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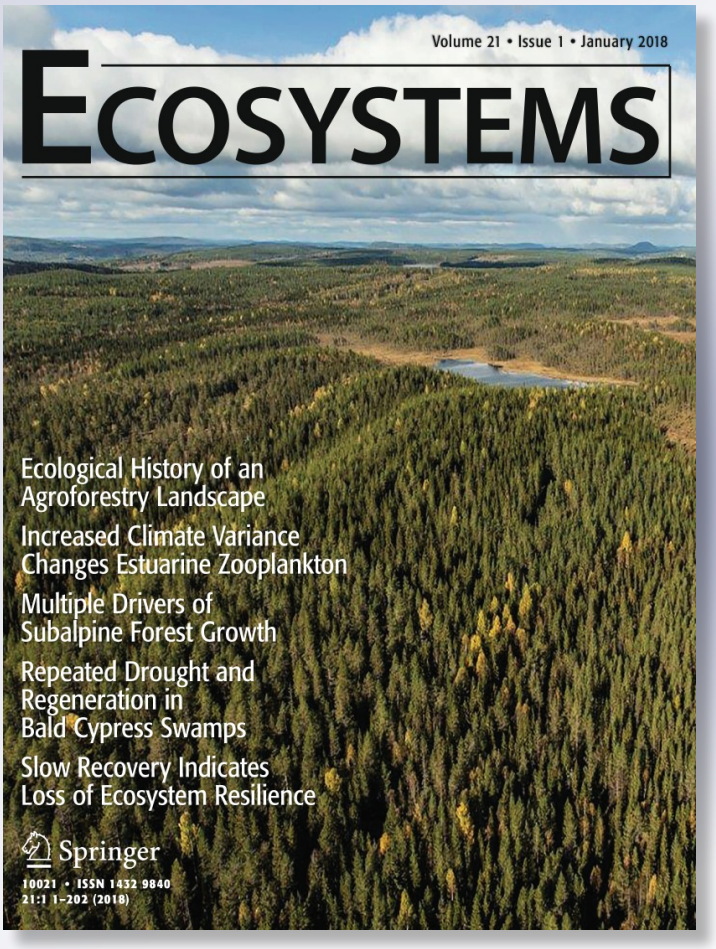

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Species, Climate and Landscape Physiography Drive Variable Growth Trends in Subalpine Forests

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Abstract

Forests around the world are undergoing rapid changes due to changing climate and increasing physiological stress, but forest response to climate at the ecosystem scale can be highly variable due to the mixed responses of different trees across heterogeneous landscapes. To determine the response of ecosystems in the Rocky Mountains to climate stress, we investigated the response of subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*), two widely distributed subalpine forest species of Rocky Mountains, to climate warming across a region characterized by gradients of elevation, aspect and soil type. We investigated the growth trend of individual trees through time, determined the climate variables most important for driving growth and quantified the interactions between climate and topography that influence long-term growth trends and potential ecological changes across the study region. Growth trends of these two species are similar through the first part of the century, but diverge during the last several decades. Since 1975, subalpine fir growth decreased through time, while Engelmann spruce growth increased. We find that aspect and warm summer temperatures are the most important factors determining growth in subalpine fir, and subalpine fir growth declines are greatest on east- and south-facing aspects. In contrast, Engelmann spruce growth is uniformly unresponsive to climate. In addition to highlighting the importance of species-level differences in growth response to climate, our results also identify interactions between climate and local physiography as controls on long-term growth trends and suggest that the local landscape physiography can mediate climate-related stress in forested ecosystems. This work advances our understanding of how forest stress is mitigated by landscape factors at the ecosystem scale, and how interactions of species, landscape and climate will control future ecosystem composition and forest growth dynamics.

Key words: Engelmann spruce; subalpine fir; basal area increment; aspect; climate–growth responses; climate change; linear-mixed effects models; Rocky Mountains; *Abies lasiocarpa*; *Picea engelmannii*.

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Author Contributions All authors contributed to formulating the idea and developing the methodology, KCK conducted the field work, KCK and MDR analyzed data and performed the modeling, KCK wrote the manuscript with substantial contributions from JCN, MDR and NNB.

Subalpine fir data: https://www.researchgate.net/publication/314180102_San_Juan_National_Forest_Raw_Ring_width_data_Subalpine_Fir. Engel mann Spruce data: https://www.researchgate.net/publication/314180522_San_Juan_National_Forest_Raw_Ring_width_data_Engelmann_Spruce.

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Introduction

Forests across the globe are experiencing rapid rates of decline and regional-scale die-offs due to drought, insects, wildfire and escalating rates of background mortality (Breshears and others 2005; Hicke and others 2006; Westerling and others 2006; Raffa and others 2008; van Mantgem and others 2009; Worrall and others 2010; Carnicer and others 2011; Smith and others 2015). Changing climate is a common driver behind many of these changes, highlighting forest growth response to climate as a key factor in predicting the future health of forest ecosystems, and a control on broader ecological changes including shifts in plant and animal communities and alteration of biogeochemical cycles. Recent forest diebacks in the southwest US have occurred at scales large enough to cause some degree of mortality on nearly 20% of the forested area of this region (Williams and others 2010), but in most cases these changes were discontinuous and highly spatially variable (Breshears and others 2005; Huang and others Huang et al. 2010; Worrall and others 2010; Huang and Anderegg 2012). Dendrochronological work examining forest response to climate suggests that a wide range of factors including species differences (Villalba and Veblen 1994; Adams and Kolb 2005; Miyamoto and others 2010) and physiographical factors such as elevation (Littell and others 2008; Lo and others 2010), aspect (Peterson and Peterson 1994) and soil type (Barger and Woodhouse 2015; Piraino and others 2015) all act to mediate climate expression at the local level. Thus, we expect that differences in species physiology and local edaphic factors can mitigate or exacerbate forest stress in response to climate conditions, but there is still considerable uncertainty as to how climate sensitivities are expressed over complex landscapes.

The timing and spatial distribution of the conditions that induce forest stress are key components of overall ecosystem health. Physiological stress in a tree is a response to unfavorable environmental conditions such as competition, cold or drought that affect a tree's physiological function. Climate-induced forest stress can occur either as a result of inter-annual variation in climate, or in response to long-term climate trends. Inter-annual variations, such as acute drought, cause severe stress and increase the chance of mortality in the short-term (Bigler and others 2007), whereas long-term trends allow stress to build over time and be carried over via factors with long residence times such as soil water content. Short- and long-term climate conditions also have interacting effects on forest stress because the presence of long-term stress factors may predispose trees to short-term acute stress (Allen and Breshears 1998; Pedersen 1998), and similarly acute stress can affect growth in subsequent years and initiate a trend of growth decline (Bigler and others 2007). These complex interactions of climate and tree physiology highlight local variation in landscape and species as key factors determining how climate impacts play out across forest ecosystems.

