Environmental Research Letters

CrossMark

LETTER

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

D M Barnard[1], H R Barnard[1,2] and N P Molotch[1,2,3]

[1] Institute of Arctic and Alpine Research, 4001 Discovery Drive, University of Colorado, Boulder, CO 80309, United States of America
[2] Department of Geography, University of Colorado, Guggenheim 210, UCB 260, Boulder, CO 80309, United States of America
[3] Jet Propulsion Laboratory, California Institute of Technology, 4800 Oak Grove Dr., Pasadena, CA 91190, United States of America

E-mail: david.m.barnard@colorado.edu

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 topoclimates 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 topoclimates 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_{air}) and mean annual soil temperature (Mean T_{soil}). Error ranges represent one standard deviation.

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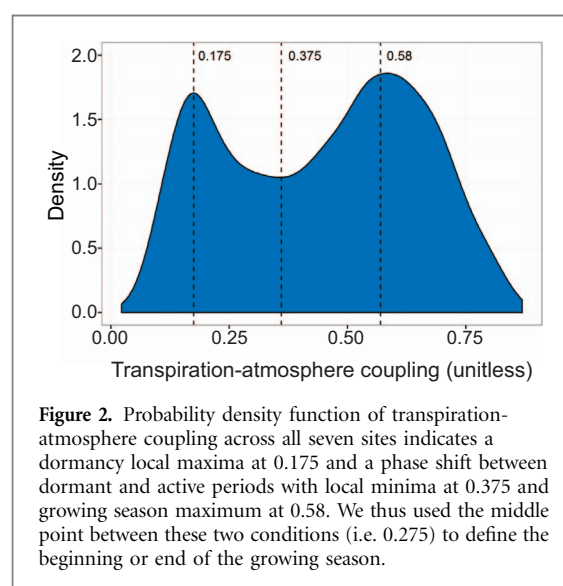
2. Methods

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_{air}) and relative humidity (RH) sensors (Vaisala HMP45AC, Vantaa, Finland) at 2 m above the ground, and soil temperature (T_{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
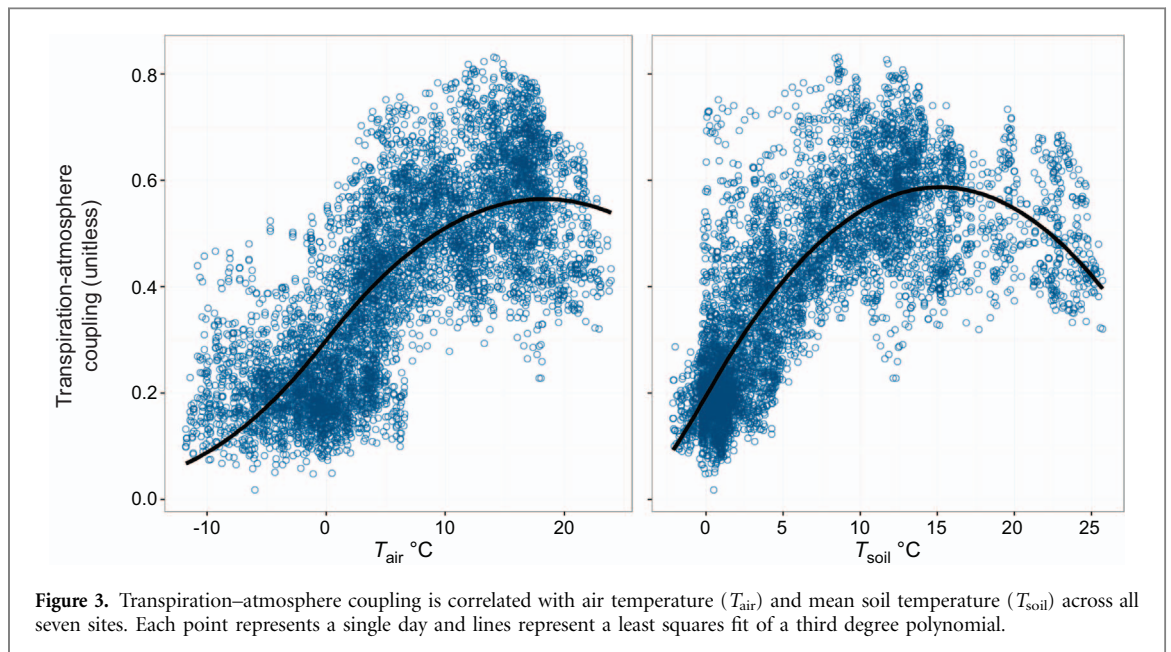
Figure 1. Transpiration-to-atmosphere coupling coefficient, measured over three years, follows distinct seasonal patterns of increased coupling through spring, a peak in summer and then declining to a winter minimum. Line color indicates site elevation. Line type represents site slope aspect. The dashed 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_{air} and RH sensors at mid-canopy height (107 L, Campbell Scientific, Logan, UT). Four of the Gordon Gulch sites were instrumented with T_{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_{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_{air}) and mean soil temperature (T_{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_{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_{end} in fall. The GSL was then calculated as GS_{end}–GS_{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

