Seasonal and Diurnal Patterns of Whole-Tree Plant Water Relations in Three Pacific Northwest Conifer Species: *Thuja plicata*, *Pseudotsuga menziesii*, and *Tsuga heterophylla*

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Abstract

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I examined the diurnal and seasonal patterns of sap flow and stem increment in a conifer stand in western Washington. The study site, at the Charles L. Pack Experimental Forest, is on a south-facing slope and at approximately 460-m elevation. Two *Pseudotsgua menziesii,* two *Tsuga heterophylla*, and four *Thuja plicata*, of various diameters and heights, were outfitted with sap flow modules and dendrometer bands. I also estimated water use efficiency for the study trees and approximated total stand transpiration by scaling up normalized daily sap flow of the study trees. *T. plicata* demonstrated a large lag in peak daily sap flow in the summer compared with the other two species, while *P. menziesii* and *T. heterophylla* appeared to down-regulate their transpiration via stomatal closure during the hottest, driest parts of the day. Normalized sap flow rates were highest in *T. heterophylla* in spring (0.24 kg per cm DBH), early summer (~0.5 kg per cm DBH), late summer (0.71 kg per cm DBH), and in the fall (0.44 kg per cm DBH). Flow rates were lowest in *P. menziesii* in spring (.02 - .04 kg per cm DBH) and early summer (0.15 kg per cm DBH in the suppressed tree), in the shortest *T. plicata* in late summer (0.13 kg per cm DBH), in the shortest and the codominant *T. plicata* in fall (0.04 and 0.03 kg per cm DBH, respectively), and in the codominant *T. plicata* and smaller *T. heterophylla* in winter. In contrast to the greater average sap flow per unit circumference noted in *T. heterophylla*, the maximum daily value noted during my study was observed in the largest *T. plicata* and was 176.32 kg (the value for the largest *T. heterophylla* on the same day was 50.72 kg). A strong drought response was evident in *T. plicata* in late summer and early fall as stomatal conductance and sap flow fell, while *T. heterophylla* and *P. menziesii* did not show such a response. Overall stem growth during the study period was lowest in *P. menziesii*. I used mean daily sap flow rates of each tree to estimate total stand transpiration, which reached 1.23 mm in late summer and fell to 0.18 mm in winter. Overall, the study provided insight into ecological and physiological differences and similarities among these three species.

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Introduction

In the Pacific Northwest, conifer forests comprise the dominant land type and are an integral component of the economy and the ecology of the region. Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), western redcedar (*Thuja plicata* Donn ex D. Don), and western hemlock (*Tsuga heterophylla* (Ram.) Sarg.) are the most common tree species in this region, particularly in low- to mid-elevation forests west of the Cascades mountain range (Case and Peterson 2005). Although they are frequently found co-occurring on the same sites (Franklin and Dyrness 1988), these three species demonstrate different tolerances for environmental conditions including shade, temperature, and drought (Carter and Klinka 1992; Drever and Lertzman 2001; Minore 1979).

Of the three species, *T. heterophylla* and *T. plicata* are the most shade-tolerant (Minore 1979). Although all three species grow fastest under higher light conditions (Harrington 2006), *T. plicata* requires only 10% above-canopy light to survive (Wang et al. 1994), while *P. menziesii* requires 20% (Mailly and Kimmins 1997). In order to reach maximal sapling growth, *P. menziesii* requires 60% above-canopy light while *T. plicata* requires just 30% (Drever and Lertzman 2001). Although *T. heterophylla* is often considered to be the most shade tolerant of the three species (Minore 1979), seedling mortality in low light regimes is lower in *T. plicata* than in *T. heterophylla* (Kobe and Coates 1997). In high light conditions, *P. menziesii* outperforms the other two species. It has a higher light-saturated photosynthetic rate than *T. heterophylla*, which in turn has a higher photosynthetic rate than *T. plicata* in old-growth forests (Winner et al. 2004), indicating a higher tolerance for and dependence on high light conditions. In a study of vertical gradients of photosynthetic light response, *T. heterophylla* was found to have greater photosynthetic rates than *P. menziesii* at low light levels and lower photosynthetic rates at high light levels, due to lower light-saturated photosynthetic rates, light compensation rates, and respiratory rates (Lewis et al. 2000).

Tolerance for extremes of soil moisture varies by species as well. *T. plicata* is able to tolerate water surplus and flooded soils (Krajina 1969) and has a higher flood tolerance than *T. heterophylla*, which in turn has a higher flood tolerance than *P. menziesii* (Minore 1968). *P. menziesii* has been found to be the most drought-tolerant of the three species (Franklin and Dyrness 1988; Minore 1979), in part because its stomata close more completely in response to drought stress than those of *T. heterophylla* (Hodges 1967). Although neither of the other two species is considered to be drought-tolerant, *T. plicata* can survive on sites which are too dry for *T. heterophylla* because of its deeper root system (Franklin and Dyrness 1988), and *T. plicata* seedlings have higher survival during drought stress than those of *T. heterophylla* (Marshall 1931).

Minore (1979) found that *P. menziesii* and *T. heterophylla* are able to initiate photosynthesis during warm, sunny days in the winter, whereas *T. plicata* does not respond in this way. However, a more recent study demonstrated that seedling shoot growth of *T. plicata* is responsive to winter warm temperatures (Grossnickle and Russell 2006).

Because water is the most limiting factor for plant growth in dry Pacific Northwest summers (Zhang and Hebda 2004), plant water relations are key to gaining an understanding of the ecology and health of a forest and its components. Conifer forests dominate the Pacific Northwest for several reasons, including that conifers maintain lower leaf temperatures and better control of water loss than competing hardwood species during summer drought (Waring and Franklin 1979). Because winters are mild in the region, conifers are also favored since they are able to conduct some photosynthesis and growth prior to leaf-out of deciduous trees. And finally, low soil nitrogen (N) in the region also favors conifers over deciduous species as they retain needles for a number of years (Waring and Franklin 1979). However, comparisons of water relations among conifers have received little attention. Walter and Ettl (2010) found more negative mid-day water potential of 3 year-old *P. menziesii* than *T. plicata* seedlings on a south-facing site, but there was no difference in water potential between the species in the evening nor predawn. The interactions between soil water availability, relative humidity, and solar radiation likely all impact water relations of Pacific Northwest conifers—likely in ways that impact stand development and species composition. Understanding species specific and relative responses to water availability and stress is an important component of understanding Pacific Northwest forest community ecology. Abiotic factors such as temperature, humidity, and wind, also play a major role in plant water demand and photosynthetic rate (Minore 1979). Historically, studying plant water relations has been challenging in large specimens because many techniques for measuring plant water status have either been destructive in nature or required containment of the whole plant (Turner 1981; Wullschleger et al. 1998). Continuous sap flow monitoring, which measures the rate at which sap ascends plant stems, allows for reliable estimation of evapotranspiration rates of whole trees in a non-destructive manner (Bequet et al. 2010; Jung et al. 2011; Vertessy et al. 1997).

Sap flow is the movement of water as it travels up the xylem, from the roots of a plant to the leaves (Burgess and Dawson 2008). Continuous sap flow monitoring can be used to determine whole-plant water use and hydraulic conductance, as well as to identify periods of photosynthetic activity (Ford et al. 2004). Sap flow monitoring permits observation of short-term changes in plant evapotranspiration in response to rapid variations in climate conditions, particularly to changing vapor pressure deficit (VPD) (Anfodillo et al. 1998). VPD is calculated using the following formula:

$$VPD = \frac{100 - RH}{100} \times SVP$$

where RH is relative humidity and SVP is saturated vapor pressure.

Sap flow measurements, in addition to providing insight into the water budgets of individual trees, can also be scaled up to provide estimates of transpiration for whole forest stands (Čermák et al. 2004; Hatton and Wu 1995; Jung et al. 2011; Kim et al. 2008; Köstner et al. 1998; Martin et al. 1997) and even whole forests (Martin et al. 2001; Wilson et al. 2001). There are several techniques for the electronic measurement of sap flow, all of which allow for frequent or continuous measurements in a minimally invasive way (Baker and Van Bavel 1987; Čermák et al. 2004; Smith and Allen 1996). The main methods used are heat pulse velocity, trunk segment heat balance, stem heat balance, heat dissipation, and heat field deformation (Čermák et al. 2004).

Additional insight into plant water relations, specifically water storage, water use, and timing of growth can be gained using dendrometer bands. Dendrometer bands are spring-loaded bands of aluminum or stainless steel tape that accurately measure incremental changes in the circumference of trees or tree limbs on which they are installed. Dendrometer band measurements can be used to illustrate both long-term radial growth of a tree bole and fluctuations resulting from daily and seasonal depletion and replenishment of water (Čermák et al. 2007; Deslauriers et al. 2007; Lassoie 1973; Lassoie 1979).

Diurnal fluctuation in stem diameter is a function of both daily tree growth and of water storage in the bole of the tree, and is driven primarily by transpiration (Zweifel et al. 2001). Typically, the boles of trees contract during the day when transpiration is at its peak, and expand at night as water is recharged (Turcotte et al. 2011). However, a lag effect in bole contraction relative to transpiration due to hysteresis is common in many systems, related to differences in VPD, leaf and stem water potentials, and soil water content (Zhang et al. 2014). Typically, there is a delay in stem response to canopy transpiration. In an extreme case Hinckley et al. (1974) noted that, on clear days at a given xylem pressure potential, the stem of a white oak (*Quercus alba*) was thinner during stem recharge than during dehydration. A hysteresis loop exists between stem circumference and leaf water potential because of the elasticity of the water conduction system. This causes a delay in the change of water potential from the stem xylem to the elastic tissues outside of the cambium (Hinckley and Bruckerhoff 1975; Hinckley et al. 1974). A similar hysteresis loop was observed in stem circumference and leaf water potential of a large *P. menziesii* (Čermák et al. 2007). Diurnal stem contraction in *P. menziesii* is related to VPD and solar radiation, as well as to air temperature in the dormant season (Devine and Harrington 2011). Several authors have asserted that daily fluctuations in stem diameter are driven primarily by changes in bark water storage, due to the relative inflexibility and more constant water status of the xylem tissue itself (Dobbs and Scott 1971; Steppe et al. 2006; Zweifel et al. 2000).

A strong inverse relationship is typical between sap flow and stem increment curves collected from dendrometer bands (Gruber et al. 2009). As transpiration increases, sap flow rates rise, and stems contract as water is moved out of the tree and into the boundary layer, the thin layer of still air surrounding the surface of a leaf. An example of this inverse relationship from a large *P. menziesii* tree at the western Washington study site is shown in Figure 1. When used in combination, monitoring of sap flow rates and changes in stem increment provides insight into the water use and presumed photosynthetic activity of trees and the ways in which trees are influenced by their abiotic environment. In turn, this helps us to understand the ecology and hydrologic function of individual trees and the environments in which they live.

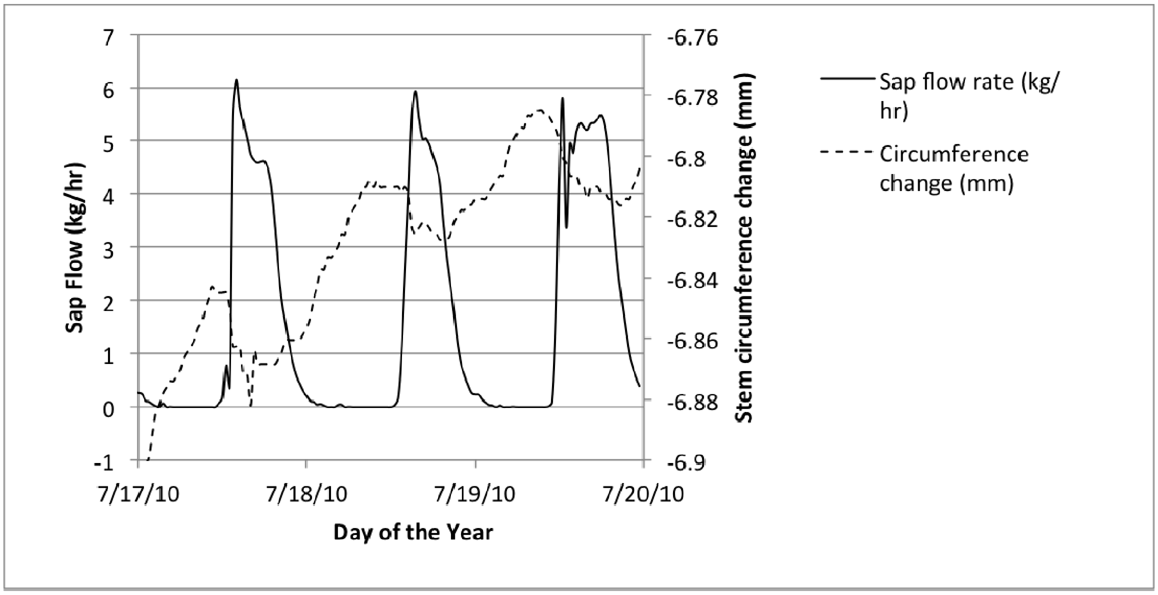


Figure 1. Demonstrating the inverse relationship between sap flow and stem increment of a 98.6-cm *P. menziesii* located within the study site.

Canopy position, or the vertical distribution of tree canopies in a forest stand, can have a substantial impact on transpiration rates and water use. Taller trees that are dominant in the forest canopy tend to have higher transpiration rates per sapwood area due in part to greater boundary layer and stomatal conductance resulting from increased exposure to solar radiation, VPD, and wind (Martin et al. 2001; Martin et al. 1997; Sellin and Lubenets 2010). For transpiration to occur, water vapor leaving the stomata of a plant must diffuse through the boundary layer to reach the atmosphere (Lambers et al. 2008). The thicker the boundary layer, the slower the rates of transpiration are likely to be. Trees with greater canopy exposure have thinner boundary layers in their upper canopies than in the lower and mid-canopies (Martin et al. 1999). Additionally, the upper canopies of trees have greater exposure to solar radiation (Hardy et al. 2004) and experience greater wind speed (Jung et al. 2011) than the canopies of shorter trees in the same stand for any given leaf area.

A study of five deciduous trees in South Korea found that tree height explained more of the variation in sap flow rates than did tree species due to increased solar radiation and wind speed at the upper canopy positions (Jung et al. 2011). In another study of sap flow rates in a mixed species deciduous forest, the relative contribution of trees to stand transpiration was driven more by sapwood area than by species differences in water use (Wullschleger et al. 2001). Because *T. plicata* and *T. heterophylla* have a higher shade tolerance than *P. menziesii*, and are able to photosynthesize more efficiently in low light conditions (Carter and Klinka 1992), they are likely to have higher sap flow than *P. menziesii* in lower canopy positions.

Substantial work has investigated the sap flow rates of mature *P. menziesii* (Bequet et al. 2010; Granier 1987). Granier (1987) used sap flow measurements to evaluate total transpiration for suppressed, codominant, and dominant *P. menziesii* trees growing in a loamy brown soil over a 4-month period, and found that transpiration declined sharply when plant-available soil water fell below 30%. Unsworth et al. (2004)

utilized sap flow measurements in combination with other methods to study water flux in an old-growth *P. menziesii* – *T. heterophylla* ecosystem in western Washington, and determined that transpiration by dominant trees on-site accounted for the majority of water-vapor flux within the system. Meanwhile, there have been few studies utilizing sap flow measurements to estimate transpiration and water use of *T. plicata* and *T. heterophylla* in the field. In a study of nighttime transpiration, Kavanagh et al. (2007) presented some sap flow study of all three species, indicating sap flow rates were highest in *T. plicata* and lowest in *T. heterophylla*, and demonstrating a higher sensitivity to VPD in *T. plicata* sap flow rates.

While diurnal patterns of sap flow and water storage have been examined for individual tree species (Čermák et al. 2007; Foote and Schaedle 1976; Herzog et al. 1995), comparisons of diurnal patterns between *T. plicata, P. menziesii,* and *T. heterophylla* have not been done. Additionally, most studies on transpiration using sap flow measurements have focused on short time periods, typically during the summer, in order to capture data during the period when the trees are most photosynthetically active (Jung et al. 2011; Unsworth et al. 2004). There is some evidence that *T. plicata* is photosynthetically active for a longer portion of the year than *P. menziesii* (Hawkins et al. 1995), but this has not been tested on mature trees in our region.

Understanding forest water use is especially important in light of potential climate change impacts. Although models vary with regard to the magnitude of climate change impacts, the Pacific Northwest overall is forecast to see greater than average impacts from climate change in the form of warmer temperatures and less summer precipitation (Jassal et al. 2009; Mote and Salathé 2010). The response of mixed-conifer forests to changing climate will depend on the interaction effects of water availability, relative humidity, light (sunny vs. cloudy days), and temperature. The relative response of the major conifer species is poorly understood, especially when considering responses across seasons and at multiple canopy levels.

Different species are likely to be impacted to varying degrees as a result of their different tolerances for extremes in environmental conditions such as sun, VPD, and plant-available water (Bovard et al. 2005). This underlines the importance of learning more about comparative tree water relations of individual species, in order to predict how species will react to changing climatic conditions. Growth of *P. menziesii* is regulated by maximum air temperature and plant available soil water, which affect growth interactively (Beedlow et al. 2013). Beedlow et al. (2013) found sharp declines in *P. menziesii* photosynthetic rates above 25 °C, and thus expected that *P. menziesii* will experience increasing temperature limitation under predicted climate models. However, if *P. menziesii* is able to take advantage of warmer days in fall, winter, and spring (Winner et al. 2004), it may be able to compensate somewhat during these seasons for lost growth in the summer.

