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## LETTER

# Topoclimate effects on growing season length and montane conifer growth in complex terrain

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## Abstract

Spatial variability in the topoclimate-driven linkage between forest phenology and tree growth in complex terrain is poorly understood, limiting our understanding of how ecosystems function as a whole. To characterize the influence of topoclimate on phenology and growth, we determined the start, end, and length of the growing season ( $GS_{start}$ ,  $GS_{end}$ , and  $GSL$ , respectively) using the correlation between transpiration and evaporative demand, measured with sapflow. We then compared these metrics with stem relative basal area increment (relative BAI) at seven sites among elevation and aspects in a Colorado montane forest. As elevation increased, we found shorter  $GSL$  ( $-50$  d  $km^{-1}$ ) due to later  $GS_{start}$  ( $40$  d  $km^{-1}$ ) and earlier  $GS_{end}$  ( $-10$  d  $km^{-1}$ ). North-facing sites had a 21 d shorter  $GSL$  than south-facing sites at similar elevations (i.e. equal to 200 m elevation difference on a given aspect). Growing season length was positively correlated with relative BAI, explaining 83% of the variance. This study shows that topography exerts strong environmental controls on  $GSL$  and thus forest growth. Given the climate-related dependencies of these controls, the results presented here have important implications for ecosystem responses to changes in climate and highlight the need for improved phenology representation in complex terrain.

## 1. Introduction

Improved understanding of spatially variable ecosystem functioning in topographically complex regions is essential given that complex terrain yields  $> 60\%$  of total carbon uptake in the western United States, covers  $> 50\%$  of the land surface globally, and is a source of uncertainty in global carbon cycling estimates (Rotach *et al* 2014, 2008, Schimel *et al* 2002). Much of this spatial variability is due to topographic-driven gradients in temperature and vegetation structure that result in a heterogeneous patchwork of topoclimate that can be decoupled from the mean regional climate (Daly *et al* 2010, Dobrowski 2011, Novick *et al* 2016). As a result, the timing of phenological events (e.g. onset of spring growth) can vary among topoclimate and influence tree growth and ecosystem productivity (Churkina *et al* 2005, Rossi *et al* 2013, Tran *et al* 2017). However, studies that include direct measurements of spatial phenological

variation in complex terrain are few despite the known impacts of phenology on regional and global climate, and forest growth and susceptibility to disturbance (Bonan 2008, Dale *et al* 2001, Kramer *et al* 2000, Peñuelas and Filella 2009, Bruening *et al* 2017).

The influence of topography on ecosystem and critical zone functioning has become the focus of renewed interest and several dendrochronological studies have identified an effect of topoclimate on tree growth and the location of tree line and ecotone boundaries (Körner 2012, Adams *et al* 2014, Tran *et al* 2017). Tree growth rates are, in general, inversely proportional to elevation due to decreasing temperatures at higher elevations (Körner and Paulsen 2004, Bruening *et al* 2017). Slope and aspect effects on solar insolation can interact with elevation changes to affect site temperature and moisture regimes as well, resulting in high spatial variability in the factors that limit growth (e.g. energy, moisture) (Bunn *et al* 2011, Salzer *et al* 2014). The effect of temperature variability

**Table 1.** Characteristics of the seven study sites including, mean annual air temperature (Mean  $T_{\text{air}}$ ) and mean annual soil temperature (Mean  $T_{\text{soil}}$ ). Error ranges represent one standard deviation.

Elevation (m)	Latitude (degrees)	Longitude (degrees)	Aspect	Species	Mean $T_{\text{air}}$ (°C)	Mean $T_{\text{soil}}$ (°C)
<b>Betasso</b>						
1884	40.0125	−105.3405	S	<i>P. ponderosa</i>	7.9 ± 3.8	10.8 ± 4.1
<b>Gordon Gulch</b>						
2478	40.0127	−105.4616	S	<i>P. ponderosa</i>	5.1 ± 3.6	6.6 ± 2.6
2536	40.0121	−105.4696	N	<i>P. contorta</i>	4.1 ± 3.8	4.8 ± 2.6
2572	40.0146	−105.4684	S	<i>P. ponderosa</i>	4.8 ± 5.6	7.7 ± 2.8
2589	40.0160	−105.4742	W	<i>P. contorta</i>	5.6 ± 3.7	5.0 ± 2.3
2675	40.0202	−105.4830	S	<i>P. ponderosa</i> and <i>P. contorta</i>	4.3 ± 3.8	5.3 ± 2.4
2691	40.0221	−105.4809	N	<i>P. contorta</i>	3.5 ± 3.7	3.5 ± 2.3

on growing season length (GSL) has received much attention, and GSL is commonly used as a predictor of tree growth and forest productivity in complex terrain (Paulsen and Körner 2014, Bruening *et al* 2017). However, GSL is typically determined as a function of air temperature alone (often averaged over periods > 1 d); an approach that likely neglects topographic and short-term effects on forest- and species-level physiological activity and phenological transitions. Given that GSL is often used to describe vegetation growth across topographic boundaries (Churkina *et al* 2005, Rossi *et al* 2013, Paulsen and Körner 2014, Tran *et al* 2017), the impact of topography on GSL and forest growth represents a substantial knowledge-gap in the current understanding of forest ecosystem function.

