient temperature. The temperature difference between the probes is proportional to the sap velocity, with the maximum temperature difference when sap flow is near zero. To estimate the sap velocity V (cm s^{-1}) from the measured temperature difference dT (°C), we used an empirical relationship defined by Granier (1985, 1987):

$$V = 0·0119K^{1·231} \tag{8}$$

where

$$K = (\mathrm{d}TM - \mathrm{d}T)/\mathrm{d}T \tag{9}$$

and dTM the temperature difference when no sap was flowing. For most of the measurement period, sap velocity measurements were made every 10 min, and measurements each night between 11 : 00 P.M. and 3 : 00 A.M.
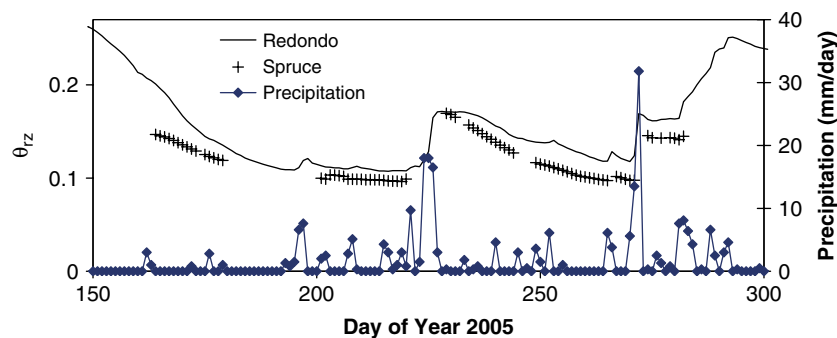

Figure 2. Root zone soil moisture, θ_{rz}, at the spruce site (average of 12 soil moisture probes) and the nearby Redondo Saddle site (average of 3 probes) during the summer of 2005. Daily precipitation is also shown.

used to determine dTM. For some periods, measurements were made every hour.

Hourly averages were calculated for each probe from the 10-min data where necessary, and daily average sap velocity calculated from the hourly data. To avoid biasing from discontinuous sampling, daily averages were retained only for those days when 24-hourly measurements were available. Measurements from the separate probes were averaged to provide a sap velocity estimate for each tree, and then the tree estimates averaged to derive the stand average flow velocity for each day.

Meteorology

Continuous meteorological records are not available for the entire study period at the two sites where we measured soil moisture and sap velocity. Continuous meteorological records exist at five stations in the Valles Caldera National Monument. As discussed above, the Redondo Saddle site is very close to the spruce research site. Therefore, we used data from the Redondo station to evaluate meteorological controls, transpiration and soil moisture, at the spruce site. We use data from the Headquarters meteorological station as a proxy for the ponderosa site. They are at similar elevations (within 100 m) but roughly 10 km apart. Both sites have extensive ponderosa pine stands.

A variety of methods have been established to estimate PET from meteorological data (Shuttleworth, 1993). The Penman–Monteith (PM) equation is believed to provide the best estimate of reference crop PET, but the data requirements for PM are substantial and are typically only satisfied with reliable data at heavily instrumented research sites (Shuttleworth, 1993; Allen *et al*., 1998; Droogers and Allen, 2002). Owing to the lack of net radiation measurements at our research sites, we use the Hargreaves equation (Hargreaves and Samani, 1982) to estimate PET (mm day^{-1}) from temperature data in conjunction with measurements of solar radiation

$$\text{PET} = aS_0(T_{\text{avg}} + b)(T_{\text{max}} - T_{\text{min}})^{0.5} \quad (10)$$

T_{avg} is the average temperature (°C) calculated from daily maximum and minimum temperatures, T_{max} and T_{min}, and S_0 is the evaporated water-depth equivalent of solar radiation (mm day^{-1}). The Hargreaves equation is empirically based, but the first term (S_0) provides an energy constraint, the second ($T_{\text{avg}} + b$) varies nearly linearly with the thermodynamic scaling term in the Penman combination equation, and the third [$(T_{\text{max}} - T_{\text{min}})^{0.5}$] indirectly factors in cloudiness (Shuttleworth, 1993). We use the parameter values ($a = 0.0025$ and $b = 16.8$) from Droogers and Allen (2002), who calibrated the Hargreaves parameters via a comparison to PM estimates derived from a coarse-resolution global meteorological dataset.

