TREE TRANSPIRATION FROM TWO FORESTS IN THE WASATCH MOUNTAINS, UTAH

by

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STATEMENT OF THESIS APPROVAL

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ABSTRACT

In many seasonally snow-covered forests, productivity is highest in the spring period when air temperature is warm enough for photosynthesis to occur and soil moisture is not limiting. Due to the relative importance of this period, even small changes in the onset date of tree activity can have large impacts on annual productivity. Therefore, understanding the environmental controls on the onset of the active season is crucial in predicting the future state of our forests. While most studies to date have focused on measuring the seasonal patterns of forest productivity using eddy-covariance or remote sensing techniques, we employed the use of thermal dissipation sap flux sensors to make year-round continuous measurements of tree activity. This approach has the advantage of allowing us to distinguish between co-located species and to assess how changes in environmental conditions are likely to affect particular tree species. After testing and verifying in a laboratory setting that thermal dissipation sap flux sensors could accurately measure transpiration during cold periods, we installed sap flux sensors in *Abies concolor* and *Populus tremuloides* at a low elevation site and *A. lasiocarpa* and *P. tremuloides* at a high elevation site to monitor seasonal transpiration patterns. Our study included two spring periods with very different precipitation and air temperature, which allowed us to compare how interannual variability in environmental conditions affected the onset of transpiration and early season transpiration patterns. We found that warmer air temperature and earlier snowmelt advanced the onset of the active season for

A. concolor and *A. lasiocarpa*, but that a shift in timing of precipitation events contributed to a delay in *P. tremuloides* activity. Overall, variability in tree activity between years was greater at the low elevation site, highlighting the susceptibility of lower elevation montane forests to climate change effects.

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1 INTRODUCTION

Spring is an especially important period of the year for trees growing in seasonally snow-covered environments (Clark et al. 2014). In these areas, the majority of precipitation falls as snow and trees rely on snowmelt water as their primary water resource (Hu et al. 2010). The snowpack acts as a reservoir of accumulated winter precipitation that can be gradually released back into the environment during the snowmelt period. For many of these forests, productivity is highest in the spring when soil moisture is not limiting, but air temperature is high enough for photosynthesis to occur (Black et al. 2000a; Monson et al. 2005; Aerts et al. 2006; Barr et al. 2009; Melaas et al. 2013). However, in many montane areas of the Western U.S., air temperature has been increasing and annual snowfall has been declining (Barnett et al. 2005; Mote et al. 2005). This puts pressure not only on the forests that rely on snowmelt as a water source, but also on the many municipalities whose reservoirs are filled by snowmelt water.

In the face of these changing conditions, there has been growing concern regarding how forests will respond. Forests account for approximately 50% of net primary production and play an important role in regulating the water cycle (Bonan 2008). For seasonally snow-covered forests, changes in precipitation patterns (amount, timing, phase) and air temperature are particularly important. These forests are generally dormant during the cold winter months. Deciduous-broadleaf species lose their leaves and remain inactive until leaf-emergence and evergreen-coniferous species downregulate photosynthetic capacity and increase xanthophyll cycle pigments to protect the leaf tissue from the damaging effects of excess light (Öquist and Huner 2003; Zarter et al. 2006a; Verhoeven 2014). However, wintertime activity in evergreen-coniferous trees has been documented in many boreal and high elevation forests (Schulze et al. 1967; Öquist and Huner 2003; Ensminger et al. 2004; Sevanto et al. 2006) and although photosynthetic capacity is reduced, it is not fully inhibited (Nippert et al. 2004; Koh et al. 2009). Evergreen-coniferous trees can respond quite rapidly when favorable conditions exist in the winter (Monson et al. 2005; Verhoeven 2014); this allows them to take advantage of intermittent warm periods and to be active for a longer extent of the year.

Changes to the length of the active season have been observed in both temperate and boreal forests, with a strong trend toward an earlier onset of the active season that has been largely attributed to warmer spring temperature (Richardson et al. 2013). Many studies have found that the date of the onset of the active season is positively correlated with annual productivity in both evergreen-coniferous and deciduous-broadleaf forests (McMillan et al. 2008; Barr et al. 2009; Richardson et al. 2009; 2013; Froelich et al. 2015). Randerson et al. (1999) showed that variation in seasonal CO_2 uptake over a 17-year period was best explained by variation in early season uptake for boreal forests. Similar results have been found in temperate forests (Monson et al. 2005; Richardson et al. 2009; Froelich et al. 2015). However, Hu et al. (2010) found that annual CO_2 uptake was lower in years with longer active seasons in a subalpine forest in Colorado. At this site, the onset of the active season was earlier in years with shallower snowpacks. Because these trees were strongly dependent on snowmelt water, moisture stress later in the season ultimately reduced annual carbon uptake. These contrasting studies demonstrate the variability in forest responses to warmer springs and the need to understand the environmental controls on the onset date of tree activity.

The transition between dormant and active states for evergreen-coniferous species is largely controlled by air temperature (Tanja et al. 2003; Monson et al. 2005; Moore et al. 2008), although soil temperature has also been shown to be important, especially in boreal forests where soils may freeze during the winter (Ensminger et al. 2004; Ensminger et al. 2008; Repo et al. 2008). Monson et al. (2005) found that the presence of an isothermal snowpack in the spring was needed before full recovery of ecosystem carbon uptake could occur. Isothermal conditions within the snowpack allowed liquid water to percolate into the soil and these daily melt cycles were an important characteristic of the early season environment in this study. Other studies have examined recovery at the leaf-level and have shown that the rate of recovery of photosynthetic capacity varies by species (Nippert et al. 2004; Koh et al. 2009) and involves the recovery of photosystem II activity, chloroplast protein synthesis, and the conversion of zeaxanthin to violaxanthin (Ensminger et al. 2004). Verhoeven (2013) measured the half recovery times of photosynthetic capacity for white pine, balsam fir, and white spruce to be 144 h, 76 h, and 40 h, showing that there are large differences in the ability of species to respond to warming.

Despite being limited by the timing of leaf-emergence, deciduous-broadleaf trees have been shown to be more responsive to springtime warming compared to evergreen conifers (Barr et al. 2009; Richardson et al. 2009). The onset of the active season for deciduous-broadleaf trees is controlled by the date of leaf emergence. As for evergreen-coniferous species, air temperature has been shown to be an important control on the onset date of tree activity in the spring (Black et al. 2000b; Richardson et al. 2013). Because the cost of leaves emerging too soon in the spring can have damaging effects on leaf tissue and subsequent productivity in the active season, some deciduous-broadleaf species also rely on photoperiod and accumulated winter chilling or accumulated spring warming as cues for leaf emergence (Kramer et al. 2000; Barr et al. 2009; Lenz et al. 2013). However, Baldocchi et al. (2005) showed that the date when mean soil temperature is equal to mean annual air temperature was an accurate predictor of the date when net carbon uptake was occurring in temperate deciduous forests. Because soil temperature and air temperature measurements are readily available from long-term records, this is an especially useful relationship in predicting the onset of the active season for deciduous-broadleaf trees.

The majority of recent research on the seasonality of plant activity has relied on eddy covariance measurements from flux tower networks and the onset of the growing season has been determined by the date when there is net carbon uptake by the forest. These studies have provided important results regarding long-term trends in phenology and carbon cycling at the forest level, but they do not allow the responses of co-located species to be distinguished. However, there are important differences between tree species in, for example, their water use patterns (Pataki et al. 2000; Link et al. 2014) and their rate of photosynthetic recovery following winter dormancy (Nippert et al. 2004; Zarter et al. 2006b; Verhoeven 2013). Therefore, being able to distinguish seasonal patterns of activity for particular tree species is important in predicting future plant distributions and forest productivity.

Measurements of stem sap flux provide a useful method of monitoring daily tree activity. While there are currently many methods being used, the thermal dissipation sap flux technique has the advantage of being low cost and having relatively easy sensor assembly and installment in the field (Smith and Allen 1996; Lu et al. 2004). Using the thermal dissipation method developed by Granier (1985), transpiration rates can be determined from sap flux measurements by a simple empirical calculation based on the temperature difference between a heated an unheated probe installed in the sapwood of a tree.

Transpiration accounts for the largest loss of water from the land surface (Jasechko et al. 2013; Good et al. 2015) and is also directly linked to primary production through stomatal conductance. Transpiration rates are controlled by leaf stomatal conductance, which is in turn influenced by light, air temperature, plant water status, and vapor pressure deficit (VPD). When the stomata are open, CO_2 diffuses into the leaf, while water evaporates at the leaf-air interface. This creates a trade-off of water lost to carbon gained. Plants have varying degrees of stomatal control depending on their environment and life history (Lin et al. 2015).