The effect of climate on forest stress can be mediated by local physiographic factors such as elevation, aspect and soil type, which alter local water and energy balance. Trees tend to experience stress related to cold temperatures at high elevations or high latitudes, and stress related to low moisture in low elevation regions, or at the lower elevational or latitudinal end of a species' range (Fritts 1974; Adams and Kolb 2005; Waring and Running 2007; Littell and others 2008; Lo and others 2010). At low elevations, warm temperatures and associated higher vapor pressure deficit (VPD) contribute to stress in trees through increased evaporation of water from soils, and physiological changes in trees that result in reduced carbon fixation (Tardieu and Simonneau 1998; McDowell and others 2008; Breshears and others 2013). Aspect also influences tree stress via controls on insolation and the resulting effects on evapotranspiration and soil moisture dynamics. Equator-facing aspects (the south-facing aspects in the northern hemisphere) generally have higher temperatures, lower relative humidity and greater VPD resulting in greater stress on forest ecosystems which is manifested by lower forest biomass and rates of regeneration (Desta and others 2004; Elliott and Kipfmueller 2011; Gutiérrez-Jurado and others 2013; Zapata-Rios and others 2015). Tree stress across aspects is also controlled by the interaction of daily maximum insolation and daily temperature fluctuations (Young and Smith 1983), which sets up important contrasts in soil water balance between east- and west-facing aspects (Desta and others 2004; Liang and others 2006) in addition to north and south. Finally, soil type also affects forest stress through its influence on water availability to trees. Soil depth, organic matter content and the proportion of fine particles such as silts and clays all alter soil available water capacity (AWC), and as a result heterogeneity in soil type drives variability in tree growth by modifying forest stress at the local scale (Pinto and others 2007; Barger and Woodhouse 2015; Kobal and others 2015; Piraino and others 2015).

Understanding the effects of local physiography in mitigating and exacerbating forest stress is particularly important in subalpine forests where complex terrain presents the potential for high ecosystem-level variability in responses to climate. Two dominant and widespread tree species, subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*), coexist throughout the subalpine forests of the southwest US. Previous dendrochronological investigations of these species have identified complex and sometimes contradictory relationships between tree growth and climate. Growth of both species is generally greatest with a longer growing season and smaller snowpack, especially in the northern portion of their range (Peterson and Peterson 1994; Splechtna and others 2000; Miyamoto and others 2010). However, on locally drier and warmer landscape positions both species respond negatively to warm summer temperatures and positively to summer precipitation, indicating stress related to local water limitation (Villalba and Veblen 1994; Peterson and others 2002; Adams and Kolb 2005). In some cases, these two species have inconsistent responses to climate even when growing in mixed assemblage stands; on drier sites growth of both species is limited by hot summers and long winters, but their responses diverge at wetter sites where subalpine fir growth is affected by climate, but Engelmann spruce is relatively unresponsive (Villalba and Veblen 1994). The complex response of these species to climate indicates that future growth under increased climate stresses will likely be highly variable, and trees of one species, or in a specific landscape position, may have different timing and magnitude of responses to climate stress. Our current knowledge of the climate–growth relationships of these species, combined with the complexity of the interactions between climate and edaphic factors, make it difficult to evaluate long-term trends of growth in response to climate conditions or to predict the impact of growth changes on a broader suite of ecological responses.

Southern Rocky Mountains subalpine forests are currently experiencing substantial climate warming, with especially high rates of warming over the past several decades (Rangwala and Miller 2010). These forests contain multiple tree species growing across a highly heterogeneous setting, and therefore, we expect that forest response to the stresses associated with warming will be highly variable. By quantifying climate–growth relationships and trends of tree growth through time across regions of complex terrain, we can gain insight into how forests respond to climate stress at an ecosystem scale. In this study, we examine the role of physical landscape and species-level physiological differences in mediating climate stress on Southern Rocky Mountain subalpine forests by exploring the following three objectives: (1) determine tree growth trends in response to warming in two co-occurring subalpine forest species; (2) identify the climate variables that most strongly influence growth in each species; and (3) investigate how climatic drivers interact with local physiographic variables to influence forest growth and trends of tree growth through time. Our results will help determine how forest stress related to ongoing climate change may be manifested across an ecosystem according to species physiology and local-scale terrain variability.

Materials and Methods

Study Area

The study was conducted in San Juan National Forest located in southwest Colorado (~38°N, 108°W; Figure 1). The climate of this region is characterized by low temperatures with high snowfall between November and April and monsoonal rainfall from July through October (Blair 1996). This region receives approximately 98 cm of precipitation annually; average maximum temperatures (~19.5°C) occur in late summer, and minimum temperatures (−13.9°C) occur mid-winter (http://www.wcc.nrcs.usda.gov/snow/). Treeline is at an elevation of approximately 3600 m. The geology of this region consists of interbedded sandstone, limestone and shale of Pennsylvanian and Mississippian age, with some Tertiary volcanics (Yager and Bove 2002). Soils are predominantly cobbly sand clay loam (NRCS).

Sampling Design and Tree Growth Data

Tree ring data were collected from 23 sites within a subalpine forest (Table 1). To produce a wide range of local temperature and moisture conditions across our study sites, we selected sites that represent a deep and a shallow soil on each aspect (north, east, south and west), across an elevational gradient from 2700 to 3400 m. Soil depth affects soil water-holding properties and slope aspect influences local energy balance and water fluxes due to the differences in insolation, so we chose to sample over gradients of these factors in order to include variation in local temperature and moisture conditions. We used soil maps produced by the National Resources Conservation Service to guide site selection, and soil depth and texture were verified in the