Measuring spatially explicit topo-climatic controls on forest productivity in complex terrain is difficult and new procedures to characterize spatially-explicit physiological activity are needed. One potential solution is to use spatially-distributed sapflow measurements of tree transpiration (Burgess *et al* 2001). Transpiration is an inevitable consequence of carbon uptake for photosynthesis (Collatz *et al* 1991, Farquhar and Sharkey 1982, Jarvis and Davies 1998) and may subsequently serve as an indicator of active canopy gas exchange. Because conifer gas exchange is well-coupled to atmospheric demand (Jarvis and McNaughton 1986), the relationship between vapor pressure deficit (VPD) and sapflow can be used as a metric for physiological activity while intrinsically accounting for the effects of temperature and moisture availability. Temporal dynamics of physiological activity can be used to identify phenological phase shifts such as the transition from dormant to active periods and vice-versa. These phenology metrics can then be compared with measurements of radial tree growth rates to clarify the relationship between GSL and forest growth in complex terrain.

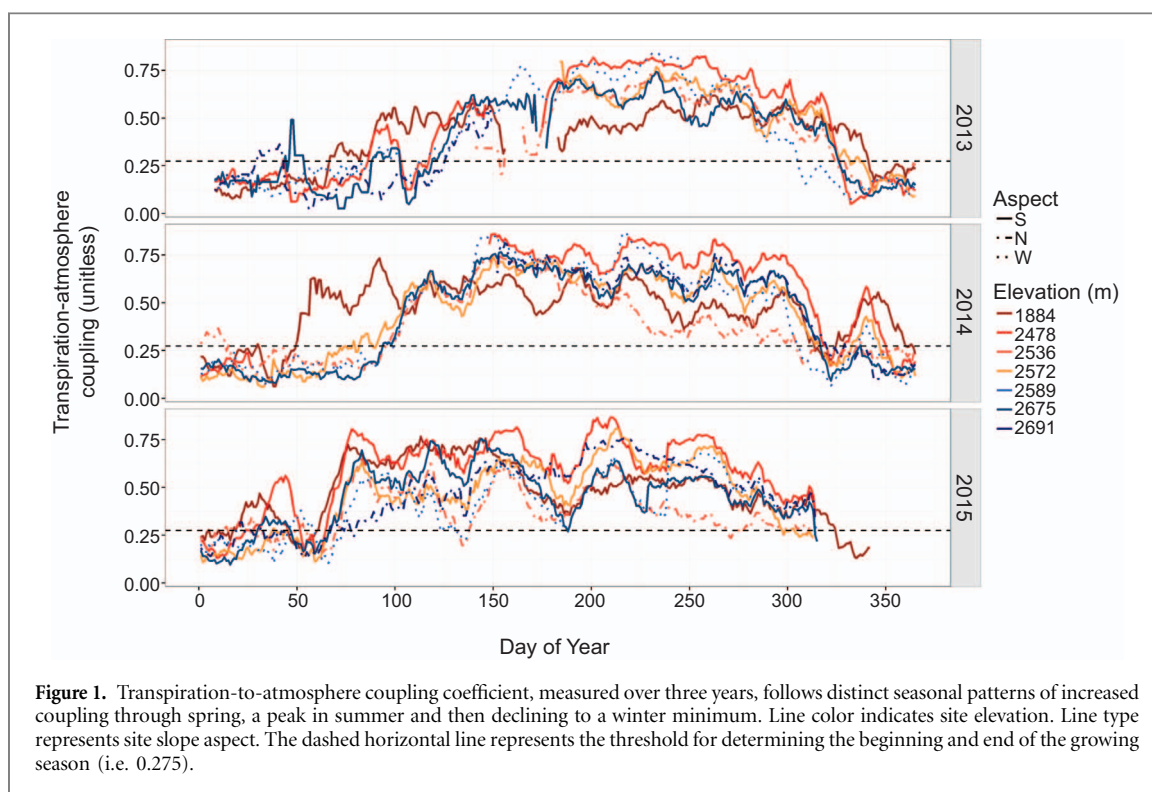
In this study, we used the correlation between transpiration and VPD (i.e. transpiration–atmosphere coupling) measured from seven spatially-distributed sapflow sites to examine forest physiological activity

throughout the year and to describe variability in the start, end, and length of the growing season ( $GS_{\text{start}}$ ,  $GS_{\text{end}}$ , and GSL, respectively). Sites were located across an 800 m elevation gradient and among slope aspects within a montane forest ecosystem. We addressed two main research questions: (1) does topoclimate variation or topographic location cause differences in growing season metrics or annual patterns of transpiration–atmosphere coupling?; (2) how does topographic variation in growing season metrics influence forest productivity as indicated by annual radial tree growth?