The ability to measure transpiration over long time periods with the sap flux technique is an appealing method because it provides a continuous measurement of tree activity. However, there have been few studies that have employed this technique for periods greater than one year (Clausnitzer et al. 2011; Yoshifuji et al. 2011; Link et al. 2014), and none have occurred in seasonally snow-covered environments. For seasonally snow-covered environments in particular, year-round sap flux measurements could provide extremely useful data regarding day-to-day variation in tree activity during the transition from winter to spring (as inferred through transpiration rates) as well as the timing of the onset of activity. Monitored over multiple years, sap flux measurements in conjunction with environmental variables could provide valuable insight into the controls on tree activity and how they vary seasonally for individual species.

This was the motivation behind our study to investigate the use of the thermal dissipation sap flux technique as a year-round measurement of transpiration in seasonally snow-covered environments. The objectives of our study were to 1) evaluate the ability of thermal dissipation sap flux sensors to accurately measure stem water transport in low temperature, 2) examine and compare the annual transpiration patterns of co-located deciduous-broadleaf and evergreen-coniferous species at different elevations, 3) determine the environmental controls on the onset of transpiration in years with different precipitation and air temperature, and 4) determine which environmental variables most influence transpiration rates in the winter-spring transition period. We hypothesized that 1) evergreen-coniferous trees would have longer active seasons than co-located deciduous-broadleaf species and that lower elevation evergreen-coniferous and broad-leaf deciduous species would have longer seasons than their higher elevation counterparts, 2a) evergreen-coniferous transpiration would begin when air temperature is above zero and after initial snowmelt has started, 2b) deciduous-broadleaf transpiration would begin when mean soil temperature was equal to mean annual air temperature, 3) low elevation transpiration patterns would be more sensitive to changes in spring weather patterns, and 4) air temperature would be the primary predictor of sap flux rates for evergreen-coniferous species in the spring, but both air temperature and soil temperature would be predictors of sap flux rates for deciduous-broadleaf species.

We tested these hypotheses by making year-round measurements of stem sap flux for *Populus tremuloides* and *Abies concolor* in a relatively low elevation forest and for *Populus tremuloides* and *Abies lasiocarpa* in a relatively high elevation forest and evaluating how seasonal patterns of transpiration responded to environmental conditions. Our study included two winter-spring periods with contrasting precipitation and air temperature, which allowed us to assess how changes in winter-spring weather affect the onset of tree activity.

2 METHODS

2.1 Site descriptions

Sap flux measurements were made at two sites varying in elevation in the Wasatch Mountains of northern Utah, USA. These sites are part of the iUTAH EPSCoR GAMUT Network (http://iutahepscor.org, iUTAH GAMUT Working Group, 2014).

2.1.1 Low elevation

The lower elevation site was located on a southeast facing slope in the Knowlton Fork drainage of Red Butte Canyon, approximately 8 km northeast of Salt Lake City, Utah, USA (2070 m a.s.l., 40.81˚N, -111.77˚W). The dominant tree species were *Abies concolor* and *Populus tremuloides* with a stand of *Pseudotsuga menziesii* adjacent to the sap flux site. Twelve *A. concolor* (white fir) and twelve *P. tremuloides* (aspen) co-located in a $60 m^2$ area were instrumented for sap flux measurements. Average DBH of study trees was 29.5 cm ± 7.4 SD and 24.2 cm ± 5.8 SD for *A. concolor* and *P. tremuloides*, respectively.

2.1.2 High elevation

The higher elevation site was located at the T.W. Daniel Experimental Forest in Logan Canyon (2620 m a.s.l., 41.87˚N, -111.51˚W), approximately 30 km northeast of Logan, Utah, USA. The site is underlain by karst bedrock and contains open meadow areas surrounded by pure stands of *P. tremuloides*, and mixed conifer forest dominated by *Abies lasiocarpa* and *Picea engelmannii*. Twelve *P. tremuloides* and twelve *A. lasiocarpa* (subalpine fir), in two separate plots, were selected for sap flux measurements. The aspen and the subalpine fir plots were each 25 m diameter and located approximately 130 m apart on level ground. Average DBH of study trees was 24.6 cm ± 8.5 SD and 31.2 cm ± 9.3 SD for *A. lasiocarpa* and *P. tremuloides*, respectively.

2.2 Sap flux field measurements

Sap flux density was measured using the Granier thermal dissipation method (Granier 1985). Note from here, the term “sap flux” will be used interchangeably with sap flux density. Pairs of sensors were assembled in the lab and consisted of a reference sensor and a heated sensor. Both sensors contained a copper-constantan thermocouple inside a 19 gauge (2 mm diameter) hypodermic needle that was cut down to 21 mm in length. The thermocouple was secured in the needle 10 mm from the base. The heated sensor was wrapped in constantan heating wire and was delivered a constant power of 0.2 W.

In the field, a small area of bark (~3 cm diameter) was removed for each sensor and pairs of sap flux sensors were installed 15 cm apart, with the heated sensor directly above the reference sensor, in the outermost sapwood layer. Sensor pairs were installed 1.3 m above the ground, in random axial directions, to capture any axial variation in sap flow. One pair of sensors was installed in each tree. Sensors were covered in reflective bubble wrap to prevent radiative influences on measurements. All instrumented trees were greater than 15 cm DBH, per recommendation of the Granier method. Among trees above this size class, individuals were selected to capture the range of stem diameters present at each site.

The sensors were wired to measure a differential voltage, such that the difference in voltage, ΔV, could be used to calculate the sap flux density, J_s (g m^{-2} s^{-1}), according to the equation:

$$\boldsymbol{J_s = 119 \times (\frac{\Delta V_{max}}{\Delta V} - 1)^{1.231}} \quad (1)$$

ΔV_{max}, the daily maximum voltage difference, occurs under zero flow conditions (i.e., at night). This acts as a baseline to which voltage differences at any point during the day (ΔV) can be compared. Shifts in the baseline occur over time or can be affected by sudden changes in temperature (data not shown); therefore, a proper measure of the baseline is important for accurate calculations of J_s. Because we were measuring sap flux over a long period of time, we used a continuously moving baseline that was calculated by using a piecewise cubic Hermite interpolation to create an interpolated line through the maximum nighttime differential voltages (Matlab 7.12.0.635 R2011a, The MathWorks, Inc., Natick, Massachusetts, USA). Each ΔV was then compared to the corresponding ΔV_{max} from the interpolated baseline. This approach assumes that there is no nighttime transpiration, which may lead to underestimation of daily sap flux rates if there was nighttime transpiration occurring (Lu et al. 2004). However, this method has the advantage of accounting for seasonal changes in baseline values and eliminating the human bias that may be present in manual baseline determination (Lu et al. 2004).

Measurements at the low elevation site commenced on 23 August 2013 and continued until 5 December when the sensors were shut off to conserve power during the first winter. Measurements were re-started on 20 February 2014 and continued until 5 July 2015, including winter. Measurements at the high elevation site commenced on 24 March 2014 at the *A. lasiocarpa* site and on 13 May 2014 at the *P. tremuloides* site. The measurement period for the high elevation site continued until 12 July 2015, including winter. Sap flux measurements were taken every 10 s and 15 min averages were logged on a CR1000 datalogger (Campbell Scientific, Inc., Logan, Utah, USA).

2.3 Sap flux data filtering

The raw sap flux data were sent through three filtering steps before the data were processed into a sap flux density measurement. First, the data for each species were separated into Winter, Fall, Spring, and Summer time periods, which were defined based on timing and magnitude of transpiration for each species and site (Table 1). Second, for each seasonal time period, all data from each tree were compiled for each 15 min period within a day, such that all daily cycles were combined and compared. Points outside the 98th and 2nd percentiles of the combined 15 min data were removed. Finally, days with less than 95% of data remaining were then removed. Sap flux rates were calculated using the filtered data and Equation 1. Two *P. tremuloides* at the low elevation site were deemed outliers, based on inconsistent daily patterns that did not match the other trees, and were removed from the dataset. Similarly, two *A. lasiocarpa* were removed from the dataset at the high elevation site.

2.4 Statistical analysis

We used multiple linear regression models to determine which combinations of environmental parameters best explained transpiration responses in each season. A full model including daily values of air temperature, maximum vapor pressure deficit, mean soil temperature, mean soil moisture, and PAR (cumulative daily sum) as predictors and cumulative daily sap flux densities as the response variable was run first and predictors were successively removed according to highest p-value using backwards elimination. Each model was ranked by Akaike Information Criterion (AIC) score and predictors were removed until the lowest AIC score was obtained. Prior to multiple regression analysis, we used individual linear regressions to determine which daily air temperature variable (mean, max, or min) to use as a predictor in the model. AIC scores and adjusted R^2 values for the multiple linear regressions were compared to corresponding values for individual linear regressions for each predictor variable to confirm that the multiple regressions provided a better fit of the data. All statistical analyses were done using the “lm” function in R version 3.2.1.

2.5 Additional field measurements

Each site (the low elevation site and both stands at the high elevation site) was equipped with a weather station measuring air temperature, humidity, photosynthetically active radiation (PAR), snow depth, soil temperature, and soil moisture (volumetric percent) at five locations down to 1 m depth. Precipitation data for snow water equivalent and rain were obtained from nearby USDA/NRCS SNOTEL sites. The data for the low elevation site came from the Louis Meadow SNOTEL site, located at a similar elevation and aspect in an adjacent canyon approximately 2000 m away. The data for the high elevation site came from the Doc Daniel SNOTEL site, located in a clearing approximately 75 m from the *A. lasiocarpa* sap flux site.

