A new approach towards climate monitoring in Rocky Mountain alpine plant communities: A case study using herb-chronology and *Penstemon whippleanus*

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**Abstract**
The alpine ecosystem of the Rocky Mountains is experiencing significant increases in growing season length, summer maximum temperatures, and shifting patterns in precipitation. Alpine herbs are specifically sensitive to these changes. Biomass accumulation and reproductive effort are often negatively affected by elevated temperatures and earlier snowmelt. Here, we assess the use of herb-chronology, the study of annual growth rings in the woody underground organs, to retroactively monitor effects of monthly to seasonal climate on growth of the alpine forb species *Penstemon whippleanus*. We explored methods for building the strongest growth chronology possible by comparing the mean interseries correlations (MICs) of the whole population to that of groupings by cohorts, spatial locations, and random groupings using a permutation procedure. MIC for the whole population was low (0.034). Our permutation grouping performed best, producing a maximum MIC of 0.263. Using the permutation-derived chronology (2008–2015), we found significant decrease in growth with increased maximum temperatures in July, decreased May rainfall, increased drought between April and August, and lower minimum temperatures in September. Herb-chronology proved useful for understanding growth dynamics with climate in this alpine system; expanding this practice to similar systems could elucidate unknown effects of shifting climate on annual growth of alpine herbaceous species.

**Introduction**
There is wide consensus that anticipated global change may be the strongest in the polar regions and high-altitude systems (Solomon et al. 2007). For the Rocky Mountains of the United States in particular, over the last four decades, the number of annual frost days has decreased while minimum temperatures in the early spring continue to rise (Pederson et al. 2011a). Monthly maximum temperatures throughout the year are also increasing (Pederson et al. 2011a). Warmer overall spring temperatures, coupled with decreases in winter snowpack and substantial declines in peak snow water equivalent, are contributing to earlier season snow melts with reduced amounts of runoff (Rajagopalan et al. 2009; Pederson et al. 2011b). Rainfall is departing from previous averages with higher mean amounts and increased variance in the spring and summer (Pederson et al. 2011a).

If these changes in annual climate continue, large changes to the growth and composition of the Rocky Mountain alpine vegetation may ensue. Over geologic time, pollen and macrofossil records reveal the cyclic nature of alpine communities; herbaceous prominence in alpine landscapes thrives during cooler geologic time periods, whereas trees and shrubs dominate in relatively warmer periods (Short 1985; Wick and Tinner 1997). Conservation and better anticipating the effects of climate change on the growth of current alpine communities, which are mostly dominated by perennial herbaceous forb species and a small presence of shrubs and subshrubs (Hadley 1987), is becoming a top research priority (Xu et al. 2009; Thomas 2011; Rayback, Lini, and Berg 2012). Preservation of current alpine and subalpine vegetation instills numerous ecosystem benefits, as resident forb communities are important belowground carbon sinks (Kato et al. 2006; Sun et al. 2011), filter streamflow draining from catchments (Mueller, Weingartner, and Alewell 2013), and host a suite of endemic plant and animal species (Bliss 1962; Tribsch and Schönswetter 2003).
Observed changes in regional temperature have had mixed effects on alpine forbs. Often, rising temperatures affect growth by inducing water stress and thus decreases in photosynthesis (Roden and Ball 1996; Pearson and Dawson 2003; Niu et al. 2008), though these effects are species specific with even the capacity of some to acclimate to changes (Niu et al. 2008). For forbs negatively affected by rising temperatures and the induced water stress, aboveground biomass often decreases over time in experimental warming plots (Lambrech et al. 2007). Alternatively, rising temperatures could play an indirect role in lengthening the growing season by decreasing the occurrence of late spring frosts (Pederson et al. 2011a), enabling earlier growth phenology (Lambrech et al. 2007) and possibly enhanced growth. To a lesser degree, increasing minimum temperatures in early fall (Pederson et al. 2011a) could also enhance growth by prolonging the time until first frost and plant senescence (Zhang and Welker 1996; Berdanier and Klein 2011).