## 2. Methods

During 2013–2015, we collected data from seven sites (each with a 10 m radius) within two catchments of the Boulder Creek watershed in the Colorado Front Range, Colorado, USA (table 1). The sites have considerable variation in topography with an elevation range of 1884–2691 m. Betasso is a south-facing, lower montane catchment that is forested with *Pinus ponderosa*. Mean annual precipitation at Betasso is 500 mm, of which 20% falls as snow (Berryman *et al* 2015). The one Betasso site was selected to represent a lower elevation extreme and because it is collocated with a meteorological station that included air temperature ( $T_{\text{air}}$ ) and relative humidity (RH) sensors (Vaisala HMP45AC, Vantaa, Finland) at 2 m above the ground, and soil temperature ( $T_{\text{soil}}$ ; Decagon EC-5, Decagon Devices, USA) at 15 and 40 cm below the soil surface.

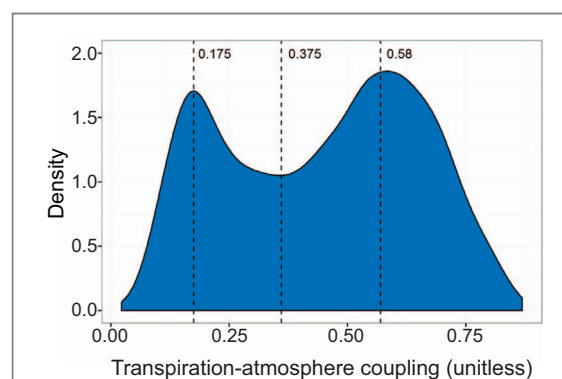
Gordon Gulch is an upper montane catchment with distinct north- and south-facing slopes. South-facing slopes are more arid with a transient snowpack and low to moderate density *P. ponderosa* (Hinckley *et al* 2014). North-facing slopes are more mesic, with a shallow seasonal snowpack and densely spaced *Pinus contorta* (Hinckley *et al* 2014). Mean annual precipitation at Gordon Gulch is 510 mm of which 50% falls as snow (Berryman *et al* 2015). The six site locations within Gordon Gulch were selected to



**Figure 1.** Transpiration-to-atmosphere coupling coefficient, measured over three years, follows distinct seasonal patterns of increased coupling through spring, a peak in summer and then declining to a winter minimum. Line color indicates site elevation. Line type represents site slope aspect. The dashed horizontal line represents the threshold for determining the beginning and end of the growing season (i.e. 0.275).

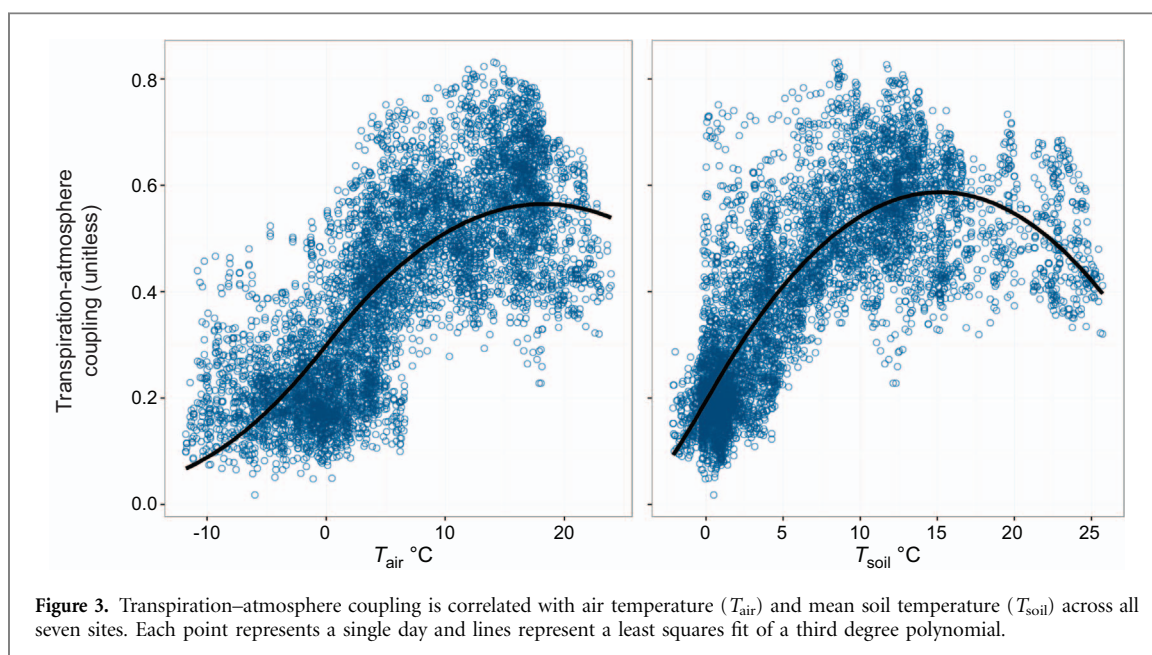
represent a range of elevations on south, west, and north facing slopes within the catchment. All Gordon Gulch sites were instrumented with  $T_{\text{air}}$  and RH sensors at mid-canopy height (107 L, Campbell Scientific, Logan, UT). Four of the Gordon Gulch sites were instrumented with  $T_{\text{soil}}$  sensors, installed at 10 and 30 cm below the soil surface (HydraProbe, Stevens Water Monitoring Systems Inc., Portland, OR) whereas, the other two (i.e. 2536 m and 2572 m) were instrumented with  $T_{\text{soil}}$  (Decagon 5TE, Decagon Devices Inc., Pullman, WA) at 5 and 25 cm. Soil temperature measurements at all sites are reported as the mean of the two sensor depths. Three sites (1884 m, 2536 m and 2572 m) were also collocated with ultrasonic snow depth sensors (Judd Communications, Salt Lake City, UT). Meteorological data was measured at 10 m intervals, which were checked for missing and duplicate entries and then averaged to 30 min intervals for comparison to sapflow measurements.