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

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.
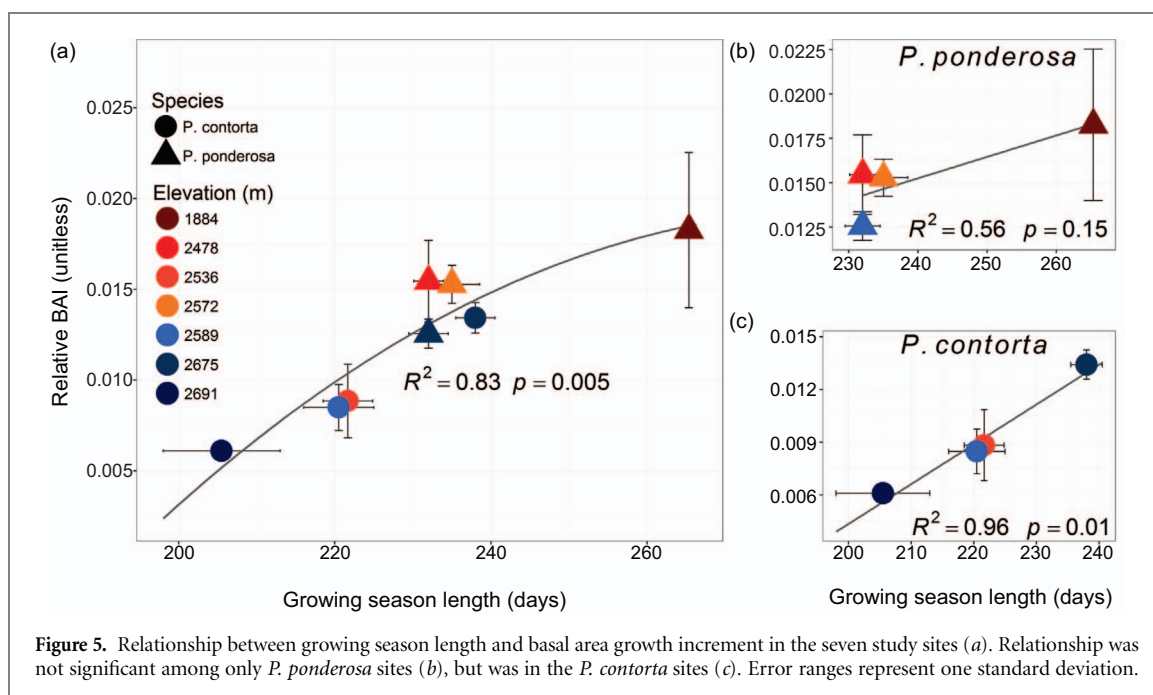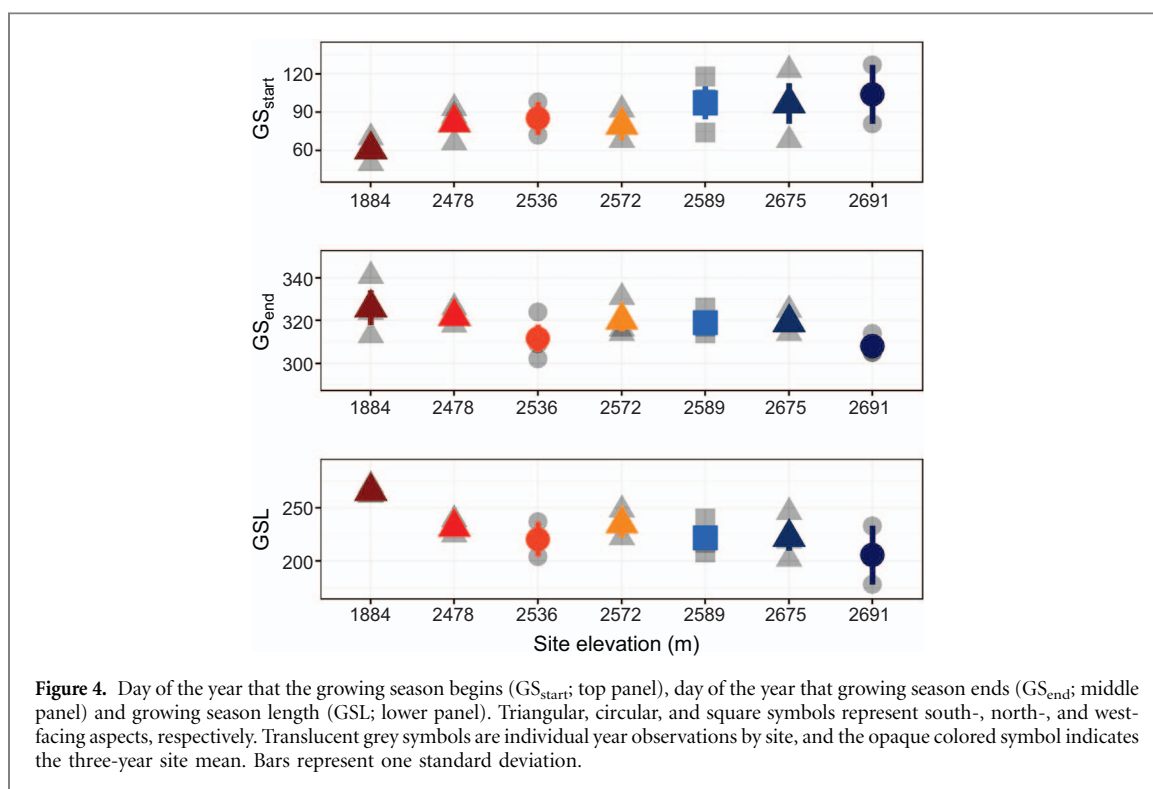
3. Results