Precipitation is another important factor in alpine forb annual growth. Primarily, runoff from winter snowpack recharges soil moisture in the spring when forbs are emerging. When a decreased amount of winter snowpack is coupled with an advanced snowmelt, the resulting lower springtime available soil moisture negatively effects aboveground forb biomass (Harte and Shaw 1995; Inouye et al. 2000; Lambrech et al. 2007). The exact timing of snowmelt is important since snow provides insulation from freezing wind exposure in the late winter and early spring, which could kill apical buds and thus interrupt the annual growth cycle (Galen and Stanton 1995; Inouye et al. 2000; Wipf and Rixen 2010; Klimešová, Doležal, and Šťastná 2013). Due to this frost damage, early snowmelt has been directly connected to decreased growth (Harte and Shaw 1995; Inouye et al. 2000; Wipf and Rixen 2010). Plant reproductive effort may also be reduced due to frost damage, which over time could decrease populations (Molau 1997; Inouye 2008; Wipf and Rixen 2010). For these reasons, many forb populations thrive in habitats with a long snow cover duration in the Rocky Mountain Alpine.

Given the anticipated changes in climate for the Rocky Mountain Alpine, and the documented effects these factors have on forb growth (Lambrecht et al. 2007; Wipf and Rixen 2010), records of growth response to recent past environments could be important for forecasting future growth, population viability, and even possible community transition away from forb dominance. Annual growth records of alpine plants are largely represented by dendrochronology research on shrub species (Bär et al. 2008; Hallinger, Manthey, and Wilmking 2010; Franklin 2013), with a paucity of similar studies on the more dominant alpine herbaceous component. Though currently not common knowledge, the annual growth of herbaceous plants too can be retrospectively observed. Many herbs contain annual growth rings in their perennial underground organs (Dietz and Ullmann 1998; Dietz and Schweingruber 2002). Like dendrochronology, herb-chronology finds significant variation between climate and annual growth increments of herbaceous species in montane (Dietz, von Arx, and Dietz 2004; von Arx and Dietz 2006; Klimešová, Doležal, and Šťastná 2013) and other landscapes (Liu and Zhang 2010; Dee and Palmer 2017; Hiebert-Giesbrecht et al. 2017). Physiologically, belowground annual growth rings correlate with annual climatic factors because the xylem in part functions in the winter storage of photoassimilate (Wargo 1979; Lacointe 2000; Dee et al. 2018).

In this study, we verify the application of herb-chronology by using this technique for uncovering the monthly climatic factors dictating growth of a Rocky Mountain perennial alpine herb Penstemon whippleanus. We predict years with warmer spring and summer months, earlier snowmelt, less winter snowpack, and less summer precipitation will lead to years with the most reduced annual growth ring areas. Additionally, years with lower minimum temperatures in the late summer and early fall could lead to increased annual growth ring areas. Since herb-chronology is a nascent field, our study also serves to establish a method to better construct herbaceous growth chronologies. Two major problems exist in the nature of obtaining a reliable master chronology from herbaceous species. First, study-wide synchronous growth patterns between individuals are often low compared to trees (Dee and Palmer 2017), possibly due to a high sensitivity to microsite environment in addition to climate (Dietz and Ullmann 1998; Dee and Palmer 2016, 2017). Second, traditional diagnostics used to cross-date and build a master chronology (Cook and Kairiukstis 2013) are mostly lost due to the short time series often found in herbs. In efforts to overcome these problems and progress toward investigating connections between climate and herbaceous growth mentioned in the preceding, our study explored a new dendrochronology-derived method for obtaining robust chronologies from herbaceous species.

**Methods**

**Site description and field methods**

Pennsylvania Mountain (PMR; 39.26463° N, −106.14203° W), located in Park County, Colorado, is 3100 to 4000 m in elevation and represents a transition zone between alpine
tundra with alpine perennial herbs, shrubs, and grasses giving way to forests dominated by Rocky Mountain bristlecone pine (*Pinus aristata*) and subalpine fir (*Abies lasiocarpa*) at the lower elevations. Typical annual climate consists of winter durations of snowpack, usually subsiding by middle May, and growing season temperatures ranging between 1°C and 15°C, until the first freeze, which usually takes place in September (http://www.usa.com/park-county-co-weather.htm). Rainfall is usually most abundant during the late spring with an average of about 650 mm growing-season accumulation (http://www.usa.com/park-county-co-weather.htm).