We measured sapflux velocity ( $V_s$ ) at 30 min intervals (i.e. 48 measurements per day) using heat-pulse sapflow sensors (Burgess *et al* 2001). Sensors were installed at 1.4 m aboveground in eight randomly selected trees per site to a depth of 2 and 5 cm inward from the cambium. Sapflux velocity is most commonly at its maximum near the sapwood-cambium boundary (Meinzer *et al* 2010) and the sapwood of *P. contorta* is commonly < 5 cm deep (Barnard *et al* 2013), therefore we used only  $V_s$  measured at 2 cm depth for this study. The highest elevation south-facing site (2675 m) was mixed-species (*P. ponderosa* and *P. contorta*), so we instrumented  $n = 4$  of each species at that site.



**Figure 2.** Probability density function of transpiration-atmosphere coupling across all seven sites indicates a dormancy local maxima at 0.175 and a phase shift between dormant and active periods with local minima at 0.375 and growing season maximum at 0.58. We thus used the middle point between these two conditions (i.e. 0.275) to define the beginning or end of the growing season.

We calculated transpiration-atmosphere coupling as the coefficient of determination ( $R^2$ ) between daily linear regressions of VPD and  $V_s$ , co-measured every 30 min (48 measurements per day) for the three years of this study (figure 1). We used a probability distribution function of values of transpiration-atmosphere coupling to characterize the threshold between periods of dormancy and non-dormancy. The probability density distribution was bimodal with two peak densities corresponding to the two main phenological phases: the mean of forest dormant periods (0.175) and the mean of the forest growing season (0.58) (figure 2). Given a transition-period minima of 0.375, we chose one-half the distance from the dormant period peak to the transition-period



**Figure 3.** Transpiration–atmosphere coupling is correlated with air temperature ( $T_{\text{air}}$ ) and mean soil temperature ( $T_{\text{soil}}$ ) across all seven sites. Each point represents a single day and lines represent a least squares fit of a third degree polynomial.

minima to represent the threshold between the two phenological phases (0.275). The  $GS_{\text{start}}$  was then quantified as the first day of a period in spring that the transpiration–atmosphere coupling 10 day moving average was greater than the threshold for more than 10 d. The converse was used to quantify  $GS_{\text{end}}$  in fall. The GSL was then calculated as  $GS_{\text{end}} - GS_{\text{start}}$ .

To characterize differences in forest productivity among the sites, we collected increment cores at 1.4 m from three dominant trees per site. Following sanding, ring widths were measured using WinDENDRO software (Regent Instrumentation, Quebec, Canada). To examine differences in stand level growth variation, we calculated relative basal area increment (relative BAI). Relative BAI normalizes individual growth rings by basal area allowing for comparisons among sites (Bigler *et al* 2004). Relative BAI was calculated as

$$\text{Relative BAI} = \frac{\pi r_t^2 - \pi r_{t-1}^2}{\text{BA}} \quad (1)$$

where  $r_t$  is stem radius at breast height (cm) at year =  $t$ ,  $r_{t-1}$  is stem radius at breast height in year =  $t-1$ , and BA is the stem basal area.

