



# Higher temperatures increase growth rates of Rocky Mountain montane tree seedlings

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**Citation:** Carroll, C. J. W., A. K. Knapp, and P. H. Martin. 2021. Higher temperatures increase growth rates of Rocky Mountain montane tree seedlings. *Ecosphere* 12(3):e03414. 10.1002/ecs2.3414

**Abstract.** Recent observational studies report weak or flat temperature – growth relationships for many tree species in temperate forests. In contrast, distribution limits of trees are strongly shaped by temperature, and studies show marked short-term temperature effects on leaf-level ecophysiology. To better determine the effects of warming on trees, we planted one-year-old seedlings of one lower montane (ponderosa pine), two upper montane (quaking aspen and lodgepole pine), and one subalpine tree species (subalpine fir) in in situ experimental gardens on an elevation gradient in the Rocky Mountains (USA) which span a 6°C range in temperature but have approximately uniform precipitation. Seedlings were lightly watered the first three growing seasons to facilitate establishment, and growth and survivorship were followed for four years. We expected a trade-off between growth and survivorship, as seedlings in high temperatures grow faster (e.g., with a longer growing season), but have higher mortality from heat stress. Compared to the coldest site, aspen (+256% wider, +337% taller), ponderosa pine (+234% wider, 270% taller), and lodgepole pine (+235% wider, 283% taller) all had strikingly higher cumulative diameter and height growth in the warmest site by the end of the study. Linear models of cumulative and annual growth in the montane species showed strong, positive relationships with growing-season temperature, but no significant relationships with growing-season precipitation. In contrast, growth of subalpine fir did not vary significantly with temperature, but increased slightly with higher growing-season precipitation. Accelerated growth did not come at the expense of survivorship in the montane species: cumulative four-year survivorship of the montane species remained robust (71.4–94.4%) in high temperatures, but caused complete mortality of subalpine fir. As long as precipitation remains adequate, these results indicate that warming is likely to strongly increase growth in seedlings of montane species with only modest decreases in survivorship despite higher evapotranspiration, especially in cooler and wetter portions of their current distributions where hydric stress is low. In contrast, warming may negatively affect seedling growth and survival in hotter and drier areas of the Rockies, and warming of +3–6°C may endanger the persistence of subalpine fir over much of its current distribution.

**Key words:** climate change; experimental gardens; global change; mixed conifer; montane tree species; Rocky Mountains; seedling growth; temperature.

**Received** 18 August 2020; accepted 31 August 2020; final version received 5 January 2021. Corresponding Editor: Debra P. C. Peters.

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## INTRODUCTION

Temperatures are rising in forests worldwide. Models forecast global temperatures to rise

1.1°–6.4°C by 2100 (compared to 1980–1999), with high-latitude forests warming by as much as 5°–8°C in the winter (Christensen et al. 2007). Temperatures have already increased sharply in

the montane ecosystems of the western USA, having risen three times faster than the global mean over the last 100 yr (Pederson et al. 2010). At the same time, precipitation patterns are changing in western mountains (e.g., the ratio of snow vs. rain; Mote et al. 2005), but only modest changes in total precipitation have been observed across the region, with a small increase (0–10%) in the central and northern Rockies (Kittel et al. 2002, Lukas et al. 2014) and a small decrease (0–5%) in the southern Rockies (Lukas et al. 2014). Climate forecasts predict these trends will continue over the next 50–100 yr in the region, with warming steadily increasing (+3°C in Colorado by 2100; Gross et al. 2016) while total precipitation remains largely unchanged (Lukas et al. 2014). Thus, increases in temperature in the coming decades are likely to have much greater effects on this system than changes in precipitation.