Much of the work performed on plant hydraulics of mature trees in the Pacific Northwest has focused on *P. menziesii* (Beedlow et al. 2013; Čermák et al. 2007; Devine and Harrington 2011; Dobbs and Scott 1971; Granier 1987). Although *P. menziesii* is a commonly occurring tree in the Pacific Northwest, it is very rare as an understory species west of the Cascades, particularly in mesic forests, likely due primarily to light limitations. By carefully selecting a site containing both large dominant and smaller trees of each of the tree study species, we were able to test some common assumptions regarding species' ecological niches and stress tolerances. Specific objectives of the study were to illustrate seasonal and diurnal sap flow and water storage patterns, to examine the relative effects of canopy position and tree species on sap flow rates, to estimate growing season length, and to approximate whole-stand transpiration. This study produced semi-continuous sap flow and dendrometer band data for two and a half years, encompassing three growing seasons. Two hypotheses of this study are that sap flow will be greater in trees occupying dominant canopy position regardless of species, and that *T. plicata* and *T. heterophylla* will experience greater sap flow rates in lower canopy positions. By studying the water relations of these three species, my broader goal was to better understand the interaction between species and canopy position, as they may affect forest community composition and stand structure.

Methods

Study Site

The study was located in a mature conifer stand in the central portion of the Charles Lathrop Pack Experimental Forest, owned by the University of Washington, in western Washington (Figure 2). The regional climate is maritime with cool, wet winters, and mild summers with an extended drought (Franklin and Dyrness 1988). Average January and July temperatures are 3.9 and 18.3˚C, respectively. Precipitation averages 97.8 cm, with 88% falling between September and May (Swanson 2006). Elevation is approximately 460 meters above mean sea level (msl) and the site is located on a south-facing aspect with approximately 35% slope.

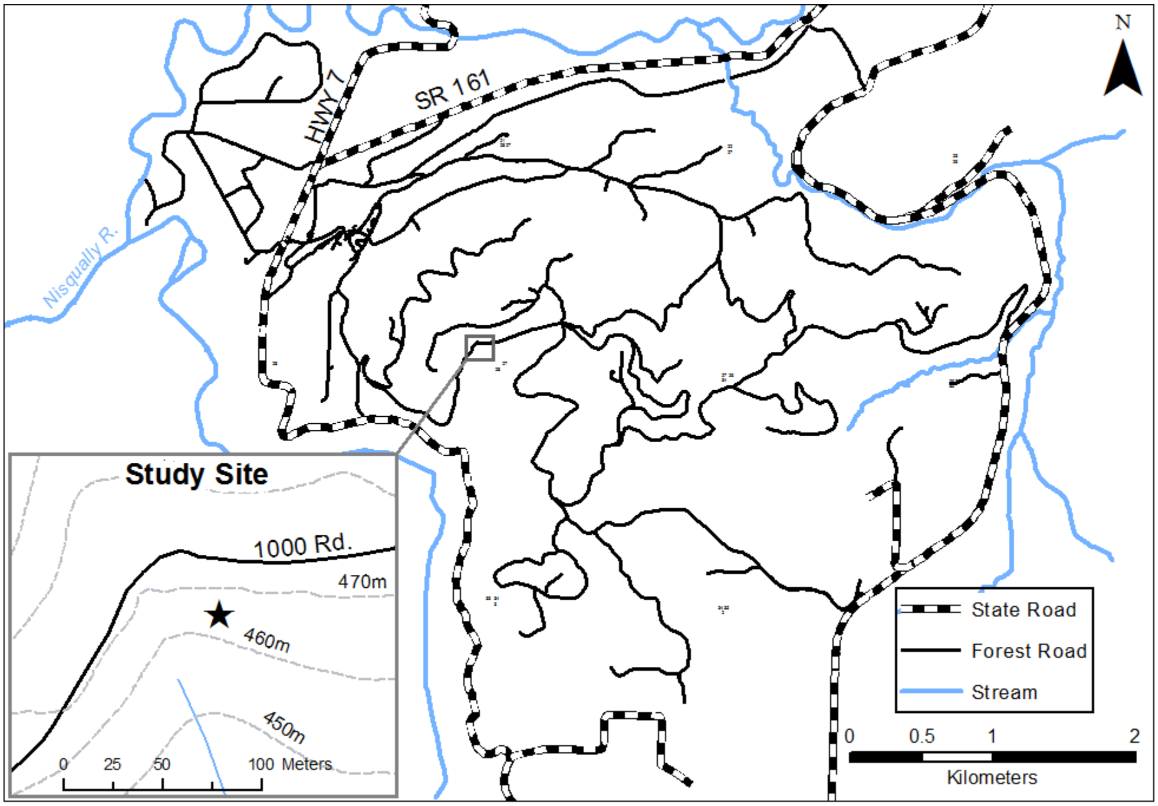


Figure 2. The study site is located within the Charles Lathrop Pack Experimental Forest in western Washington, south of Tacoma and west of Mount Rainier National Park. The site is located approximately 50 meters downslope from the 1000 Road on a south-facing aspect.

T. plicata and *P. menziesii* are the dominant species on the-site. *T. heterophylla* is common in the mid- and lower canopy. A histogram of study site tree diameters at breast height (DBH) shows a reversed *j* distribution with higher stocking of smaller trees, although there is a cohort of larger trees representing those from the pre-fire disturbance stand (Figure 3). The stand has an average basal area (BA) of approximately 90 m^2/hectare. This number is high in part due to the pre-fire remnant trees, which are consistent in size to those measured in old-growth stands in the region.

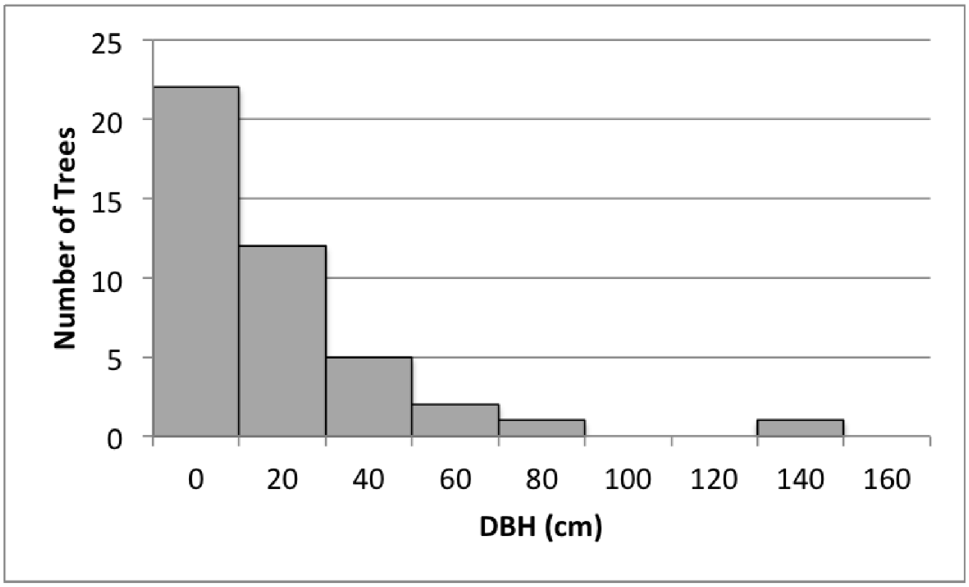


Figure 3. DBH distribution of trees in the vicinity of the project site, showing a reverse *j*-distribution with a majority small trees and a small cohort of large trees. Data are from a 0.04-hectare plot centered on the study trees.

Older trees on the site bear fire scars, evidence of the Eatonville fire that passed through the stand in 1926. Younger trees likely established following that fire, which killed all standing vegetation in other areas of the forest (Swanson 2006). Understory vegetation is sparse, and consists primarily of salal (*Gaultheria shallon*) and sword fern (*Polystichum munitum* (Kaulf.) C. Presl). Soils onsite belong to the Wilkeson series, and are a gravelly silt loam. Figure 4 shows a diagram of the site and Table 1 lists the study trees and some of their physical attributes.

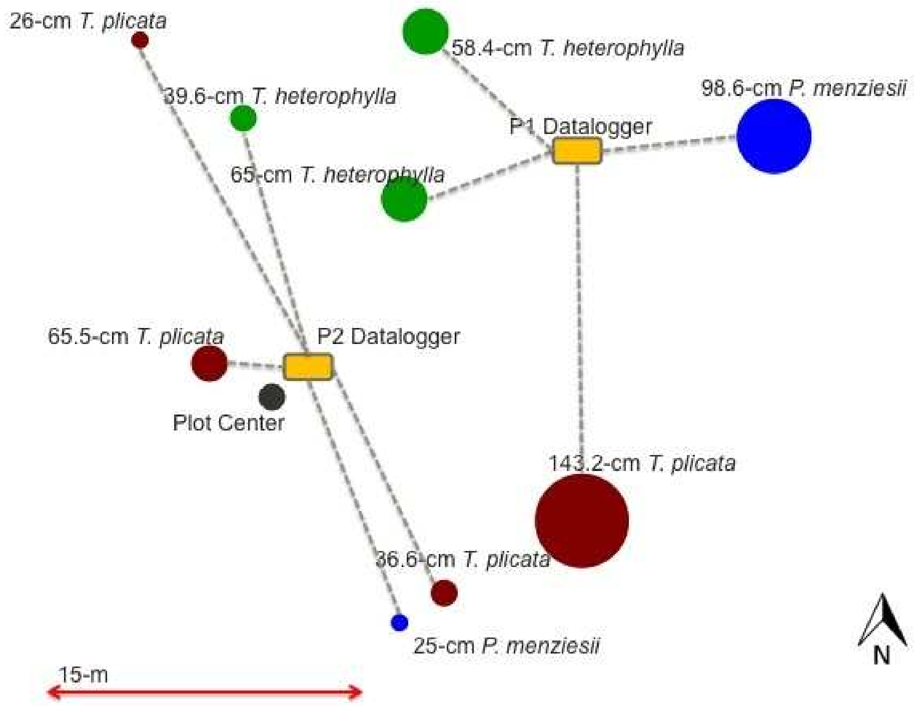


Figure 4. Site map showing locations of sap flow study trees and data loggers in relation to one another. The site includes multiple sizes of each species and is located on a south-facing slope.

Table 1. List of study trees along with their DBH, height, height to crown, crown ratio and bark thickness. Trees 1-8 were outfitted with both sap flow modules and dendrometer bands. Tree 10 was outfitted with just a dendrometer band.

Study Tree	Tag #	Species	DBH (cm)	Height (m)	Crown Ratio	Bark Thickness (cm)	Sapwood Area (cm^2)
1	2	*T. plicata*	143.3	41.8	0.74	0.7	1742
2	1	*P. menziesii*	98.6	44.7	0.65	5	3760.7
3	14	*T. heterophylla*	64	38	0.87	1	1696.5
4	45	*T. plicata*	25.9	25.2	0.7	0.3	139.1
5	31	*T. plicata*	36.6	24.8	0.88	0.4	337.7
6	43	*T. plicata*	65.5	34.8	0.78	1.3	808.8
7	33	*P. menziesii*	24.9	30.8	0.55	3.1	391.2
8	48	*T. heterophylla*	39.6	34.2	0.55	0.8	568.8
10	18	*T. heterophylla*	58.4	39.3	0.56		

The site was selected because the three study species were well represented within close proximity to one another, and the mixed-cohort nature of the stand ensured various canopy heights of each species. A photo of the project site depicts typical conditions and shows some of the instrumented trees (Figure 5). It is primarily a closed-canopy system (see Figure 6**),** although there is one clearing on-site, just south of the largest *P. menziesii*.

Figure 5. A photograph of the project site showing trees instrumented with sap flow meters and dendrometer bands. Camera is facing upslope and approximately north.

Figure 6. Looking up into the canopy at the study site from a location near the P2 datalogger. Trees shown include some of the smaller-diameter study trees.

Field Instrumentation and Sap Flow Calculations

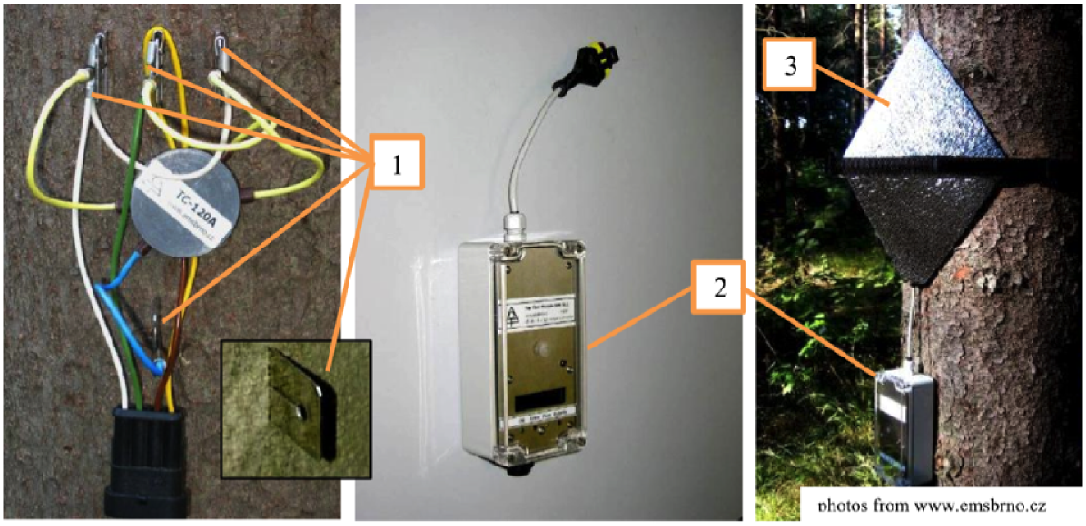
To quantify sap flow, two *P. menziesii* (one large dominant, one intermediate), two *T. heterophylla* (both co-dominant), and four *T. plicata* (one large dominant, one co-dominant, one intermediate, and one suppressed) were instrumented with sap flow modules and dendrometer bands (EMS Brno) in July 2010. Sap flow rates were measured using the thermal heat balance (THB) method. The original THB method was developed by Vieweg and Ziegler (1960), further developed by Čermák et al. (1973), and refined by Kučera et al. (1977). In the THB method, internal heat is applied via AC voltage to the tree sapwood by three 1mm-thick stainless steel plate electrodes. A fourth, unheated electrode is installed below the other three electrodes. Needle thermosensors inserted into the electrodes measure the temperature difference between the three heated plates and the lower plates. Heating is automatically controlled to maintain a 1 K temperature difference between the heated and sensor electrodes. The rate of sap flow is calculated from the heat conducted by the sap minus any measured heat losses from the sensor (Čermák et al. 1973).

The heat balance of the xylem through which the sap flows is described by the equation $P = Q \times dT \times c_w + dT \times z$, where P is the heat input power, Q is the sap flow rate in kg / sec, dT is the temperature difference in the measuring point, c_w is the specific heat of water, and z is the coefficient of heat losses from the measuring point. Sap flow is calculated using the equation:

$$Q = \frac{P}{c_w \times d \times dT} - \frac{z}{c_w}\ [\frac{kg}{s}, cm]$$

In this equation, the first term describes heat conducted by the sap flow and the second represents sensor heat losses. The resultant raw data is equal to the sap flow of a segment of sapwood, not the entire tree. To calculate whole-tree sap flow, measurements of tree circumference and bark depth are incorporated into the model. Circumference of each tree was measured and bark depth was measured using a blunt aluminum tool also instrumented with a linear gauge; bark thickness is estimated where resistance to insertion changes (EMS Brno). Whole-tree sap flow was calculated using the following equation: $Q_{tree} = Q \times (A - 6.28B)[\frac{kg}{hr}]$, in which A is equal to stem circumference and B is equal to the thickness of bark plus phloem (Kučera 2010).

Sap flow modules were installed at a height of at least 1 m on the downslope / south-facing side of the trunk, with the exception of the two largest trees. The largest *P. menziesii* was outfitted with two sap flow modules, one on the north and one on the south side of the tree bole. The largest *T. plicata* was also outfitted with two modules, but with one on the east and one on the west side of the trunk. Two sap flow modules were installed on the largest trees to describe bole variation in sap flow, and sap flow was averaged for these two modules for subsequent analysis (Čermák et al. 1995). Sap flow modules and south-facing lower tree boles receiving direct sunlight were covered with insulating foam and reflective material to protect them from precipitation and overheating due to solar radiation, both of which affect measurements. Electrodes were removed, cleaned, and reinserted in a slightly different location in the tree bole (away from the presumed sap flow of previous installation) once annually to prevent erroneous measurements resulting from resin build-up. A diagram of the sap flow sensor setup is shown in Figure 7.



photos from www.emsbrno.cz

Figure 7. Sap flow modules components: 1) Small thermo sensors, threaded through slots on the electrodes; 2) Module – a self-contained unit that measures sap flow rates. It hangs freely from the electrodes and connects to the datalogger. 3) Reflective, insulating covering to reduce error from solar radiation and precipitation. Not shown, the entire apparatus at the right was then covered in a 0.5 m by 1 m continuous sheet of reflective insulation.