Additionally, a mean annual air temperature was calculated for each site from long-term records of mean daily air temperature from the SNOTEL sites above in order to test our hypothesis that *P. tremuloides* transpiration would begin when mean soil temperature was equal to mean annual air temperature. The mean annual air temperature for the low elevation site was based on 14 years of data and the high elevation site was based on 7 years of data. Mean soil temperature was measured at 5 cm depth which corresponds to Baldocchi et al. (2005).

Cumulative degree days were also determined for *P. tremuloides* as a metric for the onset of the active season. These were calculated by summing the number of degrees above zero for daily mean air temperature from 1 May to the date when transpiration was first observed.

Predawn and midday water potential measurements were taken in 2014 between 8 April and 24 October at the low elevation site and between 10 June and 29 October at the high elevation site to determine if the trees were water-stressed over the course of the active season. Measurements were made with a Scholander pressure chamber (PMS Instrument Co., Corvallis, Oregon, USA), approximately biweekly at the low elevation site and monthly at the high elevation site.

2.6 Sap flux laboratory measurements

In order to test the ability of the Granier sensors to accurately measure water flow in cold stems and to withstand subfreezing stem temperatures, we designed a laboratory set-up, based on system described in Bush et al. (2010), that allowed us to directly measure stem water transport for comparison with concurrent sap flux sensor measurements (Fig. 1). Sap flux sensors were installed radially in a stem segment of *A. concolor*, according to the field protocol above, along with a separate thermocouple measuring stem temperature at the depth of the sap flux sensors. Stem diameters ranged from 5.5 cm to 6.5 cm. Approximately 1 m segments were cut in the field, bagged in dark plastic, and brought back to the lab. Immediately before beginning experiments, both ends of the stem segment were recut underwater such that the remaining segment was about 50 cm in length. The stem segment was suspended in a beaker of 20 mM KCl solution on a balance (LP34000P, Sartorius, Goettingen, Germany) and sensors were connected to a CR1000 datalogger (Campbell Scientific, Inc., Logan, Utah, USA). Measurements were logged every 10 s.

Stem temperature was controlled by wrapping a copper coil (~6 mm diameter), attached to a recirculating water bath, around the stem segment. The entire stem plus coil system was then covered in reflective bubble wrap for insulation. Silicone heat transfer fluid (Syltherm XLT, Dow Chemical Company, Midland, Michigan, USA), which maintains a low viscosity at subfreezing temperature, was put in the water bath (VWR Scientific, Model 1157) to enable temperatures below zero to be attained. The entire set-up was kept in a cold room at 4˚C to minimize the temperature gradient between the stem and its surroundings. For each trial, the water bath was set at a given temperature between -20˚C and 20˚C and the stem was left overnight to allow stem temperature to equilibrate. During this time, a zero-flow baseline, which is a requirement of the Granier method, was also established. A constant vacuum of 17 kPa (5 inHg) was then applied to the top of the stem for a period of 5-6 h using a vacuum pump (GE Motors, G8GCX). Stem water transport rate was directly measured from the change in mass on the balance. This was then compared to the flow rates measured by the sap flow sensors. The sapwood area of each stem was determined at the end of each trial by dying the stems using Safranin O solution (0.05%). The dye was pulled through the stems using a vacuum pump in the same way that the sap flux trials were done. The vacuum was run for approximately 1 h.

Table 1. Seasonal periods for each species at the low and high elevation sites.

Species	**Site**	**Season**	**Season Code**	**Start Date**	**End Date**
Abies concolor	Low	Winter	D	6 November	23 February
		Spring	A	24 February	8 April
		Summer	B	9 April	28 August
		Fall	C	29 August	5 November
Populus tremuloides	Low	-----	-----	-----	-----
		Spring	A	5 May	18 June
		Summer	B	19 June	23 September
		Fall	C	24 September	25 October
Abies lasiocarpa	High	Winter	D	21 November	4 April
		Spring	A	5 April	3 June
		Summer	B	4 June	1 October
		Fall	C	2 October	20 November
Populus tremuloides	High	-----	-----	-----	-----
		Spring	A	30 May	8 July
		Summer	B	9 July	11 September
		Fall	C	12 September	1 October

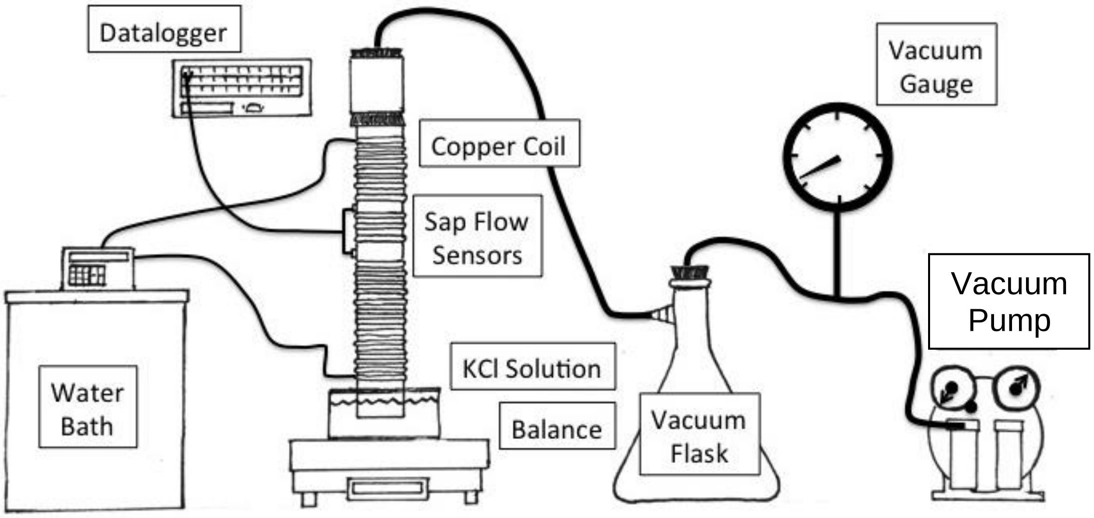

Figure 1. Laboratory system to test sap flux measurements as a function of stem temperature. A stem segment of *A concolor* was cut and suspended in a beaker of KCl solution on a balance. A rubber gasket attached to the top of the stem was connected to a vacuum pump via an Erlenmeyer flask. Thermal dissipation sap flux sensors were installed in the stem segment and sap flux measurements were compared with water transport rate based on the loss of mass from the balance as KCl solution was pulled through the stem. A copper coil around the stem connected to a recirculating water bath allowed control of stem temperature.

3 RESULTS

3.1 Sap flux laboratory tests

We found a strong linear relationship between the measured flow rates and the sap flux sensor measurements (linear regression, $R^2 = 0.86$). This held true for stem temperatures measuring as low as 0.5˚C and stem temperature did not influence this relationship (Fig. 2, A). When stem temperature dropped below freezing, we were not able to pull water through the stem. This was evident from the balance and the sap flux sensor measurements (i.e., there was no change in the raw mV output). However, the stems were able to go through a freezing event, then thaw, and still be able capable of transporting water. Rates of sap flux were often lower after a freezing event, but were still detectable. The ability of sap flux sensors to detect water and accurately measure water transport was not affected by undergoing freeze-thaw cycles.

Our results deviated from the Granier calibration curve, $J_s = 119*K^{1.231}$ (Fig. 2, B); however, we still used the Granier equation when processing all raw sap flux measurements from the field. This discrepancy deserves consideration when using the Granier sap flux technique in cold temperature, but because our laboratory tests were only done on one of our three study species, we were not able to discern if this was a general pattern. As our study relied on relative rather than absolute differences in sap flux densities, the equation used to convert raw data into sap flux densities did not affect the patterns investigated.

3.2 Seasonal transpiration patterns

There were clear differences in the length of the active transpiration periods (here referred to as the active season) at the high and low elevation sites. The low elevation *P. tremuloides* had a longer active season than the higher elevation population (Fig. 3). In 2014, the active season started on day of year (DOY) 136 (16 May) for the low elevation *P. tremuloides* and on DOY 162 (11 June) for the high elevation *P. tremuloides* (Table 2). In total, the active season was approximately one month longer at the low elevation site. In 2015, the active season began on DOY 149 (29 May) for *P. tremuloides* at the low elevation site and DOY 165 (14 June) for *P. tremuloides* at the high elevation site (Table 2).