In the early fall of 2016 we excavated 40 *Penstemon whippleanus* individuals from Pennsylvania Mountain with global positioning system (GPS) locations and elevation positions recorded for each. *Penstemon whippleanus* (Figure 1) is a perennial herb of the Plantaginaceae family with a local distribution spanning from the alpine down through subalpine and lower elevations. *Penstemon whippleanus* contains a primary lateral root that gives way to secondary and finer roots. Each spring a new basal rosette emerges from underground buds. Xylem anatomy is semi-ring porous. Several other herbs in the *Penstemon* genus contain semi-ring porous anatomy with distinguishable growth rings (https://www.wsl.ch/dendropro/xylemdb/index.php?TEXTID=2379andMOD=1).

**Lab methods**

Following excavation, roots were separated from above-ground mass, cleaned of debris, and stored in Mason jars containing 75% alcohol. Drawings of roots were used to track locations of sections and their relative sizes. In the lab, we dissected roots and determined sectioning locations based on location nearest the stem and least disturbed tissue. Root sectioning was performed using a mini sledge microtome. Sections of approximately 15 µm thickness were then bleached for 5 minutes and washed with water to enhance the subsequent staining. Two drops of a 1:1 mix of Astra blue and Safranin (Schweingruber, Börner, and Schulze 2011), which turns parenchyma cells blue and lignified cells red to help enhance ring borders, were used for staining. After 3 minutes, excess stain was washed away with 95% alcohol. Sections were then mounted onto glass slides, allowing images of each stained section to be taken using a compound scope at 40× (Figure 1). Images were scaled by finding the pixel distance of a 1-mm scale of imaged ruler under the same 40× magnification. Image analysis proceeded with ROXAS (von Arx and Carrer 2014) software to digitize ring boundaries and determine annual ring area. In cases where the complete root cross section was not present, we estimated ring area by taking the area measured, its arc length, and the diameter of the section, and then calculating total area of the ring assuming a perfect circle shape.

**Constructing a master growth chronology for *P. whippleanus***

Individual ring area series were standardized and plotted out both through time and by age via spaghetti plots constructed using the plotting functions under the gplots library in R version 3.4.3 (Warnes et al. 2009; R Core Team 2017). Standardization of individual series consisted of subtracting the mean ring area from each area in a series and dividing by the standard deviation of the series. Mean interseries correlation (MIC) and mean sensitivity for the entire population were then calculated (Cook and Kairiukstis 2013). Given our efforts in establishing a master ring-area

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**Figure 1.** Excavated *P. whippleanus* in its common habitat at PMR, along with an example of the semi-ring porous root anatomy observed after staining a root section, visualized at 40× and 100× magnification, respectively. Features delineating the start of a new growth ring are shown: specifically, an earlywood parenchyma band stained blue followed by large earlywood vessels.
chronology with the strongest possible ability correlation with local environmental factors, MIC would be of primary importance because of its ability to assess the consistency of annual growth amongst individuals in a group. In past studies with herb-chronology, MICs for populations improved to as high as 0.45 when subgrouping on a predetermined biological context (Dee and Palmer 2017). In this study we assumed a similar phenomenon would occur; stronger chronologies based on groupings by a predefined biological context would emerge with higher MICs compared to those for the entire population, thus maximizing a common signal and our ability to associate annual herbaceous growth with a source (e.g., climate).