The THB method measures sap flow rates accurately and is sensitive to even small changes in flow rates (Schulze et al. 1985). It allows for estimation of whole-tree transpiration with low error rates, although error is somewhat higher when the study trees are under drought stress conditions (Čermák et al. 1995). The results of individual tree measurements can be scaled to the stand level by estimating sap flow per tree by diameter and multiplying the number of trees of each size.

To quantify water storage and tree growth, dendrometer bands were installed at approximately 1.5 m aboveground on all of the sap flow study trees as well as an additional *T. heterophylla*. The DR 26 dendrometer bands consist of stainless steel tape, whose length variations are measured with an attached rotary position sensor (EMS Brno) (Figure 8). Output data have a resolution of 1 µm and represent a change (Δ) in stem circumference. A change in band length results in a change of the rotary position, which is converted into exact electrical voltage for transmission to a datalogger.

Figure 8. Dendrometer module, showing stainless steel band and rotary position sensor. The band is placed under tension during installation and changes in rotary position are recorded with 1 µm precision.

Sap flow modules and dendrometer bands transmitted data to two EMS Mini32 dataloggers. The four dominant and co-dominant trees, three outfitted with both sap flow and dendrometer modules, one outfitted with only a dendrometer band, were connected to datalogger P1 and the five smaller trees were connected to datalogger P2. The dataloggers recorded sap flow and stem increment at 30-minute time intervals. Each datalogger was powered by a 12-volt rechargeable car battery, which was charged from a solar panel. Battery failures occurred due to cold temperatures, and other difficulties with maintaining electrical equipment in the field for 2 ½ years resulted in loss of data from one or both dataloggers for time periods of varying lengths.

Two weather stations were also installed on-site. Station 1 was installed at approximately 1 m above the ground in a small clearing subject to intermittent sun (Figure 9). Station 2 was installed in the lower canopy of a dominant (non-study) tree 20 m above the ground (Figure 10). Each station consisted of sensors measuring air temperature, relative humidity, soil temperature, solar radiation [W/m^2], and wind speed. Each station was connected to an independent datalogger that recorded values every 10 minutes (Figure 9). Data from all dataloggers were uploaded to a field laptop several times per month. Data were collected from early July 2010 through early December 2012.

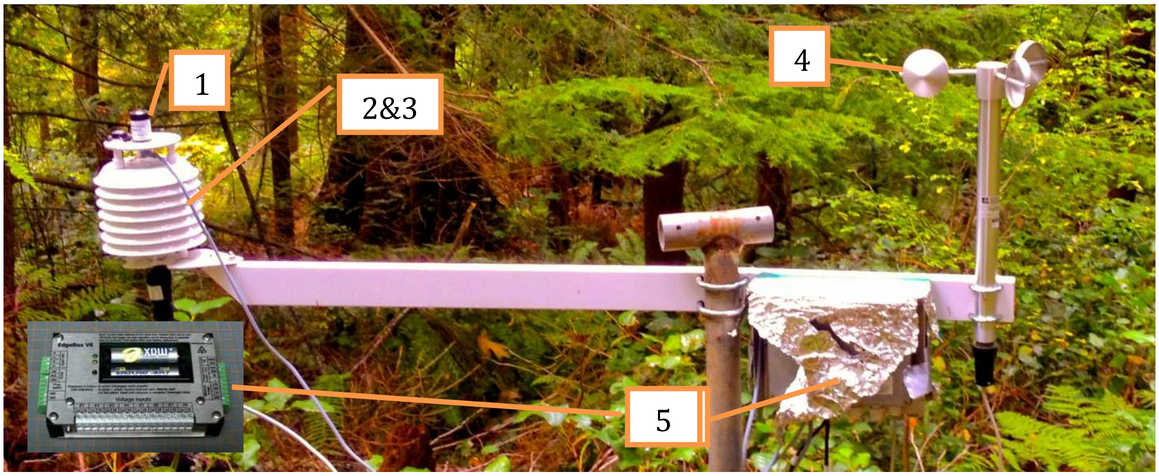


Figure 9. Ground-level weather station. Components are as follows: 1) solar radiation sensor; 2 and 3) temperature and relative humidity sensors encased in radiation shield; 4) anemometer to measure windspeed; and 5) datalogger.

Figure 10. Canopy-level weather station mounted approximately 20 m above the ground. Components are the same as those in Figure 9.

Qualitative Data Analysis

Time series of sap flow and dendrometer data were examined by season to compare differences among species, tree sizes, and canopy position. Patterns in sap flow and stem increment data were visualized at daily, seasonal, and longer time periods.

ANOVA

Analysis of variance (ANOVA) was used to test for differences in sap flow among species and canopy position. Stem diameter has been found to explain 87-88% of variation in transpiration in two hardwood species (Vertessy et al. 1995) and tree basal area explained 91.1-99.9% of variation in *Abies amabilis* (Martin et al. 2001), so prior to ANOVA, I converted daily sap flow to a per-DBH unit value (i.e. daily sap flow per centimeter of DBH) in order to normalize sap flow for trees of various sizes. I then created datasets of total daily sap flow for series of days by season. In the first set of tests, I compared trees by species, and then in a separate test by height class.

The first ANOVA test compared total daily sap flow of each species without regard to height. In a second analysis, I compared total daily sap flow of each of three height classes – under 30 m, 30-35 m, and over 35 m – without regard to tree species. Each test was run multiple times, for each season for which we had a minimum of 30 days of data. Subsequently, I ran ANOVA tests comparing sap flow rates for just the three dominant trees to one another, and then just of the three smallest trees to one another. These tests were also run for each season for which data were available.

Stand Transpiration

To produce an estimate of stand transpiration, I first categorized all the trees in the study site into height classes (less than 30 m, 30 to 35 m, and over 30 m). I then calculated the mean normalized total daily sap flow rates for each of the study trees. I used these rates to calculate the sap flow of all the trees within the 0.04-hectare plot, based on tree size, by multiplying the mean per cm sap flow rate of the closest in size study tree by the DBH of the non-study trees. This value was converted to mm of transpiration per day, which is equivalent to 10 m^3 per hectare per day. I performed this calculation for spring (April 1 – May 31), early summer (June 1 – July 14), late summer (July 15 – September 15), fall (September 16 – November 15), and winter (November 16 – March 31).

Water Use Efficiency

I estimated tree water use efficiency (WUE) for all months of the growing season for which both sap flow and stem increment data were available to compare WUE by species and canopy position. To perform this analysis, I calculated the basal area increment (BAI) for each month, using the dendrometer band data, and the total monthly sap flow of each study tree. Monthly WUE was calculated as the ratio of BAI to total sap flow for each tree. I also estimated three-year WUE for each of the three largest trees and two-year WUE for the five smaller trees. For this estimate, I calculated the ratio of BAI from growth rings of tree cores to estimated annual transpiration of each tree. Annual transpiration of each tree is based on seasonal daily means, which were calculated using any available data.

Tree Vigor

Because stemwood production is a secondary priority to root and shoot growth for plants, a method of assessing tree vigor by determining the proportion of carbon allocated to stem growth has been suggested (Waring et al. 1980). Waring et al. (1980) found that in young *P. menziesii* the ratio of basal area growth to sapwood basal area was a reliable indicator of stemwood-volume production per unit of leaf area. To determine tree vigor of the study trees, I calculated the area of the 2012 growth rings for each tree as well as their 2012 sapwood area and computed the ratio of the two values for each tree.

Results

Bole Variation in Sap Flow in Dominant P. menziesii and T. plicata

Two sap flow modules were installed on the two largest trees, and the differences between sap flow measurements at different locations on the tree boles are depicted in Figures 11 and 12. The sap flow patterns demonstrate synchrony, with increases and decreases in flow occurring at the same time in both sap flow modules. However, in the *P. menziesii*, the south-facing module depicts changes of greater magnitude than the north-facing module. In the *T. plicata*, the two sap flow curves are very similar until late August, when the decline in sap flow is steeper in the west-facing module.

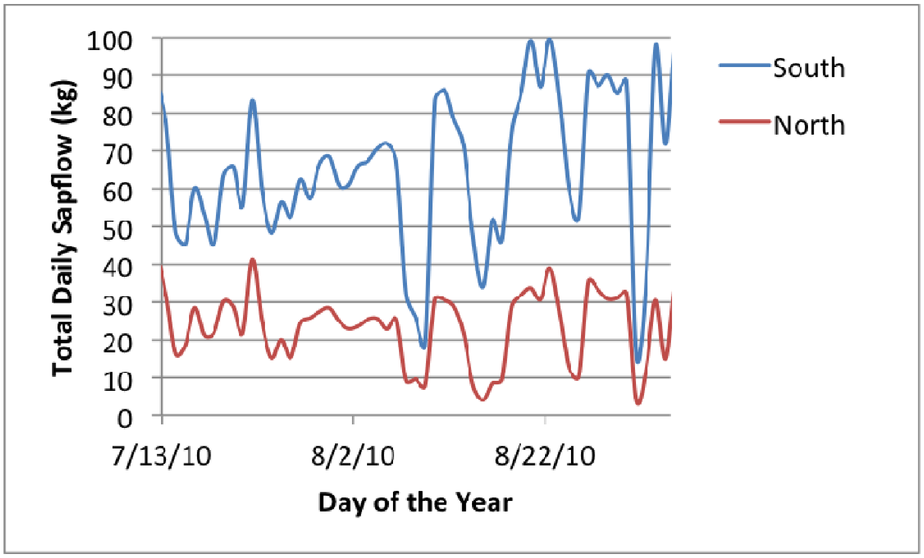


Figure 11. Total daily sap flow rates for 98.6-cm *P. menzeisii*, illustrating the difference between measured sap flow rates on the north and south sides of the tree bole.

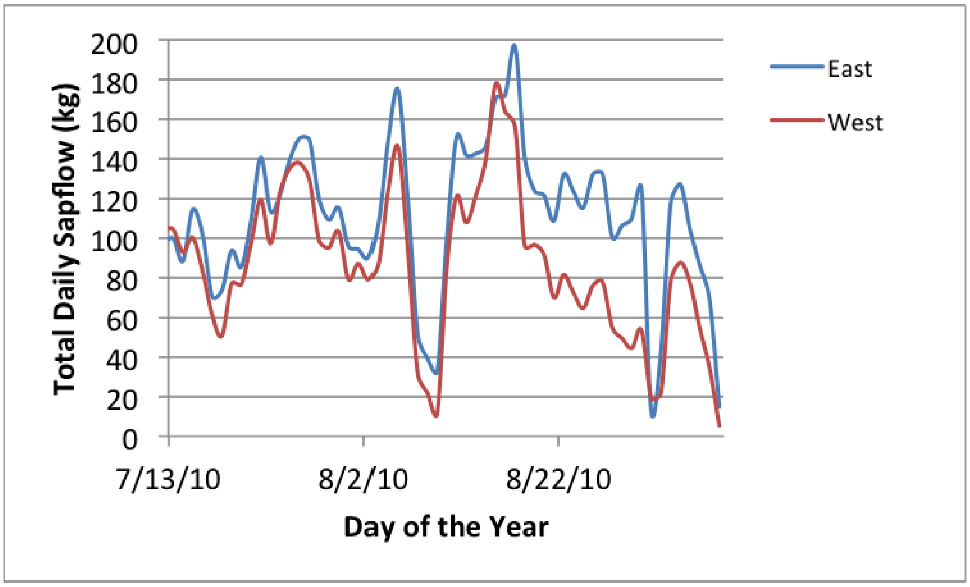


Figure 12. Total daily sap flow rates for 143.3-cm *T. plicata*, illustrating the different sap flow rates on the east and west sides of the tree bole.

Diurnal and Seasonal Sap Flow Patterns

All trees shared the same general sap flow curve – an increase in flow in the early afternoon, peaking sometime in the afternoon, and then declining into the evening – but patterns differed by species, especially during summer months. *T. plicata* demonstrated a more bell curve-shaped diurnal pattern, particularly on days with lower levels of light and

VPD, and its sap flow levels peaked later in the day (Figure 13). *T. heterophylla* and *P. menziesii* initiate activity more abruptly, reach their peak earlier, and then decline gradually throughout the evening. In the summer months, this pattern held true for trees of all sizes, indicating species uniformity regardless of canopy position. On July 22, 2010, a fairly cloudy day particularly in the morning, sap flow initiated at approximately the same time for the three largest trees of each species, at around 0800 h. It initiated earliest in *T. heterophylla* and latest in the small *P. menziesii*. Sap flow peaked at around 1500h for the large *P. menziesii* and *T. heterophylla* and at 1600h for the dominant *T. plicata*. Both *P. menziesii* and *T. heterophylla* sap flow curves demonstrate a flattening after nearing their peaks. On July 23, 2010, when light levels were higher, all three dominant trees demonstrate a sharp dip in sap flow rates, which coincides with peak solar radiation at the ground-level weather station (Figure 13). *P. menziesii*, the most drought-tolerant of the three species, maintains a fairly constant sap flow rate for a much longer portion of the day than the other two trees, although the dominant *T. plicata* maintains measurable sap flow later into the evening on both summer days.

Magnitude of flow is also quite different for the three trees. For all the study trees, sap flow was slightly higher on July 22, indicating that sap flow rates may be limited by higher VPD and light levels on the sunnier day. On July 22, *T. plicata* reaches a maximum sap flow of 13.3 kg/hr, while *P. menziesii*'s maximum flow is 6.6 and *T. heterophylla*'s is 5.8. However, when sap flow rates are transformed to a scalable unit by calculating sap flow per centimeter DBH, differences in magnitude are smaller. Per cm DBH, sap flow rates for these two summer days are highest in the smaller *T. heterophylla*, followed by the dominant and co-dominant *T. plicata.* Per-unit sap flow rates are lowest in the smallest *T. plicata* and the smaller *P. menziesii* (Figure 14). Fall diurnal sap flow rates for the three dominant trees are similar in magnitude, with *P. menziesii* peaking earlier in the day than the other two trees (Figure 15) On these same dates in the smaller trees, the same basic curves are evident for most trees. When sap flow measurements of the smaller trees are scaled to sap flow per cm DBH, *T. heterophylla* has the highest peak flow rate.

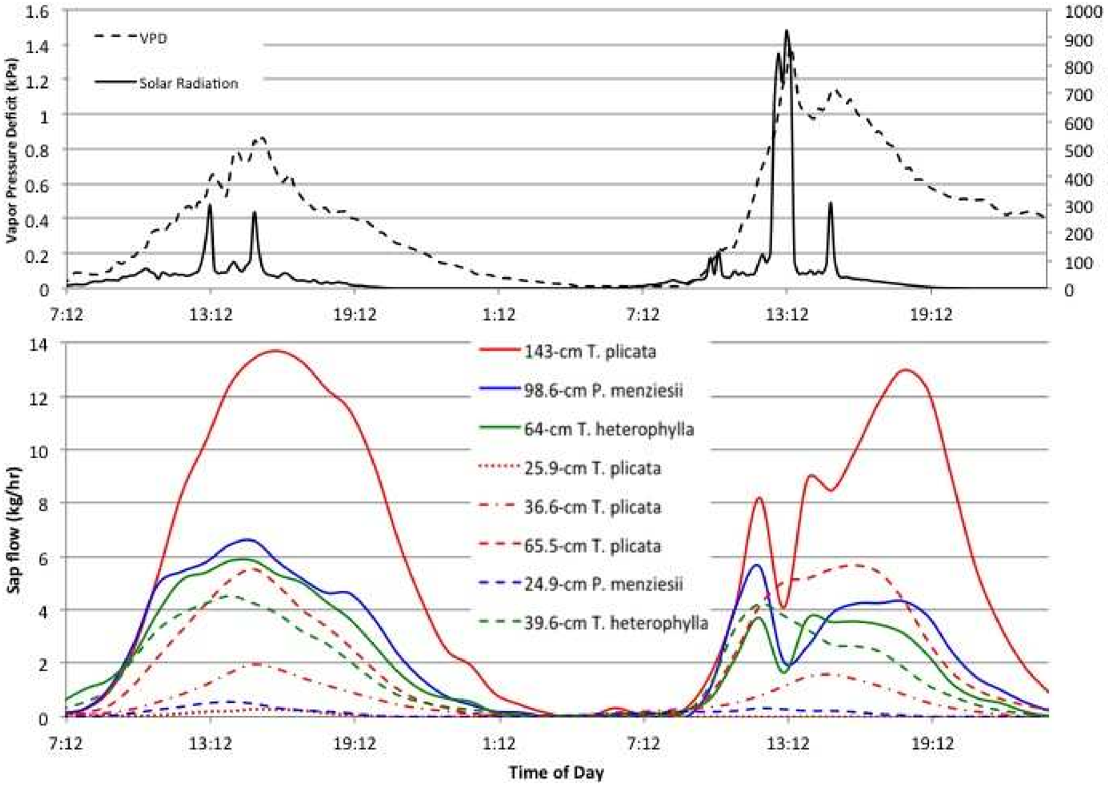


Figure 13. Diurnal sap flow curves for all study trees on July 22, 2010, a somewhat cloudy day, and July 23, 2010, a sunny day. Sap flow is shown in kg/hr for whole trees. Solar radiation and VPD taken at Weather Station 1, at 1m height, are shown above.