The first signs of transpiration for *A. concolor* at the low elevation site were observed on DOY 35 (4 February) in 2015, which fell during the winter period. Due to a power limitation at the low elevation site in 2014, we were not able to measure sap flux from 8 December 2013 to 20 February 2014. From the start of sap flux measurements on 21 February 2014, we first saw signs of transpiration on DOY 56 (25 February) for *A. concolor* (Table 2). In contrast to the low elevation *A. concolor,* high elevation *A. lasiocarpa* did not transpire during the winter period (Fig. 3). These trees stopped transpiring on DOY 305 (1 November) and did not show any signs of transpiration until DOY 118 (28 April) in 2015. In 2014, sap flux sensors were not turned on until DOY 95 (5 April), but no transpiration was observed until DOY 124 (4 May).

3.3 Interannual variability in environmental conditions during the winter-spring transition period

In order to examine differences in transpiration patterns between species and sites, we compared precipitation patterns (amount, timing, phase) and air temperature between the two study years. We were fortunate to experience two very different winter-spring periods during this time.

Total precipitation at the low elevation site in the January – June period was 490 mm in 2014. In 2015, the total was 503 mm (Fig. 4, C). Despite similar total precipitation amounts, the percentage of rain versus snow differed greatly between the two years. In 2014, 65.3% of the January – June precipitation was snow and 34.7% was rain. In 2015, 40.4% was snow and 59.6% was rain. Peak SWE was 401 mm in 2014 and 361 mm in 2015. The site became snow-free on DOY 127 (7 May) in 2014 and on DOY 92 (2 April) in 2015, although a few minor snow events occurred after this date (Fig. 4, A).

Total precipitation at the high elevation site in the January – June period was 815 mm in 2014 and 406 mm in 2015 (Fig. 4, D). In 2014, 95.3% of January – June precipitation was snow and 4.7% was rain. In 2015, 68.1% was snow and 31.9% was rain. Peak SWE was about two times higher in 2014 than 2015 960 mm versus 505 mm. The site became snow-free on DOY 157 (6 June) in 2014 and DOY 130 (10 May) in 2015. It is important to note that the snow-free dates were determined from snow depth sensors and soil temperature measurements at each site. Because there was so much spatial heterogeneity in snow cover, snow-free dates for a particular site are better determined by site-specific measurements. However, the SNOTEL data are useful for estimating snow water inputs, which cannot be determined from snow depth measurements alone (Fig. 4, A and B).

At both sites, there was a shift in the timing of precipitation events between years. The majority of January – June precipitation occurred between January and March in 2014, with February having the highest precipitation totals at both sites. In 2015, the majority of precipitation during this period occurred in May. Almost all May precipitation was rain at the low elevation site, while approximately half fell as rain and half as snow at the high elevation site.

Average monthly air temperature at the low elevation site was higher in every month except May during the January – June period in 2015 compared to 2014. The greatest discrepancy between years was seen in June, when mean monthly air temperature was 3.6°C higher in 2015 (Fig. 5, A and B). At the high elevation site, January – June air temperature followed a similar pattern between years with mean monthly temperature in 2015 being higher in all months except May (Fig. 5, B and C).

Neither the evergreen-deciduous nor the deciduous-broadleaf species showed signs of water stress throughout the active season in 2014 (Table 3). Measurements were not taken in 2015.

3.4 Onset of transpiration and transpiration responses to environmental variables early in the growing season

We used multiple linear regression analysis to determine which environmental variables best predicted sap flux rates during each season. However, when examining the conditions needed for the growing season to start, we found that examining time series data more clearly demonstrated how particular events influenced the initiation of transpiration. The seasonal time periods, which were determined based on timing and magnitude of transpiration for each species and site, are shown in Figure 3 and Table 1. Here we focused on the winter and spring activity, although the summer season is also included in Table 4 for comparison.

3.4.1 Low elevation initiation of transpiration

3.4.1.1 A. concolor. In the winter of 2014/2015, the onset of transpiration for *A. concolor* was detected following a large melt period when there was an increase in soil moisture at all measured depths (down to 100 cm) and air temperature above zero (Fig. 6, A, C, E). After this initial melt event, transpiration was detected on all subsequent days when air temperature was above zero. Following the initiation of transpiration, maximum daily VPD, soil temperature, soil moisture, and PAR were found to be the best predictors of sap flux rates during the winter 2014/2015 period (multiple regression, $p < 0.0001$, $R^2 = 0.43$, Table 4).

While we only have one complete season of winter sap flux measurements, we had two spring periods to compare. In the spring period of 2014, our full multiple regression model including maximum daily air temperature, maximum daily VPD, soil temperature, soil moisture, and PAR best predicted sap flux rates in 2014 (multiple regression, $p = 0.0001$, $R^2 = 0.43$, Table 4). In the spring period of 2015, soil temperature, maximum VPD, and PAR were the primary predictors (multiple regression, $p < 0.0001$, $R^2 = 0.76$, Table 4). Sap flux rates were higher overall during the spring of 2015 compared to 2014 (Fig. 3).

3.4.1.2 P. tremuloides. In 2014, *P. tremuloides* transpiration began in mid-May and corresponded closely with an increase in soil temperature following the completion of snowmelt (Fig. 7, A and C). However, in 2015, transpiration did not begin until approximately 40 days after the site became snow-free. This can be seen in Figure 7D as the time between the first soil temperature oscillations (approximately 1 April) and the first sap flux peaks. The date when mean 5 cm soil temperature passed the mean annual air temperature (6˚C) was DOY 125 (5 May) in 2014 and DOY 113 (23 April). The accumulated degree days between May 1 and the start of the growing season were 103 in 2014 and 359 in 2015. Overall, sap flux rates during the spring 2015 period were best explained by the combination of soil moisture, soil temperature, and PAR (multiple regression, $p < 0.0001$, $R^2 = 0.76$, Table 4). In 2015, soil temperature alone was the best predictor for the spring period (multiple regression, $p < 0.0001$, $R^2 = 0.71$, Table 4).

3.4.2 High elevation initiation of transpiration

3.4.2.1 A. lasiocarpa. There was no transpiration for *A. lasiocarpa* during the winter period (Fig. 3). Overall, air temperature was lower at the high elevation site, but even in the presence of above zero air temperature, transpiration did not occur until the spring season (Fig. 3). In both years, transpiration began in the spring period when the site was still snow-covered. Like the low elevation *A. concolor*, there was initial melt event percolating down to 100 cm depth that was concurrent with the first signs of transpiration (data not shown).

The best predictor variables of sap flux rate in the spring of 2014 were minimum air temperature and soil moisture (multiple regression, $p < 0.0001$, $R^2 = 0.58$, Table 4). In contrast, maximum air temperature, soil temperature, and PAR best explained sap flux rates in the spring of 2015 (multiple regression, $p < 0.0001$, $R^2 = 0.53$, Table 4). Sap flux rates were lower overall during the spring period of 2015 compared to 2014 (Fig. 3).

3.4.2.2 P. tremuloides. Similar to *P. tremuloides* at the low elevation site, the soil environment was an important control on the start of the growing season and transpiration began soon after the site became snow-free in both years (Fig. 8). In 2014 the snow-free date was DOY 157 and transpiration started on DOY 162. In 2014, the snow-free date was 130 and transpiration began on DOY 165. The date when mean 5cm soil temperature passed the mean annual air temperature (3˚C) was DOY 157 (6 June) in 2014 and DOY 132 (12 May). Despite soil temperature warming earlier in 2015, air temperature was much cooler in the period preceding the snow-free date compared to 2014 and the accumulated degree days between May 1 and the start of the growing season in both years was nearly the same (281 degree days in 2014 and 268 degree days in 2015).

Following the initiation of transpiration, soil moisture and maximum air temperature were the best predictors of sap flux in spring 2014 (multiple regression, $p < 0.0001$, $R^2 = 0.62$, Table 4). In the spring of 2015, soil temperature and maximum VPD were the best predictors (multiple regression, $p < 0.0001$, $R^2 = 0.54$, Table 4).