Higher temperatures will fundamentally impact the ecology of western forests, and evidence of warming's effects is accumulating, especially in altered disturbance regimes (e.g., Veblen et al. 2003) and insect outbreaks (e.g., Brown and Wu 2005), but how higher temperatures are influencing tree demography in the region has received less attention. A key question is how life-history trade-offs and growth hierarchies between species are altered, as such changes will have a large influence on how forest communities are shaped by climate change (Canham and Murphy 2016, Buechling et al. 2017). In forests, life-history trade-offs commonly manifest as an interspecific trade-off between growth and survivorship (e.g., Kobe et al. 1995, Martin et al. 2010), for example due to constraints in the plasticity of different physiological (e.g., rates of metabolism; Körner 2016), morphological (e.g., leaf shape; Royer et al. 2009), and phenological (e.g., conservative dormancy strategies to avoid freezing temperatures; Howe et al. 2003) traits needed to optimize growth and survivorship across a range in temperatures (e.g., Rehfeldt et al. 1999). In particular, adaptations needed for freeze tolerance may limit growth rates in trees (Loehle 1998).

Numerous models have been developed to address how climate change will impact forests, especially correlative climate envelope models (CEMs; e.g., Iverson et al. 2004) and

ecophysiological process models (e.g., VEMAP 1995), and both predict large and rapid shifts in ranges and increases in forest productivity. Yet despite increasing sophistication, for example, incorporating the role of local adaptation (Gray and Hamann 2013), functional-type (Dobrowski et al. 2015), and trait-based (Anderegg 2015) perspectives, the realism of CEMs has been called into question due to key assumptions common in these models (e.g., distributions remain in equilibrium with climate; e.g., Pearson and Dawson 2003, Heikkinen et al. 2006) and validation of CEMs remains problematic (Araújo et al. 2005). Many models also rely on presence–absence data, but long lags common in forest dynamics mean current distributions unlikely reflect how trees are responding to ongoing climate change (Clark et al. 2011).

Ecophysiological and dendroecological studies of trees and temperature—as well as a number of recent field-based observational studies on climate and forests (e.g., Buechling et al. 2017)—offer empirical counterpoints to models. Ecophysiological studies—usually conducted in growth chambers inside or on potted seedlings outside—provide direct insights into temperature effects on growth, but such studies typically use plants that have undergone a pre-acclimation treatment (Way and Oren 2010), are rarely replicated over a range of climates, infrequently use full in situ field conditions (e.g., including a dormant period), and tell us little about the effects of warming on survivorship. Retrospective tree ring analyses have provided little clarity on these issues as well, with studies showing both increased and decreased growth with warming, depending on temperature levels (the divergence problem; D'Arrigo et al. 2008). Finally, observational studies along climate gradients, which offer direct insights into in situ patterns, report many tree species having a flat growth response over a wide range in temperature (Canham and Thomas 2010, Coomes et al. 2014, Canham and Murphy 2016, Buechling et al. 2017), despite temperature gradients strongly shaping the distribution patterns and range limits of trees (Martin and Canham 2020). Observational studies, however, can have confounding effects (e.g., local adaptation, covariation in temperature and moisture) that make isolating the role of temperature challenging.

Collectively, these approaches leave us with conflicting evidence on how forests will respond to warmer temperatures, and highlight the need for more controlled, in situ studies of temperature's role in tree performance, especially studies that follow both growth and survivorship for multiple years. This is especially pressing in the western USA given the rates of warming in the region. To address these issues, active warming experiments are increasingly utilized, with whole-plant chambers (e.g., Barton et al. 2010, Sigurdsson et al. 2013), infrared heaters (e.g., Kueppers et al. 2017a), or coupled plant and soil warming treatments (Reich et al. 2015) imposed on naturally or experimentally established seeds or plants, but such climate experiments remain underrepresented in woody biomes, due to considerable logistical and financial constraints (Wu et al. 2011).