### 3. Results

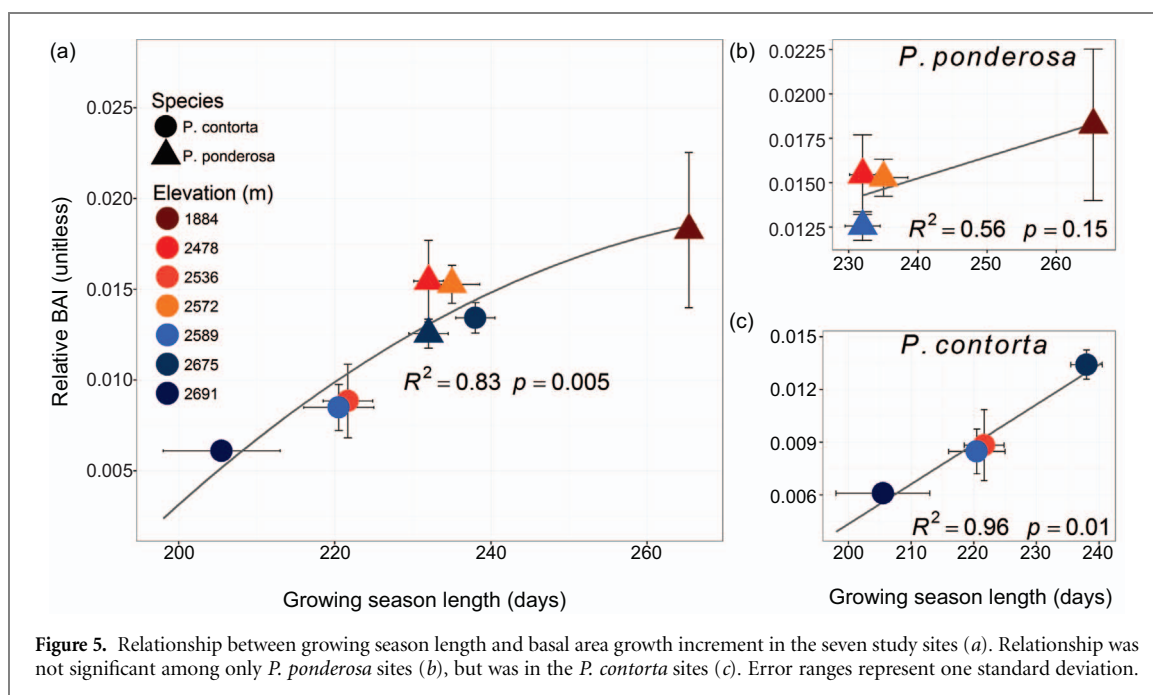
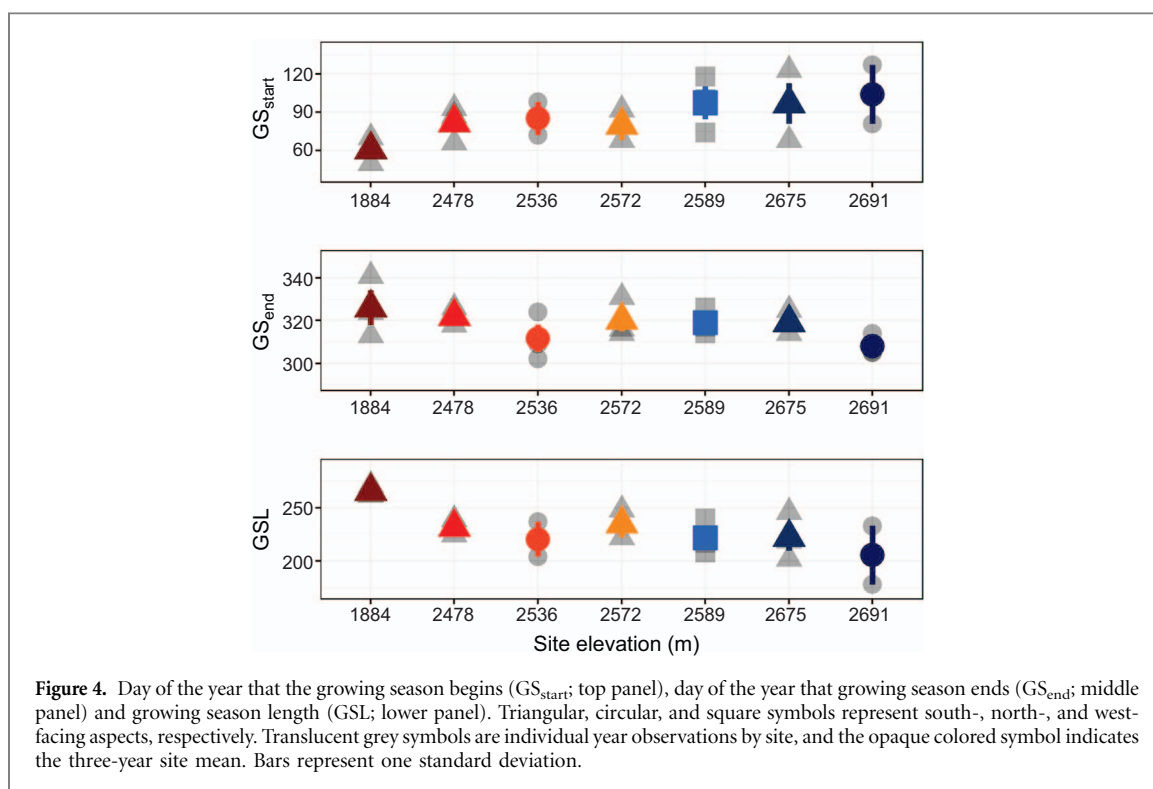
The largest differences in topoclimate were between the Betasso and Gordon Gulch catchments whereas the differences among sites at Gordon Gulch were not significant except for  $T_{\text{soil}}$  (table 1). Annual  $T_{\text{air}}$  at Betasso was on average 4.4 °C warmer than the mean of  $T_{\text{air}}$  at all of the Gordon Gulch sites ( $p < 0.01$ ). Mean annual  $T_{\text{air}}$  among sites at Gordon Gulch did not differ significantly by elevation or aspect ( $p = 0.51$  and  $p = 0.13$ , respectively). Annual  $T_{\text{soil}}$  was highest at the 1884 m site (10.8 °C) and significantly different than the mean of the six Gordon Gulch sites (5.9 °C,