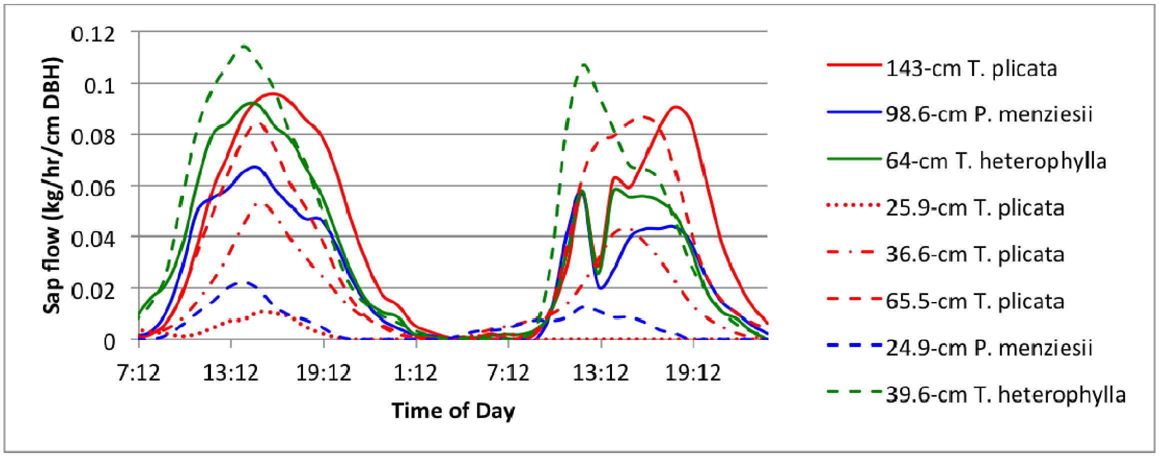


Figure 14. Normalized hourly sap flow rates for all study trees on July 22 and 23, 2010.

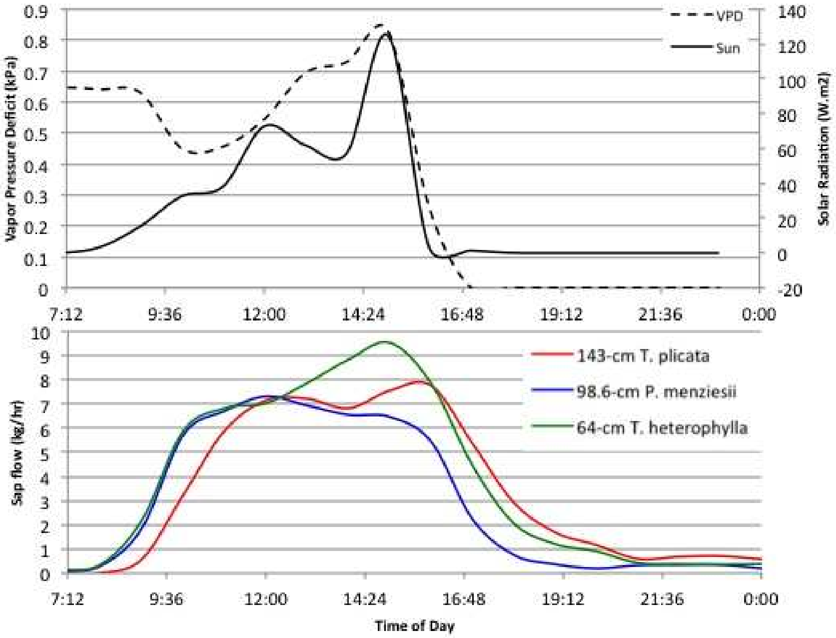


Figure 15. Hourly sap flow and weather data for the three dominant study trees on October 14, 2010.

Winter daily sap flow was much lower, and patterns were less apparent, particularly for trees in lower canopy positions (Figures 16 and 17). Maximum sap flow rates are much lower in Figure 16 than in Figure 13, and lower still in Figure 17. Sap flow curves of the large *P. menziesii* and *T. heterophylla* were similar in shape to those curves in summer days, and although the magnitude was much less, these trees still maintained measurable rates. Regardless of size, *T. plicata* demonstrated very little winter activity on cold, cloudy days.

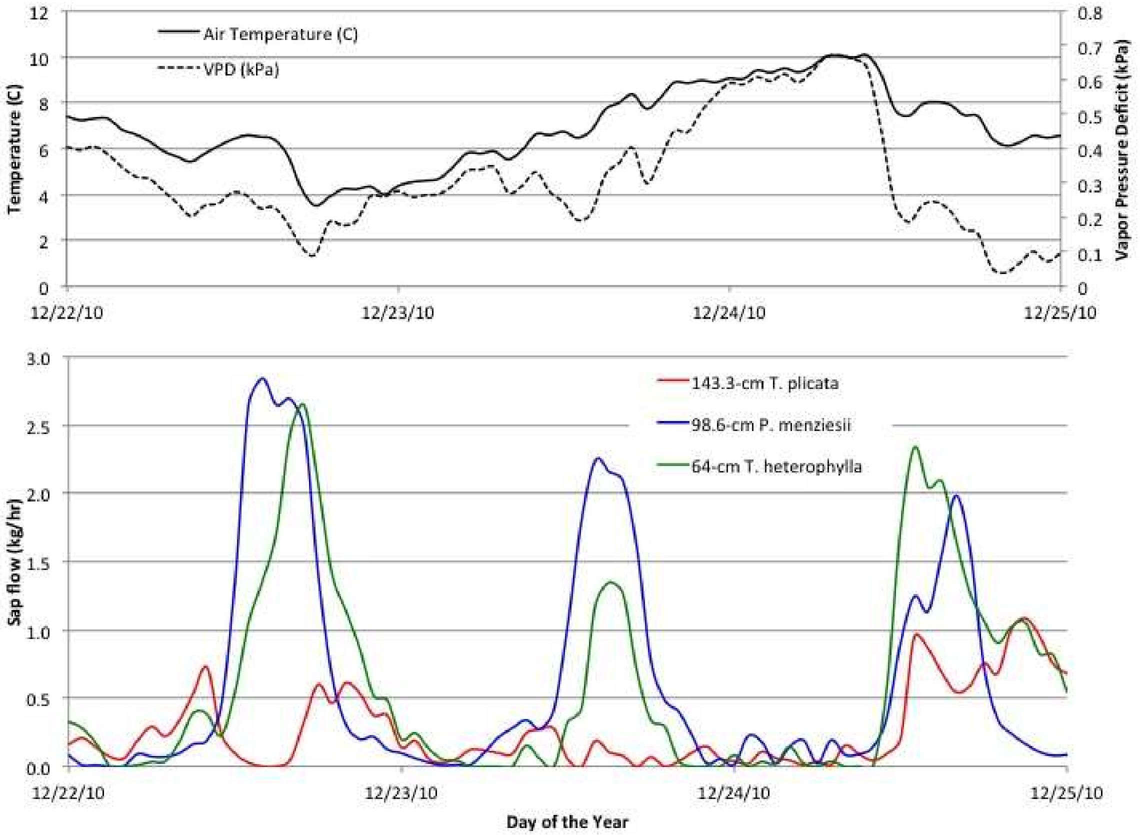


Figure 16. Diurnal sap flow rates of the three largest study trees on three cold, cloudy, winter days. Sap flow is shown in kg/hr for whole trees. Air temperature and VPD at the ground-level weather station are shown above, for the same time period.

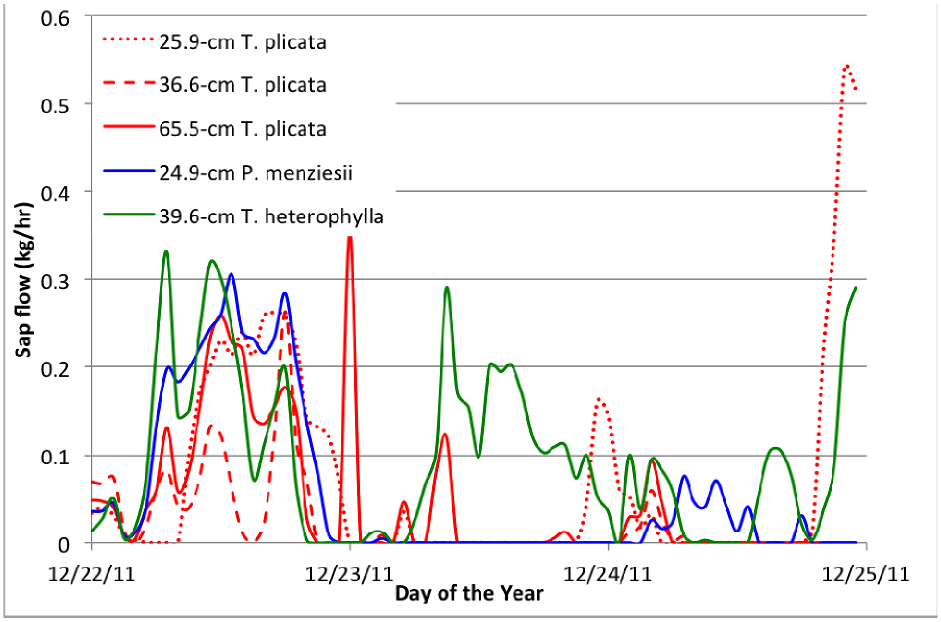


Figure 17. Diurnal sap flow rates of the smaller study trees on cold, cloudy winter days. Although some synchronous response is evident on December 22nd, overall patterns are much less regular than on warm days.

The sap flow rates of *T. plicata* began dropping earlier in the fall than the other two species. In the spring, *T. plicata* sap flow rates appeared to increase later in the year than those of *P. menziesii* and *T. heterophylla*. Unfortunately, inadequate data were available to illustrate the spring increase in sap flow. Figure 18 depicts most of a year of sap flow rates for the three dominant trees. Sap flow is shown in kilograms per day of sap flow per tree, and values represent a five-day running average of total daily flow. Figure 19 shows data for the same time period, but values represent total daily flow per cm DBH. Figure 20 and 21 show a full year of five-day averaged total daily sap flow, for the whole tree and per cm DBH, respectively, for the five smaller study trees. Average whole-tree daily sap flow for each season is depicted in Table 2.

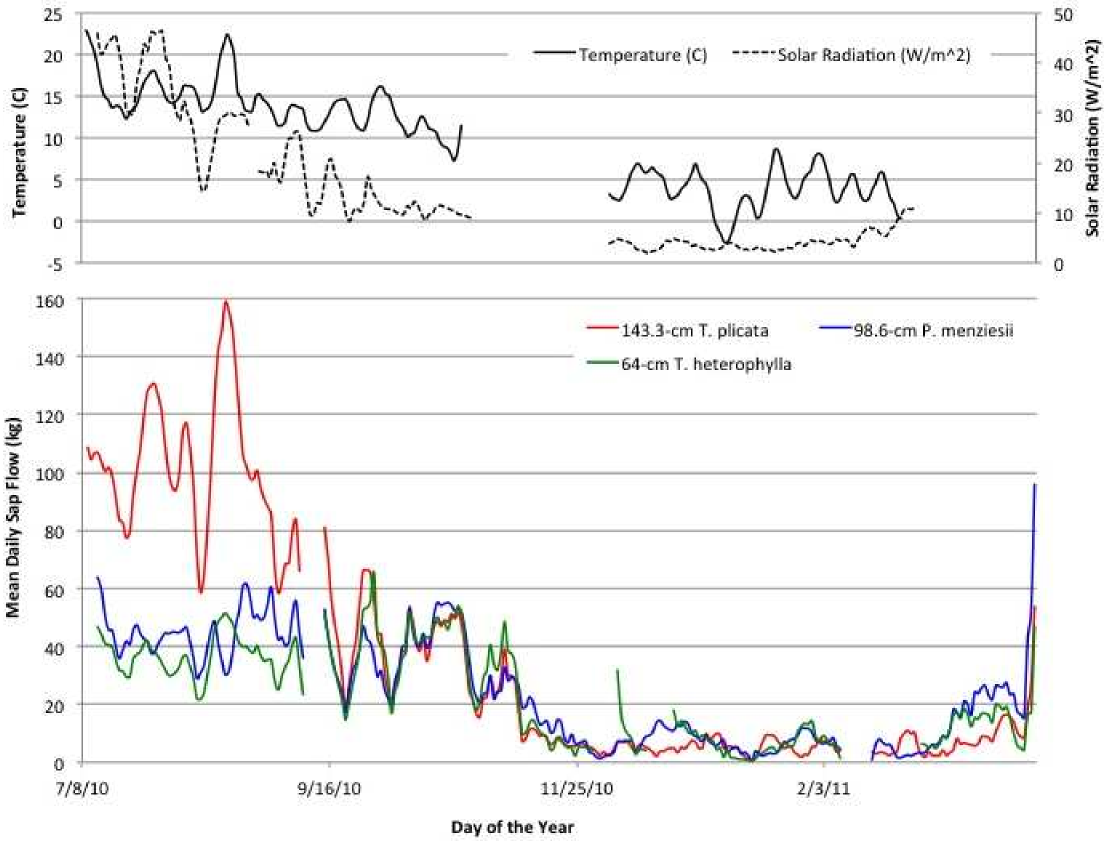


Figure 18. Five-day running averages of total daily sap flow for the three dominant trees, from July 2010 to April 2011. Five day running averages of patchy temperature and solar radiation data from the ground-level weather station are shown for the same time period.

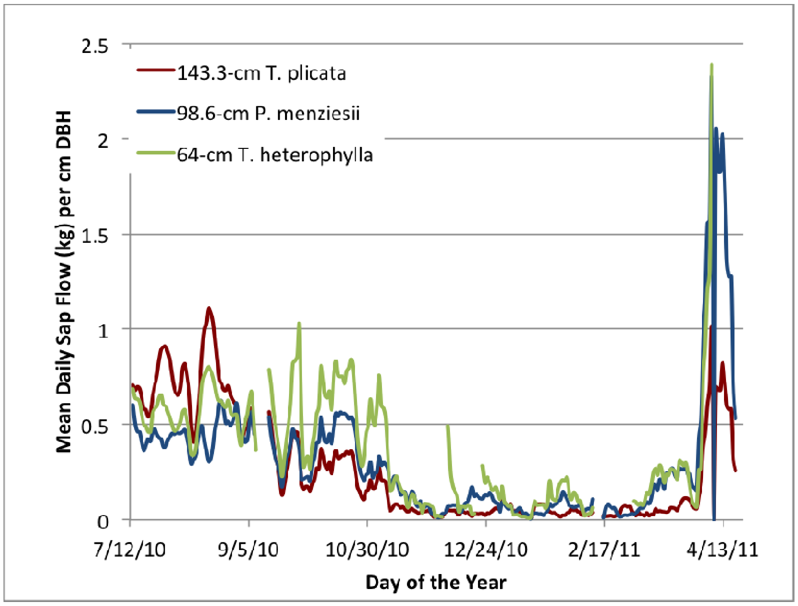


Figure 19. Five-day running averages of total daily sap flow for the dominant study trees, in kilograms per cm DBH, from July 2010 to April 2011.

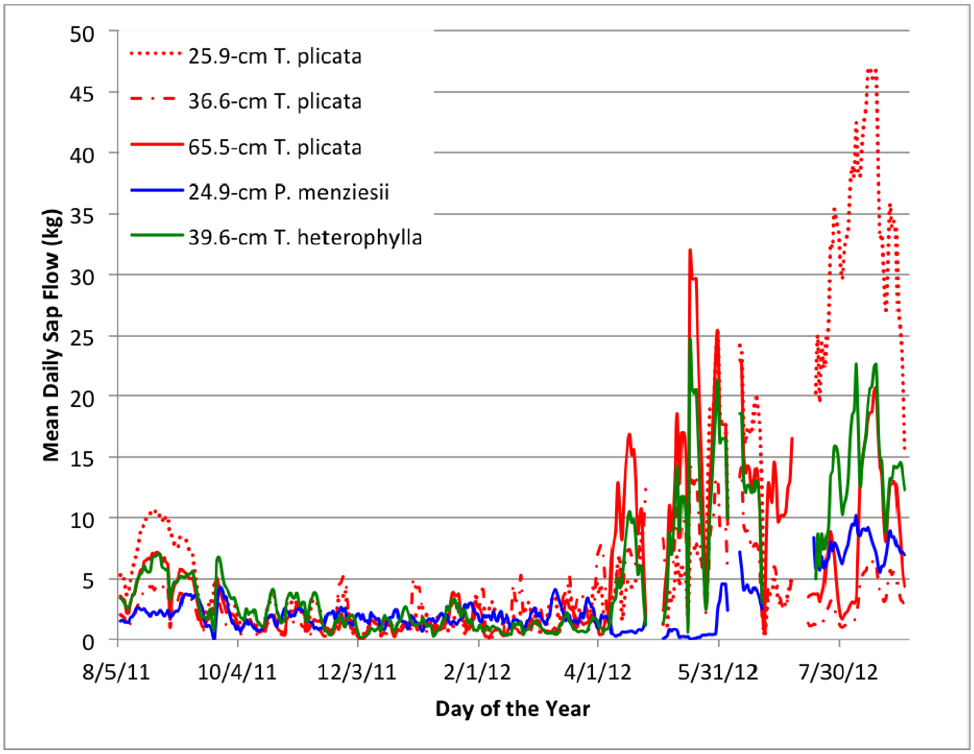


Figure 20. Five-day running averages of total daily sap flow for the five smaller trees.