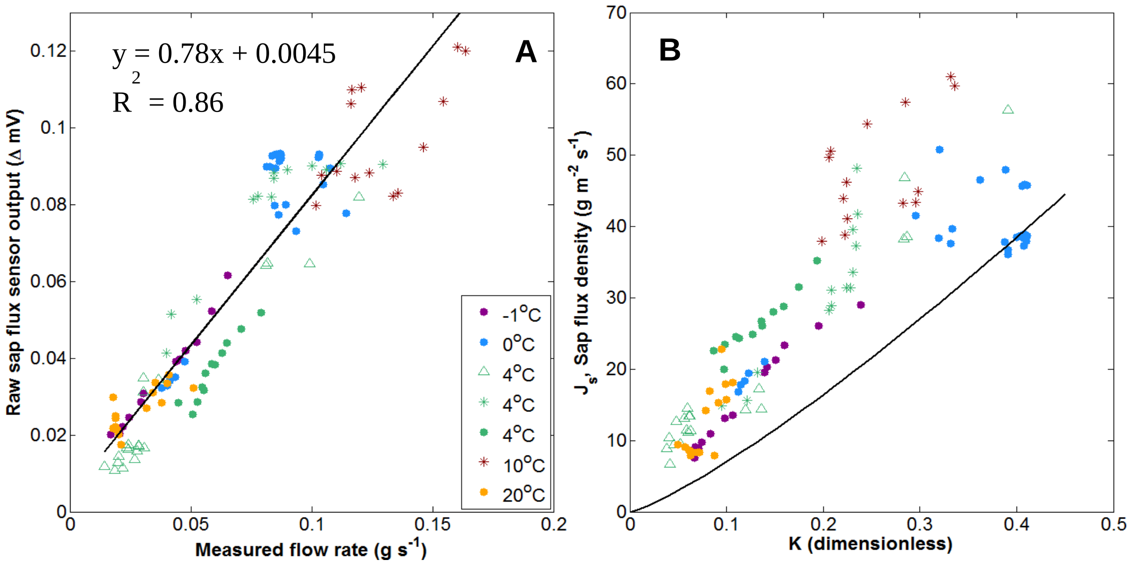

Figure 2. Sap flux lab test results as a function of stem temperature. Each color represents a different water bath temperature and symbols denote different stems. Stem temperature was above water bath temperature at -1 to 4˚C and the lowest stem temperature recorded for the data shown was approximately 0.5˚C. **A)** Thermal dissipation sensor output, shown as the difference from a baseline zero flow condition (ΔmV) versus water transport rate measured by loss of mass on balance (linear regression line shown). **B)** Water transport rates measured from the balance were converted to sap flux density (g m^{-2} s^{-1}) using the sapwood area for each sample stem segment and are shown relative to K values, corrected by sapwood depth using the Clearwater method (Clearwater et al. 1999). The calibration curve, $J_s = 119*K^{1.231}$, is shown for comparison (Granier 1985).

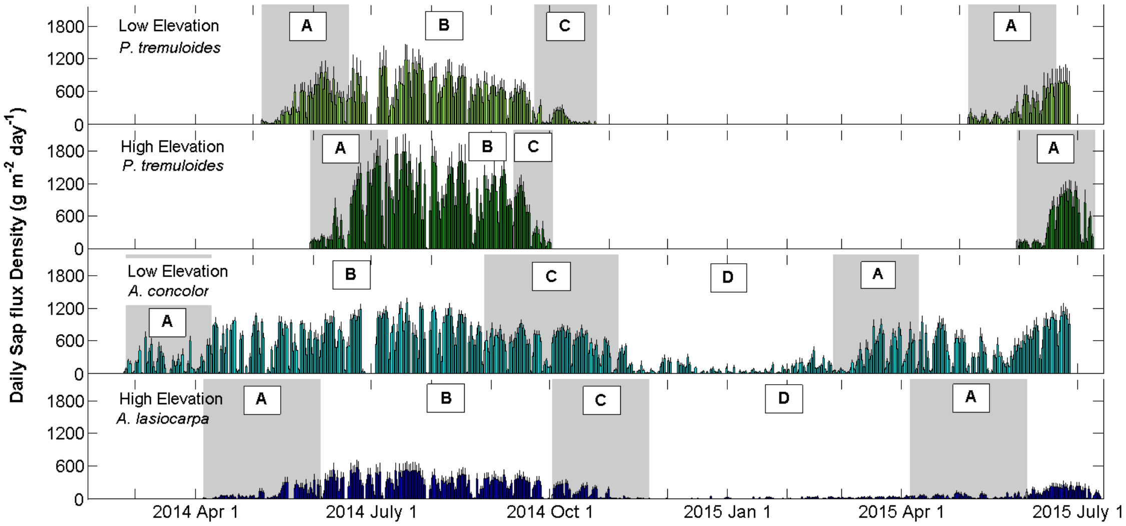

Figure 3. Seasonal daily sums of sap flux densities for all study species in 2014-2015. Error bars represent + SE (n = 12 trees, *A. concolor* & high elevation *P. tremuloides*; n = 10 trees, low elevation *P. tremuloides* & *A. lasiocarpa*). Letters correspond to seasonal time periods for each site and species and are described in the text and Table 1 (A = Spring, B = Summer, C = Fall, D = Winter).

Table 2. Active season start dates (day of calendar year) based on sap flux data and snow-free dates based on snow depth measurements at each site.

Year	**Low** ***A. concolor***	**Low** ***P. tremuloides***	**Low Snow - free**	**High** ***A. lasiocarpa***	**High** ***P. tremuloides***	**High Snow-free**
2014	56*	136	127	124	162	157
2015	35	149	92	118	165	130

***** Sap flux measurements were not started until DOY 52 in 2014.

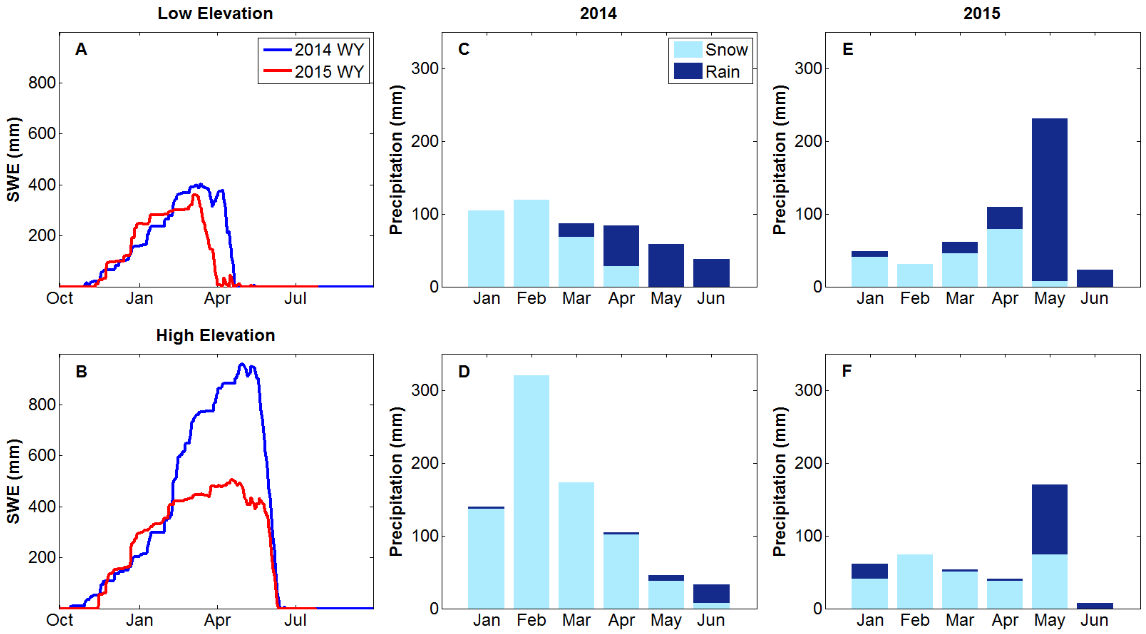

Figure 4. Precipitation at high and low elevation sites in 2014 and 2015. **A – B)** Snow water equivalent (SWE) hydrographs for water years 2014 and 2015 at the low (A) and high (B) elevation sites. **D – F)** Total monthly precipitation in January – June in each year for both sites.

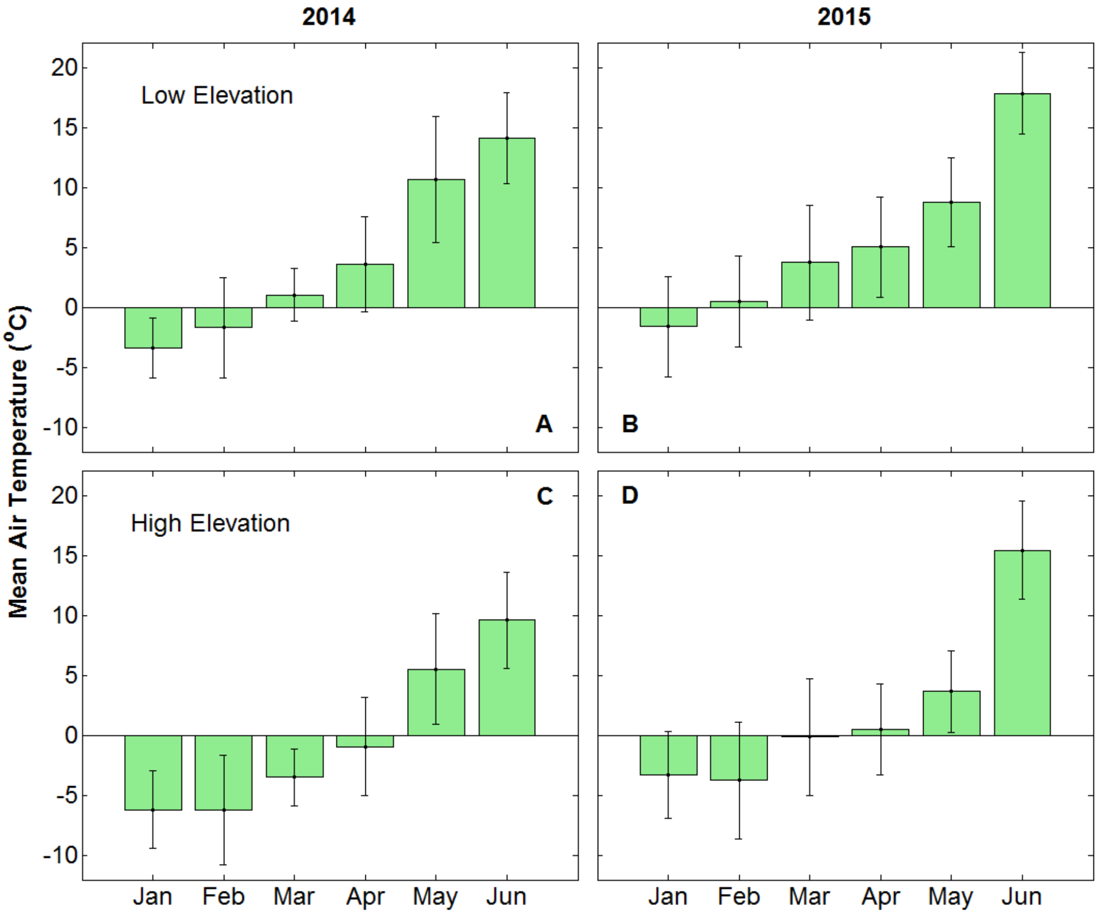

Figure 5. Mean monthly air temperature at the low (A and B) and high (C and D) elevation sites in January – June for each year. Error bars represent ± SD.