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_{soil} (table 1). Annual T_{air} at Betasso was on average 4.4 °C warmer than the mean of T_{air} at all of the Gordon Gulch sites ($p < 0.01$). Mean annual T_{air} among sites at Gordon Gulch did not differ significantly by elevation or aspect ($p = 0.51$ and $p = 0.13$, respectively). Annual T_{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_{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_{soil} ($p < 0.01$, 3rd degree polynomial adjusted $R^2 = 0.65$) and T_{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_{start} occurred an average of 4–6 d later, and GS_{end} 12–14 d earlier than south-facing sites at similar elevations. The west-facing site at 2589 m had an average GS_{start} three days later and a GS_{end} one day earlier than the south-facing site at 2572 m. The variation in GS_{start} and GS_{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

Figure 4. Day of the year that the growing season begins (GS_{start}; top panel), day of the year that growing season ends (GS_{end}; middle panel) and growing season length (GSL; lower panel). Triangular, circular, and square symbols represent south-, north-, and west-facing aspects, respectively. Translucent grey symbols are individual year observations by site, and the opaque colored symbol indicates the three-year site mean. Bars represent one standard deviation.

Figure 5. Relationship between growing season length and basal area growth increment in the seven study sites (*a*). Relationship was not significant among only *P. ponderosa* sites (*b*), but was in the *P. contorta* sites (*c*). Error ranges represent one standard deviation.

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 d km^{-1} and −50 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 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_{air} and T_{soil}; GS_{start}; GS_{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_{air} or T_{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_{end} at north- versus south-facing sites which is notable given that previous studies have shown GS_{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_{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_{air} difference between the south-facing sites at 2478 and 2675 m was similar to the T_{air} difference between north- and south-facing aspects at similar elevations (i.e. about 0.9 °C). However, the difference in GS_{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_{air} influences on GS_{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_{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_{start} or GS_{end}, or with T_{air} or T_{soil}. It was particularly surprising that relative BAI was not linked with GS_{start} or T_{air} variation. Earlier studies identified the spring onset-timing of radial cell growth, often determined by T_{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_{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_{air} difference of 4.4 °C, which is within the range of forecasted increase in T_{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_{start} and GS_{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_{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_{start} and changes in moisture availability, any error in the characterization of GS_{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_{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.