We use hourly measurements of temperature, vapour pressure, and solar radiation to calculate the meteorological limitations on transpiration (Jarvis, 1976; Noilhan and Planton, 1989; Chen and Dudhia, 2001). We set all parameter values for 'needle-leaf evergreen trees' in the Noah land surface model (Chen and Dudhia, 2001). When the air temperature, T_{a}, is above or below the optimal temperature, T_{ref}, the fractional reduction in transpiration is

$$F_{\text{temp}} = 1 - 0.0016(T_{\text{ref}} - T_{\text{a}})^2 \quad (11)$$

The commonly used value for T_{ref} is 25 °C. The vapour pressure limitation on transpiration is expressed as

$$F_{\text{vp}} = \frac{1}{1 + h_{\text{s}}[e_{\text{s}}(T) - e_{\text{a}}]} \quad (12)$$

where h_{s} represents the sensitivity to the vapour pressure deficit, here the difference between the saturation vapour pressure at the air (or leaf) temperature, $e_{\text{s}}(T)$, and vapour pressure of the air, e_{a}. F_{vp} is of the same form as the vapour pressure deficit reduction term in the Penman–Monteith equation, which makes sense as they are both resistance-based representations of the vapour flux (Jarvis, 1976; Monteith and Unsworth, 1990). The light limitation is expressed as

$$F_{\text{rad}} = \frac{\dfrac{R_{\text{cmin}}}{R_{\text{cmax}}} + f}{1 + f} \quad \text{and} \quad f = 0.55\frac{R_{\text{g}}}{R_{\text{gl}}}\frac{2}{\text{LAI}} \quad (13)$$

where R_{cmax} and R_{cmin} are the maximum and minimum values for canopy resistance, LAI is leaf area index, R_{g} is the visible solar flux and R_{gl} is an adjustment parameter (Noilhan and Planton, 1989).

RESULTS

Time series

We first show time series of soil moisture and sap velocity. We display the results for 2006, the interval when data was continuous at both sites (Figures 3 and 4).

Ponderosa. Soil moisture increases following snowmelt, as does sap flow (Figure 3). Then the soil dries out and sap flow decreases. During this spring interval with significant transpiration, the day-to-day fluctuations in sap velocity are not large. Between days 170 and 190, there is 130 mm of rainfall, yielding an increase in soil moisture and transpiration. This is followed by more than 300 mm rainfall after day 200, yielding a period of ~2 months with the highest θ_{rz} observed during the year. Sap velocity is also high during this interval, although there are local minima that last for one to several days when sap velocity is relatively slow. The correspondence between θ_{rz} and sap velocity is similar during the period of 2005, for which both records are continuous (not shown).