The central goal of this study is to address how warming is impacting tree ecology in Rocky Mountain forests, studying tree seedlings in situ across a wide temperature gradient. Using experimental gardens along an elevational gradient with a 6°C range in mean annual temperature but only modest variation in precipitation (Appendix S1: Table S1), we test how climate impacts multi-year, in situ growth and survivorship of seedlings from four dominant tree species—quaking aspen (*Populus tremuloides*), lodgepole pine (*Pinus contorta*), ponderosa pine (*Pinus ponderosa*) and subalpine fir (*Abies lasiocarpa*)—in Rocky Mountain forests. With this design, we can examine how warming impacts life-history strategies; for example, as it warms, do species adapted to hotter, lower elevation forest have higher fitness than species from colder high elevation forests? Growth in high elevation tree species can be temperature limited (Way and Oren 2010), while seedling growth in similar high elevation conditions can be moisture limited (Moyes et al. 2015), suggesting variation in both variables will be important for seedling demography. Overall, we expect higher temperatures will increase seedling growth in Rocky Mountain forests when precipitation is constant or increased, as predicted for large areas of the region. At the same time, we expect there will be a trade-off between growth and survivorship, as seedlings which benefit from warmer temperatures (e.g., by growing

faster due to a longer growing season) are also at increased risk of stress and mortality due to moisture stress (e.g., cavitation, desiccation) even when precipitation is held constant, due to higher moisture stress from increased evapotranspiration.

## METHODS

### Study sites

We investigated the role of temperature on the growth and survivorship of tree seedlings in three experimental gardens established in 2014. As Colorado is expected to experience + 3°C of warming by 2100 (Gross et al. 2016), we used 800-m resolution PRISM data from 1994 to 2013 (PRISM Climate Group 2015) to select closely located sites with ~3°C differences in mean annual temperature (MAT) and similar annual and growing-season (April–September) precipitation (Appendix S1: Table S1). The gardens were located at 1570 m (N°40.5884, W°105.1414), 2460 m (N°40.6247, W°105.3350), and 2750 m (N°40.5723, W°105.5909) elevation along a 1,200 m elevation transect in the Front Range of Colorado (Fig. 1). The low and the intermediate elevation gardens are ~16 km apart, and intermediate and high elevation gardens are ~22 km apart. At the high elevation site, the forest is presently dominated by pole-sized trees and large saplings of lodgepole pine and quaking aspen, and seedlings and saplings of subalpine fir and Engelmann spruce (*Picea engelmannii*), all regrowing after the stand-replacing Hourglass fire in 1994; the intermediate elevation site is dominated by a matrix of adult-sized trees of Douglas fir (*Pseudotsuga menziesii*), quaking aspen, ponderosa and lodgepole pines, and some nearby open grass and herbaceous areas created by the High Park fire in 2012. The low elevation site is in a fallow field owned by the Colorado State Forest Service Nursery.

### Experimental design

To study the direct and indirect effects of temperature on seedling performance, we standardized several key factors across gardens—topographic exposure (slope and aspect), light availability, long-term mean growing-season precipitation, competitive environment, seedling age and population source, and soils. We did not