$p < 0.01$ ). Among all sites at Gordon Gulch,  $T_{\text{soil}}$  was significantly different ( $p < 0.01$ ), generally decreasing as elevation increased. These differences were especially distinct between north- and south-facing sites (4.5 and 6.7 °C, respectively;  $p < 0.01$ ). North-facing sites at Gordon Gulch accumulated a shallow (30–40 cm) seasonal snowpack. Betasso and the south-facing sites at Gordon Gulch had transient snowpack development, typically with shallow, semi-persistent, heterogeneous snow cover (10–20 cm).

Transpiration–atmosphere coupling followed a general pattern with defined periods of physiological activity in late-spring through fall, dormancy in winter and early spring, and a few periods of physiological activity that were out of phase with the overall annual cycle (figure 1). Outside of the growing season, the lowest elevation south-facing site (1884 m) had the greatest percentage of days within the year with transpiration–atmosphere coupling  $> 0.275$  (29%) and the highest elevation north-facing site had the fewest (16%). Across all sites, transpiration–atmosphere coupling was significantly correlated with  $T_{\text{soil}}$  ( $p < 0.01$ , 3rd degree polynomial adjusted  $R^2 = 0.65$ ) and  $T_{\text{air}}$  ( $p < 0.01$ , 3rd degree polynomial adjusted  $R^2 = 0.56$ ; figure 3).

Both elevation and aspect had significant impacts on growing season metrics across all sites (figure 4). At north-facing sites,  $GS_{\text{start}}$  occurred an average of 4–6 d later, and  $GS_{\text{end}}$  12–14 d earlier than south-facing sites at similar elevations. The west-facing site at 2589 m had an average  $GS_{\text{start}}$  three days later and a  $GS_{\text{end}}$  one day earlier than the south-facing site at 2572 m. The variation in  $GS_{\text{start}}$  and  $GS_{\text{end}}$  resulted in GSLs that were 21 d longer on average at south-facing sites than north-facing sites at Gordon Gulch, with the west-facing site having an eight day longer GSL than the closest elevation north-facing site (2536 m). The GSL was up to 50 d longer at the lowest versus highest





elevation south-facing sites. Also at 2675 m, *P. contorta* had a GSL that was ten days longer on average than the co-occurring *P. ponderosa* with  $GS_{start}$  occurring four days earlier and  $GS_{end}$  occurring six days later in *P. contorta*.

Growing season metrics generally varied linearly with elevation, but did not vary significantly ( $p > 0.05$ ) with mean site  $T_{air}$  or  $T_{soil}$ . Across all sites, the  $GS_{start}$  occurred later, and the GSLs were shorter with increasing elevation ( $40 \text{ d km}^{-1}$  and  $-50 \text{ d km}^{-1}$ , respectively,  $p < 0.01$  for both, figure 4). We acknowledge that the lowest and highest points being

south- and north-facing, respectively, may influence these regression slopes but we found no significant interactions among elevation, aspect, or species ( $p > 0.20$  for all). The  $GS_{end}$  was not significantly correlated with elevation across all sites ( $p = 0.11$ ), but there was an interaction between aspect and elevation ( $p = 0.01$ ). There was a significant linear trend of earlier  $GS_{end}$  with increasing elevation for south-facing sites ( $-10 \text{ d km}^{-1}$ ,  $p < 0.01$ ) but not for north- or north- and west-facing sites ( $p > 0.2$  for all comparisons).

Growing season length was the best predictor of relative BAI, explaining  $> 83\%$  of the variance among

sites, species, and aspects (figure 5). In general, north-facing sites with only *P. contorta* had lower relative BAI than sites with only *P. ponderosa*. However, the mixed species site at 2675 m suggests that growth differences may not be due to only north- versus south-facing topoclimates given that individuals of *P. contorta* had a higher relative BAI and longer GSL than the co-located *P. ponderosa*. When all sites were subsampled by species, GSL was not a significant predictor of relative BAI in *P. ponderosa*, but was for *P. contorta*, explaining 96% of the variance in relative BAI. We also tested mean site  $T_{\text{air}}$  and  $T_{\text{soil}}$ ;  $GS_{\text{start}}$ ;  $GS_{\text{end}}$ ; and the total number of days with transpiration–atmosphere coupling  $> 0.275$  as predictors of relative BAI, but none produced significant relationships ( $p > 0.05$  for all).