Ponderosa sap velocity varies strongly with θ_{rz} (Figure 3). The correspondence with shallow soil moisture, for example, volumetric water content at 15 cm (θ_{15}), is also high. In contrast, there is little similarity between the water content at 60 cm (θ_{60}) and sap velocity (Figure 3). θ_{60} does not respond to the spring snowmelt or summer rainfall until day 230. In contrast, we observed nearly
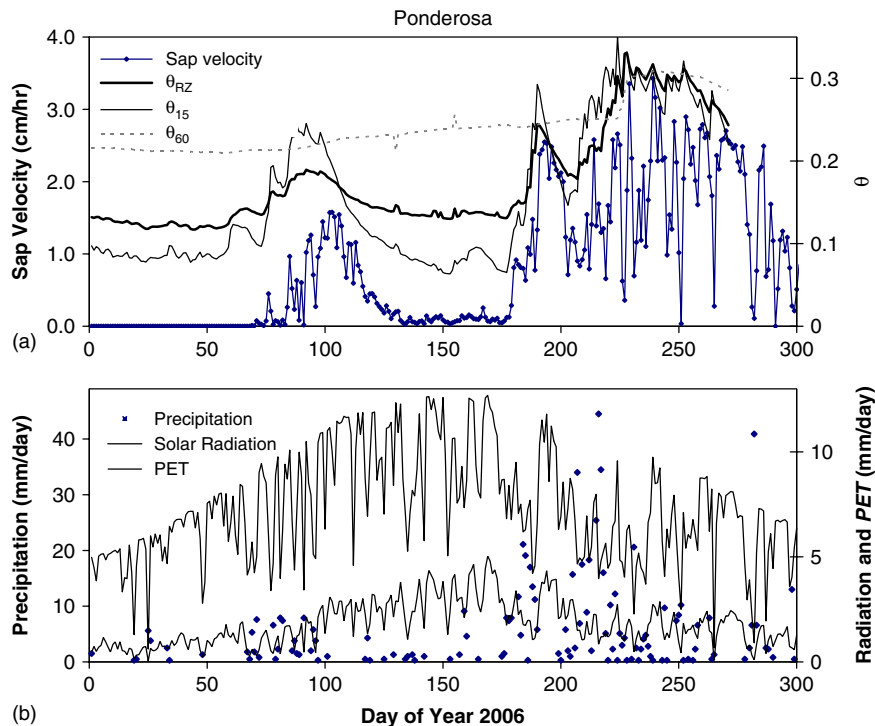
Figure 3. (a) Time series of sap velocity and soil moisture from the ponderosa site during 2006. Root zone soil moisture, θ_{rz}, and soil moisture at depths of 15 and 60 cm are plotted. (b) Daily precipitation, PET, and solar radiation. The latter is converted to units of mm day^{-1} using the latent heat of vaporization.
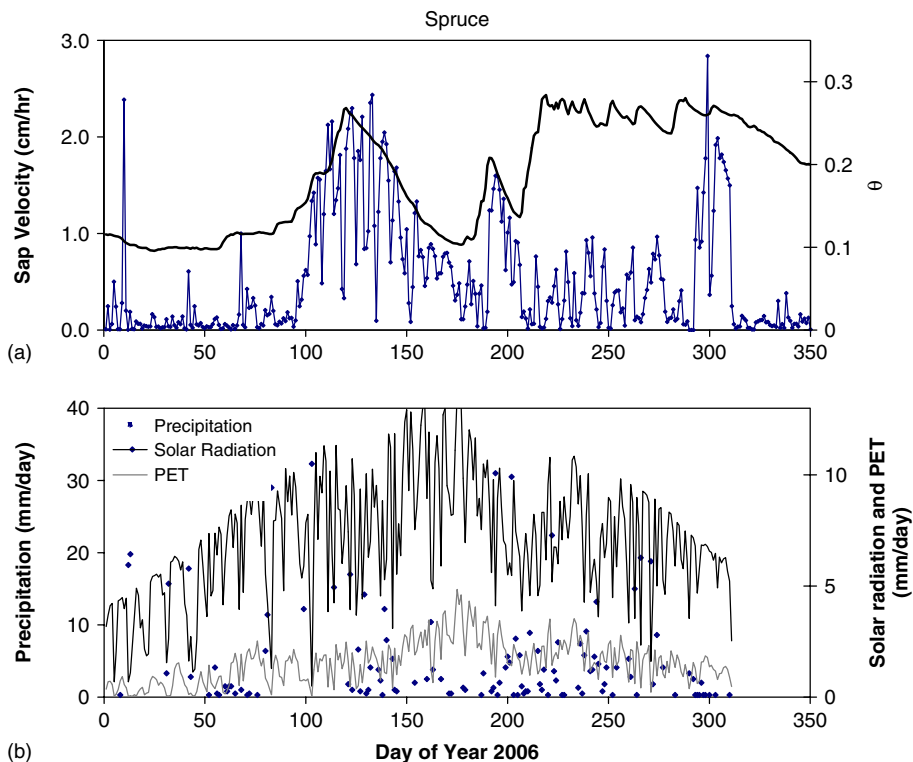

Figure 4. Same as Figure 3, but for the spruce site. The soil moisture time series is from the Redondo Saddle site.

entire range of sap velocity magnitude prior to day 230, when θ_{60} increases.