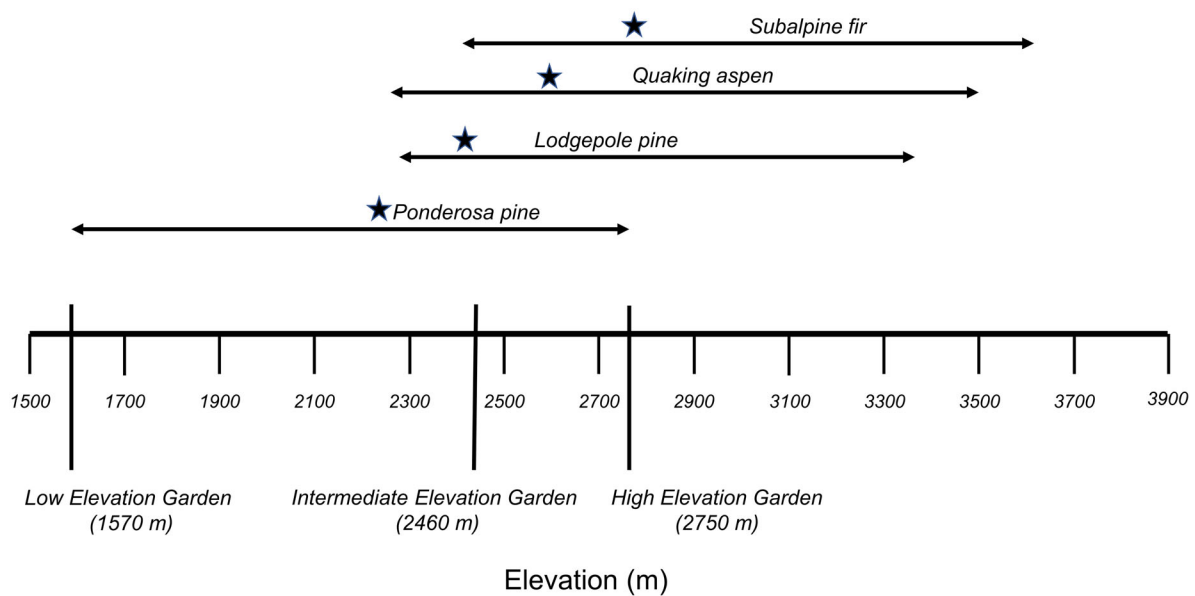


Fig. 1. Elevation ranges (m) of the four study species in northern Colorado—quaking aspen (*Populus tremuloides*), lodgepole pine (*Pinus contorta*), ponderosa pine (*Pinus ponderosa*), and subalpine fir (*Abies lasiocarpa*). Elevation range data were compiled from Peet (1981), Huckaby et al. (2003), Veblen and Donnegan (2005), and from the Colorado State Forest Service. The approximate seed source elevation for each species is denoted with a star, and the elevation of each of the gardens in this study is shown with vertical lines.

standardize soil moisture levels, letting variation in evapotranspiration (an indirect effect of higher temperatures) and inter-seasonal variation in precipitation influence soil moisture levels. At each site, we selected a flat area with a neutral aspect and full-sun exposure and removed all vegetation (e.g., cut down extant saplings). To provide homogeneous edaphic conditions, we removed the top ~30 cm of soil from a 37 m<sup>2</sup> area (4.3 × 8.6 m) at each site and filled these areas with soil collected from the intermediate site. The soil was moved to the new locations immediately within two hours of excavation and was then tilled in place. Plots were weeded bi-annually, and we placed a 2 m high fence around each site to limit herbivory. Starting June 2015, at each site we measured air temperature and precipitation with a Hobo Pro weather station fit with a ventilated radiation shield (Onset), and soil temperature and soil volumetric water content (VWC) with four 5TM sensors (Decagon Devices) deployed horizontally at a depth of 5 cm. We used PRISM data (Appendix S1: Table S1) for estimates of snow and total winter precipitation

at each site as Hobo Pro weather stations do not accurately measure snowfall.

As our goal was to evaluate warming effects on the ecology of tree seedlings, we transplanted one-year-old seedlings into different temperature regimes and followed their growth and survivorship for four growing seasons. Our study was not designed for insights into warming's effects on seed ecology, germination, or first-year seedling establishment. Seedlings used in the study were germinated and grown under identical conditions for one year at the nursery run by the Colorado State Forest Service in Fort Collins, Colorado. We used seedlings of four species dominant in the Rocky Mountains of northern Colorado: one species dominant in the lower montane forest zone, ponderosa pine; two species dominant in the upper montane forest zone, quaking aspen and lodgepole pine; and one species dominant in the subalpine forest zone, subalpine fir (zones per Peet 1981). While each of these species occurs over a wide elevation range (Fig. 1), we refer to lodgepole pine and aspen as upper montane species, as these species attain

their highest abundance in elevations below the subalpine forests dominated by Engelmann spruce and subalpine fir, and ponderosa pine as a lower montane species as it dominates in the lower elevations of the Front Range. Seeds were collected from a single stand per species in sites in the nearby Roosevelt National Forest, which minimizes within-species differences between individuals due to local adaptation; seed was collected at 2250 m for ponderosa pine, 2450 m for lodgepole pine, 2600 m for quaking aspen, and 2750 m for subalpine fir (Fig. 1). The intermediate elevation site overlaps with the current elevational distributions of all four species in the Front Range (Fig. 1); the low elevation site is well below the elevational distributions of subalpine fir, lodgepole pine, and quaking aspen and just below the range of ponderosa pine; and the highest site overlaps with the distributions of subalpine fir, lodgepole pine, and quaking aspen and is slightly above the typical range of ponderosa pine, whose range tops out at ~2740 m except on warmest south-facing slopes where it can occur up to ~3050 m in elevation (Huckaby et al. 2003).