As with prior studies, building the strongest possible master chronology first began by evaluating MICs for the entire population. After MICs were assessed, we proceeded with forming a priori groupings by cohort and by spatial location along an elevational gradient. Three groups were formed from the elevational gradient, each separated by approximately 250 m between 3600 and 3750 m. For each cohort and elevational group, we ran a permutation test with 10,000 iterations to assess how the MIC of the grouping compares to randomly placing individuals into a subgrouping of the same size. The test statistic was the MIC of the actual grouping; therefore, the associated p value represented the percentage of the 10,000 random iterations with a higher MIC compared to the grouping. We concluded a significant MIC at p \( \leq 0.05 \). In addition, in case grouping by cohort or spatial location failed to produce MICs that were improved over the population MIC, we proceeded with running a permutation scheme with 10,000 iterations of randomly shuffling individuals into groupings of 75% of the total population (n = 20). Though 75% may appear arbitrary, we choose this percentage since 25% of the total amount of series in a forb chronology typically have low pairwise correlations with other series, and most of the time this likely has to do with microsite conditions not accounted for within the study (Dee and Palmer 2016, 2017). Only the permutation group with the highest MIC was considered in further growth and climate analyses.

**Climatic correlations with chosen chronology(s)**

For the subsequent climatic analysis, chronologies from cohort and elevational groups were considered if their MICs were higher than that of the entire population. If neither cohorts nor elevation groupings produced higher MICs, and also failed permutation tests, then the 75% permutation group was used, given it had a higher MIC relative to the entire population. Overall, if none of these groupings produced an MIC of \( \geq 0.20 \), a minimum metric for prior successful studies (Dee and Palmer 2016, 2017), climatic analysis did not proceed.

For the years 2008–2015 (with 2008 representing the first year a sample depth of at least four individuals was achieved) we used daily PRISM data (Daly et al. 2008) downloaded from http://www.prism.oregonstate.edu. Interpolated PRISM data for the site included daily minimum and maximum temperature, daily precipitation, and daily maximum vapor pressure deficit (VpdMax hereafter). These climatic variables were first averaged by calendar month and then correlated with each other to remove collinear variables (r \( \geq 0.70 \)) prior to correlative analysis with the master chronology. In addition, these monthly averages were also averaged into 3- to 4-month seasonal periods (January through March, April through August, and September through December).

Other climatic variables considered included last date of snowpack for each year along with drought severity for each of the three to four seasonal month periods. Landsat 7 and 8 satellite images (https://glovis.usgs.gov/imagery) were used to estimate the last day of snow cover at the site each year. Landsat imagery is available on a roughly 2-week time step. We cycled through available images between the months of April and July each year to assign an approximate date of last snow cover for the whole site. We excluded 2012 and 2014 from the analysis because all image dates between April and July were obscured by clouds. Datasets of Palmer Drought Severity Index (PDSI hereafter) for Colorado Climate Division 4 were compiled at a monthly resolution for 2008–2015 (Avail: https://www.ncdc.noaa.gov/temp-and-precip/drought/historiPALMERS/).

For any significant correlations among ring area and climate variables, we carried out permutation tests to reduce the possibility of spurious relationships. These permutation tests involved keeping the master ring area chronology constant while randomly shuffling yearly values of the climatic variable being considered and then assessing correlations value for each of 10,000 iterations. The test statistic was the actual correlation between the climatic variable and ring area, with the p value representing the percentage of the 10,000 random iterations with a higher correlation. We concluded that there is a significant relationship if p \( \leq 0.05 \) for the permutation test. All these analyses were done in R version 3.4.3 (R Core Team, 2017).
Results

Building chronology(s) for *P. whippleanus*

Twenty-seven individual series of annual ring area were constructed with ROXAS image analysis software. Ring anatomy was semi-ring porous with the latewood to earlywood transition easily identified except in cases when rings were compact on outer portions of the roots (Figure 1). On average, individual series had a mean length of 6.03 (SD = 2.19) years. Year-to-year variation in ring area amongst individuals was high, translating to a very low MIC of 0.034 (Figure 2). Average mean sensitivity across the population was 0.25. From 2008 to 2015 (sample depth of at least four individuals), ring area increased between 2008 and 2010, declined in 2011 and 2012, and strongly increased from 2013 onward (Figure 2 and see Figure 7, shown later). When plotted by age, rather than calendar year, we found no obvious age-related trends in ring area (results not shown).