Spruce. In 2006, the precipitation and soil moisture time series at the spruce site are similar to those observed at the ponderosa site (Figure 4). Soil moisture increases following spring snowmelt, although about 30 days later than at the ponderosa site. θ_{rz} then decreases to the pre-melt value, before rainfall around day 180 yields a soil moisture pulse that lasts roughly 20 days. Substantial

rainfall after day 200 yields high θ_{rz} for the remainder of the year.

The correlation between sap velocity and θ_{rz} is not as tight as at the ponderosa site. If one considers the days with the highest observed sap flow, over intervals of several days to a week, then spruce sap velocity increases and decreases with θ_{rz} for the pulses of soil moisture following melt and the subsequent rainy period. The maxima are clearly correlated with soil moisture, but there are many days when sap velocity is very low, sometimes only 20% of the maxima observed on adjacent days.

The correlation between the highest sap velocity values and θ_{rz} observed during the first part of the year does not exist after day 210. For most of the remainder of the summer and fall, θ_{rz} remains at nearly its maximum value observed all year, but sap velocity is very low. There is a 15-day period around day 300 when sap velocity increases to the springtime values.

The pattern in 2007 is similar (not shown). θ_{rz} increases following snowmelt and then decreases through the spring. Sap velocity peaks in the late spring. After day 200, sap velocity decreases somewhat, even though θ_{rz} is relatively high because of summer rainfall. The decrease following day 200 is not as dramatic as in 2006. Similar to 2006, there are substantial day-to-day fluctuations in sap velocity: velocity varies by nearly an order of magnitude between different days, while θ_{rz} remains relatively constant. It is apparent that sap velocity is responding to something other than soil moisture.

Soil moisture–transpiration relationships

Ponderosa. The relationship between sap velocity and θ_{rz} is roughly consistent with the widely applied model of soil moisture restrictions on transpiration described in Equation (2) (Figure 5(a)). Below an apparent θ_{wilt}, roughly $\theta = 0.13$, there is no transpiration. For higher values of θ, the highest observed sap velocity values increase linearly with θ_{rz}, levelling off above $\theta = 0.22$. Although this general relationship is apparent, roughly

one-third of the points fall clearly below the envelope drawn on Figure 5. Nearly all of the points that fall far below the envelope are from days when PET is lower than the mean PET from 2006. This is the case for days when θ_{rz} is high but sap velocity is very low. Conversely, nearly all the points that plot along the maximum envelope have high PET. This suggests that PET should be considered when modelling transpiration of ponderosa pine.

Spruce. The relationship at the spruce site has a similar overall shape, although four differences are apparent (Figure 5(a)). First, the apparent θ_{wilt} is lower ($\theta = 0.09$), consistent with the soil texture at this site being coarser. Second, the slope of sap velocity with θ_{rz} is roughly half as steep, reaching the maximum sap velocity values of 2 cm h^{-1} when $\theta = 0.22$. Third, a much larger portion of the data falls far below the envelope at the spruce site than at the pine site. Fourth, many of the data points that fall far below the envelope of maximum sap velocity are from days when PET is higher than the annual average. One possibility is that the shallow soil at the spruce site is occasionally waterlogged, yielding low transpiration values. Alternatively, limitations other than PET may be critical at the spruce site. We evaluate this further below.