#### 4. Discussion

This study is, to our knowledge, the first to explore how complex terrain can influence variation in direct measurements of montane forest GSL. In this context, we found that GSL varied greatly over small spatial scales but was not clearly linked with differences in site  $T_{\text{air}}$  or  $T_{\text{soil}}$ , indicating that complex topography–environment interactions may ultimately drive phenology and subsequently tree growth (Adams *et al* 2014, Salzer *et al* 2014, Tran *et al* 2017, Bruening *et al* 2017). Within Gordon Gulch, sites separated by as little as 0.3 km of linear distance (i.e. north- versus south-facing sites) had GSLs that varied by up to 21 d. The large differences in GSL between aspects were primarily due to earlier  $GS_{\text{end}}$  at north- versus south-facing sites which is notable given that previous studies have shown  $GS_{\text{end}}$  to be determined by temperature or day length (Kramer *et al* 2000, Rossi *et al* 2007). Because plant-perceived photoperiod is responsive to direct, diffuse, and reflected light (Holmes and Smith 1977), it was not likely to vary among slope aspects and was thus doubtful to have influenced the timing of  $GS_{\text{end}}$  in this study. It is also improbable that species differences in sensitivity to day length drove this disparity given that *P. contorta* had a greater GSL than *P. ponderosa* at the mixed-species site, contrary to the aspect-driven trend. In addition, the  $T_{\text{air}}$  difference between the south-facing sites at 2478 and 2675 m was similar to the  $T_{\text{air}}$  difference between north- and south-facing aspects at similar elevations (i.e. about 0.9 °C). However, the difference in  $GS_{\text{end}}$  was disproportionately greater between the sites on opposing aspects (up to 12 d) versus those at the different elevations (2 d).

The absence of clear day length or  $T_{\text{air}}$  influences on  $GS_{\text{end}}$  suggests that other environmental factors may drive phenological transitions e.g. enhanced stem and canopy surface temperature due to radiative warming (Smith *et al* 1984). Previous studies have shown that conifer leaf and stem temperatures can

exceed  $T_{\text{air}}$  by up to 4 and 15 °C, respectively, on clear days with high insolation (Pomeroy *et al* 2009), but this effect would be substantially limited on north-facing slopes during fall and winter when solar angles are low (Wang *et al* 2002). While a comprehensive analysis of the mechanisms that drive dormancy onset was beyond the scope of this study, it is probable that limited amplification of stem and canopy temperature on north-facing sites due to lower insolation may have inhibited thermal recovery (i.e. leaf and stem thaw) following strong freeze events. This lowered thermal recovery could have resulted in the earlier dormancy onset we observed at the north- versus south-facing sites. Future studies would benefit from co-measuring air, stem, and canopy temperatures, and radiation and moisture regimes on different aspects in conjunction with transpiration–atmosphere coupling to clarify the impact of different components of the whole-plant energy balance on phenological shifts and plant growth.

Our analysis confirms that radial-stem growth was correlated with GSL, but not with  $GS_{\text{start}}$  or  $GS_{\text{end}}$ , or with  $T_{\text{air}}$  or  $T_{\text{soil}}$ . It was particularly surprising that relative BAI was not linked with  $GS_{\text{start}}$  or  $T_{\text{air}}$  variation. Earlier studies identified the spring onset-timing of radial cell growth, often determined by  $T_{\text{air}}$ , as a key determinant of annual radial growth (Lupi *et al* 2010, Oberhuber *et al* 2014, Rossi *et al* 2013, Royce and Barbour 2001) and that this period can shift overtime in relation to mean night time temperature (Sullivan *et al* 2015). Other studies have identified a photoperiodic control on radial growth rates that lead to peak growth in early July and ending in August (Cuny *et al* 2012, Oberhuber *et al* 2014, Rossi *et al* 2006, Seo *et al* 2011). Hence, an earlier  $GS_{\text{start}}$  would expand the period of growth unilaterally. In contrast, Rossi *et al* (2006) identified the onset of summer drought as responsible for declines in radial growth and Adams *et al* (2014) found a significant relationship between interannual precipitation variability and ring growth in Gordon Gulch, both suggesting that moisture availability may control radial growth rates. It is more likely that the GSL influence on growth varies with topographic gradients in temperature in our study domain. For example, Villalba *et al* (1994) found moisture- versus energy-limitations on growth to vary with slope aspect, Trujillo *et al* (2012) found moisture limitations on photosynthetic capacity to be elevation dependent, and Maxwell and Condon (2016) identify ground water depth as a key determinant of transpiration (and thus photosynthesis).