Table 3. Mean predawn and midday stem water potential taken in 2014 ± SE (n = 5, *A. concolor*, *A. lasiocarpa*, and high elevation *P. tremuloides*; n = 3, low elevation *P. tremuloides*).

Species	Site	DOY	Predawn Ψ (MPa)	Midday Ψ (MPa)
A. concolor	Low	98	----	-1.35 ± 0.20
		104	----	-0.63 ± 0.11
		126	-0.63 ± 0.09	-0.99 ± 0.14
		141	-1.23 ± 0.12	-1.39 ± 0.08
		155	-0.69 ± 0.03	-1.37 ± 0.07
		183	-0.68 ± 0.08	-1.60 ± 0.06
		213	-0.81 ± 0.09	-1.63 ± 0.18
		258	-1.04 ± 0.02	-1.78 ± 0.07
		297	-1.35 ± 0.06	-1.29 ± 0.04
P. tremuloides	Low	104	----	-1.29 ± 0.19
		126	-0.74 ± 0.01	-1.28 ± 0.02
		141	-0.52 ± 0.03	-0.60 ± 0.04
		155	-0.33 ± 0.02	-0.88 ± 0.05
		183	-0.31 ± 0.01	-1.38 ± 0.05
		213	-0.27 ± 0.02	-1.58 ± 0.11
		258	-0.87 ± 0.09	-1.93 ± 0.04
		297	-1.66 ± 0.15	-1.34 ± 0.09
A. lasiocarpa	High	161	-0.66 ± 0.04	-1.56 ± 0.06
		190	----	-1.26 ± 0.05
		191	-0.59 ± 0.04	----
		227	-0.67 ± 0.07	-1.68 ± 0.13
		260	-0.81 ± 0.04	-1.65 ± 0.11
		302	-1.07 ± 0.12	-1.14 ± 0.03
P. tremuloides	High	161	-0.50 ± 0.03	-0.75 ± 0.04
		190	----	-0.84 ± 0.03
		191	-0.21 ± 0.01	----
		227	-0.30 ± 0.01	-1.50 ± 0.07
		260	-0.78 ± 0.04	-1.20 ± 0.06
		302	-2.66 ± 0.16	-0.79 ± 0.05

Table 4. Multiple linear regression models for each species during the winter, spring and summer seasons. Best predictor variables of sap flux rates were determined from backwards elimination. All p-values were 0.0001 or less.

Species	Site	Season	Season Code	Year	Predictor	F value	Adjusted R^2
A. concolor	Low	Spring	A	2014	Max Air T + Soil T + Soil Ɵ + Max VPD + PAR	6.96	0.43
	Low	Summer	B	2014	Max Air T + Soil T + Soil Ɵ + PAR	31.6	0.48
	Low	Winter	D	2014/2015	Max VPD + PAR + Soil T + Soil Ɵ	32.2	0.53
	Low	Spring	A	2015	Soil T + Max VPD + PAR	45.3	0.76
P. tremuloides	Low	Spring	A	2014	Soil T + Soil Ɵ + PAR	47.2	0.76
	Low	Summer	B	2014	Max VPD + Soil T + PAR	37.2	0.55
	Low	Spring	A	2015	Soil T	103.8	0.71
A. lasiocarpa	High	Spring	A	2014	Min Air T + Soil Ɵ	39.5	0.58
	High	Summer	B	2014	Max Air T + PAR	64.4	0.51
	High	Winter	D	2014/2015	Min Air T + Soil T + Max VPD + PAR	35.6	0.51
	High	Spring	A	2015	Max Air T + Soil T + PAR	23.2	0.53
P. tremuloides	High	Spring	A	2014	Max Air T + Soil Ɵ	33.2	0.62
	High	Summer	B	2014	Max Air T + PAR	28.2	0.46
	High	Spring	A	2015	Soil T + Max VPD	24.3	0.54

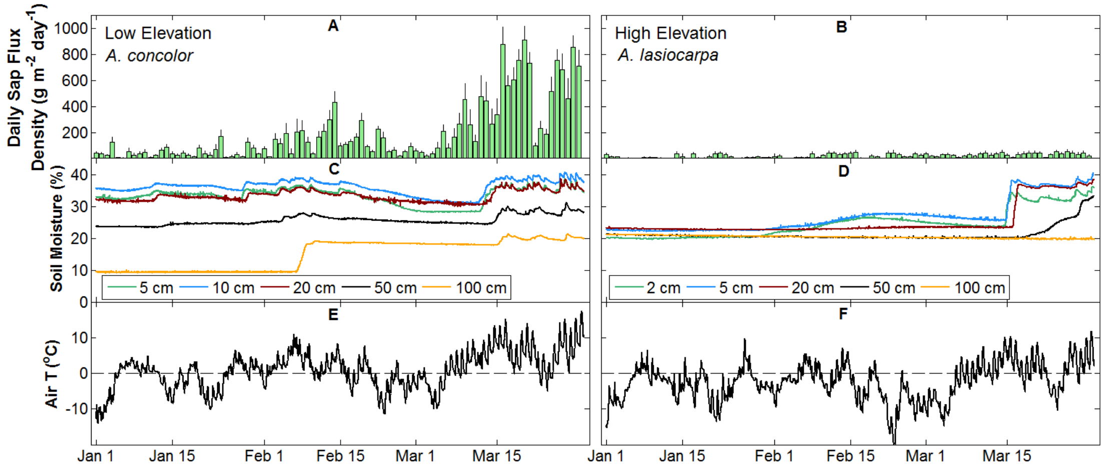

Figure 6. January – March 2015 season daily sums of sap flux densities compared with soil moisture and air temperature for evergreen-coniferous species at high and low elevation sites. **A – B)** Daily sum of sap flux densities for *A. concolor* and *A. lasiocarpa*. Error bars represent + SE (n = 12 trees, *A. concolor;* n = 10 trees, *A. lasiocarpa*). **C – D)** Soil moisture at various depths. **E –F)** Air temperature (dashed line indicates 0˚C).

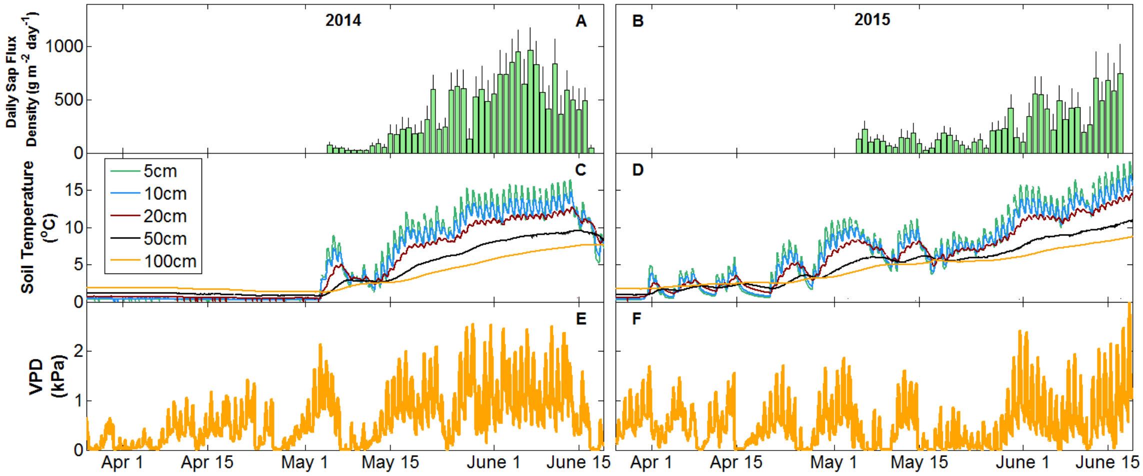

Figure 7. Low elevation *P.tremuloides* daily sum of sap flux densities at the start of the active season in 2014 and 2015 compared with soil temperature and VPD. **A – B)** Daily sum of sap flux densities. Error bars represent + SE (n = 10 trees). **C – D)** Soil temperature at various depths. **E – F)** Vapor pressure deficit (VPD). Note there were no sap flux data collected prior to 5 May in either year.