Influence of PET

We first describe the magnitude and variability of PET calculated from temperature and solar radiation. The high elevation, and therefore low air temperature, yields relatively low PET values (Droogers and Allen, 2002). PET varies seasonally with solar radiation (Figures 3(b) and 4(b)). After day 170, deviations below the seasonal-cycle envelope become more common at both sites. The low PET values are the result of clouds and lower temperatures.

We scale the observed daily sap velocity by PET, separately for each day in the record, to isolate the F_{soil} functional relationship (e.g. Emanuel *et al.*, 2007).
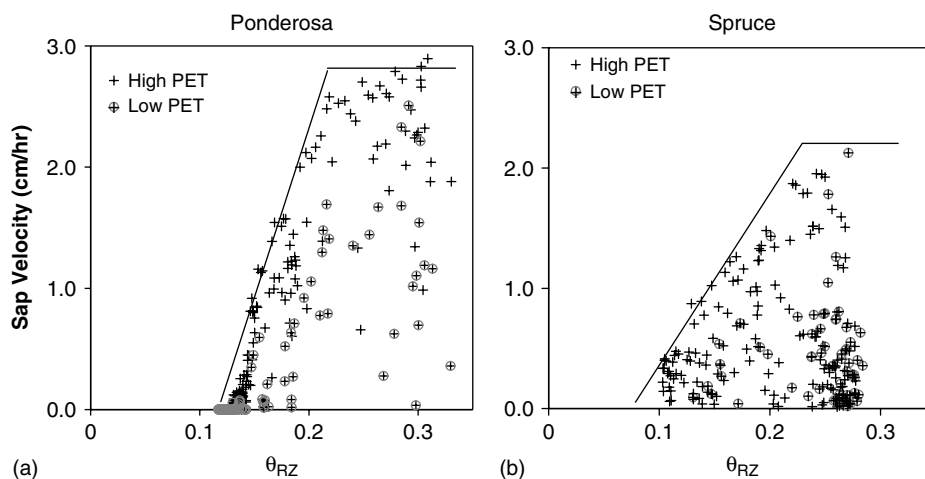
$$F_{soil} = \frac{T}{PET} \qquad (14)$$

Figure 5. (a) Scatter plot of sap velocity *versus* θ_{rz} at the ponderosa site. Data points from days when PET is less than the average value (low PET) are circled. The envelope is drawn by eye. (b) Same for the spruce site.

At the ponderosa site, transpiration varies linearly with θ_{rz}, once the scaling by PET in Equation (3) is applied (Figure 6(a)). Comparing this result to that in Figure 5 demonstrates that a significant portion of the observed scatter in the sap velocity *versus* θ_{rz} relationship can be eliminated by including a PET term. This does not prove that energy limitations are the ultimate cause of the scatter in Figure 5(a). Instead, fluctuations in the variables included in the PET calculation (here radiation and temperature) may be key factors. There are several notable outliers in Figure 6(a). For example, the circled outlier is from day 251. On that day, there is a significant dip in PET (Figure 3). However, sap velocity drops to nearly zero, and the normalization by PET does not fully compensate for the low sap velocity value.

The result is very different at the spruce site (Figure 6(a)). Normalizing by PET does not eliminate the scatter in the sap velocity *versus* θ_{rz} relationship or clarify the F_{soil} function. The scatter in Figure 5(b) and Figure 6(b)) are nearly identical. Many of the points that fall far below the envelope are from after day 200, when θ_{rz} is high but sap velocity is low (Figure 4). At the spruce site, modelling transpiration according to Equation (3) will not yield reasonable results. This suggests that more complex methods are required.