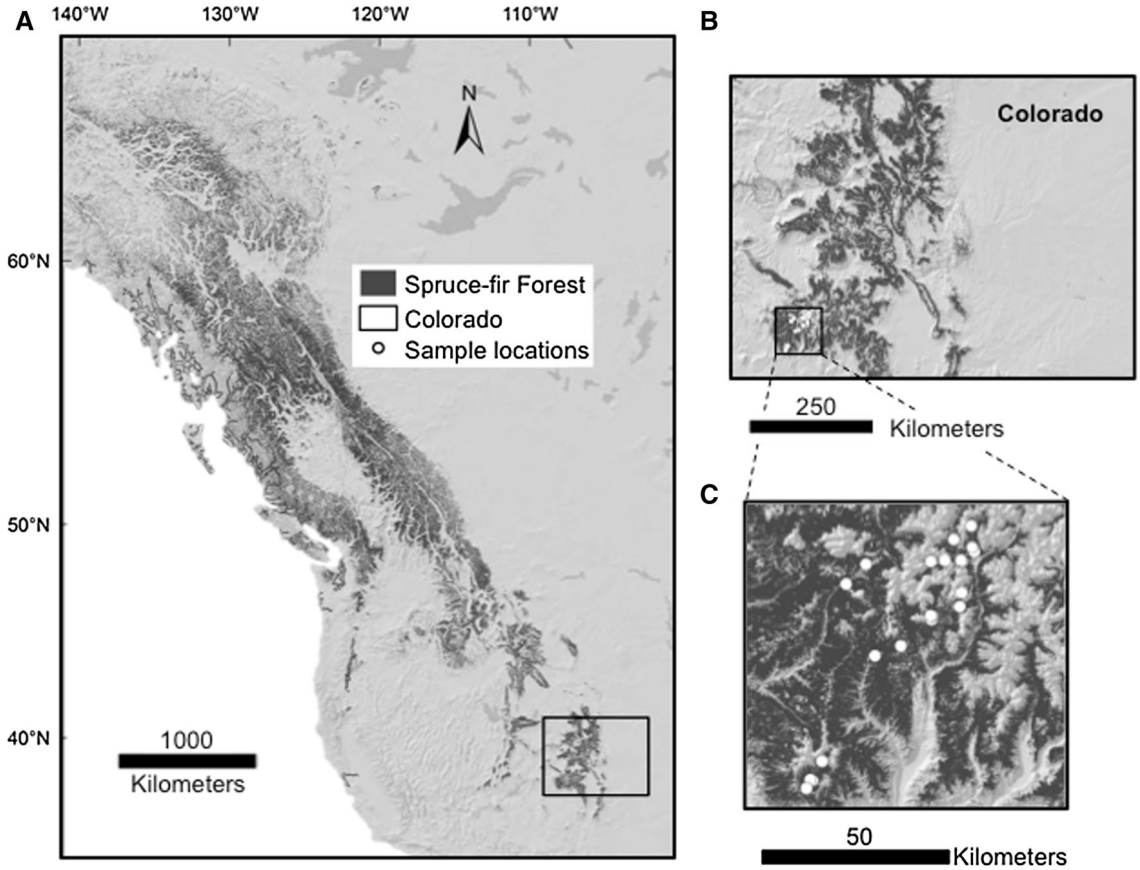

Figure 1. **A** Distribution of spruce–fir-type subalpine forest through North America, and location of Colorado; **B** location of sampling sites within Colorado; **C** distribution of study plots.

field. At each site, we selected approximately 20 individuals of both subalpine fir and Engelmann spruce for approximately 40 trees total. A 50-m transect was established perpendicular to the slope, and trees were selected as those closest to the transect that were greater than 20 cm diameter at breast height (DBH) with no visible damage to crowns or stems. At sites where both species were present, subalpine fir is generally more abundant than Engelmann spruce, but equal numbers of both trees were sampled from each species. At sites where subalpine fir was not present (eight sites total), only Engelmann spruce was sampled.

We collected a total of 450 cores from Engelmann spruce and 210 cores from subalpine fir. An increment borer was used to extract one core from each tree at a height of 1.3 m. The cores were mounted and then sanded with progressively finer grades of sand paper in order to produce a flat surface on which tree rings were easily visible. Cores were measured using the Velmex ring-measurement system (Velmex Inc., Bloomfield, NY) and cross-dated visually and statistically. Cross-dating accuracy was checked using the program COFECHA (Holmes 1983; Grissino-Mayer 2001).

Physiographic Variables

At each site, we also obtained measurements of site elevation, aspect and soil AWC. Elevation and aspect were measured at three points along the 50-m transect (at 0, 25 and 50 m). AWC was calculated from soil texture, organic matter and soil depth (Saxton and Rawls 2006). To quantify soil texture, we collected six soil samples (10 cm in depth) at each site. Soils were then sieved through a 2-mm sieve; the greater-than-2 mm fraction was weighed as gravel and the less-than-2 mm fraction was used to estimate percent sand, silt and clay using the hydrometer method (Gee and Or 2002). Soil depth at each site was determined at six locations along the transect by inserting a 2-m soil probe into the soil until resistance. Where the probe was fully inserted without meeting bedrock, the soil depth was recorded as greater than 2 m. We used the estimates of soil depth and percentage sand, silt,

Table 1. Site Characteristics of Tree Ring Sampling Sites

Site	Latitude	Longitude	Elevation (m)	Aspect	AWC (cm)	Precipitation (cm)	*T* max (°C)	*T* min (°C)	Species Sampled
1	37.72	−107.71	3366	N	355.0	78.9	9.3	−6.0	ES
2	37.81	−107.70	3011	N	117.0	76.7	8.9	−6.9	ES/SF
3	37.81	−107.70	3019	E	81.8	76.7	8.9	−6.9	ES/SF
4	37.83	−107.67	2940	N	273.5	57.6	9.2	−6.9	ES
5	37.84	−107.68	2997	W	244.7	57.6	9.2	−6.9	ES/SF
6	37.88	−107.68	3365	N	237.3	66.7	8.3	−6.9	ES/SF
7	37.65	−107.85	3114	E	217.6	69.5	10.5	−5.6	ES/SF
8	37.39	−108.06	2979	N	273.1	61.2	9.8	−5.5	ES/SF
9	37.39	−108.07	2793	N	274.3	61.2	9.8	−5.5	ES
10	37.37	−108.08	2710	N	242.9	61.2	9.8	−5.5	ES
11	37.43	−108.04	3041	W	178.9	69.1	8.8	−5.4	ES
12	37.81	−107.74	3001	E	405.0	66.2	8.1	−6.8	ES
13	37.81	−107.74	2998	W	136.7	74.4	8.7	−6.6	ES/SF
14	37.85	−107.72	3254	W	215.3	63.6	8.7	−6.7	ES/SF
15	37.81	−107.78	3095	S	145.0	70.2	7.6	−7.1	ES/SF
16	37.70	−107.78	3235	E	155.2	78.8	9.7	−5.6	ES/SF
17	37.71	−107.77	3320	N	158.7	78.8	9.8	−5.6	ES/SF
18	37.75	−107.71	3379	S	288.0	72.8	9.1	−6.6	ES/SF
19	37.75	−107.70	3388	E	75.6	72.8	9.1	−6.6	ES/SF
20	37.71	−107.78	3380	N	300.9	78.8	9.8	−5.6	ES/SF
21	37.77	−107.98	2874	N	147.1	57.8	9.3	−7.0	ES/SF
22	37.77	−107.98	2924	N	235.7	57.8	9.3	−7.0	ES
23	37.80	−107.93	3125	S	280.3	62.3	8.3	−7.8	ES

Climate data were calculated from PRISM modeled climate data.
AWC—available water capacity; precipitation—annual mean precipitation; T max—annual mean monthly maximum temperature; T min—annual mean monthly minimum temperature; N—north; S—south; E—east; W—west; ES—Engelmann spruce; SF—subalpine fir.

clay and gravel from each site to calculate soil AWC by subtracting the wilting point (θ_{1500}) from field capacity (θ_{33}), which we calculated following the equations in Saxton and Rawls (2006), and multiplying by the soil depth.

Climate Data and Variable Selection

Long records of measurement of mountain climate are not available in our study area, and therefore to investigate relationships between climate and tree growth, we chose to use gridded climate data from the PRISM climate group (PRISM data hereafter). PRISM data are based on observational data, which are used as input for algorithms that anticipate how precipitation and temperature vary over regions of complex terrain (PRISM 2004). The resulting data product is produced at a spatial resolution of 4 km^2. We chose to use this dataset because it provides climate information for each site that accounts for the variable topography of this region. Estimating precipitation in mountainous environments is challenging and unreliable estimates could lead to erroneous climate growth relationships, so therefore we chose to confirm our results of the climate–growth relationships by also developing these relationships with data from the NOAA National Climate Data Center (Divisional data hereafter) which consist of monthly temperature and precipitation values computed from area-weighted observational data (Karl and Koss 1984). Both datasets yielded the same results regarding which climate variables were most important for driving tree growth, so we chose to use PRISM data through the remainder of the analyses and discussion because of this dataset's superior spatial resolution.