In June 2014, we planted the one-year-old seedlings bare-rooted in each site. Each 37-m<sup>2</sup> garden received 42 seedlings each of quaking aspen, lodgepole pine, and subalpine fir, and 36 seedlings of ponderosa pine due to spacing limitations. Each garden consisted of two adjacent plots with seedlings planted in a 9 × 9 grid resulting in 162 total seedlings per garden or 81 seedlings per plot. Each seedling was planted with a spacing radius of ~26.5 cm to reduce root competition. The southernmost row in each plot was planted with the shortest statured species at planting (subalpine fir), with consecutive rows containing taller and taller species to minimize shading. From 2014 to 2017, height (root collar to tip of terminal bud) and diameter (at D5, 5 cm above the root collar) were measured monthly during each growing season (April–September). Studies indicate that several years of higher moisture is associated with successful initial seedling recruitment in the region (e.g., Brown and Wu 2005)—hence, to facilitate initial establishment, each garden was hand-watered (to control quantities) in 2014 and 2015 twice a month from June through September with the equivalent 4 cm of water spread evenly across

the entire plot, a ~8–10% increase above average growing-season precipitation per PRISM data (Appendix S1: Table S1). In 2016, each garden was watered once a month with 4 cm of water from June through September and then stopped entirely for the remainder of the study.

### Statistical analysis

To build models of seedling growth, we focused on diameter growth, which is generally preferable to height growth when modeling growth in seedlings (e.g., Martin and Marks 2006) and saplings (e.g., Martin et al. 2010). First, we used linear mixed-effects models to test for mean differences in mean annual diameter growth between sites, using initial size, the interaction between site and species as fixed effects, and individual as a random effect to account for repeated measures; mean site-level differences were assessed using Tukey's HSD post hoc adjusted pairwise comparisons.

Next, we used linear mixed-effects models to evaluate continuous predictors of temperature and precipitation for each species. We examined potential predictor variables (Appendix S1: Table S2) with Pearson correlations, examining multicollinearity and calculating cross-correlations to avoid regression pitfalls (Neter et al. 1996). We evaluated predictors of annual, growing-season and winter temperature and precipitation, and growing-season soil moisture (VWC). Growing-season climate (mean daily growing-season air temperature and cumulative growing-season precipitation from April 1st through September 30th) and VWC were summarized from the weather stations and soil moisture sensors deployed at each site, and annual and winter climate were summarized from 800-m resolution PRISM data. Variables with a cross-correlation > 0.50 were not used in the same model. Only seasonal measures of temperature and precipitation were suitable for inclusion in full models (Appendix S1: Table S2). Seedlings were likely impacted by transplant effects in year one, and thus, we excluded all 2014 data from statistical analyses of growth.

With the subset of suitable predictor variables (i.e., cross-correlation ≤ 0.50), we then modeled seedling growth (a) as a function of climate and cumulative diameter growth (calculated from September 2014 to September 2017), and (b)

climate and annual diameter growth (calculated from each September to September; e.g., 2015 growth is change in D5 from 9/2014 to 9/2015). To assess cumulative growth, we used species-specific multiple linear regressions to model three years of growth as a function of mean growing-season temperature and growing-season precipitation averaged at each site, and a size term to account for variation in initial diameter. For annual growth, we used linear mixed effects to model annual growth as a function of year-to-year variation in growing-season temperature and growing-season precipitation at each site from 2015 to 2017, a seedling size term as a fixed effect, and a random effect of individual seedling to account for repeated measures of individual seedlings over time. An interaction between growing-season temperature and growing-season precipitation and minimum annual temperature or cumulative winter precipitation (November 1st to March 31st in the months preceding a growing season) were also included as candidate predictors in the annual models; the mixed-effects model dataset had more statistical power, but not enough to include minimum annual temperature and cumulative winter precipitation simultaneously in a model. Linear mixed-effects models were constructed using the lmer function in the lme4 R package (Bates et al. 2015). A series of models were developed for each species and full models evaluated size and year-to-year variation in climate in a linear mixed-effects framework:

$$\begin{aligned}
 \text{Diameter growth} = & \text{mean growing – season temperature} \\
 & + \text{total growing – season precipitation} \\
 & + \text{mean growing – season temperature} \\
 & \times \text{total growing – season precipitation} \\
 & (\text{interaction}) + \text{size} \\
 & + \text{minimum annual temperature or total} \\
 & \text{winter precipitation (one per model run)} \\
 & + \text{random effect (for repeated measures)} \\
 & (1)
 \end{aligned}$$

The final model was selected using AIC with 2-unit support intervals ( $\Delta\text{AIC} < 2$ ) to choose among the best, most parsimonious models. A Type III ANOVA with Satterthwaite's method

was used to test the significance and importance of the fixed effects, and partial  $R^2$  values for each fixed effect was determined using the Nakagawa and Schielzeth approach in the R package r2glmm (Jaeger 2017).

Probability of mortality was assessed for each seedling at each time step via Cox Proportional Hazard models using the survival Package in R (Therneau 2015)—which allow for dynamic predictors of mortality while controlling for repeated measures (Chalita et al. 2006)—as a function of site (i.e., temperature), change in diameter growth, and change in allocation ratio (height:basal area) of a seedling at annual time-steps. Ties were accounted with the Efron approximation. Statistics were calculated in R (3.5.1). Initial seedling survival was also likely impacted by transplant effects and thus we excluded all 2014 data, and any stems killed by herbivory (which was minimal) in 2015–2017, from statistical analyses of survivorship.

## RESULTS

### *Temperature and moisture*

Annual and growing-season air temperatures were consistently  $\sim 3^\circ\text{C}$  different between neighboring sites, providing a full  $6^\circ\text{C}$  range in MAT from the lowest to the highest site in the study (Fig. 2A–C, Appendix S1: Table S1), which is greater than any other in situ study reported in a meta-analysis of 100 + warming studies (Lin et al. 2010). 2015 was the warmest and 2017 was the coolest growing season, but the relative differences in temperature between sites remained consistent across years. Soil temperatures were closely correlated with air temperatures (Fig. 2D). Annual precipitation varied between sites, mostly due to higher winter precipitation at the higher elevation sites, and precipitation had more interannual variability than temperature, but growing-season precipitation was similar between sites (Fig. 2A–C): mean growing-season precipitation in 2015–2017 was 280 mm at the low elevation site, 299 mm at the intermediate elevation site, and 282 mm at the high elevation site. Precipitation received in the sites during the study was similar to the long-term averages (Appendix S1: Table S1), with 2014 consistent with the 10-year average (12–16% wetter across