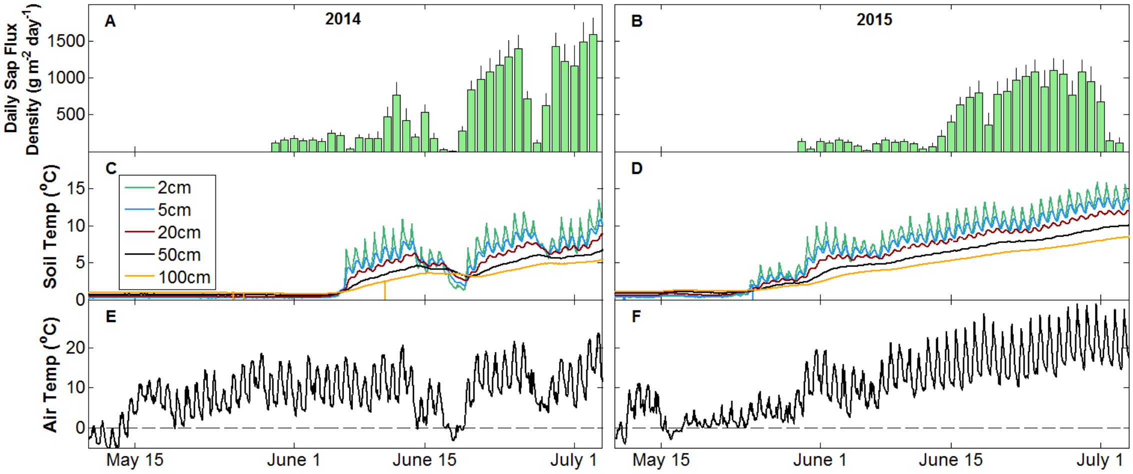

Figure 8. High elevation *P. tremuloides* daily sum of sap flux densities at the start of the active season compared with soil temperature and air temperature. **A – B)** Daily sum of sap flux densities. Error bars represent + SE (n = 12 trees). **C – D)** Soil temperature at various depths. **E – F)** Air temperature (dashed line indicates 0˚C). Note there were no sap flux data collected prior to 30 May in either year.

4 DISCUSSION

Changes in the onset date of the active season have important implications for annual forest productivity. The use of continuous sap flux measurements in our study has allowed us to evaluate variability in the onset of the active season for individual species in a high and low elevation forest and the environmental conditions that control early season transpiration rates.

4.1 Changes in onset of transpiration in response to environmental variation between years

4.1.1 Evergreen-coniferous

Warmer air temperature in 2015 compared to 2014 allowed *A. concolor* at the low elevation site to be active during the winter period (Fig. 6, A). We observed transpiration from these trees on days when air temperature was above zero in February through April. Increased air temperature has been shown to be a primary control on the recovery of photosynthesis for many evergreen-coniferous species in seasonally snow-covered forests (Tanja et al. 2003; Monson et al. 2005; Thum et al. 2009). In warm winter periods, many evergreen-coniferous species are able to switch between active and inactive states when conditions are favorable for photosynthesis (Monson et al. 2005; Zarter et al. 2006b; Moore et al. 2008; Verhoeven 2014). However, it was not air temperature alone that enabled transpiration at the low elevation site. Soil moisture was also important. Activity corresponded with periods where melt events occurred under the snowpack and maximum daily air temperature was above zero, which supported our hypothesis that transpiration would occur in evergreen-coniferous trees when air temperature was above freezing and there is daily percolation of snowmelt water into the soil (Fig. 6, A, C, E).

An important difference during the *A. concolor* winter period in 2015 compared to 2014 was that there were periodic melt events occurring and increases in soil moisture could be seen under the snowpack (Fig. 6, C). This contrasts with many other seasonally snow-covered forests, where soil moisture conditions from the fall persist throughout the winter and spring beneath the snowpack (Maurer and Bowling 2014). While a stable soil moisture environment was present in 2014 (data not shown), the warmer air temperature in 2015 led to comparatively early melt events. Monson et al. (2005) found that the snowpack becoming isothermal in the spring was an important event in the recovery of tree activity, as isothermal conditions permit liquid water in the snowpack to percolate through to the soil. We did not measure snow temperature, but the frequent increases in soil moisture observed under the snowpack are indicative of an isothermal snowpack. These soil conditions, along with long periods of above zero air temperature enabled *A. concolor* transpiration as earlier as DOY 35 (4 February).

Although air temperature was also comparatively warmer at the high elevation site in 2015 compared to 2014, *A. lasiocarpa* did not respond to intermittent periods of above zero air temperature (Fig. 6, B, D, F). Unlike the low elevation site, there were not periodic melt events occurring under the snowpack that affected deep soil moisture (Fig. 6, D). Soil moisture stayed fairly constant throughout the winter-spring period and it was not until soil moisture began to increase and minimum air temperature was above zero that sap flux was detectable (data not shown). In addition, the rate of photosynthetic recovery may be slower at the higher elevation site and delayed by freezing events (Ensminger et al. 2004).

Despite soil moisture and temperature constraints on activity during much of the winter period, there were still earlier signs of transpiration in 2015 compared to 2014. Similar to *A. concolor, A. lasiocarpa* began to transpire soon after we observed an increase in soil moisture at 100 cm depth in both 2014 and 2015. That event occurred earlier in 2015, and consequently, transpiration also began earlier (data not shown). However, soon after daily transpiration had begun in 2015, a long period of rain followed in the month of May. This resulted in low VPD and low transpiration.

4.1.2 Deciduous-broadleaf

The initiation of *P. tremuloides* transpiration is limited by the timing of leaf emergence in spring and there can be considerable variation in the onset of the growing season date between years (Black et al. 2000b). Baldocchi et al. (2005) suggested that the onset of the growing season of deciduous-broadleaf forests corresponds to the day when mean soil temperature is equal to mean annual air temperature. This relationship approximated the start of the growing season fairly well in 2014 for *P. tremuloides* at both the high and low elevation sites. At the high elevation site, transpiration was first observed 5 days after the soil temperature threshold was met and at the low elevation site, there was a 10-day delay. However, in 2015, there was a 33-day delay between the day the soil temperature threshold was met and the day when transpiration was first observed. Similarly, at the low elevation site, there was a 36-day delay.

The delay in the onset of transpiration relative to soil warming in 2015 may be explained by the difference in spring weather patterns. Both sites became snow-free much earlier in 2015 compared to 2014 and January – April mean monthly air temperature was higher. The low elevation site was snow-free 35 days earlier and the high elevation site 27 days earlier. There is an abrupt increase in soil temperature following the completion of snowmelt and based on the hypothesis of Baldocchi et al. (2005), we expected that earlier snowmelt would lead to an earlier start to the growing season. However, precipitation was much higher during the month of May in 2015 and mean monthly air temperature was lower (Fig. 4, E and F; Fig. 5, B and D). It is likely that cooler air temperature delayed leaf emergence, and consequently the onset transpiration in 2015.

There were also important differences in the onset of transpiration between the high and low elevation *P. tremuloides* in 2015. While snowmelt occurred earlier than in 2014 at both sites, the onset date was nearly the same in both years at the high elevation site, but was delayed by almost 2 weeks compared to 2014 at the low elevation site. At this site, the soil temperature threshold was not met until 21 days following snowmelt. Therefore, phenology was likely first delayed by a limitation in soil temperature. After passing the soil temperature threshold, there were a few short periods of sunny, warm days and then a 2-week period of rain at the end of May. It is possible that leaves had emerged in the warm periods prior to these rain events and that low VPD was preventing transpiration at this time. We found that the number of degree days from May 1 to the first day of transpiration were much higher in 2015 than 2014. Therefore, it is not likely that there was a temperature limitation on the start of the active season at this site.

At the high elevation site, the soil temperature threshold was met soon after the site became snow-free, as was observed in 2014. However, the delay in the onset of transpiration may have been driven by cooler air temperature at the end of May. Accumulated degree days can also be useful predictors of the timing of leaf emergence (Lechowicz 1984; Barr et al. 2009). When we calculated the degree days from May 1 to the onset of transpiration, we found that degree days were higher in 2014 than 2015 (281 in 2014 and 268 in 2015). Therefore, the combined effects of soil and air temperature were important drivers of the onset of transpiration in 2015.

Black et al. (2000b) found that air temperature was highly correlated with the timing of leaf emergence for a boreal *P. tremuloides* stand; years with higher April – May air temperature had earlier leaf emergence. Soil temperature was also important, but air temperature was the dominant control of leaf emergence. Similarly, the timing of leaf emergence for many temperate deciduous forests is largely driven by air temperature (Hunter and Lechowicz 1992; Richardson et al. 2009; Richardson et al. 2013). Although we found cumulative degree days explained, in part, the onset date for *P. tremuloides* at the high elevation site, we did not find a clear pattern between springtime air temperature and the onset date of transpiration.