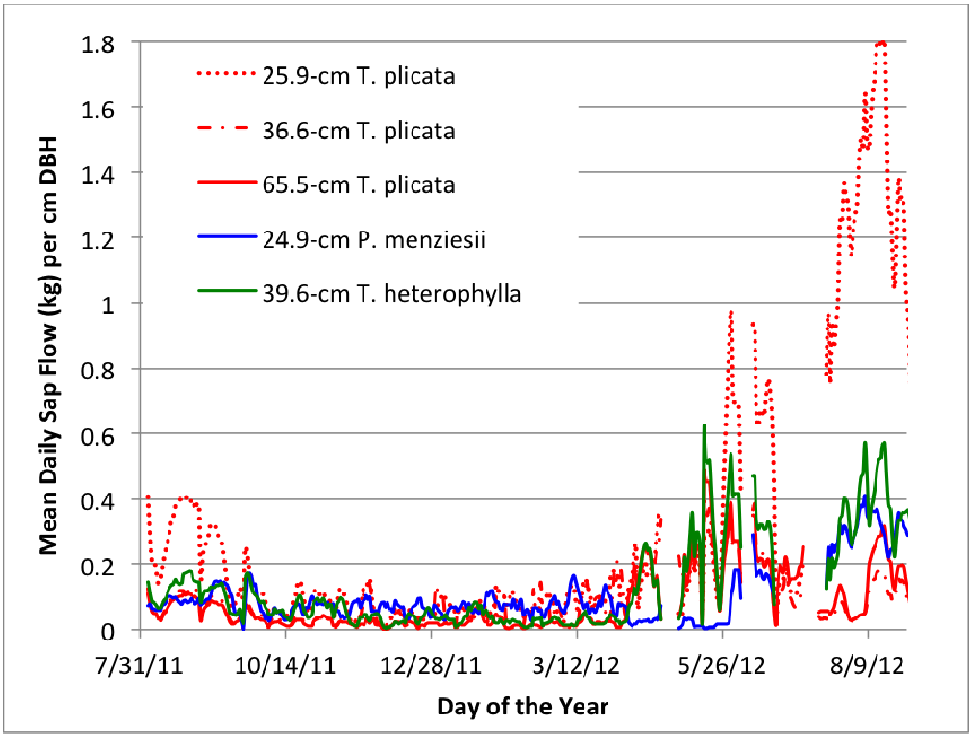


Figure 21. Five-day running averages of total daily sap flow for the smaller study trees, in kg per cm DBH.

Table 2. Average daily sap flow and average daily sap flow per-cm DBH daily sap flow for each study tree for spring (Apr 1-May 31), early summer (June 1 – July 14), late summer (July 15 – Sept 15), fall (Sept 16 – Nov 15), and winter (Nov 16 – Mar 31). All days for which data are available are included in the calculation, so some seasons have more robust data than others. Few data were available for spring.

Tree	Spring	Early Summer	Late Summer	Fall	Winter
143.3-cm *T. plicata*	8.55	35.68	70.48	23.75	6.81
98.6-cm *P. menziesii*	2.00	23.85	39.70	28.65	8.88
64-cm *T. heterophylla*	--	35.35	45.68	27.93	9.00
25.9-cm *T. plicata*	7.28	7.65	16.77	3.73	1.94
36.6-cm *T. plicata*	7.47	5.97	4.63	1.47	2.15
65.5-cm *T. plicata*	13.75	11.32	11.52	1.91	1.28
24.9-cm *P. menziesii*	0.91	3.66	4.51	1.45	1.87
39.6-cm *T. heterophylla*	9.52	20.05	14.78	3.32	1.24

Tree	Spring	Early Summer	Late Summer	Fall	Winter
143.3-cm *T. plicata*	0.06	0.25	0.49	0.17	0.05
98.6-cm *P. menziesii*	0.02	0.24	0.40	0.29	0.09
64-cm *T. heterophylla*	--	0.55	0.71	0.44	0.14
25.9-cm *T. plicata*	0.28	0.30	0.65	0.14	0.07
36.6-cm *T. plicata*	0.20	0.16	0.13	0.04	0.06
65.5-cm *T. plicata*	0.21	0.17	0.18	0.03	0.02
24.9-cm *P. menziesii*	0.04	0.15	0.18	0.06	0.08
39.6-cm *T. heterophylla*	0.24	0.51	0.37	0.08	0.03

ANOVA Results

The results of the ANOVA show the effects of tree height and tree species on total daily sap flow rates vary by season. Comparing all trees, both species and height class have significant effects on total daily sap flow by cm DBH in summer, fall, and winter (Figure 22). In all three seasons, sap flow is highest in *T. heterophylla*. In summer and fall, there was no significant difference between total sap flow of *T. plicata* and *P. menziesii*. In the winter, both species effect and height class effect are somewhat diminished, and sap flow was lowest in *T. plicata*.

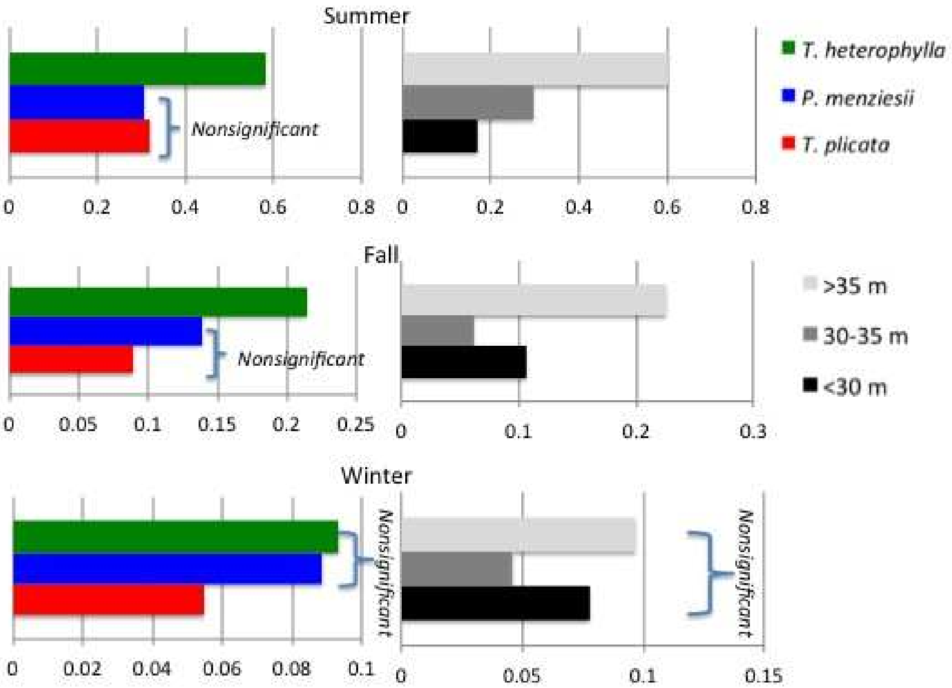


Figure 22. Results from ANOVA tests comparing total daily sap flow per cm DBH between the three study species and between height classes for three seasons. Values shown are in kilograms / cm DBH / day.

In comparing total daily sap flow per cm DBH of the three dominant trees, sap flow rates was highest in *T. heterophylla* in all seasons tested, although in late winter it was not significantly different than *P. menziesii* (Figure 23). In the fall and winter, sap flow was lowest in the dominant *T. plicata*.

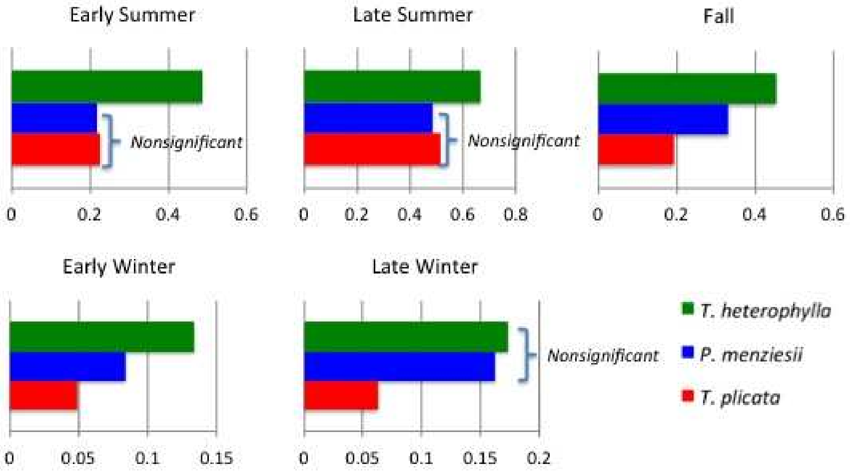


Figure 23. Results from ANOVA tests comparing total daily sap flow per cm DBH between the three largest trees of each species. Values shown are in kilograms / cm DBH / day.

Finally, comparing sap flow of the three smallest-diameter trees of each species (Figure 24), *T. plicata* had the highest sap flow in the spring, summer, and fall. Sap flow was lowest in the small *P. menziesii* in all seasons except winter, when its sap flow was not significantly different from that of *T. plicata*.

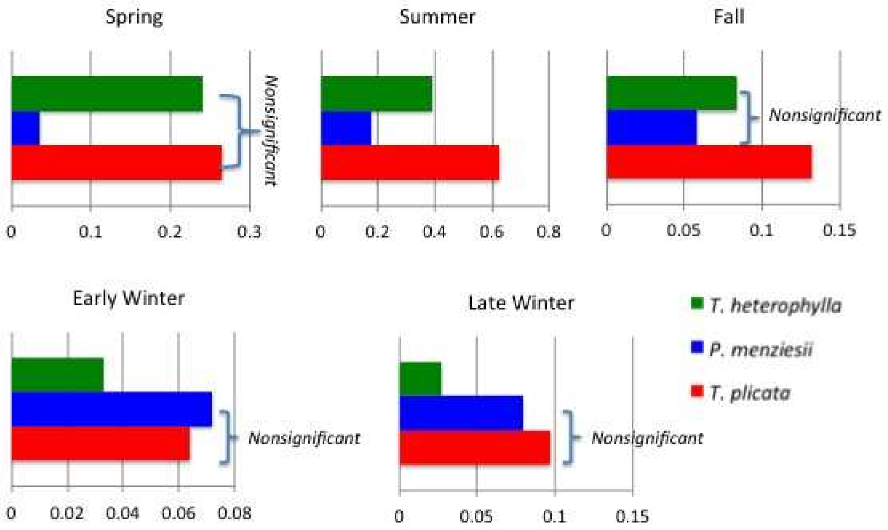


Figure 24. Results from ANOVA tests comparing daily sap flow per cm DBH among the three smallest trees of each species. Values shown are in kilograms / cm DBH / day.

Tables showing means, p-values, and post-hoc tests for all three tests are included in the Appendix.

Diurnal and Seasonal Stem Increment Patterns

In order to examine diurnal stem increment patterns, I first transformed all the dendrometer data (removing differences in starting rotational measurement of sensors) to begin at 0 mm at the beginning of the study period. I then graphed stem increment changes over short time periods (Figure 25). During the time period from July 10th to August 4th, both the rate and the magnitude of stem expansion are greatest in the dominant *T. plicata*. Stem circumference also increases greatly in the two large *T.*

heterophylla and the smallest *T. plicata*. Day-to-day fluctuations are greatest in these four trees as well. During this time period, there is minimal overall stem expansion in the two *P. menziesii* and the 65.5-cm *T. plicata*, and the small *T. heterophylla* and 36.6-cm *T. plicata* lose stem circumference. These five trees also demonstrate less day-to-day fluctuation, with the 36.6-cm *T. plicata* remaining the most static within days.

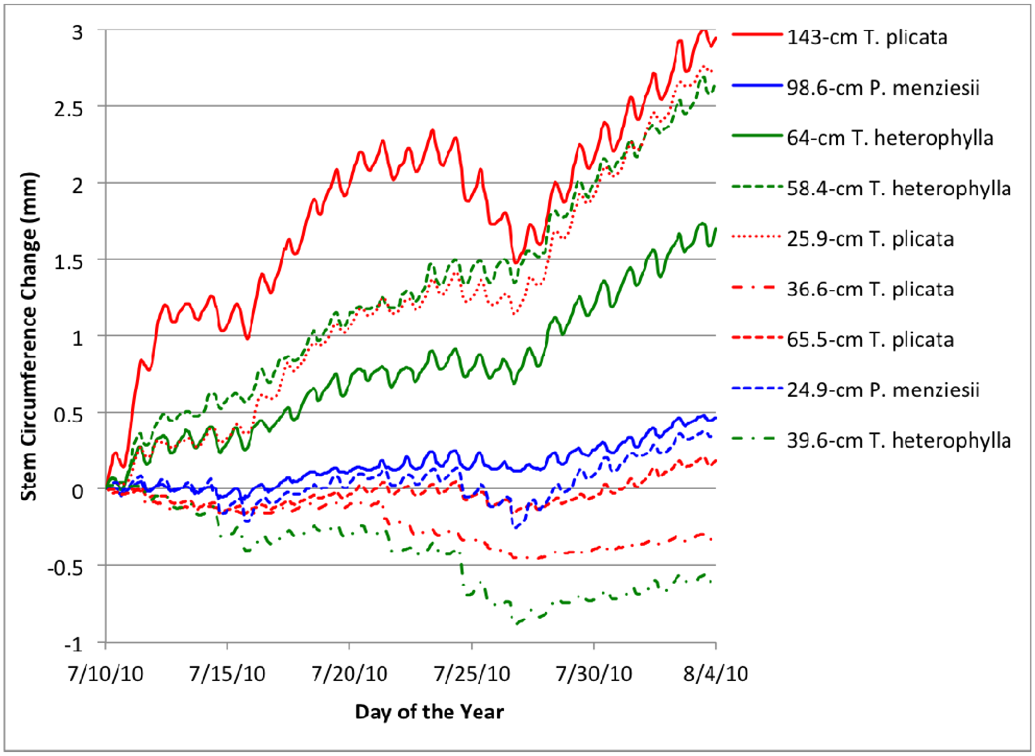


Figure 25. Diurnal stem circumference fluctuations for all study trees from July 10th – August 4th, 2010, demonstrating both day-to-day fluctuations as well as growth trends.

In the winter, there is much less within-day fluctuation in stem circumference for all the study trees (Figure 26). In November and December 2011, the greatest changes in stem circumference occurred in the three larger *T. plicata*, and the smallest changes occurred in the two *P. menziesii* and the smallest *T. plicata*. Species appeared to more strongly affect patterns of stem increment change than did canopy position during the winter, when light levels are low for all trees regardless of height.

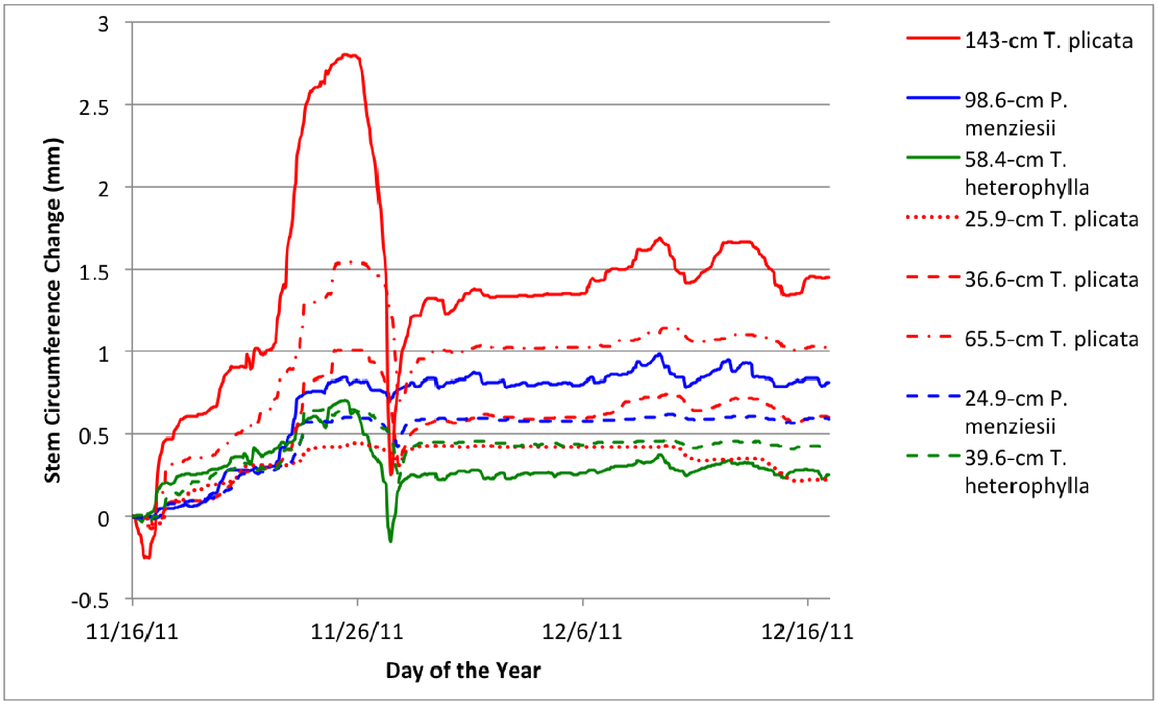


Figure 26. Diurnal stem circumference fluctuations for the study trees from November 16th – December 16th, 2011, demonstrating both day-to-day fluctuations as well as growth trends. Stem expansion appears to continue, albeit slowly, into late November for all study trees.