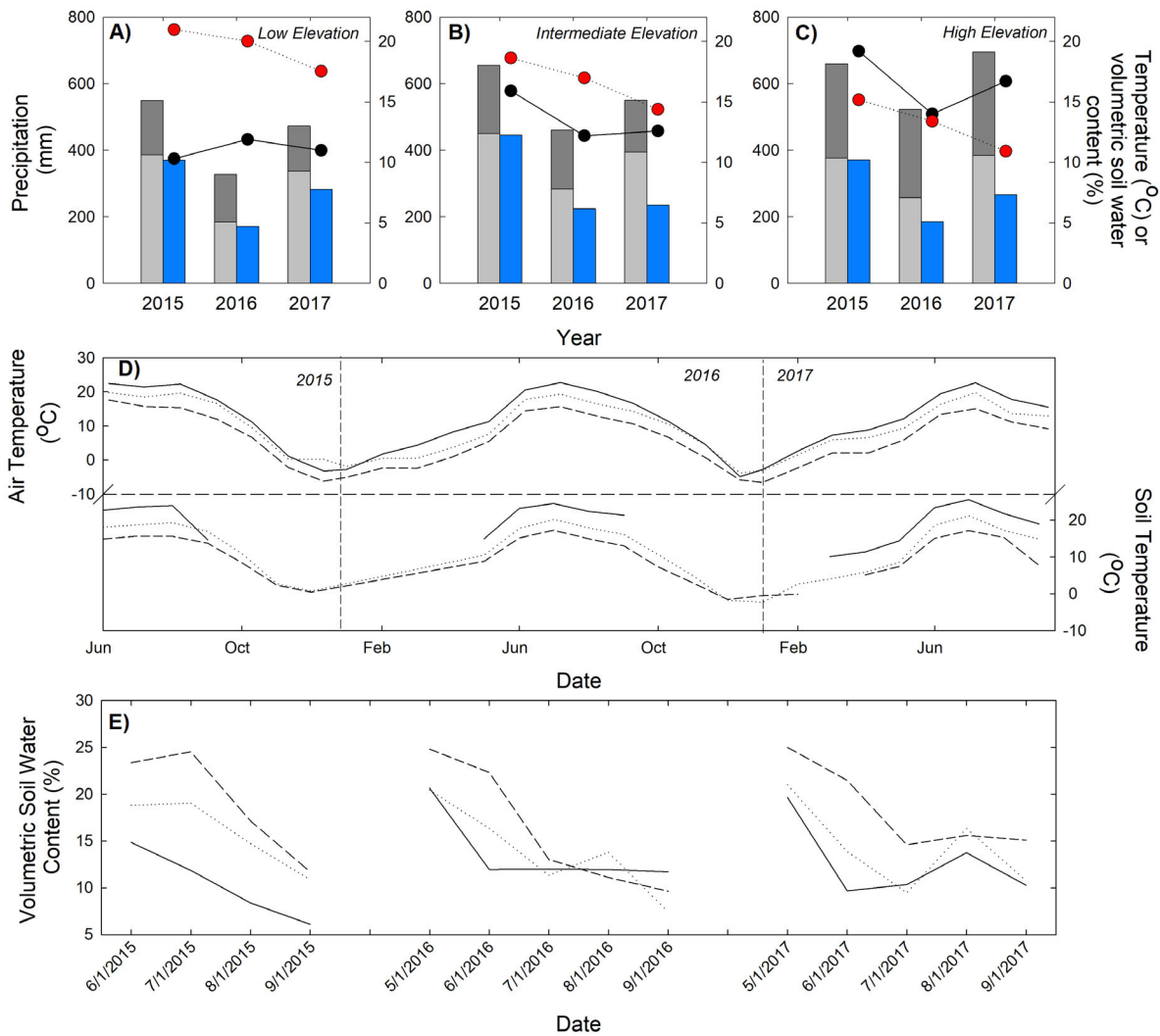


Fig. 2. Panels (A–C): Annual and growing-season precipitation, air temperature, and soil moisture in three experimental gardens along a temperature gradient in the Rocky Mountains. Annual (dark gray bars) and April 1<sup>st</sup>–September 30th (light gray bars) combined precipitation are from 800-m resolution PRISM data, and April 1<sup>st</sup>–September 30th (blue bars) precipitation are from on-site with weather stations. Mean daily air temperature (red dot) and soil moisture (black dot) from June 1st to September 31st were measured on-site. Panel (D): Daily mean air and soil temperatures from June 2015 to September 2017. Panel (E): Mean monthly volumetric water content (%). In (D and E), the low site is solid (–), intermediate site is dotted (…), and high site is dashed (– –).

the three sites), 2015 above-average (23–32% wetter), 2016 below-average (12–35% drier), and 2017 above-average (12–25% wetter). Despite similar growing-season precipitation, there were modest but consistent differences in growing-season soil moisture between the sites: the low site averaged 10.8% volumetric water content (VWC), the intermediate site 13.2% VWC, and the high site 16.7%

VWC. Differences in VWC between sites were primarily due to differences in temperature: VWC was strongly correlated ( $r = 0.63$ ) with growing-season temperature, but only weakly with growing-season ( $r = 0.11$ ) and winter ( $r = 0.25$ ) precipitation (Appendix S1: Table S2). There was no detectable change in VWC levels after water additions were ended (Fig. 2E).