4.2 Environmental controls on sap flux rates during the winter-spring period

We used multiple linear regression analysis to determine which environmental variables best predicted sap flux rates during each season. These models help to explain which variables are most important in understanding process-based relationships between different environmental variables and sap flux rates. In some cases, these results are difficult to interpret because all of the possible predictor variables show up in the final model and there are no clear dominant factors. This can be seen for *A. concolor* during

Spring 2014 and Winter 2014/2015. In this type of analysis it is also unlikely that highly correlated predictors will both end up in the final model. For example, air temperature and VPD may both be important factors, but because they are so correlated, usually only one of them would show up in the final model (although that is not always the case).

These models highlight that there are a suite of environmental variables that are controlling transpiration rates in the spring and that the major predictors of transpiration rates vary between season and between years. Some of the general patterns we can pull from these models are that the soil environment was a major driver of sap flux rates for *P. tremuloides* at the low elevation site during both spring periods. While soil temperature was important in both years, it was the sole predictor of transpiration rates in spring 2015. These results partially support our hypothesis that soil temperature and air temperature would be the dominant controls on spring transpiration for *P. tremuloides.* Air temperature was surprisingly unimportant at the low elevation site, but it was a predictor for transpiration rates of *P. tremuloides* at the high elevation site. However, here, soil temperature was only a predictor in 2015. The differences we found between the high and low elevation *P. tremuloides* may be, in part, explained by acclimation to different climates. The high elevation *P. tremuloides* has a higher risk of freezing damage during leaf emergence and during the spring period and they also have a much shorter growing season (Fig. 3). The fact that they are more responsive to air temperature may be a strategy to maximize productivity during a relatively short active season (Lenz et al. 2013).

We hypothesized that air temperature would be the primary control of transpiration rates during the spring period for the evergreen-coniferous species. Air temperature and/or VPD were predictors of spring transpiration rates for both evergreen-coniferous species in both years, but they were not the only predictors (Table 4). Soil temperature and PAR were also predictors. Soil temperature is correlated with rates of photosynthetic recovery and many studies have found that cold soil temperature can delay recovery (DeLucia 1986; Day et al. 1989; Day et al. 1990; Mellander et al. 2004). A notable exception was spring 2014 for the high elevation *A. lasiocarpa*. Here, air temperature and soil moisture were the primary predictors. An important difference between 2014 and 2015 at the high elevation site was that soil moisture was dramatically lower throughout the winter in 2014 (data not shown). Soil moisture is generally assumed not to be a limiting factor for early season evergreen-coniferous tree activity (Sevanto et al. 2006; Thum et al. 2009). However, soil moisture was below 10% (volumetric percent) during the winter of 2014, which is well below moisture levels that have been shown to limit transpiration in *A. lasiocarpa* during the summer (Pataki et al. 2000). Maurer and Bowling (2014) showed that soil moisture conditions from the fall persist throughout the winter under the snowpack. Therefore, it is possible drier fall conditions may limit photosynthetic recovery in the spring.

4.3 Contrasting transpiration patterns between evergreen-coniferous and deciduous-broadleaf trees

The differences we saw in seasonal transpiration patterns support our hypothesis that evergreen-coniferous species would have longer active seasons than co-located deciduous-broadleaf species and that the low elevation species would have longer active seasons than their high elevation counterparts. These results corroborate the findings of Barr et al. (2009). In a study examining the seasonal patterns of net ecosystem production in stands of jack pine, black spruce, and aspen, they found that the pine and spruce growing season was 50 days longer than the aspen. The aspen were much more productive during the middle of the growing season, while the conifers maximized carbon uptake in the shoulder seasons. We saw similar patterns between the deciduous-broadleaf and evergreen-coniferous trees at both of our sites. Additionally, we observed a shorter growing season for the high *P. tremuloides* compared to the low and likewise, a shorter growing season for *A. lasiocarpa* compared to *A. concolor* (Fig. 3).

However, in contrast to other studies, we did not find a comparative advantage for deciduous-broadleaf trees over evergreen-coniferous in response to warmer spring temperature. While the onset of transpiration was advanced for both evergreen-coniferous species in 2015 when air temperature was warmer and snowmelt occurred earlier, the start of the active season was delayed for *P. tremuloides* at both sites.

In the context of the widespread *P. tremuloides* mortality that has been documented across the Western U.S. (Bartos and Campbell 1998; Brown et al. 2006; Worrall et al. 2008; Anderegg et al. 2013), our findings suggest an additional stress that may occur due to a delayed onset of the active season. Anderegg et al. (2013) found that extreme drought led to mortality in *P. tremuloides* in western Colorado and that these trees were especially susceptible to drought because they relied on shallow soil water and exhibited little stomatal control in response to water stress. The combination of a shallower snowpack, earlier melt and increased delay between snow-free date and the onset of transpiration that we observed for the high and low elevation *P. tremuloides* may lead to increased drought stress during the summer. In the previous year, soil moisture was highest immediately following the completion of snowmelt. This is a common characteristic of seasonally snow-covered forests (Bales et al. 2011). The fact that *P. tremuloides* was not active during this period in 2015 will likely have consequences not only by shortening the length of the active season, but also by missing a period with favorable soil moisture.

4.4 Climate change implications

There has been a general trend toward increasing winter and spring temperature in the Western U.S. (Barnett et al. 2005) which has been accompanied by a decline in annual snowfall (Mote et al. 2005). In Utah, January – March snowfall has decreased by 9% over the last 50 years and the proportion of precipitation falling as rain has increased (Gillies et al. 2012). Similar patterns have been found in Colorado, where the timing of snowmelt and peak streamflow have advanced 2 – 3 weeks since 1978 (Clow 2010). Additionally, large-scale tree mortality events have become more frequent in response to drought and insect infestation (van Mantgem et al. 2009; Adams et al. 2012; Anderegg et al. 2013), leading to growing concern regarding the future of our forests. The extent to which forests can respond to these changes will have ecological, hydrological, and economic consequences (Barnett et al. 2005; Bonan 2008; Adams et al. 2012). The two years of our study, which had contrasting winter-spring precipitation and air temperature, provided us an opportunity to examine how decreasing snow cover and increasing air temperature affects transpiration.

We found that transpiration patterns at the low elevation site were more affected by the variability in environmental conditions that we observed. This site is more susceptible to major snow to rain shifts compared to the high elevation site, due to its warmer climate. However, while the warmer winter and earlier melt events in 2015 allowed transpiration to begin earlier for the low elevation *A. concolor*, transpiration of the co-located *P. tremuloides* was delayed, at least in part, by a much wetter May, when leaf emergence and transpiration had occurred in the previous year.

Although other studies have found deciduous-broadleaf trees to be relatively more responsive to spring warming than evergreen-coniferous trees (Barr et al. 2009; Richardson et al. 2009), we found that major shifts in the timing of precipitation, with more precipitation falling in May, was an important factor in the timing of growing season onset for the deciduous-broadleaf trees in our study. There has been less agreement among climate models on how precipitation amounts and patterns are likely to change, so it is difficult to make conclusions regarding how long-term spring transpiration patterns will be affected (Barnett et al. 2005). However, Bales et al. (2011) has shown that soils dry out faster following rain events than snowmelt events. Therefore, shifts in precipitation phase from rain to snow are likely to result in drier soils even if total precipitation amount does not change. We predict then, that a long-term shift toward more rain may increase summer water stress in these lower elevation forests. Our study highlights the fact that air temperature alone is not enough to predict the onset of transpiration and that variability in the timing of precipitation events will be important to consider in the future.

4.5 Conclusions

To our knowledge, this study is the first to utilize year-round sap flux measurements in a seasonally snow-covered forest. This has allowed us to examine the annual transpiration patterns of co-located deciduous-broadleaf and evergreen-coniferous species, which is not possible using forest-level measurements. Our analysis, focusing on the environmental controls on the onset of transpiration and early season transpiration rates, has shown that warmer winter temperature can lead to earlier onset of transpiration for evergreen-coniferous species, if accompanied by melt events from the snowpack that percolate into the deep soil. Contrary to our hypothesis, the timing of soil warming did not consistently predict the onset of transpiration for *P. tremuloides.* Variation in spring weather events complicated this relationship and emphasized the importance that shifts in the timing of precipitation may have on phenology. Due to the relatively short length of our dataset, it is difficult to make general predictions regarding the impact that interannual variability in environmental conditions will have on early season transpiration. However, our study has demonstrated that co-located deciduous-broadleaf and evergreen-coniferous species respond differently to spring conditions and that there was more variability in spring phenology at our lower elevation site. Looking forward, future studies of year-round sap flux could benefit from adding leaf-level measurements and phenological observations to more fully understand the physiological processes that control transpiration and early season tree activity.

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