Stem increment curves over a calendar year for the largest trees of each species demonstrate both short-term fluctuations in water storage status and longer-term growth of the tree boles (Figure 27). The two similar-sized *T. heterophylla* demonstrate almost identical curves of stem increment change, suggesting that species plays a vital role in water storage and growth patterns. The large *T. plicata* shows the greatest short-term fluctuation in bole water status, while short-term fluctuation is minimal in the large *P. menziesii*. Onset of spring-time growth and/or stem recharge occurs earliest in *T. heterophylla* and latest in *T. plicata*. Stem circumference of the dominant *T. plicata* dips sharply at approximately the same time that *T. heterophylla* initiates growth, in late May. The overall trend is for an increase in circumference, and while this is greatest during the summer, surprisingly, there appears to be a small expansion during the winter as well.

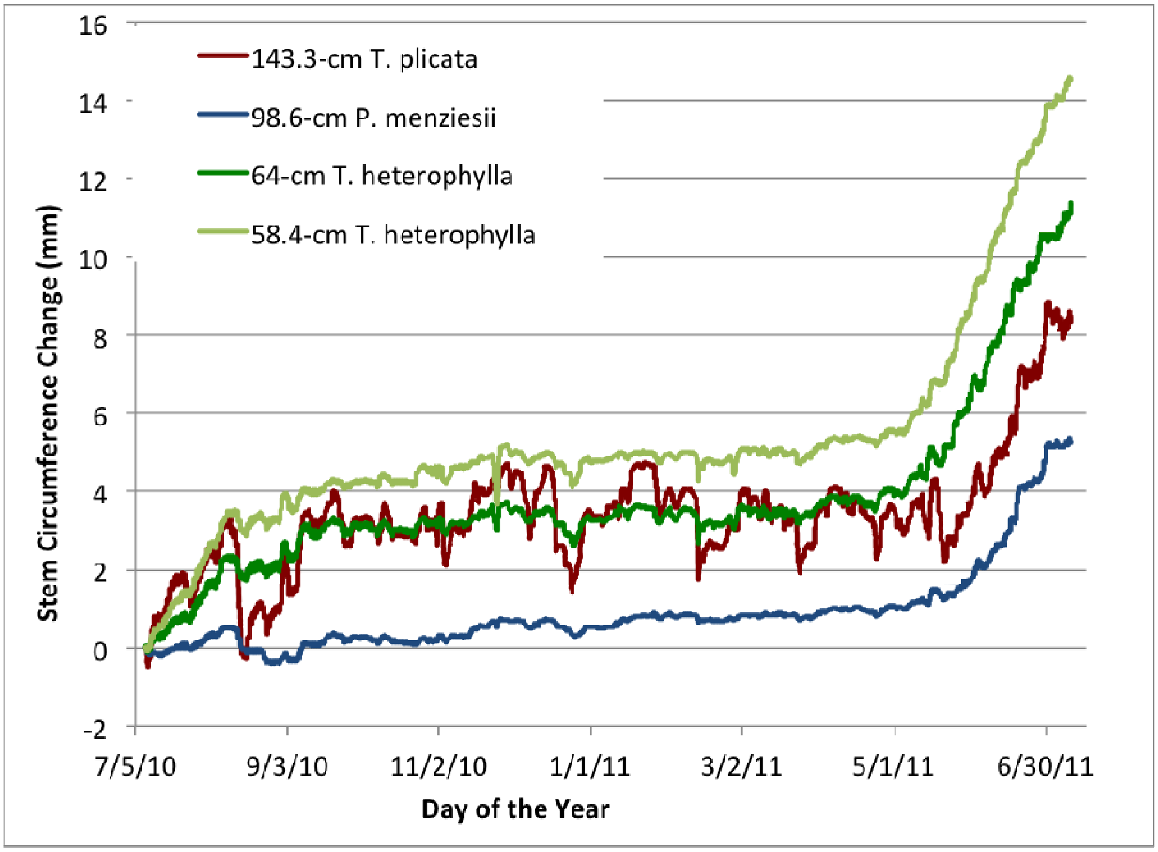


Figure 27. Stem increment changes for dominant trees across a full year.

These patterns are mirrored, although less evidently, in Figure 28, which depicts a calendar year of stem increment change for the five smaller trees. Here the strongest similarities are between the two larger *T. plicata*. The 25.9 cm *T. plicata* shows little short-term fluctuation and little long-term growth, reflecting its status as a suppressed tree in a closed-canopy system. The 39.6 cm *T. heterophylla* demonstrates a shallower spring growth curve than the larger trees in Figure 27, likely a result of canopy position-induced growth limitations. Despite drastically different sizes and canopy positions, the two *P. menziesii* demonstrate patterns of similar magnitude (Figures 26 and 27).

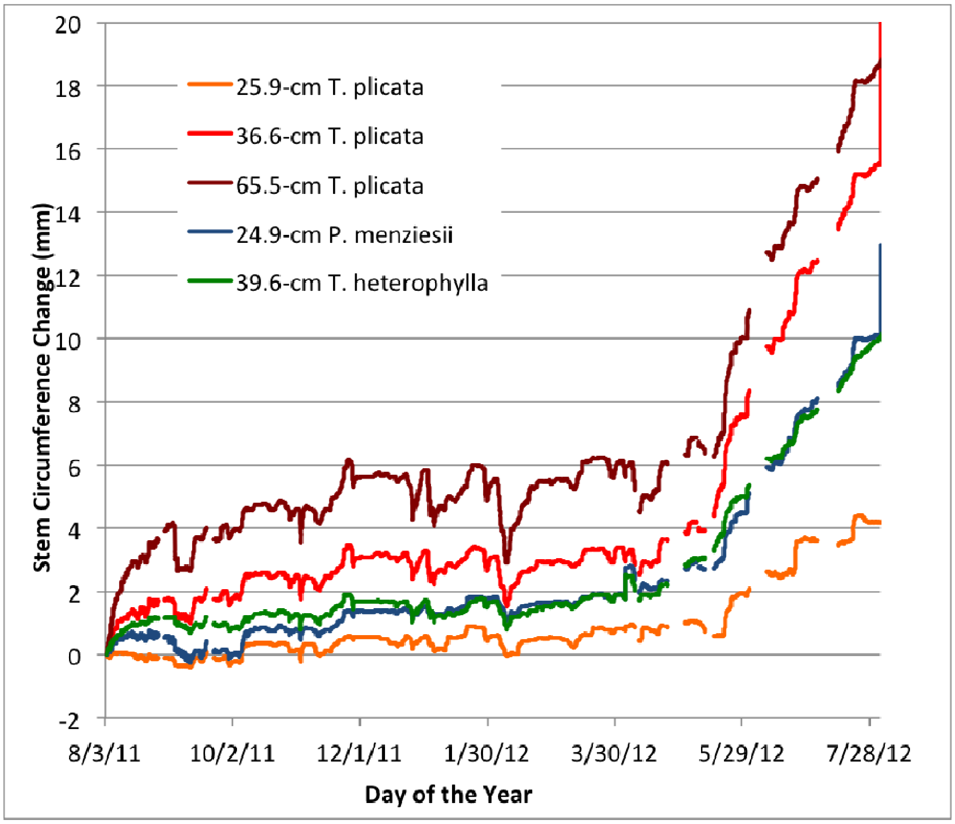


Figure 28. Stem increment changes for intermediate and suppressed trees across a full year.

Overall length of growing season appears to be influenced both by tree species and canopy position. *T. heterophylla* onset of growth occurs earliest in the year regardless of tree height. Next to initiate growth are the suppressed to intermediate *T. plicata* and the suppressed *P. menziesii*, followed by the dominant *P. menziesii* and finally the dominant *T. plicata.* Cessation of summer stem growth is more variable, but occurs earliest in *T. plicata*, with the exception of the 65.5-cm tree, and latest in the co-dominant *T. heterophylla*. These results are summarized in Table 3.

Table 3. Approximate start and end dates of seasonal stem expansion for all study trees based on dendrometer band data.

Tree	Height Class*	Start Date	End Date	Days in Growing Season
143.3-cm *T. plicata*	3	5/21	7/29	69
98.6-cm *P. menziesii*	3	5/19	8/3	76
64-cm *T. heterophylla*	3	5/7	8/11	96
25.9-cm *T. plicata*	1	5/16	7/21	66
36.6-cm *T. plicata*	1	5/16	8/3	79
65.5-cm *T. plicata*	2	5/17	8/26	101
24.9-cm *P. menziesii*	2	5/16	8/3	79
39.6-cm *T. heterophylla*	2	4/20	8/3	105
58.4-cm *T. heterophylla*	3	4/27	8/14	109

*Height class 1<30m; class 2 30-35m; class 3 > 35m

I used stem increment data to determine overall circumference growth of all the study trees during the time period from July 2010 to December 2012, and then calculated BAI. Overall BAI during this period was highest in the 143.3-cm *T. plicata* (181.85 cm^2 BAI), the 65.5-cm *T. plicata* (155.01 cm^2 BAI), and the 58.4-cm *T. heterophylla* (122.58 cm^2 BAI). The lowest recorded overall BAI occurred in the 25.9-cm *T. plicata* (3.22 cm^2 BAI), followed by the 24.9-cm *P. menziesii* (44.19 cm^2 BAI).

Total Stand Transpiration

I calculated total stand transpiration by multiplying the mean total daily sap flow rates per study tree across all 46 trees in the study plot, converting to kilograms per hectare, and then converting to mm per day (10 m^3 per hectare per day). I approximated the total stand transpiration per hectare for spring, summer and fall (Table 4). Although only six of the 46 trees were over 50 cm in diameter, these trees accounted for nearly half of transpiration across all three seasons. Transpiration rates were much higher in the summer than in the fall or winter, and were approximately twice as high in the fall as in the winter.

Table 4. Approximate stand-level transpiration rates, per hectare, based on extrapolating daily sap flow rates for the study trees across all trees within the study plot.

	Total Average Daily Stand Transpiration (mm)				
Tree DBH (cm)	Spring	Early Summer	Late Summer	Fall	Winter
> 50	0.26	0.45	0.48	0.19	0.05
25-50	0.22	0.28	0.36	0.09	0.06
< 25	0.24	0.25	0.39	0.09	0.07
Totals	0.56	0.98	1.23	0.37	0.18

Water Use Efficiency

Monthly WUE of each study tree was calculated for August through October of 2010, August through October of 2011, and May through September of 2012 (Figure 29). WUE is highest in *T. plicata* throughout most of the growing season, and WUE fluctuates more in the smaller trees than in the dominant and co-dominant trees. No other strong patterns are evident across study years. In 2010, WUE of the dominant *T. plicata* and *P. menziesii* increased from August through October (greatest in *T. plicata*), while it decreased somewhat in the large *T. heterophylla.* In 2011, WUE of all trees dipped from August into September and then increased again in October. This effect was most strongly seen in the three larger *T. plicata.* Solar radiation was lower in mid-late September 2011 than during the same time period in 2010 (see Appendix). In 2012, WUE of the mid-sized *T. plicata* showed a bell-shaped curve from May through September, while the WUE of all the other study trees either decreased or maintained constant over the same time period.

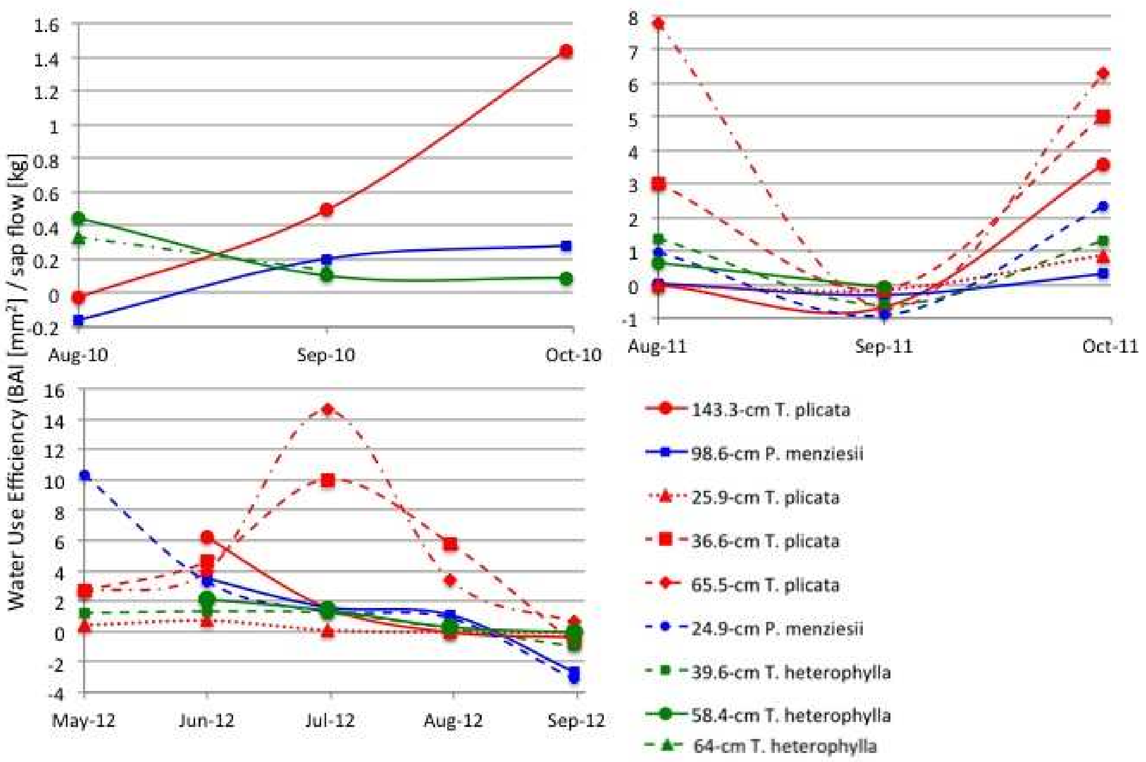


Figure 29. Estimates of water use efficiency (WUE) for all growing season months for which both sap flow and stem increment data are available for some or all of the study trees.

I used measurements of tree rings to estimate WUE over longer time periods – two years for the five smaller trees and three years for the three largest trees – by calculating the ratio of growth ring BAI to estimated annual transpiration (Table 5). WUE was highest in the 65.5-cm *T. plicata*, followed by the dominant *T. plicata* and the co-dominant *T. heterophylla*. It was lowest in the smaller *P. menziesii* and *T. heterophylla.* When calculated using normalized (per cm DBH) sap flow rates rather than whole-tree sap flow, the ranking of WUE is the same, but the difference between the 65.5-cm and the 143.3-cm *T. plicata* is smaller (see Figure D in Appendix).

Table 5. BAI measurements and WUE estimates over three years (three largest trees of each species) and two years (five smaller trees). WUE was calculated as the ratio of BAI to annual transpiration.

Study Tree	BAI (mm^2)	WUE
143.3-cm *T. plicata*	4819.8	0.55
98.6-cm *P. menziesii*	1246.4	0.19
64-cm *T. heterophylla*	1187.0	0.52
25.9-cm *T. plicata*	160.4	0.12
36.6-cm *T. plicata*	675.9	0.29
65.5-cm *T. plicata*	1673.4	1.99
24.9-cm *P. menziesii*	166.0	0.05
39.6-cm *T. heterophylla*	498.5	0.07

Tree Vigor

Tree vigor was calculated as the ratio of the basal area of the 2012 growth ring to the 2012 sapwood area (Figure 30). Tree vigor was highest in *T. plicata* and lowest in *P. menziesii*. There did not appear to be a strong relationship between stem diameter and tree vigor.

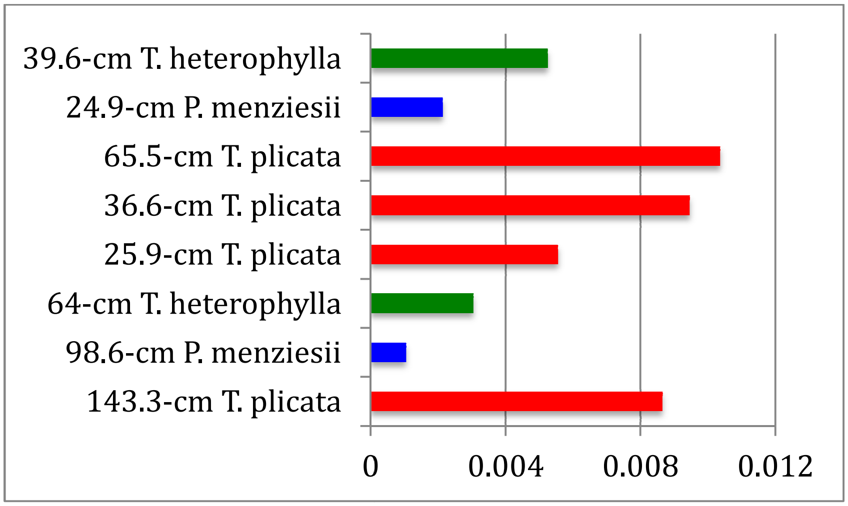


Figure 30. Tree vigor calculated as the ratio of tree ring basal area to sapwood area, per the method described in Waring et al. (1980). *T. plicata*, *T. heterophylla*, and *P. menziesii* are shown in red, green, and blue, respectively.