Acknowledgments

References

Adams H R, Barnard H R and Loomis A K 2014 Topography alters tree growth—climate relationships in a semi-arid forested catchment *Ecosphere* **5** 1–16

Adams W W, Demmig-Adams B, Rosenstiel T N, Brightwell A K and Ebbert V 2002 Photosynthesis and photoprotection in overwintering plants *Plant Biology* **4** 545–57

Allen C D, Macalady A K, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A, Breshears D D and Hogg E T 2010 A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests *Forest Ecol. Manage.* **259** 660–84

Baldwin C, Wagner F H and Lall U 2003 Rocky Mountain / Great Basin Regional Climate-Change Assessment Report for the US Global Change Research Program (Boulder, CO: Utah State University Press)

Barnard D M, Lachenbruch B, McCulloh K A, Kitin P and Meinzer F C 2013 Do ray cells provide a pathway for radial water movement in the stems of conifer trees? *Am. J. Bot.* **100** 322–31

Berryman E M, Barnard H R, Adams H R, Burns M A, Gallo E and Brooks P D 2015 Complex terrain alters temperature and moisture limitations of forest soil respiration across a semiarid to subalpine gradient *J. Geophys. Res. Biogeosci.* **120** 707–23

Bierkens M F, Bell V A, Burek P, Chaney N, Condon L E, David C H, de Roo A, Döll P, Drost N and Famiglietti J S 2015 Hyper-resolution global hydrological modelling: what is next? 'Everywhere and locally relevant' *Hydrologic Processes* **29** 310–20

Bigler C, Gričar J, Bugmann H and Čufar K 2004 Growth patterns as indicators of impending tree death in silver fir *Forest Ecol. Manage.* **199** 183–90

Bonan G B 2008 Forests and climate change: forcings, feedbacks, and the climate benefits of forests *Science* **320** 1444–9

Bruening J M, Tran T J, Bunn A G, Weiss S B and Salzer M W 2017 Fine-scale modeling of bristlecone pine treeline position in the Great Basin, USA *Environ. Res. Lett.* **12** 014008

Bunn A G, Hughes M K and Salzer M W 2011 Topographically modified tree-ring chronologies as a potential means to improve paleoclimate inference *Climatic Change* **105** 627–634

Burgess S S, Adams M A, Turner N C, Beverly C R, Ong C K, Khan A A and Bleby T M 2001 An improved heat pulse method to measure low and reverse rates of sap flow in woody plants *Tree Physiol.* **21** 589–98

Churkina G, Schimel D, Braswell B H and Xiao X 2005 Spatial analysis of growing season length control over net ecosystem exchange *Glob. Change Biol.* **11** 1777–87

Collatz G J, Ball J T, Grivet C and Berry J A 1991 Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: a model that includes a laminar boundary layer *Agr. Forest Meteorol.* **54** 107–36

Cuny H E, Rathgeber C B, Lebourgeois F, Fortin M and Fournier M 2012 Life strategies in intra-annual dynamics of wood formation: example of three conifer species in a temperate forest in north-east France *Tree Physiol.* **32** 612–25

Dale V H, Joyce L A, McNulty S, Neilson R P, Ayres M P, Flannigan M D, Hanson P J, Irland L C, Lugo A E and Peterson C J 2001 Climate change and forest disturbances: climate change can affect forests by altering the frequency, intensity, duration, and timing of fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, windstorms, ice storms, or landslides *BioScience* **51** 723–34

Daly C, Conklin D R and Unsworth M H 2010 Local atmospheric decoupling in complex topography alters climate change impacts *Int. J. Climatol.* **30** 1857–64

Dobrowski S Z 2011 A climatic basis for microrefugia: the influence of terrain on climate *Glob. Change Biol.* **17** 1022–35

Farquhar G D and Sharkey T D 1982 Stomatal conductance and photosynthesis *Annu. Rev. Plant Phys.* **33** 317–45

Hinckley E-L S, Ebel B A, Barnes R T, Anderson R S, Williams M W and Anderson S P 2014 Aspect control of water movement on hillslopes near the rain–snow transition of the Colorado Front Range *Hydrol. Process.* **28** 74–85