We investigated trends in temperature over the last century for the entire region of study using a time series correlation analysis between temperature from the NOAA Divisional data and year (Figure 2). The NOAA Divisional dataset is a superior choice for analyzing trends because these data are derived from area-weighted means of observational data, in contrast to PRISM data which are modeled and less reliable for long-term trends. Further, all of our study sites fall within one grid cell of the Divisional data, so this dataset provides climate trends representative of the entire study area.

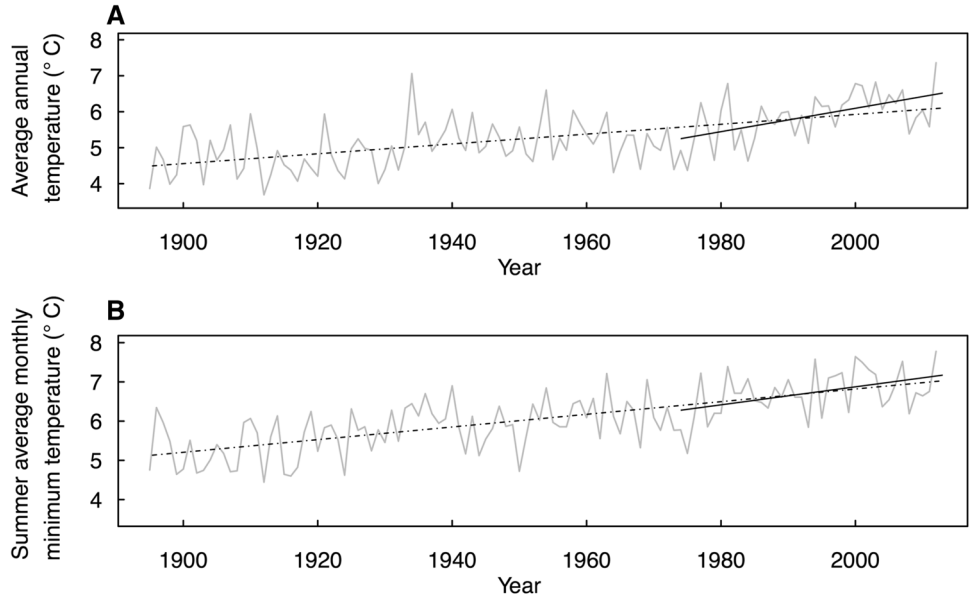

Figure 2. **A** Average annual temperature and **B** summer average monthly minimum temperature from NOAA divisional data for western Colorado during the period 1895 through 2012. The *dashed line* shows the temperature trend from 1895 through 2012, and the *solid line* shows the temperature trend from 1975 through 2012. The slopes and correlations for 1895 through 2012 are 0.014 and 0.61 ($p < 0.00$), respectively, for **A** and 0.016 and 0.71 ($p < 0.00$), respectively, for **B**. The slopes and correlations for 1975 though 2012 are 0.033 and 0.55 ($p < 0.00$), respectively, for **A** and 0.029 and 0.44 ($p = 0.004$) for **B.**

Tree Growth Analysis

The annual radial growth in a tree varies according to both annual climate conditions and the age and size of the tree. For this reason, researchers have developed many different methods of analyzing radial growth data depending on the intent of the analysis. In this study, each of our three objectives requires a different analysis method of radial growth data. Here we describe the reasoning behind choosing these growth metrics, and we provide a full description of each methodology in the following sections.

To explore trends in growth through time (Objective 1), we used the trend of basal area increment (BAI) over time. BAI is the cross-sectional area of new growth that a tree produces each year according to the following formula:

$$\mathrm{BAI} = \pi\left(R_n^2 - R_{n-1}^2\right) \tag{1}$$

where R is the radius of the tree and n is the year of ring formation. BAI provides a meaningful metric of tree growth because it more accurately reflects the amount of new biomass accrued annually than raw ring width, and BAI values can remain high even when there is an apparent decline in raw ring width (West 1980). Furthermore, BAI is a useful measure of tree health because low levels of growth are commonly considered an indicator of increased risk of tree mortality (Wyckoff and Clark 2000; Bigler and Bugmann 2003, 2004).

To identify the climate variables that most strongly influenced growth in our study species (Objective 2), we standardized tree ring width data from each tree to remove growth patterns resulting from tree age and local stand dynamics. This standardization process yields a unitless ring width index (RWI) where all values for a given tree have a mean of one, and values less than one indicate a year of below average growth, while values greater than 1 indicate a year of above average growth. RWI values were then correlated with climate variables to determine climate–growth relationships. This method was chosen because it is the most widely used methodology for determining climate–growth relationships within trees, and the details of the detrending procedure are further described below.

To investigate the interaction of climatic drivers and local physiography in driving forest growth (Objective 3), we used a measure of standardized BAI. BAI generally increases through a tree's life, particularly in younger trees, and so we chose to standardize BAI by the basal area (BA) of the tree in the year of ring formation: (BAI/BA). This method is supported by McDowell and others

(2010) and Bigler and Bugmann (2004). This method provides a growth metric that is standardized by tree size, but still allows for analysis of site-scale physiographic effects. The detrended RWI data from the analysis described above are not appropriate for addressing Objective 3 because the detrending procedures make it impossible to evaluate the effect of site-scale physiographic variables (elevation, aspect, soil type) on growth.

Analysis of Long-Term Growth Trends

To assess trends in tree growth through time (Objective 1), we examined BAI through time for subalpine fir and Engelmann spruce from 1895 to the present. We further focused our analysis of trends in BAI on the time period 1975–2012 because this modern period is when we see evidence of the strongest warming in the San Juan Mountains (Figure 2), and when there is the most sustained positive temperature anomaly in mean annual surface air temperature (Rangwala and Miller 2010). To evaluate trends of BAI in this modern period of warming, 1975–2012, we calculated annual BAI for each tree and then used Pearson product moment correlations to determine the correlation of BAI and year, which is equal to the trend of growth over time. The result is one value for each tree indicating the magnitude and direction of its growth trend since 1975. To determine whether specific physiographic variables were important in determining the sign and magnitude of the growth trends from 1975 to the present, we used these trends as the response variable in a generalized linear-mixed effects modeling framework.

We used a random intercepts model to estimate the effect of predictor variables on the growth trend over time. Five models were constructed including a null model. The physiographic variables included in the mixed models were elevation, AWC and aspect (included separately as the categorical variables north, south east and west and as the continuous variable of azimuth from true north). The diameter of each tree was included as a fixed effect (*lmer* function in the R package lme4; Bates D., Bolker B., and Walker S., 2014, R Core Development Team) to account for variably sized trees. To code these models in R, east-facing aspects were coded as the reference level. For each model, we determined the Akaike information criteria (AIC) and Bayes information criteria (BIC; MuMIn package, Bartón, K., 2014, R Core Development Team). AIC and BIC are model evaluation metrics that reward simple models and penalize complex models. We based our model selection on BIC because the sample size we use here greatly exceeds the parameter space of the model (Aho and others 2014). To determine the goodness of fit, we use a pseudo-R^2 calculated according to the recommendation of Nakagawa and Schielzeth (2013), which provides a 'variance explained' term for generalized linear-mixed effects models.