Discussion

Bole Variation in Sap Flow of Dominant P. menziesii and T. plicata

Differences were greater between the two sap flow meters on the large *P. menziesii* than on the *T. plicata*, which is most likely because of the greater difference in sunlight between north and south than between east and west, although some of it may be attributable to traits specific to the species or the individual trees (Figures 11 and 12). These two species also have different water-conducting systems. Vite and Rudinsky (1959) describe *P. menziesii* and *T. heterophylla* as having a sectorial, winding ascent, whereas *T. plicata* has a sectorial, straight ascent. A sectorial, winding ascent permits a more adaptive means of water distribution than a sectorial, straight ascent (Rudinsky and Vite 1959), which may partly explain the greater difference in flow between the two modules on the *P. menziesii* than on the *T. plicata.* Although differences may have been less substantial in the co-dominant and suppressed trees, a single sap flow meter on the south side of the trees likely represents a high estimate of sap flow across the entire tree, particularly when the tree is exposed to varying environmental conditions according to its position and microsite.

Diurnal Patterns

Daily sap flow patterns differ by species and by canopy position. On warm summer days, all but the smallest trees demonstrated a similar curve, but the sap flow curve of *T. plicata* was much more bell-shaped than the others (more left-skewed) regardless of tree size, especially on cloudier days (Figures 13 and 14). Although all three species initiate photosynthetic activity at approximately the same time of day in the summer, *P. menziesii* and *T. heterophylla* reach peak transpiration earlier in the day than *T. plicata*. Because *T. plicata* is considered to be less drought-tolerant than *P. menziesii* (Minore 1979), it may regulate water loss through its stomata less well. This could explain why the sap flow curves of *T. plicata* appear to approximate the curve of available solar radiation rather than responding as strongly to elevated VPD. However, Minore (1979) also ranked *T. heterophylla* even lower than *T. plicata* on drought tolerance. And previous research has found that increasing VPD does decrease foliage conductance and net photosynthesis in *T. plicata* seedlings (Grossnickle et al. 2005). Additionally, VPD was found to explain more variability in sapflux of *T. plicata* than in *P. menziesii* or *T. heterophylla* (Kavanagh et al. 2007). Sap flow of *P. menziesii* dips earliest in the day, perhaps indicating a superior ability to regulate water loss, in turn reflecting its status as a drought-tolerant species. Hinckley and Scott (1971) found that when soil moisture is low, there is no correlation between temperature and sap flow in young *P. menziesii,* demonstrating that plant processes (i.e. stomatal closure) can override the expected results based purely on the physical gradient and indicating an adaptation to reduce water loss. Both *P. menziesii* and *T. heterophylla* are considered to be conservative with regard to stomatal control of water loss (Bond and Kavanagh 1999).

Summer sap flow of *P. menziesii* and *T. heterophylla* reached its peak earlier in the day than *T. plicata* (Figure 13), indicating that they may be closing their stomata to conserve water during the hottest part of the day. The dominant *P. menziesii* is able to maintain a high sap flow rate for a longer portion of the day than the other two dominant trees, reaching its peak sap flow earliest and does not decline sharply until 2000 h in midsummer. *T. plicata* maintains measurable sap flow later into the evening, but at low levels. Xylem morphology may play a role in this phenomenon, if tracheids of *T. plicata* are smaller and have higher capacitance than the other two species. Tracheids of *P. menziesii* are elongate and 1-4 mm in length and 10-55 μm in diameter (Domec et al. 2008). Another source approximates the tracheid diameter range from 35-55 μm in *P. menziesii*, 30-50 μm in *T. heterophylla,* and 30-45 μm in *T. plicata* (Hoadley 1990).

A study of hydraulic capacitance and xylem hydraulic safety by McCulloh et al. (2013) helps to explain patterns in diurnal sap flow curves observed in our trees. In that study, it was found that small branches of *T. plicata* can withstand more negative water potentials than *P. menziesii* or *T. heterophylla.* In the early part of the summer, I found that *T. plicata* sap flow was higher than that of the other two trees, which reflects the findings of McCulloh et al. (2013) that *T. plicata* is less conservative with regard to stomatal closure than *T. heterophylla* or *P. menziesii*. The more pronounced midday depression I observed in *P. menziesii* and *T. heterophylla* sap flow rates may be explained by the lower hydraulic safety margins observed in the branches of these two species relative to *T. plicata* (McCulloh et al. 2013).

Winter diurnal sap flow curves were much less smooth overall, and distinct patterns were more difficult to discern (Figures 16 and 17). Overall, sap flow rates of the dominant *T. plicata* were lower than those of the other two dominant trees, despite a larger tree size. This finding is consistent with Winner et al. (2004), who found that *T. plicata* is less able to photosynthesize during occasional warm, sunny winter days than the other two species. *T. plicata* undergoes cold hardening during low temperatures, resulting in a concurrent decrease in photosynthesis (Weger et al. 1993).

Seasonal Patterns

Patterns emerged in sap flow and stem increment values across seasons. The dominant *T. plicata* has higher sap flow rates in the middle of the summer, even per centimeter DBH, than the other two dominant trees, but its sap flow rate begins to decline much more rapidly in late summer and early fall (Figures 16 and 17). *T. heterophylla* and *P. menziesii* maintain slightly lower sap flow rates through August than *T. plicata*, but maintain those rates steadily through late October, when they drop substantially for the winter. It is likely that *T. plicata* is demonstrating a drought response at the end of the summer, while *T. heterophylla* and *P. menziesii*, better able to maintain photosynthetic activity in drier conditions, remain active until daylight and temperature become limiting factors. A study of water stress on *P. menziesii* found no evidence of osmotic adjustment in response to water deficit, but did find that drought resulted in large, reversible changes in cell-wall water content and elasticity (Joly and Zaerr 1987). There is some evidence that ectomycorrhizal relationships reduce the effect of drought on *P. menziesii* as well (Parke et al. 1983).

Throughout the winter, *T. heterophylla* and *P. menziesii* maintain higher levels of sap flow, indicating that they are better able to utilize low levels of light in the winter. *T. plicata* winter photosynthesis is limited by minimum ambient air temperatures and shoot growth does not occur below 4°C (Grossnickle and Russell 2006). Although our sap flow data for springtime is patchy, it appears that flow rates of *T. plicata* increase later in the year and more slowly than the other two species, indicating a shorter overall growing season. This is contrary to the findings of previous studies (Hawkins et al. 1995; Minore 1979; Mitchell 1965; Williams 1968), which found that of the three species, *T. plicata* had the longest growing season and *P. menziesii* the shortest. It is possible that this trend is a result of drier site conditions in our study than in the previous studies. Long-term dendrometer data demonstrate that onset of spring-time growth occurs earliest in *T. heterophylla* and latest in *P. menziesii*. Initiation of growth occurs at slightly different times for the three tree species. *T. heterophylla* appears to initiate growth the earliest, in late May. *T. plicata* circumference dips sharply at approximately the same time that *T. heterophylla* initiates growth, which may indicate a sharp increase in transpiration and concurrent loss of stored water.

Interactions between tree size and species became evident in the graphs of total daily sap flow by cm DBH for the five smaller study trees (Figure 19). The tree with the consistently highest sap flow per cm DBH was the *T. plicata* with the smallest DBH, while the lowest rates were found in the 36.6-cm *T. plicata* (the shortest of its species in the study) and the 24.9-cm *P. menziesii*. All five trees recorded very low rates of sap flow in the winter, although here the highest rates more often occurred in *T. plicata*. Similar to the dominant trees, *T. plicata* demonstrated a drop in sap flow activity earlier in the year, in August, and an increase in rates later in the year than *T. heterophylla*. The suppressed *P. menziesii* maintained consistently low rates throughout the year, increasing only gradually in the spring, indicating that it is more strongly impacted by light availability due to canopy position than the other two species regardless of season. *P. menziesii* is known to have lower shade tolerance than *T. plicata* and *T. heterophylla* (Carter and Klinka 1992), and our results support that understanding. Additionally, tracheid diameter is significantly greater in released *P. menziesii* than in suppressed trees of the same species, which likely effects magnitude of sap flow rates (Renninger et al. 2006).

Comparison of the effects of tree height and tree species on total daily sap flow vary by season. During summer and fall months, species and height both significantly impact total daily sap flow by cm DBH, with sap flow highest in *T. heterophylla*. The tallest trees also had higher sap flow rates, supporting findings by previous researchers (Jung et al. 2011; Unsworth et al. 2004). In the winter, when total daily sap flow was uniformly low, species and height effect were somewhat diminished though still yielded significant differences. Canopy position is likely less important in the winter when light levels are low for all trees regardless of height. The overall higher sap flow rates in *T. heterophylla* may be explained by the higher trunk conductance relative to *P. menziesii* and *T. plicata*, particularly when water is abundant (McCulloh et al. 2013)

Comparing sap flow of the dominant trees and the sub-canopy trees as groups shows contrasting results. In the dominant trees, sap flow was highest in *T. heterophylla* throughout summer, fall, and early winter (Figure 23). Sap flow of *T. plicata* and *P. menziesii* were not significantly different in the summer months, but *T. plicata* sap flow is significantly lower in the fall. Because light is unlikely to be a limiting factor for the dominant *T. plicata*, it is probable that the tree's photosynthetic activity decreases in the late summer and early fall as a result of limited water availability. Interestingly, no such drought response was apparent in *T. heterophylla*, considered by some to be less drought-resistant than *T. plicata* (Lassoie et al. 1985). Among the smallest-diameter trees, sap flow was lowest in *P. menziesii* in the spring, summer, and fall, and in the summer was highest in *T. plicata* (Figure 24). This *P. menziesii*, despite being five meters taller than the *T. plicata* in this test, is showing clear signs of light limitations, unsurprising considering the higher light requirements of the species (Carter and Klinka 1992; Minore

1979). Because lower sap flow rates were seen in the 36.6-cm *T. plicata*, it is possible that the high rates in the smallest-diameter *T. plicata* are a result of something unique to that tree. The recorded high sap flow rates could be an artifact of sap flow module placement on the tree. The module was moved to a different location on the bole each season, and recorded much higher values in 2012 than in the two years preceding.

Yearly graphs of stem circumference change provided additional information about tree water use and length of growing season, both by species and by tree size. In Figure 20, the two *T. heterophylla* expand and contract synchronously, indicating a strong effect of species on tree increment. *T. plicata* demonstrated larger short-term fluctuations than the other dominant trees, indicating that it may do less to regulate water loss than the other two species below a threshold of drought stress. In the dominant trees, *T. heterophylla* experienced the greatest overall stem expansion, while *P. menziesii* demonstrated the least. The small circumference change in *P. menziesii* may be in part because the much thicker bark on these trees prevented contact with the extensible tissue; an increase in growth in the second season likely reflects better contact following bark compression in year one. Among the smaller trees (Figure 22), stem expansion and contraction occurred at nearly identical times for all the study trees, although the magnitude of change was smallest for the 25.9-cm *T. plicata*.

An examination of stem increment by month showed that tree boles continued to expand into the fall for *T. plicata*, despite a substantial drop in sap flow rates at the end of the summer. It is likely that the trees are utilizing stored carbon in order to continue growing when water is limiting. Both water storage and carbon storage serve as buffers in times of seasonal stress in conifer species (Hinckley and Lassoie 1981).

Overall stem expansion across the study period was lowest in the smallest *T. plicata*. Although *T. plicata* has a high shade tolerance and can survive well in the understory, when this species is in a suppressed position it may focus its development on new root growth (Eis 1973). It is possible that because this tree was conducting so much sap per cm DBH, as shown in Figure 18, its water storage status did not change substantially as any water taken up by its roots was immediately utilized for transpiration and new growth occurred primarily belowground. Overall stem growth was also low in the dominant *P. menziesii*. This was a surprising finding, since *P. menziesii* is a fast-growing species and can maintain rapid height growth for more than 200 years (Curtis et al. 1974). This study did not examine height growth, so it is possible that this tree did grow substantially in height during the study period but that its growth was not reflected in its bole size. Most likely, however, stem expansion of the two *P. menziesii* was masked by the very thick, corky bark. The dendrometer bands were not in direct contact with the trees' extensible tissue. However, examination of tree rings from 2010-2012 also demonstrates little growth in *P. menziesii.*

Stand Transpiration

Although I found no previous studies that have used sap flow data to calculate total stand transpiration for *T. plicata*-dominated forests, the values calculated within this study for summer stand transpiration fall within the range of other studies on conifer forests. No comparable studies were performed in the fall and winter, so it is unclear how our calculations compare to other forests during those time periods. In a 24-year-old *P. menziesii* forest stand, mean daily transpiration was 0.17 mm for a study period from

June 1 to September 24 (Granier 1987). In a sap flow study of pine-spruce forest, stand mean daily transpiration was 0.77 mm for a dry period in the summer (Čermák et al. 1995). A study extrapolating sap flow to stand transpiration in an *Abies amabilis* forest found mean daily transpiration rates ranging from .37 to 3.37 mm in the summer (Martin et al. 2001). And in an eddy-covariance study of *P. menziesii* forests, a 58-year-old stand had mean daily transpiration of 1.09 mm over the course of a calendar year (Jassal et al. 2009). When extrapolating to the stand level I found that the largest trees account for much of the total stand transpiration. Of the 46 trees within the study plot, the six largest trees were calculated to be conducting almost half of the stand transpiration regardless of season.

Water Use Efficiency

In an analysis of monthly growing season WUE, no consistent patterns emerged by species or tree size. *T. plicata* seedlings have been shown to have fairly stable WUE across a range of VPD condition (Grossnickle et al. 2005), in contrast to our study, in which the species demonstrated considerable variability during the growing season. WUE dips for all the study trees in September of 2011. In 2011, there is a large drop in daily solar radiation from August to September, whereas in 2010 this decrease is more gradual (see Appendix Figure 1 and 2). This may indicate greater rainfall during September 2011, and decreasing WUE in response. In the WUE analysis of two- and three-year tree ring basal area, WUE was approximately three times higher in the 65.5-cm *T. plicata* than in the next two-highest trees, which were the dominant *T. plicata* and the dominant *T. heterophylla*. Long-term WUE was lowest in the small *P. menziesii* and *T. heterophylla*.

Higher WUE in *T. plicata* is consistent with previous findings that WUE is higher in water-stressed conifer seedlings (Zhang and Marshall 1994). In order to gain a clearer understanding of WUE in the study site, isotope analysis to measure carbon partitioning within the tree rings from the study period should be conducted as well.

Tree Vigor

Tree vigor was universally highest in *T. plicata* and lowest in *P. menziesii* without regard to tree height. The tree vigor values calculated in this study were substantially lower than previous results for a *P. menziesii* stand, in which one-year tree vigor ranged from 0.049 to 0.075 (Waring et al. 1980). However, the trees in our study were all significantly larger than those in the previous study, and conifer growth slows as trees age (Tappeiner et al. 1997). The low vigor demonstrated by the small *P. menziesii* was unexpected, as it is a shade-intolerant tree growing in a suppressed position, but the low vigor of the dominant *P. menziesii* was surprising. The codominant trees appeared to have the highest vigor, a finding also seen in Waring et al. (1980); perhaps because codominant trees receive sufficient light but experience lower VPD and water stress than dominant trees. Tree vigor indices of individuals in a stand have been used to determine the relationship of mean tree vigor to total stand growth (Hinckley and Lassoie 1981).

Impacts of Climate Change

Studies of tree water relations such as this one can be useful in determining the potential impacts future climate change on forest ecosystems. Because Pacific Northwest summers are predicted to become both hotter and drier, it is likely that *P. menziesii* will increasingly outperform the other two species, particularly in dominant and co-dominant canopy positions. Although *T. heterophylla* is considered to be less drought-tolerant than *T. plicata* (Marshall 1931; Minore 1979), in our study a seasonal drought effect was apparent in *T. plicata* but not in *T. heterophylla.* These results suggest that the growing season of *T. plicata* may be shortened by drier summers. Both heat and drought result in higher seedling mortality in *T. plicata* than in the other two study species (Gashwiler 1971), so establishment of the species may decline as the climate gets hotter and drier. However, *T. plicata* seedlings across multiple populations have also been shown to increase their drought tolerance in response to drought (Grossnickle and Russell 2010; Major et al. 1994), so the species may prove to be adaptable to a drier climate. Additionally, our data suggest that since temperature and soil moisture are the most limiting factors for *T. plicata*, it may be able to take advantage of warmer winters and springs, when neither heat nor drought are problematic.

Study Limitations

The greatest challenge associated with this study was keeping complex electronic equipment properly functioning at a remote site location in often-adverse weather conditions. For frequent and sometimes large periods of time, one or more of the dataloggers was not functioning. The P2 datalogger failed early in 2010, causing the loss of almost a year of data as repair attempts on the system failed and it was then shipped back to the manufacturer for repair. Frequent gaps in the data made analysis more difficult as well.

An additional limitation was the small number of study trees. For quantitative analyses such as the ANOVA tests performed, it would be preferable to have repetition in the form of multiple individuals (trees) rather than multiple days. However, the study was limited to a small number of trees within a small study site by the number of data loggers and length of wiring.