Holmes M G and Smith H 1977 The function of phytochrome in the natural environment—II. The influence of vegetation canopies on the spectral energy distribution of natural daylight *Photochem. Photobiol.* **25** 539–45

Huntington T G 2006 Evidence for intensification of the global water cycle: review and synthesis *J. Hydrol.* **319** 83–95

Jarvis A J and Davies W J 1998 The coupled response of stomatal conductance to photosynthesis and transpiration *J. Exp. Bot.* **49** 399–406

Jarvis P G and McNaughton K G 1986 Stomatal control of transpiration: scaling up from leaf to region *Adv. Ecol. Res.* **15** 49

Kelly A E and Goulden M L 2016 A montane Mediterranean climate supports year-round photosynthesis and high forest biomass *Tree Physiol.* **36** 459–68

Körner C 2012 *Alpine Treelines: Functional Ecology of the Global High Elevation Tree Limits* (Basel: Springer Science & Business Media)

Körner C and Paulsen J 2004 A world-wide study of high altitude treeline temperatures *J. Biogeogr.* **31** 713–732

Kramer K, Leinonen I and Loustau D 2000 The importance of phenology for the evaluation of impact of climate change on growth of boreal, temperate and Mediterranean forests ecosystems: an overview *Int. J. Biometeorol.* **44** 67–75

Litton C M, Raich J W and Ryan M G 2007 Carbon allocation in forest ecosystems *Glob. Change Biol.* **13** 2089–109

Lupi C, Morin H, Deslauriers A and Rossi S 2010 Xylem phenology and wood production: resolving the chicken-or-egg dilemma *Plant Cell Environ.* **33** 1721–30

Maxwell R M and Condon L E 2016 Connections between groundwater flow and transpiration partitioning *Science* **353** 377–80

McDowell N, Pockman W T, Allen C D, Breshears D D, Cobb N, Kolb T, Plaut J, Sperry J, West A and Williams D G 2008 Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytol.* **178** 719–39

Meinzer F C, McCulloh K A, Lachenbruch B, Woodruff D R and Johnson D M 2010 The blind men and the elephant: the impact of context and scale in evaluating conflicts between plant hydraulic safety and efficiency *Oecologia* **164** 287–96

Novick K A, Oishi A C and Miniat C F 2016 Cold air drainage flows subsidize montane valley ecosystem productivity *Glob. Change Biol.* **22** 4014–27

Oberhuber W, Gruber A, Kofler W and Swidrak I 2014 Radial stem growth in response to microclimate and soil moisture in a drought-prone mixed coniferous forest at an inner Alpine site *Eur. J. Forest Res.* **133** 467–79

Oleson K W, Lawrence D M, Gordon B, Flanner M G, Kluzek E, Peter J, Levis S, Swenson S C, Thornton E and Feddema J 2010 Technical description of version 4.0 of the Community Land Model (CLM)

Paulsen J and Körner C 2014 A climate-based model to predict potential treeline position around the globe *Alpine Botany* **124** 1–12

Penn C A, Bearup L A, Maxwell R M and Clow D W 2016 Numerical experiments to explain multiscale hydrological responses to mountain pine beetle tree mortality in a headwater watershed *Water Resour. Res.* **52** 3143–61

Peñuelas J and Filella I 2009 Phenology feedbacks on climate change *Science* **324** 887

Pomeroy J W, Marks D, Link T, Ellis C, Hardy J, Rowlands A and Granger R 2009 The impact of coniferous forest temperature on incoming longwave radiation to melting snow *Hydrol. Process.* **23** 2513–25

Pribulick C E, Foster L M, Bearup L A, Navarre-Sitchler A K, Williams K H, Carroll R W and Maxwell R M 2016 Contrasting the hydrologic response due to land cover and climate change in a mountain headwaters system *Ecohydrology* **9** 1431–8

Rangwala I and Miller J R 2012 Climate change in mountains: a review of elevation-dependent warming and its possible causes *Climatic Change* **114** 527–47

Rossi S, Anfodillo T, Čufar K, Cuny H E, Deslauriers A, Fonti P, Frank D, Gričar J, Gruber A and King G M 2013 A meta-analysis of cambium phenology and growth: linear and non-linear patterns in conifers of the Northern Hemisphere *Ann. Bot. (Lond.)* **112** 1911–20

Rossi S, Deslauriers A, Anfodillo T and Carraro V 2007 Evidence of threshold temperatures for xylogenesis in conifers at high altitudes *Oecologia* **152** 1–12