Climate–Growth Relationships

To identify the climate variables that most strongly influence growth (Objective 2), we determined the correlation between climate and growth from PRISM climate data and detrended RWI values for the time period 1895 through 2012. Detrended RWI values were determined by fitting a cubic smoothing spline with a 50% frequency response cutoff of 20 years, followed by an autoregressive model to remove autocorrelation present within each series (dplR package, Bunn 2008, R Core Development Team).

We used correlations between RWI and climatic variables to identify the most important climate variables influencing growth. Specifically, Pearson product moment correlations were used to compare growth in a given year within a given tree to the seasonal climate time series from the PRISM data from 1895 to 2012. We calculated the correlation between growth and aggregated seasonal variables because seasonal variables can be better than monthly climate data at approximating the actual ecophysiological mechanisms leading to annual growth–climate correlations (Fritts 1976; Watson and Luckman 2002; Littell and others 2008). Furthermore, seasonal aggregations are less likely to produce spurious significant correlations. Seasonal aggregations for this study were created as follows: Spring was defined as April through June, Summer was defined as June through August, Fall was August through October, and Winter was defined as November through February. We chose to include many months in the seasonal aggregations in order to attempt to capture the complex ecohydrology of this region. Some months were included in spring and summer seasonal aggregations, but these aggregations are always used in separate models so they are non-overlapping during any individual analysis. The climate variables we investigated were monthly maximum temperature, monthly minimum temperature, monthly average VPD and monthly total precipitation. Maximum temperature, minimum temperature and VPD were averaged over these time periods to produce seasonal aggregations, and monthly precipitation was

summed. We evaluated the correlation between growth and the concurrent year climate conditions as well as the previous year's climate conditions.

The most important climatic variables were identified as those that yielded the highest median correlation between climate and growth. Correlations were calculated from each individual tree, rather than chronologies, according to the suggestion of Galván and others (2014) who show that an individual tree-scale approach to quantifying climate–growth relationships is necessary to investigate the climate sensitivity of trees. In addition to calculating the median correlation between climate and growth, we also determined which climate variable had the highest proportion of individual trees displaying a significant relationship ($p < 0.05$) between their individual growth and annual climate.

Modeling the Effects of Climate and Physiography on Tree Growth

We used linear-mixed effects models to investigate how climatic drivers interact with local physiological variables to influence forest growth (Objective 3) for the time period 1895 through 2012. Standardized BAI, calculated as BAI/BA, was used as the response variable in our generalized linear-mixed models with seasonal climatic variables and site-scale physiographic variables as predictor variables. We used a random intercepts model to estimate the effect of the predictor variables on tree growth. The intercepts for tree and site were nested and were included as random effects (*lmer* function in the R package lme4; Bates D., Bolker B., and Walker S., 2014, R Core Development Team).

We established 24 candidate models using different combinations of climatic and site-scale physiographic variables and their interactions, with the 25th model as a null model that did not include any climatic or physiographic variables (SI Table 1). The specific climatic variables used in the models were: summer average monthly maximum temperature, summer average monthly minimum temperature and summer total monthly precipitation. Two climate variables were never included in the same model. The specific physiographic variables included in the models were elevation, aspect and AWC. The seasonal variables were chosen according to the results of the climate–growth correlation analyses. We included candidate models with all possible combinations of one climate variable and one physiographic variable, with and without interactions. The response variable, BAI/BA, was transformed using a logarithmic transformation to produce a normal distribution prior to analysis. All climate and physiographic variables were centered and scaled such that the mean value is equal to zero and the standard deviation is equal to 1. East-facing aspects were coded as the reference level for the categorical variable of aspect. All models with a ΔBIC less than 2 were selected, and we calculated the pseudo-R^2 to estimate the amount of variance explained by the model. The climatic and physiographic variables and interactions present in the best-fitting model were taken as the variables most important for determining growth.

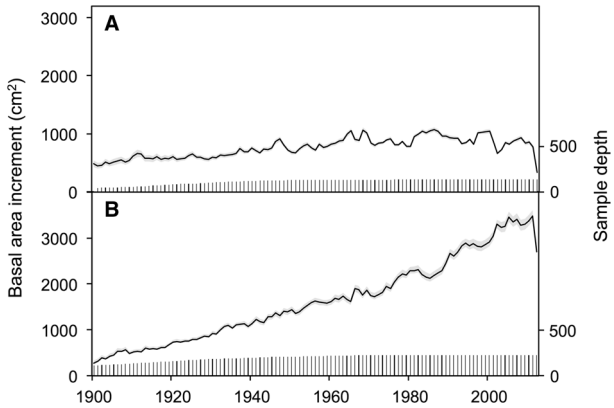

Figure 3. Mean basal area increment (BAI) and sample depth through time for **A** subalpine fir and **B** Engelmann spruce. *Gray shading* represents the 95% confidence intervals on the mean.

Results

Long-Term Growth Trends

Subalpine fir and Engelmann spruce showed similar trends of increasing BAI through time from 1895 through the latter half of the twentieth century, but in the last several decades the BAI trends of the two species diverged (Figure 3). BAI of Engelmann spruce increased through time, but subalpine fir BAI stopped increasing and began to decrease. According to our analysis of growth from 1975 to 2012, subalpine fir growth declined through time during this period in one half of the trees investigated in this study (Figure 4A). The best-performing model of the growth trend of subalpine fir though time included aspect, rather than elevation or soil AWC (pseudo-R^2 = 0.36, Table 2). Trees growing on east-facing aspects had the largest declines (negative trends) in growth (Figure 4C) followed by those trees growing on south- and west-facing aspects, respectively. Only subalpine fir growing on north-facing aspects had