Our first approach to identifying the strongest correlated chronology (compared to the low MIC of 0.03 for the whole study) was grouping individuals by cohort. Six cohorts, 10 to 3 years of age, were established based on pith years of each individual (Figure 3, only four out of six total cohorts shown). Overall,
grouping by cohort produced unsatisfactory results. MICs among cohort groups were inconsistent and, on average, comparable to the low MIC for the entire population. Only the oldest cohort (10 years old) and our fifth oldest cohort (4 years old) had higher MICs than the entire population (Figure 3). The oldest cohort had the highest MIC of 0.849. Ring area of individuals in this cohort declined sharply between 2006 and 2008 and maintained low year-to-year variation thereafter (Figure 3). The fifth cohort showed a consistent increase in ring area between 2013 and 2014, followed by a large decline in 2015 for four out of the five individuals (Figure 3).

Grouping by elevation resulted in three spatially clumped groups, each containing nine or 10 individuals. Overall, this grouping method was the least successful in terms of improving MICs above that of the entire population. MICs for all groups were close to zero, with no significant permutation results suggesting any were stronger than the whole population (Figure 4). By comparison, grouping by cohort produced higher MICs, though neither methodology produced adequate results (consistent MICs ≥ 0.20) for climatic analysis.

With unsatisfactory results based on grouping by cohort or elevation, we proceeded with randomly permuting different groups with 20 individuals (75% of our total sample size). After 10,000 iterations, our highest permutation group MIC was 0.26 (Figure 5), considerably higher than for the entire population (0.03). We compared this MIC to the average MIC of 50 highest 75% permutation groups resulting from 50 separate runs of this process using random numbers replaced into the time series for all 27 individuals. We found the average MIC from these 50 runs was 0.139, considerably less than the 0.26 we found using actual data. This confirms that the MIC from this procedure using actual data was much larger than an MIC generated from random data. Visually, the year-to-year variation among individuals in the permutation group with an MIC of 0.26 appeared to be diminished compared to the entire population chronology, but with both showing the same pronounced 2013–2015 growth increase. Moving forward, the master chronology from this 20-member randomly permuted group was used for subsequent climatic analysis.

**Climatic analysis**

Correlations among growth and monthly climate variables are summarized in a heat map (Figure 6). The highest correlation represented a positive relationship between ring area and minimum September temperature ($r = 0.83$, Figure 6). Following this, previous and current July VpdMax were the next strongest correlations with a negative association ($r = -0.82$, $r = -0.81$, respectively, Figure 6). Precipitation in November and May had

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**Figure 4.** Standardized ring area spaghetti plots grouped by spatial location along with the mean interseries correlation for each. Permutation results were not significant for any grouping.
strong positive associations with ring area as well ($r = 0.80$ and $r = 0.74$, respectively, Figure 6). Daily high temperature in the previous July, August, and current July also had strong inverse relations to ring area ($r = -0.74$, $r = -0.67$, $r = -0.74$, respectively, Figure 6). Figure 7 provides a visual reference, with the
time series of the master chronology plotted alongside each of these mostly highly correlated climatic variables. Overall, permutation tests showed significance with these and another 12 climatic variables (Table 1).

**Discussion**

**Building a site herb-chronology**

Similar to previous herb-chronology work (von Arx and Dietz 2006; Liu and Zhang 2010; Dee and Palmer 2017), the entire chronology time span for *P. whippleanus* was close to one decade. Series of this length nullify using more traditional dendrochronology techniques in efforts for cross-dating and building a site chronology (Grissino-Mayer 2001). In addition, high variability in annual growth, leading to low MICs, may be experienced across herbaceous individuals due to microsite variability (Dietz and Ullmann 1998; Dee and Palmer 2016, 2017). To overcome these issues, we adopted the chronology building practice of attempting to group by cohort, spatial location, and randomly permuting, all the while inspecting for improved chronology MICs over that of the whole population.