Rossi S, Deslauriers A, Anfodillo T, Morin H, Saracino A, Motta R and Borghetti M 2006 Conifers in cold environments synchronize maximum growth rate of tree-ring formation with day length *New Phytol.* **170** 301–10

Rotach M W, Andretta M, Calanca P, Weigel A P and Weiss A 2008 Boundary layer characteristics and turbulent exchange mechanisms in highly complex terrain *Acta Geophys.* **56** 194–219

Rotach M W, Wohlfahrt G, Hansel A, Reif M, Wagner J and Gohm A 2014 The world is not flat: implications for the global carbon balance *Bull. Am. Meteorol. Soc.* **95** 1021–8

Royce E B and Barbour M G 2001 Mediterranean climate effects. II. Conifer growth phenology across a Sierra Nevada ecotone *Am. J. Bot.* **88** 919–32

Salzer M W, Larson E R, Bunn A G and Hughes M K 2014 Changing climate response in near-treeline bristlecone pine with elevation and aspect *Environ. Res. Lett.* **9** 114007

Schaberg P G 2000 Winter photosynthesis in red spruce (*Picea rubens* Sarg.): limitations, potential benefits, and risks *Arct. Antarct. Alp. Res.* **32** 375–80

Schimel D, Kittel T G, Running S, Monson R, Turnipseed A and Anderson D 2002 Carbon sequestration studied in western US mountains *Eos. T. Am. Geophys. Un.* **83** 445–9

Seo J-W, Eckstein D, Jalkanen R and Schmitt U 2011 Climatic control of intra-and inter-annual wood-formation dynamics of Scots pine in northern Finland *Environ. Exp. Bot.* **72** 422–31

Sevanto S, Suni T, Pumpanen J, Grönholm T, Kolari P, Nikinmaa E, Hari P and Vesala T 2006 Wintertime photosynthesis and water uptake in a boreal forest *Tree Physiol.* **26** 749–57

Smith W K, Young D R, Carter G A, Hadley J L and McNaughton G M 1984 Autumn stomatal closure in six conifer species of the Central Rocky Mountains *Oecologia* **63** 237–42

Sullivan P F, Mulvey R L, Brownlee A H, Barrett T M and Pattison R R 2015 Warm summer nights and the growth decline of shore pine in Southeast Alaska *Environ. Res. Lett.* **10** 124007

Tague C L and Band L E 2004 RHESSys: regional hydro-ecologic simulation system-an object-oriented approach to spatially distributed modeling of carbon, water, and nutrient cycling *Earth Interact.* **8** 1–42

Tran T J, Bruening J M, Bunn A G, Salzer M W and Weiss S B 2017 Cluster analysis and topoclimate modeling to examine bristlecone pine tree-ring growth signals in the Great Basin, USA *Environ. Res. Lett.* **12** 014007

Trenberth K E 1999 Conceptual framework for changes of extremes of the hydrological cycle with climate change *Clim. Change* **42** 327–39

Trujillo E, Molotch N P, Goulden M L, Kelly A E and Bales R C 2012 Elevation-dependent influence of snow accumulation on forest greening *Nat. Geosci.* **5** 705–9

Verhoeven A S, Adams W W III and Demmig-Adams B 1999 The xanthophyll cycle and acclimation of *Pinus ponderosa* and *Malva neglecta* to winter stress *Oecologia* **118** 277–87

Villalba R, Veblen T T and Ogden J 1994 Climatic influences on the growth of subalpine trees in the Colorado Front Range *Ecology* **75** 1450–62

Wang S, Chen W and Cihlar J 2002 New calculation methods of diurnal distribution of solar radiation and its interception by canopy over complex terrain *Ecol. Model.* **155** 191–204

Westerling A L 2016 Increasing western US forest wildfire activity: sensitivity to changes in the timing of spring *Phil. Trans. R. Soc. B.* **371** 20150178

Wigmosta M S, Vail L W and Lettenmaier D P 1994 A distributed hydrology-vegetation model for complex terrain *Water Resour. Res.* **30** 1665–79

Winchell T S, Barnard D M, Monson R K, Burns S P and Molotch N P 2016 Earlier snowmelt reduces atmospheric carbon uptake in midlatitude subalpine forests *Geophys. Res. Lett.* **43** 8160–8