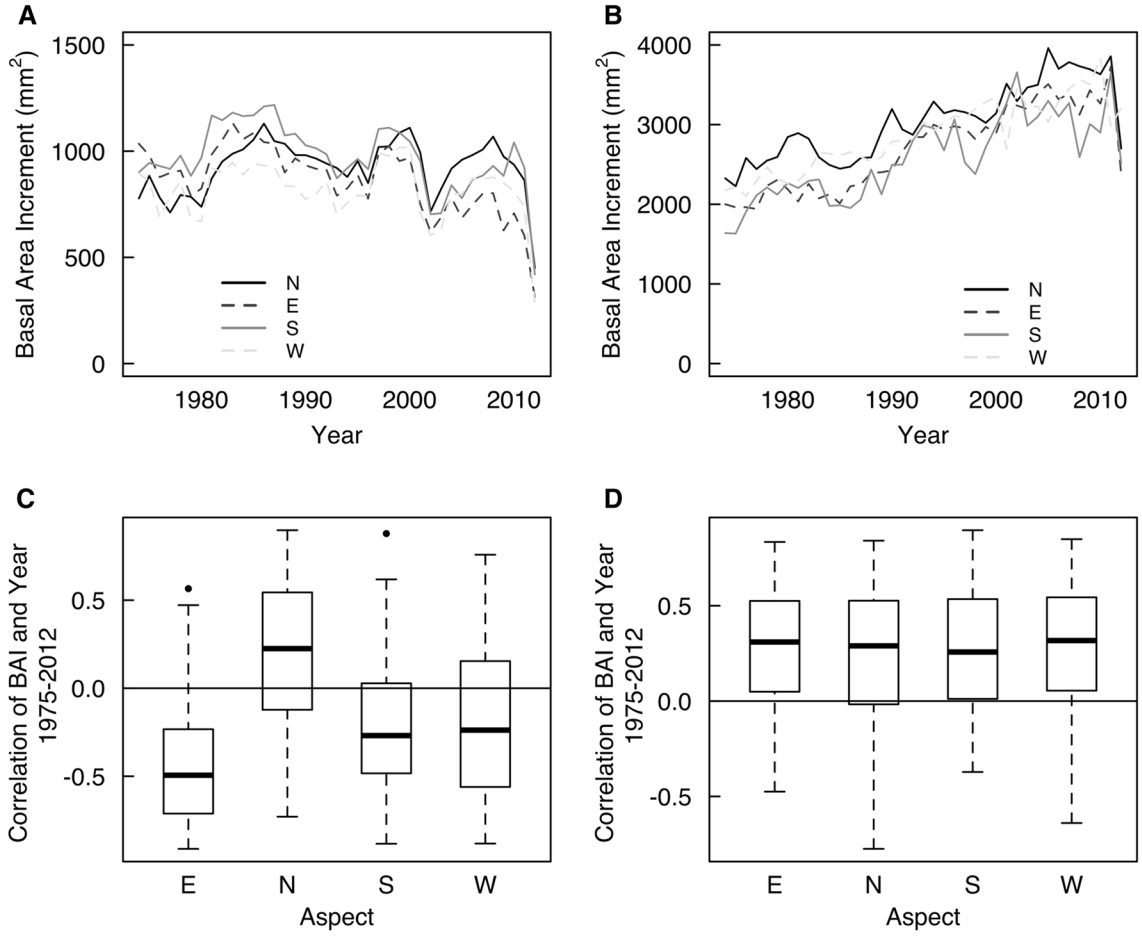

Figure 4. *Top* mean basal area increment (BAI) through time for trees located on different aspects: north (N), south (S), east (E), west (W), for **A** subalpine fir and **B** Engelmann spruce. *Bottom* box plot of BAI trend (correlation of BAI and year) from 1975 to 2012 by aspect for **C** subalpine fir and **D** Engelmann spruce; *bars* represent median trend, *boxes* represent 25–75 quartiles, whiskers represent range, and solid circles are outliers.

Table 2. Factors Affecting Forest Growth Trends Through Time

Parameter	Estimate	SE	*t*
Subalpine fir			
Intercept	−0.424	0.069	−6.121
Diameter	−0.127	0.029	−4.311
Aspect; north	0.625	0.094	6.609
Aspect; south	0.194	0.122	1.585
Aspect; west	0.229	0.107	2.139
Engelmann Spruce			
Intercept	0.253	0.027	9.238
Diameter	−0.019	0.018	−1.031

Parameter estimates for the fixed effects in the linear-mixed model of the basal area increment trend for subalpine fir (top) and Engelmann spruce (bottom). For both species, these were the best-performing models as evaluated by both AIC and BIC. East-facing aspects were coded as the reference level for the categorical variable of aspect. For subalpine fir, the best-performing model included tree diameter and aspect; pseudo-R^2 = 0.36. For Engelmann spruce, the best-performing model included only tree diameter; pseudo-R^2 = 0.08.

an average positive trend of growth through time. In contrast, Engelmann spruce growth increased through time from 1895 to the present.

Climate Growth Relations

Subalpine fir growth was reduced the most in years with high spring VPD and high summer average monthly minimum temperatures (Figure 5A). High spring VPD and summer minimum temperatures were significantly negatively correlated with growth in 49% and 46% of individual trees, respectively. Subalpine fir growth was also negatively correlated with high minimum temperatures in spring as well, and 39% of trees displayed significant negative correlations between growth and spring minimum temperature. In terms of precipitation, subalpine fir responded positively to years with more spring and summer precipitation (Figure 5A), and approximately 25% of trees had significant positive correlations with spring and summer precipitation. Current year climate conditions had stronger correlations with growth than the previous year's climate conditions. Engelmann spruce was largely unresponsive to any climate variables (Figure 5B). Fewer than 10% of trees showed significant correlations between annual growth and any seasonal climate variable.

Interactions of Climate and Physiography

Climate and physiography were both important drivers of subalpine fir growth and had interacting effects on growth. Summer average monthly minimum temperature, aspect and the interaction between temperature and aspect were all included in the best-performing model of subalpine fir growth (Table 3). Consistent with the results from the correlation analysis, average summer minimum temperature was among the most important climatic variables determining growth of subalpine fir and had a strong negative effect on subalpine fir growth. The interaction between temperature and aspect identified in the top-performing model of subalpine fir growth indicated that the negative effect of high summer minimum temperatures varied according to the dominant slope aspect. In particular, trees growing on north-facing slopes

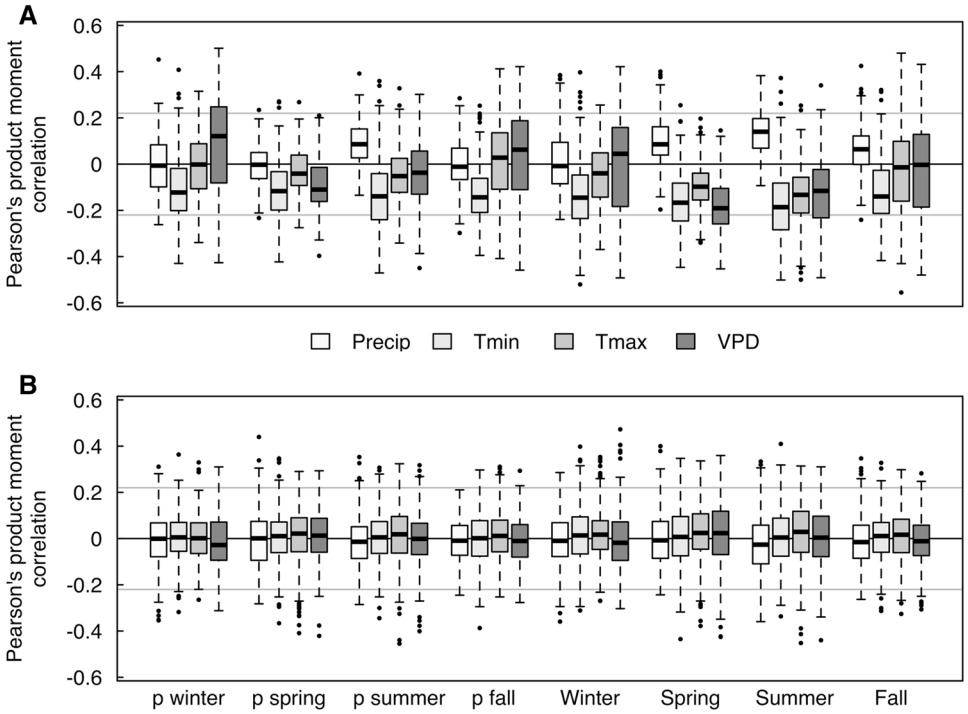

Figure 5. Median Pearson's product moment correlation of ring width index and seasonal climate variables calculated from PRISM climate data for **A** subalpine fir and **B** Engelmann spruce. Spring was defined as April–June, Summer was defined as June–August, Fall was defined as August–October of the year of ring formation, and Winter was defined as November–February starting in the year preceding ring formation. *Lines* represent the median, bars represent the interquartile range, *whiskers* represent the range, and solid circles are outliers. The *gray horizontal lines* show the significance threshold at <0.05 given the sample size. *Abbreviations*: *Precip* seasonal total precipitation, *Tmax* seasonal average monthly maximum temperature, *Tmin* seasonal average monthly minimum temperature.