Though not successful in our study, grouping by cohort has biological justification. One can hypothesize that individuals germinating in a drought period may experience relatively more sensitive annual growth rates pertaining to water availability compared to cohorts from years when water resources are plentiful (Chapin, Schulze, and Mooney 1990; Walter and Reich 1997; Schwinning and Sala 2004). Thus, a low MIC for a whole site chronology may be the result of a diffuse distribution of cohorts and/or periodic events, such as drought or other influential environmental changes. MICs of our six cohorts were mostly not improved over that of our entire population, suggesting that grouping by cohort was not beneficial. Only two of our six cohorts produced high pairwise correlation values, with no biological reasoning to help explain and distinguish this result from a random chance. The germination years of these two respective cohorts (2006 and 2012) present no evidence for consistencies in climate conditions that may have induced higher consistency in growth of only these two cohorts. Nevertheless, we recommend attempting grouping by cohort in future studies since timing of germination could have an overarching effect on growth. This “cohort effect” may overall depend on annual fecundity rates (Herrera 1991; Saavedra et al. 2003) and periodicity of the leading limiting growth factors.

Grouping by spatial location also proved unsuccessful in improving chronology MICs. No groups produced MICs > 0.1. This suggests that there may be a strong

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**Table 1.** Correlation coefficient and each respective permutation result for the top 15 strongest correlations between the master chronology and climatic variables (2008–2015). Note. Correlations for each monthly variables are shown in the Figure 6 heat map. Abbreviations are as follows: VpdMax = the average of daily maximum vapor pressure deficit values, Precip = precipitation, PDSI = Palmer Drought Severity Index, and Prev = correlation for previous year’s variable.

| Correlation Coefficient | Permutation Test | P Value |
|-------------------------|------------------|--------|
| Sep Avg Daily Min Temp  | 0.833            | 0.001  |
| Jul VpdMax              | –0.813           | 0.001  |
| Nov Sum Precip          | 0.799            | 0.006  |
| Jul VpdMax Previous     | –0.817           | 0.001  |
| May Sum Precip          | 0.745            | 0.017  |
| Sep Avg Daily Min Temp  | 0.791            | 0.006  |
| Prev                    | –0.735           | 0.001  |
| Jul Avg Daily Max Temp  | –0.735           | 0.001  |
| Apr Sum Precip          | 0.700            | 0.014  |
| VpdMax Apr–Aug          | –0.690           | 0.035  |
| Nov_Avg Daily Min Temp  | –0.689           | 0.044  |
| Jul Avg Daily Max Temp  | –0.736           | 0.001  |
| Prev                    |                  |        |
| PDSI Apr–Aug            | 0.674            | 0.024  |
| PDSI Sep–Dec            | 0.657            | 0.010  |
| Aug VpdMax Prev         | –0.697           | 0.007  |
| Aug Avg Daily Temp Prev | –0.667           | 0.009  |

**Figure 7.** Trends between the standardized master chronology for ring area (middle 95% confidence interval [CI] panel) and highly correlated climatic variables (surrounding panels). Correlation coefficients can be found within the Figure 6 heat map. The sample depth (out of 20) for the master chronology was 5 for 2008, 8 for 2009, 11 for 2010, 12 for 2011, 17 for 2012, and 20 for 2013–2015.
Implications of climatic variability on the growth of P. whippleanus

Growing season length appears to have the strongest effect on the ring area of P. whippleanus. A positive effect of increasing September minimum temperatures between 2011 and 2015 likely provided an extra few weeks for carbon assimilation, subsequent storage, and enlarged ring area (Chapin, Schulze, and Mooney 1990; Lacointe 2000). Likewise, the positive effect of higher prior year September minimum temperature also could improve current year growth due to increased reserves (Chapin, Schulze, and Mooney 1990). In several alpine landscapes, increasing growing season length enhances herbaceous biomass production compared to years with shorter growing seasons (Zhang and Welker 1996; Berdanier and Klein 2011). This is the case for shrubs and subshrubs in the alpine and subalpine as well (Rayback, Lini, and Berg 2012; Franklin 2013). Timing of increased minimum or maximum temperatures may be important for the response of forbs in terms of biomass accumulation due to seasonality of soil moisture availability. For example, forb reduction in biomass in response to experimental warming (Harte and Shaw 1995; Inouye et al. 2000; Lambrecht et al. 2007) may occur because of an overriding negative effect from increased temperatures during the summer period, likely from enhanced water stress (Lambrecht et al. 2007). Increased temperatures during the late summer and early fall may not amplify water stress but rather lengthen optimal growing conditions (Zhang and Welker 1996; Berdanier and Klein 2011; Rayback, Lini, and Berg 2012; Weijers et al. 2012). In contrast, there is the possibility that warmer conditions at the end of the growing season may negatively affect winter hardness preparations within the plant, therefore subjecting them to winter damage or kill (Wipf and Rixen 2010).