Future Work

Additional analysis could be done using the data that has already been collected. Much of this analysis would involve more intensive use of the weather data collected on-site. Although the weather station sensors experienced periodic equipment failure as well, much of the missing data was filled in using regression analysis to another nearby weather station (Miller 2013). Reconstruction of these weather variables created a robust dataset of daily and seasonal climate conditions at the study site. An excellent objective for future work would be to further explore the effects of these various environmental conditions (VPD, temperature, precipitation, soil moisture, wind speed, and solar radiation) on sap flow and water storage patterns (Bovard et al. 2005; O'Brien et al. 2004; Price and Black 1990). The evaporative demand of the atmosphere, which is impacted by temperature, wind speed, and VPD, can affect transpiration rates. In general, transpiration rates are positively correlated with temperature, wind, VPD, solar radiation, and soil moisture content (Leopold and Langbein 1960). A study of two deciduous tree species found that stomatal conductance and transpiration rates increased with increasing photosynthetically active radiation (PAR) and VPD, and decreased with depletion of soil moisture (Oren and Pataki 2001). When soil moisture is not a limiting factor, light and

VPD have the strongest effect on transpiration rates of deciduous trees (Jung et al. 2011). Microclimatic data, sap flow data, and daily dendrometer band fluctuations could be compared using regression analysis and general linear models to determine the relative influence of the weather variables on sap flow and water storage of the study trees.

Although some analysis was done to determine the effects of canopy position / height and tree species on sap flow rates, more work could be done to determine the relative effect of each. Using a scalable sap flow measurement, such as sap flow per cm DBH or sap flow per unit sapwood, regression analysis could be applied to determine how much variability in daily sap flow can be explained by tree canopy position relative to species (Jung et al. 2011), and what interaction exists, if any, between the two factors. To determine the differential effects of height and species on water storage, one could compare length of stem expansion period to canopy position and tree species, also using regression analysis.

More precise estimates of WUE could be calculated using carbon isotope analysis of the tree rings from within the study period.

Conclusions

In some cases, our results reflect findings of previous studies. For instance, it has been established that mature *P. menziesii* has greater winter photosynthetic capacity than *T. plicata* (Nippert et al. 2004), and this was the case in our study as well. Additionally, *T. plicata* showed what appeared to be a strong drought response at the end of the summer and into early fall, with sap flow dipping dramatically while temperatures and light levels were still high. This is consistent with previous studies, which found that *T. plicata* is a drought-intolerant species (Carter and Klinka 1992).

Other results, however, were unexpected. *T. heterophylla* is often described as a drought-intolerant species (Brix 1979; Lassoie et al. 1985), but we found little to no drought response in this species. *T. heterophylla* maintained high sap flow rates and grew both earlier and later than the other species. Additionally, previous studies found that *P. menziesii* has a shorter growing season than *T. plicata* (Hawkins et al. 1995; Mitchell 1965; Williams 1968), the opposite of what was found in our study. Those studies, however, were conducted in different regions: Idaho, the United Kingdom, and upper-slope regions of Oregon and Washington, respectively. It is possible that in the maritime climate of the Pacific Northwest, decreasing fall and winter light conditions are more important in affecting seasonal water use change in these species than decreasing temperatures.

Our study indicates that *T. heterophylla* and *T. plicata* have higher transpiration rates than *P. menziesii* when trees are in a suppressed to intermediate position in the canopy. Although the smallest diameter *T. plicata* did not appear to grow substantially during the study period, it had higher sap flow rates during the summer than the suppressed trees of the other two species. In most other cases, sap flow rates were highest in *T. heterophylla* in all canopy positions.

Overall, this study provides insight into the ecological and physiological differences and similarities among three common conifer species. Comparisons of tree hydraulics performed in this study indicate that despite their co-occurrence, these trees demonstrate clear differences in seasonal and diurnal sap flow and stem increment patterns by species. Most research into mature tree hydraulics has thus far focused largely on growing-season sap flow and water storage, under the assumption that winter transpiration is too low to be of interest. However, the results of this study indicate that although differences and patterns by species are more evident in growing season measurements, they do appear throughout the year as well, demonstrating the value of non-growing season monitoring. By examining sap flow and water storage patterns over multiple years, we were able to gain a deeper understanding of complex stand dynamics in a multi-species, mixed-age stand, and in particular gained insight into the water relations of the under-studied species *T. plicata* and *T. heterophylla*.

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Appendix

Table 1. Means, *p*-values, and post-hoc tests from ANOVA tests comparing total daily sap flow per cm DBH between the three study species and between three height classes for three seasons.

	T. plicata (1)	*P. menziesii (2)*	*T. heterophylla (3)*	<30 m (x)	30-35 m (y)	>35 m (z)
Summer (June 1 – Sept 15)						
Means	0.32	0.31	0.58	0.17	0.30	0.60
p-value	<.0001			<.0001		
post-hoc	1 vs 2 *nonsig*, 1 vs 3 *p*<.01, 2 vs 3 *p*<.01			x vs y *p*<.01, x vs z *p*<.01, y vs z *p*<.01		
Fall (Sept 16 – Nov 15)						
Means	0.09	0.14	0.21	0.11	0.06	0.23
p-value	<.0001			<.0001		
post-hoc	1 vs 2 *nonsig*, 1 vs 3 *p*<.01, 2 vs 3 *p*<.01			x vs y *p*<.05, x vs z *p*<.01, y vs z *p*<.01		
Winter (Nov 16 – Mar 31)						

Means	0.05	0.09	0.09	0.08	0.05	0.10
p-value	0.003303			0.000207		
post-hoc	1 vs 2 *p*<.05, 1 vs 3 *p*<.05, 2 vs 3 *nonsig*			x vs y *p*<.05, x vs z *nonsig*, y vs z *p*<.01		

Table 2. Means, *p*-values, and post-hoc tests from ANOVA tests comparing total daily sap flow per cm DBH between the three largest trees of each species.

	T. plicata (1)	*P. menziesii (2)*	*T. heterophylla (3)*
Early Summer (June 1 – July 14)			
Means	0.23	0.22	0.49
p-value			<.0001
post-hoc	1 vs 2 *nonsig,* 1 vs 3 *p*<.01, 2 vs 3 *p*<.01		
Late Summer (July 15 – Sept 15)			
Means	0.51	0.49	0.67
p-value			<.0001
post-hoc	1 vs 2 *nonsig,* 1 vs 3 *p*<.01, 2 vs 3 *p*<.01		
Fall (Sept 16 – Nov 15)			
Means	0.19	0.33	0.45
p-value			<.0001
post-hoc	1 vs 2 *p*<.01, 1 vs 3 *p*<.01, 2 vs 3 *p*<.01		
Early Winter (Nov 16 – Feb 15)			
Means	0.05	0.081	0.13
p-value			<.0001
post-hoc	1 vs 2 *p*<.05, 1 vs 3 *p*<.01, 2 vs 3 *p*<.01		
Late Winter (Feb 16 – Mar 31)			
Means	0.06	0.16	0.17
p-value			0.000157
post-hoc	1 vs 2 *p*<.01, 1 vs 3 *p*<.01, 2 vs 3 *nonsig*		

Table 3. Means, *p*-values, and post-hoc tests from ANOVA tests comparing total daily sap flow per cm DBH between the three smallest trees of each species.

	T. plicata (1)	*P. menziesii (2)*	*T. heterophylla (3)*
Spring (Apr 1 – May 31)			
Means	0.27	0.045	0.24
p-value			<.0001
post-hoc	1 vs 2 p<.01, 1 vs 3 *nonsig,* 2 vs 3 *p*<.01		
Summer (June 1 – Sept 15)			
Means	0.63	0.18	0.39
p-value			<.0001
post-hoc	1 vs 2 *p*<.01, 1 vs 3 *p*<.01, 2 vs 3 *p*<.01		
Fall (Sept 16 – Nov 15)			
Means	0.13	0.06	0.08
p-value			<.0001
post-hoc	1 vs 2 *p*<.01, 1 vs 3 *p*<.01, 2 vs 3 *nonsig*		

Early Winter (Nov 16 – Feb 15)			
Means	0.06	0.07	0.03
p-value			<.0001
post-hoc	1 vs 2 *nonsig*, 1 vs 3 *p*<.01, 2 vs 3 *p*<.01		
Late Winter (Feb 16 – Mar 31)			
Means	0.10	0.08	0.03
p-value			<.0001
post-hoc	1 vs 2 *nonsig*, 1 vs 3 *p*<.01, 2 vs 3 *p*<.01		

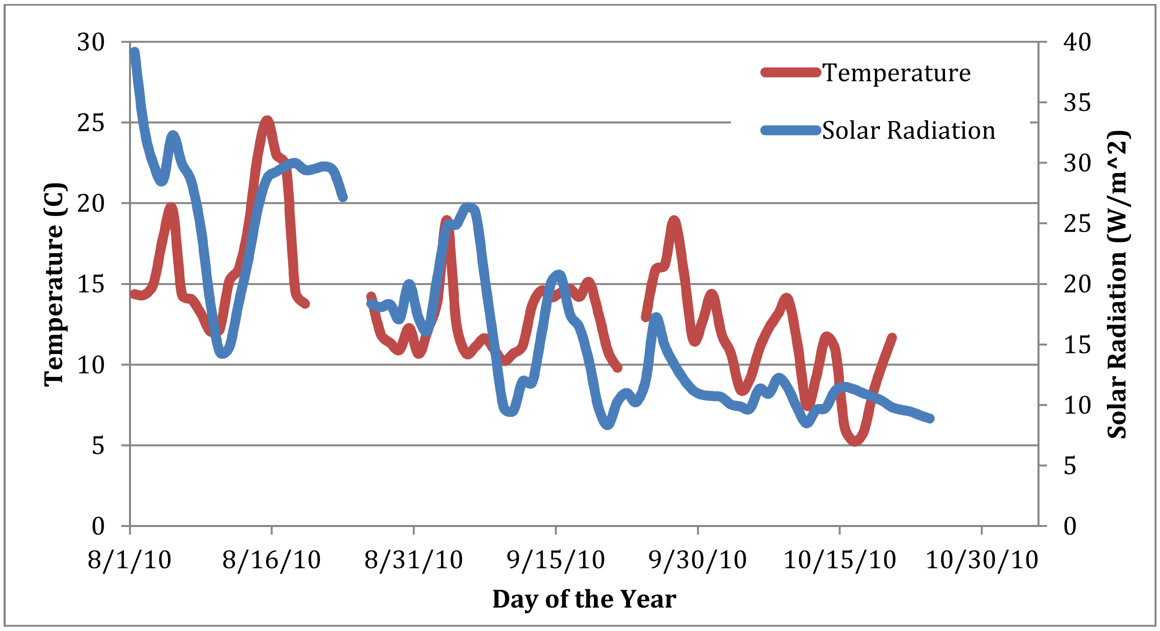

Figure A. Temperature and solar radiation recorded at the ground-level weather station for August through October, 2010.

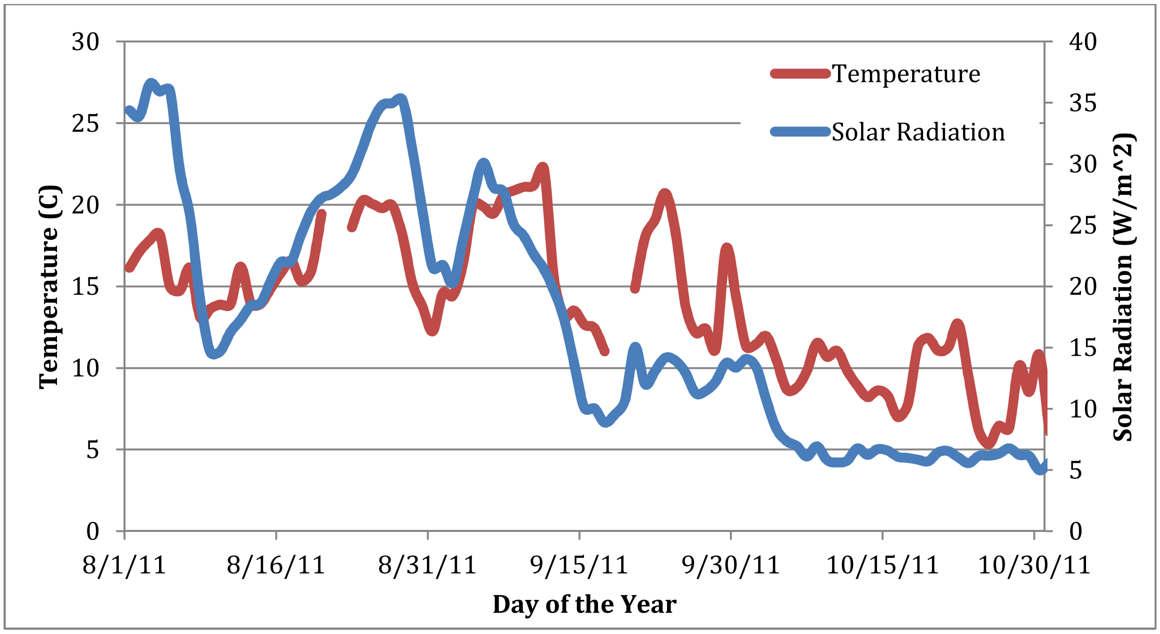

Figure B. Temperature and solar radiation recorded at the ground-level weather station for August through October, 2011.

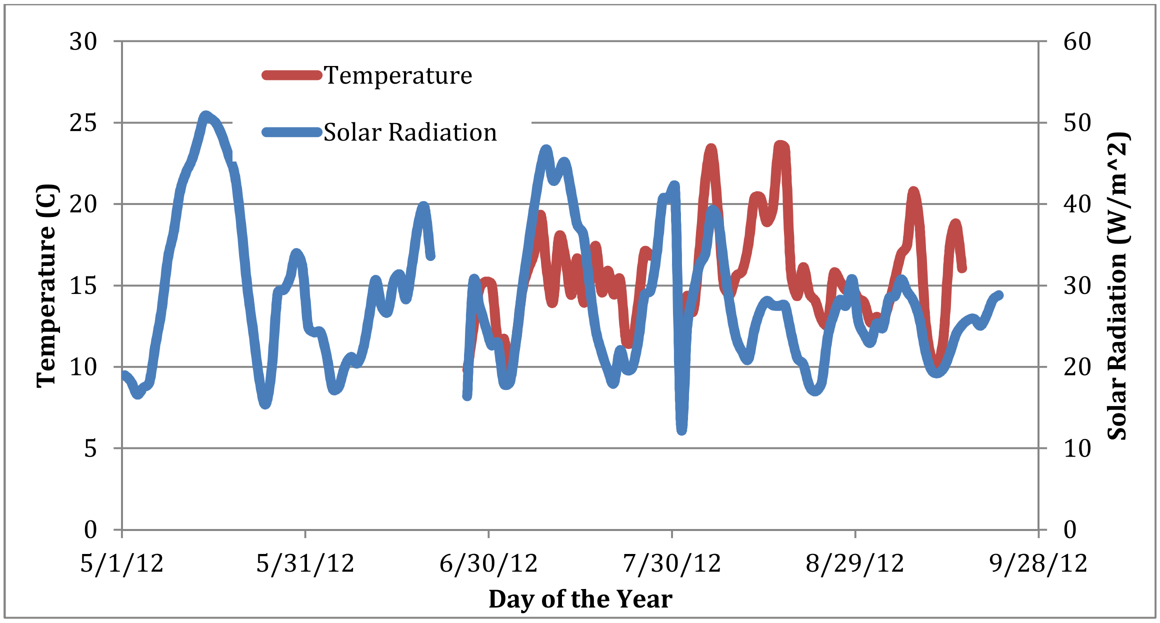

Figure C. Temperature and solar radiation recorded at the ground-level weather station for May through September, 2012.

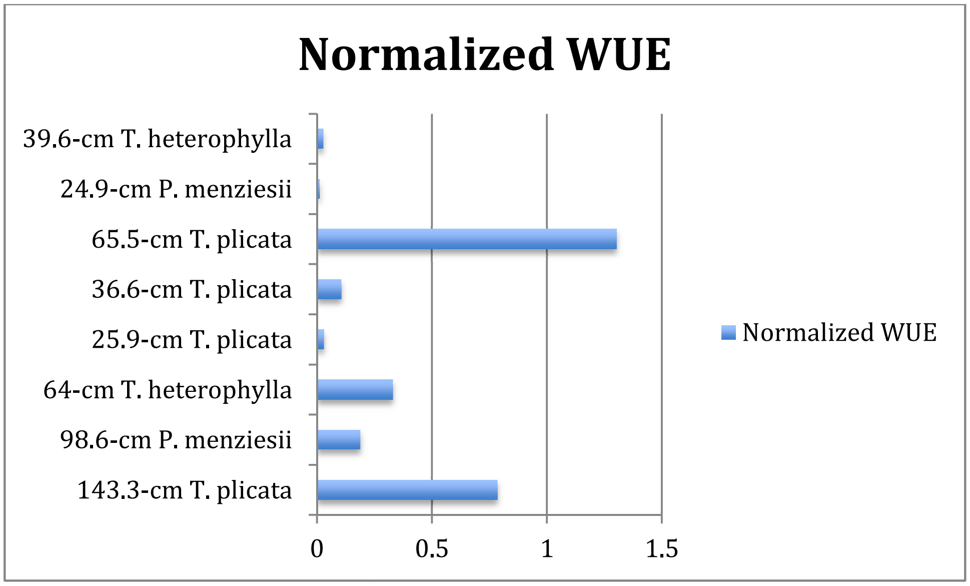

Figure D. WUE estimates over three years (three largest trees of each species) and two years (five smaller trees). WUE was calculated as the ratio of BAI to annual normalized (per cm DBH) transpiration.