Table 3. Effects of Physiography and Climate on Tree Growth

Parameter	Estimate	SE	*t*
Subalpine fir			
Intercept	−3.76	0.093	−40.16
Aspect (north)	−0.126	0.126	−1.00
Aspect (south)	0.075	0.164	0.46
Aspect (west)	−0.011	0.144	−0.08
Summer T min	−0.339	0.014	−23.50
Aspect (north) × Summer T min	0.134	0.019	6.87
Aspect (south) × Summer T min	−0.028	0.027	−1.03
Aspect (west) × Summer T min	−0.039	0.024	−1.65
Engelmann spruce			
Model 1			
Intercept	−3.84	0.066	−57.78
Elevation	−0.025	0.065	−0.39
Summer T max	−0.20	0.013	−16.14
Model 2			
Intercept	−3.84	0.066	−57.59
AWC	0.003	0.065	0.05
Summer T max	−0.206	0.012	−16.14

Parameter estimates for the fixed effects in the linear-mixed model of the effect of physiography and climate on tree growth expressed as basal area increment normalized by basal area for subalpine fir (top) and Engelmann spruce (bottom). For both species, these were the best-performing models as evaluated by both AIC and BIC. East-facing aspects were coded as the reference level for the categorical variable of aspect. For subalpine fir, the best-performing model included summer average monthly minimum temperature (Summer T min) and elevation and their interaction; pseudo-R^2 = 0.40. For Engelmann spruce, the two best-performing models differed by only 0.6 AIC units and 0.5 BIC units. The two best-performing models included summer average monthly maximum temperature (T max) and elevation (pseudo R^2 = 0.18) and summer average monthly maximum temperature (T max) and AWC (pseudo-R^2 = 0.18), respectively.

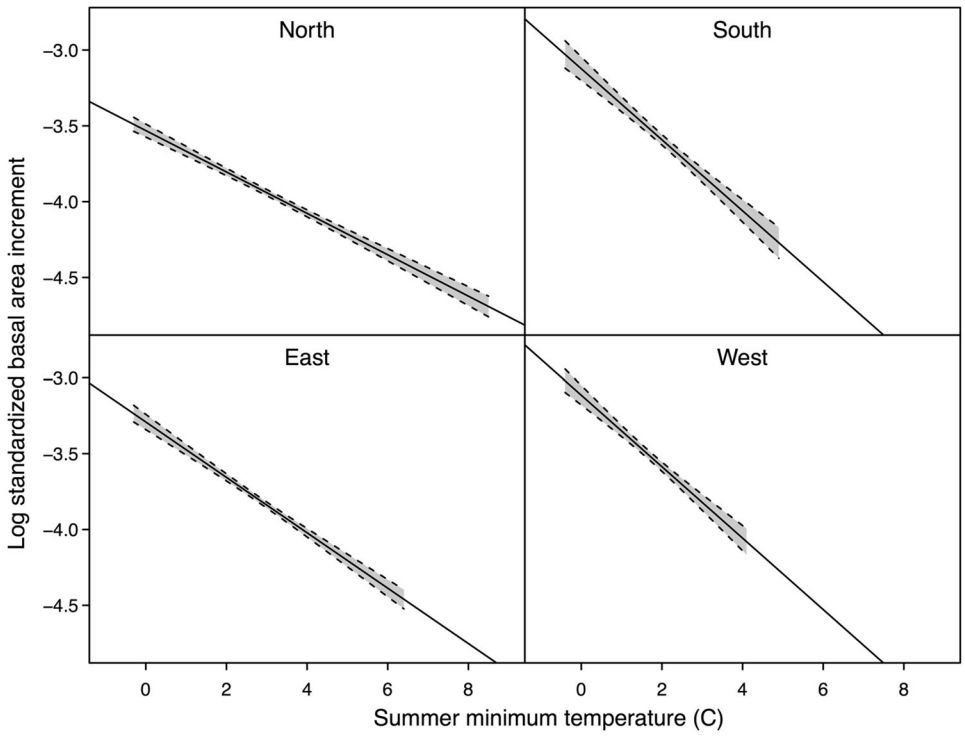

Figure 6. Interaction effect of summer average monthly minimum temperature by aspect on tree growth (expressed as the logarithm of basal area increment standardized by basal area; BAI/BA) for subalpine fir. Growth versus temperature is shown for each of the four aspects: north, south, east and west. This interaction was identified in the top-performing model (evaluated by BIC) generated in a generalized linear-mixed modeling framework. *Dashed lines* denote the 95% confidence intervals.

were much less sensitive to high summer minimum temperatures compared to trees growing on south-, east- and west-facing slopes (Figure 6).

Mixed models of Engelmann spruce growth explained a smaller proportion of the inter-annual variation in growth than models of subalpine fir

(Table 3). Evaluation of generalized linear-mixed models of Engelmann spruce growth indicated that two models performed similarly in predicting growth. The first model included summer maximum temperature and elevation, and the second model included summer maximum temperature and AWC. These two models were differentiated by only 0.6 units BIC and explained only a small proportion of the inter-annual variation in growth (pseudo-R^2 of 0.18 and 0.18, respectively; Table 3).

Discussion

Subalpine regions are characterized by complex terrain and inhabited by species vulnerable to warming climate; therefore, understanding the role of the physical landscape in mediating the effects of climate stressors is a critical component of anticipating forest response to climate change in these regions. We found that subalpine fir and Engelmann spruce, two important subalpine forest species of the intermountain west, show widely divergent growth patterns during the last several decades of climate warming in the Southern Rocky Mountains: Subalpine fir growth decreased through time from 1975 to the present, whereas the growth of Engelmann spruce increased through time. Subalpine fir grew less in years with warm summer temperatures and high vapor pressure deficit, whereas Engelmann spruce growth was unresponsive to climate. Our modeling analyses indicated that the negative effect of summer temperature on fir growth varied by aspect, and these results were confirmed by our observations of greatest declines in subalpine fir growth through time on east- and south-facing aspects. The growth patterns we observed in subalpine fir build upon recent studies indicating increasing climate-induced stress for high elevation forests by identifying species, landscape and climate interactions as drivers of forest stress at the ecosystem scale. Even in the absence of wide-scale mortality events, increased stress such as we observe in subalpine fir in specific landscape positions could change competition overtime and ultimately alter forest composition and growth dynamics.