Influence of meteorological variables

We do not evaluate the influence of meteorological variables, other than PET, at the ponderosa site for two reasons. First, nearly all of the fluctuations in sap velocity are explained by the combined effects of θ_{rz} and PET. Second, we do not have hourly meteorological data at the ponderosa site. We use hourly measurements of air temperature, radiation, and vapour pressure from Redondo Saddle to further investigate the sap velocity fluctuations at the spruce site. Figure 7 shows a time series of daily average F_{met} for the spruce site, calculated from hourly meteorological data at the nearby (1 km away) Redondo Saddle site. The expected restrictions in transpiration from vapour pressure deficit, F_{vp}, are also shown. F_{met} is low during winter and highest during summer, owing to the seasonal fluctuations in air temperature and solar radiation. In contrast, F_{vp} is lowest during the summer when the vapour pressure deficit is the highest.

Sap velocity does not vary strongly with any of the individual meteorological limitations or the combined effect of all variables, F_{met} (Figure 7). As expected, sap velocity tends to decrease as vapour pressure deficit increases ($r^2 = 0.42$ for a second-order polynomial). This weak relationship is consistent with the results of
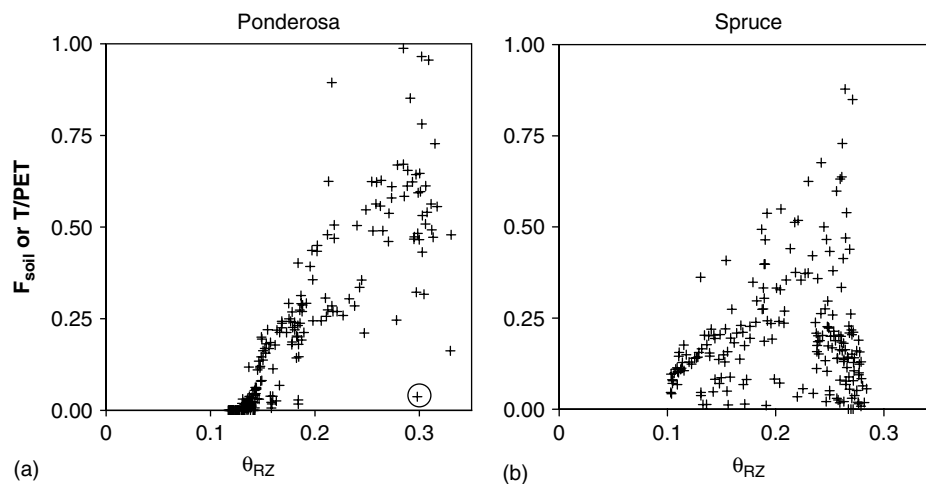

Figure 6. (a) Scatter plot of sap velocity divided by PET *versus* θ_{rz} at the ponderosa site. The data are normalized so that the maximum value equals 1·0. The circled outlier is discussed in the text. (b) Same for the spruce site.
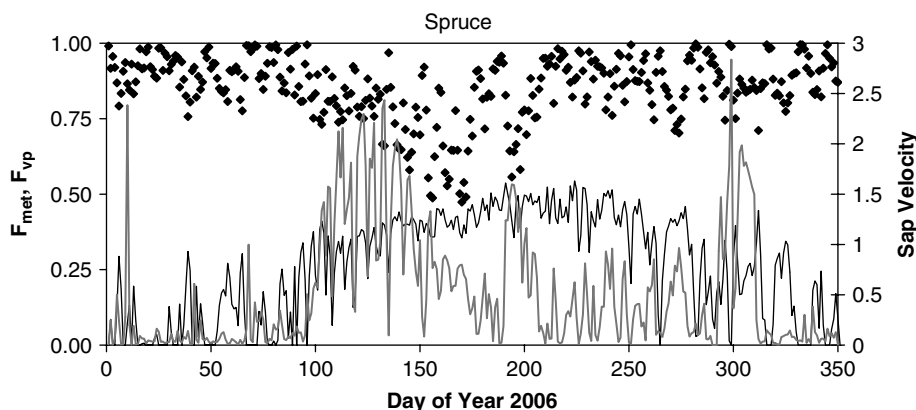