In this study, GSL was a significant predictor of relative BAI across all sites, but it was more predictive for north and west-facing sites (*P. contorta*) than at south-facing sites with *P. ponderosa*. The significant relationship between GSL and relative BAI at north-facing sites suggests an energy limitation to radial tree growth whereas the lack of relationship at south-facing sites implies that any beneficial effect of increasing

GSL may be constrained by other resource limitations (e.g. water, nutrients), such as that reported in previous dendrochronological studies (e.g. Tran *et al* 2017). Given our findings and variation in results from past studies, it would be beneficial to investigate radial growth rates relative to total carbon uptake at finer temporal scales in conjunction with measurements of transpiration–atmosphere coupling to better determine the effects of growing season metrics on forest growth.

The mid-winter periods of physiological activity that we report confirms previous studies that have identified the ability of evergreen conifer forests to rapidly upregulate physiological activity in response to warm synoptic climate patterns (Adams *et al* 2002, Sevanto *et al* 2006, Verhoeven *et al* 1999). These periods of mid-winter photosynthesis have also been shown to contribute significantly to annual sums of carbon uptake in Mediterranean montane forests (Kelly and Goulden 2016). In this study however, adding mid-winter periods of physiological activity to the GSL did not improve the prediction of radial tree growth, suggesting that winter-time carbon uptake is not partitioned to stem radial growth in montane ecosystems. Overall biomass accumulation is not well correlated with ecosystem productivity (Litton *et al* 2007) and winter photosynthate production is often stored for use in spring (Schaberg 2000), potentially explaining the disparity in results between this study and Kelly and Goulden (2016). Nevertheless, we urge future studies to consider mid-winter physiological activity as it has the potential to influence annual sums of carbon, water, and energy exchange.

The 791 m elevation difference between the lowest and highest south-facing sites resulted in a mean annual  $T_{\text{air}}$  difference of 4.4 °C, which is within the range of forecasted increase in  $T_{\text{air}}$  in the Rocky Mountains by the year 2100 (Baldwin *et al* 2003). Comparisons between these two sites may provide a proxy for predicting forest responses to future climates. A temperature increase of 4.4 °C at our highest south-facing site could extend the GSL by 50 d or more and potentially shift elevational growth dependencies on moisture availability (Trujillo *et al* 2012). While our results indicate a positive relationship between GSL and radial growth, as climate warming is amplified in mountainous regions and the hydrologic cycle intensifies (Huntington 2006, Rangwala and Miller 2012, Trenberth 1999), the potential strain of a longer growing season on plant available water may be augmented by shifting precipitation patterns, potentially increasing forest disturbance, mortality, and fire severity and influencing the hydrologic cycle (Allen *et al* 2010, McDowell *et al* 2008, Westerling 2016, Penn *et al* 2016, Pribulick *et al* 2016).

The spatial variability in growing season metrics we report has implications for modeling watershed

hydrology and vegetation–atmosphere exchange. Hydrologic and land-surface models often use static dates for phenology or, in the case of dynamic phenology sub-models, apply singular  $GS_{\text{start}}$  and  $GS_{\text{end}}$  to the entire watershed or model-pixel (Oleson *et al* 2010, Tague and Band 2004, Wigmosta *et al* 1994). Given that we show a 21 d variability in GSL within a relatively small watershed, future efforts need to concentrate on improving spatial resolution of topography-vegetation interactions in complex terrain (Bierkens *et al* 2015). We also show that up to 29% of the days outside of the growing season have measurable responses of transpiration to atmospheric demand which will likely be neglected in standard hydrologic models. Moreover, accurate characterization of  $GS_{\text{start}}$  is essential in systems where the majority of annual water inputs, become available in spring. A recent study (Winchell *et al* 2016) found that in subalpine forests, seasonal snowpack > 1 m can completely melt in as little as 17 d and up to 30% of total annual ecosystem carbon uptake can occur during this period. Due to the spatial and temporal interplay between  $GS_{\text{start}}$  and changes in moisture availability, any error in the characterization of  $GS_{\text{start}}$  during this brief period in the annual water cycle may lead to substantial errors in the timing of the biological component of evapotranspiration.

## 5. Conclusion

Using a novel approach to analyzing sapflow data, we found that relative elevation differences among sites and slope aspect have greater influence on montane forest phenology and tree growth than site specific environmental variables. Growing season length was linearly correlated with site elevation, resulting in GSL decreasing by 50 d per km of elevation gain. This difference in GSL was primarily due to higher-elevation and north-facing sites having earlier  $GS_{\text{end}}$ . There was also a large difference in GSL between north- and south-facing sites (up to 21 d) at similar elevation and the number of days outside of the growing season with physiological activity increased from 18% at the coldest and highest elevation site to 29% at the lowest and warmest site, with implications for calculating annual sums of water, carbon, and energy fluxes. The influence of spatial variability in growing season metrics may be especially important in estimates of carbon flux given the strong relationship between GSL and radial tree growth. While the true driver of growth differences among sites is more likely to be a suite of environmental variables, in this study domain a generalized topographic representation of elevation and slope aspect provided the greatest predictive power of GSL and tree growth. These findings underscore the need for high spatial resolution representations of ecosystem processes in complex mountainous terrain.

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