Species-Related Growth Trends and Response to Climate

Growth trends of subalpine fir and Engelmann spruce in mixed assemblage stands in San Juan National Forest have diverged during the last several decades (Figure 3), and these divergent trends are likely driven by changing stand dynamics (Quicke and others 1994), an external stressor such as drought or insects (Pedersen 1998; Hogg and others 2002), or by climate warming (Jump and others 2006; Camarero and others 2015). Based on evidence from this study, it appears that growth declines in subalpine fir are due to the effect of recent climate change exacerbated by physical factors related to landscape aspect and associated water and energy balance; however, we also explore the possibility of internal stand dynamics as the driver of these patterns. Differing life history strategies and related stand dynamics may initiate divergent growth patterns in these species. Engelmann spruce are longer lived and ultimately more abundant in the canopy than subalpine fir, but the high shade tolerance and greater rates of regeneration and recruitment of subalpine fir make them more abundant in the understory (Oosting and Reed 1952; Whipple and Dix 1979; Veblen 1986). Therefore, a potential decline in sunlight available to subalpine fir when they are overtopped by Engelmann spruce as the forest matures could be responsible for the observed declines in BAI. Shading and competition from Engelmann spruce may contribute to the greater climate sensitivity of subalpine fir because less vigorous or suppressed trees can be particularly prone to drought stress (Vose and Swank 1994; Orwig and Abrams 1997; Pichler and Oberhuber 2007). However, there are a number of reasons why it appears that competition alone does not explain the patterns observed here. First, Engelmann spruce are taller than subalpine fir on every aspect, but forest decline in BAI is only observed in certain settings (Table 1). Second, our data do not indicate a change sensitivity of subalpine fir growth through time as would be expected if their growth sensitivity was related to competition from overstory trees. Finally, a more detailed examination of the climate response of subalpine fir growth patterns shows they are consistent with climate-induced physiological stress in specific landscape positions.

The results of this study strongly suggest that the decline in subalpine fir is caused by physiological stress related to climate. In a general sense, this conclusion is supported by the synchrony between declining BAI in subalpine fir and the time period of increasing temperature in this region (Figures 2, 4; Rangwala and Miller 2010). More specifically, we found that high summer temperatures decreased growth rates in subalpine fir (Figure 5) and the negative effect of warm temperatures on growth varied by aspect, consistent with expectations of seasonal and aspect-driven water limitation (Table 3, Figure 4). South-facing aspects receive

the greatest insolation and have the highest rates of evapotranspiration (Desta and others 2004; Broxton and others 2009; Gutiérrez-Jurado and others 2013; Hinckley and others 2014; Holdaway and others 2014), creating the potential for forest physiological stress related to low moisture or high temperature on these aspects. In spruce–fir forests of the Southern Rocky Mountains, east-facing aspects are also warmer and drier than north-facing aspects (Zapata-Rios and others 2015) and have the potential to induce physiological stress because these slopes see the most sun and warmest temperatures in the morning when photosynthesis is greatest for the day (Knapp and Smith 1981; Beadle and others 1985; Johnson and others 2004), in contrast to west-facing slopes where the timing of maximum insolation coincides with afternoon clouds and monsoonal rain (Young and Smith 1983; Blair 1996). Our observations of the greatest growth declines on east-facing aspects followed by south-facing aspects are consistent with the variations in water and energy balance across aspects, particularly because our south-facing sites are on average at a slightly higher elevation that the east-facing sites due to the distribution of subalpine fir in this region. Conversely, the growth rate of both Engelmann spruce and subalpine fir was greatest on north facing slopes where growth in both species increased through time, suggesting a lack of physiological limitation to growth for either species on these aspects (Figure 4A, B).

Differences in plant physiology among species can also control ecosystem-scale response to climate. In the Southern Rockies, the presence of growth declines in subalpine fir but not Engelmann spruce, and the contrasting climate growth relationships of these species are consistent with differences in their physiology. Engelmann spruce demonstrate greater control of water loss under dry conditions than subalpine fir (Knapp and Smith 1981; Kaufmann 1982), and they have an extensive rooting habit that may allow them to obtain soil water from snow-free areas in the spring when subalpine fir cannot (Day and others 1989). Subalpine fir also show seasonal adjustments in transpiration indicative of stomatal control over water loss (Pataki and others 2000), but they are particularly vulnerable to cavitation and therefore need to maintain high water tension (Sperry and others 1994). These physiological differences combined with variable edaphic conditions may increase stress in subalpine fir on specific landscape positions, such as east- and south-facing slopes, and make these trees more vulnerable to other environmental stresses or disturbances.

The Ecological Implications of Climate Stress

Subalpine forests of the Southern Rockies are experiencing increasing moisture stress and accelerating rates of background tree mortality over the past 30 years (Smith and others 2015). Such climate-related stress can make trees more vulnerable to insects or pathogens (Ayers and Lombardero 2000), and recent work shows that subalpine fir are being disproportionately affected by insects and pathogens in regions of Colorado's subalpine forest where local climate conditions are warmer and drier (Reich and others 2016). Our results indicate that subalpine fir experienced the most acute climate stress on east-facing aspects, followed by south and west, but we do not see similar signs of stress in Engelmann spruce. This contrast highlights the interaction of species, landscape position and climate as interacting controls on forest stress at the ecosystem scale. These interactions and the resulting contrast in growth responses between species and among landscape positions could lead to changes in subalpine forests through time; reduced growth in subalpine fir relative to Engelmann spruce will alter stand structure and forest growth dynamics, even in the absence of subalpine fir mortality. The differences in growth dynamics among species could be exacerbated if forest change is further facilitated by conditions such as subalpine fir decline (Harris 2003; Reich and others 2016), or other insects, pathogens or disturbance. Disturbances can affect trees of either species, such as the large spruce beetle outbreak currently ongoing in southern Colorado, but contrary to expectations based on other parts of San Juan National Forest, the Engelmann spruce in this study were not impacted by this outbreak and do not show signs of stress. Our results suggest that climate effects on spruce–fir forests of the Southern Rockies will be driven by complex interactions of species, landscape and climate that create localized conditions of forest stress and thus control future forest composition and growth dynamics.

Forests of the southwestern US are currently undergoing many changes that could influence the future state of these ecosystems. The Southern Rocky Mountain region warmed 1°C between 1895 and 2005, with the majority of the warming occurring in the last several decades (Rangwala and Miller 2010). Downscaled regional climate models predict that by 2070 both minimum and maximum temperatures will increase by at least 2°C in all seasons (Rangwala and others 2012). Future warmer temperatures could impose greater physiolog-

ical stress on subalpine fir and other subalpine species both by reducing soil moisture, and through effects on photosynthesis and metabolism. Our study suggests that both species-specific differences in growth response to climate stress, and variable growth patterns within species driven by aspect, will be important in determining future forest growth. Existing research on the physiological differences between subalpine fir and Engelmann spruce suggests that the contrasting growth responses we observe here may be related to plant–water relations; however, studies comparing the physiology of these two species are limited, particularly regarding how each species responds to the types of stressors likely to occur with climate warming. This work advances our understanding of how landscape factors can mitigate or exacerbate forest physiological stress related to climate change and lays the groundwork for future experimental research on the mechanisms responsible for driving differences in growth among species, and across variable physiography, which ultimately have implications for future growth dynamics and forest ecosystem composition.

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