Figure 7. Time series of daily average F_{met} (black line), F_{vp} (black diamonds), and sap velocity (grey line) at the spruce site.
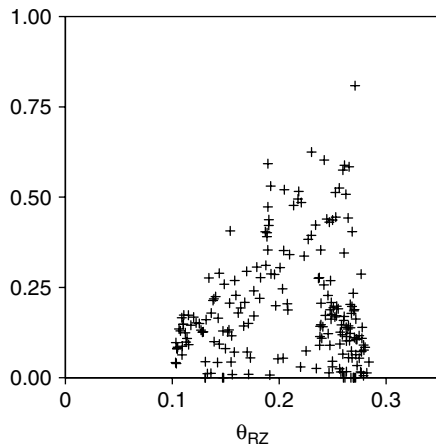
Figure 8. Same as Figure 6, but sap velocity is normalized by both F_{met} and PET at the spruce site.

McDowell *et al.* (this issue). Using a different dataset, they found no significant relationship between transpiration and vapour pressure deficit at the spruce site, most likely because the dataset was not large enough. In addition, no clear linkage exists between sap velocity and either solar radiation ($r^2 = 0.12$) or air temperature ($r^2 = 0.31$), using the relationships described in Equations (11) and (13). Considering all meteorological factors together does not improve the relationship. Sap velocity is highest during the spring, when F_{met} is still less, only roughly 0.3. When F_{met} is highest, sap velocity is relatively low. This is the opposite of what is predicted by Equation (6), indicating meteorological factors are not the primary controls on transpiration, at least given the formulations and parameters described above. Some of the daily fluctuations in sap velocity do correspond to short-term low fluctuations in F_{met} and F_{vp}.

When sap velocity from the spruce site is scaled by both PET and F_{met},

$$F_{soil} = \frac{T}{F_{met}\text{PET}} \qquad (15)$$

little or none of the scatter in the sap velocity *versus* θ_{rz} relationship is removed (Figure 8 *vs* Figures 4 and 5). Therefore, the model described by Equation (6) does not explain the fluctuations in sap velocity any better than the simpler soil moisture functions (Equations (3) and (4)).

We evaluated whether freezing nighttime temperatures were a source of the scatter in the sap velocity *versus* θ_{rz} relationship. During 2006, we did not observe daily minimum temperatures below $0\,^\circ$C between days 135 and 270. Therefore, freezing nighttime temperatures cannot explain the numerous occurrences of high soil moisture and low sap velocity shown in Figure 4(a). We do expect that freezing temperatures are a factor earlier in the spring and later in the fall, when sap velocity was less than 0.5 cm s^{-1} almost everyday even though soil moisture was high.

CONCLUSIONS

Ponderosa sap velocity varies with root zone soil moisture, as stated in many simple models of root water uptake by plants. Sap velocity varies more strongly with soil moisture at 15 cm depth than 60 cm depth, even though ponderosa roots are observed to depths greater than 2 m. Nearly all of the scatter in the ponderosa sap velocity *versus* soil moisture relationship can be predicted using a simple model of potential ET that depends only on measured incident radiation and air temperature. Therefore, simple hydrologic models of ponderosa pine transpiration are warranted, at least given conditions similar to those at the field site studied here.

In contrast, spruce sap velocity does not clearly covary with soil moisture. Following snowmelt and in early summer, the sap velocity *versus* soil moisture relationship is strongest. Later in the summer, low sap velocities are observed even when soil moisture is high, possibly indicating a reduction of transpiration due to waterlogged soils. Including variations in potential ET does not clarify the relationship between sap velocity and soil moisture. Likewise, variations in radiation, air temperature, and vapour pressure do not explain the observed fluctuations in sap velocity, at least according to standard models and parameters for meteorological restrictions on transpiration. It is possible that this result reflects the problems with the sap velocity or soil moisture data. However, we suggest that both the simple and more complex models commonly used to predict transpiration are not adequate to model the water balance in the spruce forest studied here. Models that explicitly account for interactions between soil moisture and meteorological conditions (e.g. Emanuel *et al.*, 2007) may be necessary.

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