We found strong direct evidence that drought in summer months negatively affected P. whippleanus growth. We found that growing season PDSI (averaged for April through August) was positively correlated with ring area. We also found a strong negative association growth and July VpdMax. High levels of July VpdMax (and previous July VpdMax) between 2008 and 2012 were associated with relatively small ring areas. Production in this particular location, and plausibly belowground allocation of carbon resources (Chapin, Schulze, and Mooney 1990; Lacointe 2000), may reach high levels during July, as demonstrated by NDVI satellite imagery being at its highest values during this month. Thus, any impediment to carbon assimilation, such as drought and high vapor pressure deficit, could translate to decreased ring areas that we observed. Interestingly, other herb-chronology studies in completely different regions of the United States, such as the oak savannah and the tallgrass prairie (Dee and Palmer 2017), demonstrate similar responses. Pollen records indicate periods of herbaceous dominance that are usually associated with cooler periods in these
systems as well (Camill et al. 2003), suggesting no doubt that summer drought may play an important role in limiting herbaceous growth across landscapes.

Even with evidence that both the length of the growing season and the availability of soil moisture in the driest parts of the growing season limit growth, it is surprising that annual snowfall amount and estimated snowpack duration (from satellite imagery) had no significant effects. Though lengthening of the growing season could be expected to have positive effect on growth, most past work highlights the negative effect of earlier snowmelt on growth and abundance (Harte and Shaw 1995; Inouye et al. 2000; Wipf and Rixen 2010; Klimešová, Doležal, and Šťastná 2013), with a primary reason that earlier snowmelt may expose apical buds to damage from frost (Molau 1997; Inouye 2008; Wipf and Rixen 2010). One factor that may help explain the apparent lack of effect from snow related variables is the rugged terrain of the alpine, which may cause large variation in the actual microsite accumulation and duration. Large microsite variation in snow accumulation and duration of snowpack may be a large factor in the disparate snowfall effects seen on individual growth chronologies. In addition, use of LANDSAT, PRISM, MODIS, and so on may be too coarse for accurately recording snowmelt timing in microsites. To help rectify this, we recommend that future studies that focus on plant individuals rather than populations be more diligent in obtaining improved snowmelt data for respective microsites.

**Conclusions**

Growth, composition, and existing ecosystem services of Rocky Mountain alpine ecosystems are under threat with anticipated increases in growing season length, growing season temperature, and altered rainfall patterns (Solomon et al. 2007; Pederson et al. 2011a). Alpine ecosystem services will likely change if a shifting climate causes community transition from herbaceous-dominated to more woody dominance over the next several decades (Harsch et al. 2009; Elliott and Kipfmuller 2011). Indeed, many observations are made in alpine habitats on the positive growth response and establishment of sagebrush (*Artemisia tridentata*) in response to warmer temperatures, given its greater tolerance to drought (Harte and Shaw 1995; Loik and Harte 1997; Maier et al. 2001; Perfors, Harte, and Alter 2003). Our study provides a framework for documenting herb growth response to annual climate so these relationships can be better understood and future compositional changes may even be better anticipated. In this effort, it is vital to separate more traditional dendrochronology techniques from ones that are necessary for the shorter and microsite-sensitive time series related to herbaceous species. Moving forward, we recommend chronology analyses include iterative grouping processes in attempts to improve the accuracy of herb chronologies. With these techniques, we were able to improve chronologies and find significant correlations between annual *P. whippleanus* growth and several climate variables. Further connecting these growth patterns to aboveground production, through either remote sensing or other means, will bolster the value of herbaceous root chronologies for understanding future growth dynamics in the face of climate change.

**Disclosure statement**

No potential conflict of interest was reported by the authors.

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