### Growth

We investigated how in situ variation in temperature and precipitation influenced the growth of transplanted one-year-old seedlings, while holding light, soils, seedling age, and seed source all approximately constant. Based on ~19,000 measurements on > 400 individual seedlings, we found that higher temperatures markedly increased cumulative and annual growth rates in the lower montane (ponderosa pine) and two upper montane species (aspen and lodgepole pine; Tables 1 and 2, Fig. 3), especially in the hottest site which is at an elevation lower than the current range limits of all three species in the Front Range region (Fig. 1). In contrast, seedlings of subalpine fir showed no significant variation in growth rates across the range of temperatures in the study. In the montane species, we observed faster rates of growth at higher temperatures both in the first part of the study when moisture was comparatively high (from higher precipitation and watering) and in the second when moisture was comparatively low (from lower precipitation and no watering; Figs. 2 and 3). Comparing the warmest site to the coldest, aspen (+256% higher), ponderosa pine (+234% higher), and lodgepole pine (+235% higher) all had significantly higher cumulative diameter growth by the end of the study ( $P$ -values all <0.0001 per Tukey's HSD post hoc tests, familywise error rate < 0.05; Table 1 and Appendix S1: Table S3). Mean height growth was also markedly higher in the warmest site compared to the coldest, with aspen (+337% higher), ponderosa pine (+270% higher), and lodgepole pine (+283% higher) all substantially taller by the end of the study. Aspen ( $P = 0.028$ ) and ponderosa pine ( $P = 0.007$ ), but not lodgepole pine ( $P = 0.963$ ), also grew significantly faster in diameter at the intermediate site compared to the coldest site, while subalpine fir ( $P = 0.018$ ) grew significantly slower at the warmest site compared to the intermediate site (Appendix S1: Table S3). Growth differences between species within a site are shown in Appendix S1: Table S4.

Simple linear models of cumulative growth in the montane species showed strong, positive relationships with growing-season temperature, which accounted for 48% of variation in growth rates in aspen, 58% in lodgepole pine, and 66% in ponderosa pine (Table 2). Cumulative growth

in the montane species had no significant relationships with mean growing-season precipitation. In contrast, cumulative growth of subalpine fir did not vary significantly with temperature (partial  $R^2 = 0.002$ ,  $P = 0.759$ ), but increased slightly with higher growing-season precipitation (partial  $R^2 = 0.099$ ,  $P = 0.014$ ; Table 2).

Patterns in annual growth rates were similar to cumulative growth. However, due to limited statistical power caused by high mortality by 2017, subalpine fir would not converge in a mixed-effects model; hence, mixed-effects models are only presented for the montane species. Annual growth models allowed us to assess the influence of growing-season precipitation (via year-to-year variation) and account for the vagaries of individual seedling performance. In these models, annual growth in the montane species again responded foremost to variation in growing-season temperature (partial  $R^2 = 0.325$ – $0.445$ , all  $P < 0.001$ ; Table 2). In contrast, the relative importance of growing-season precipitation (partial  $R^2 = 0.007$ – $0.197$ ) and the interaction between temperature and precipitation (partial  $R^2 = 0.005$ – $0.012$ ) were low for all species, especially compared to temperature (Table 2), and winter precipitation and minimum annual temperature were dropped via AIC for all species (Appendix S1: Table S5).

### Survivorship

Survivorship differed markedly across sites and species. Between planting in June 2014 and the end of the growing season in 2015, there was an initial pulse of mortality for all of the species in most of the sites despite the supplemental water in this period, likely due to transplant shock. Nevertheless, aspen (79–89%) and ponderosa pine (85–94%) had notably high cumulative four-year survivorships at all sites (Table 1). Subalpine fir experienced 100% mortality at the warmest site by year four and had cumulative four-year survivorships of 47.5% at the intermediate site and 85.7% at the coldest site. Lodgepole pine's cumulative survivorship patterns were the most variable, attaining a high of 71% at the warmest site and a low of 30% at the intermediate site. After 2015, year-to-year survivorship rates were very high, ranging from 91% to 100% (mean 98%) for 10 of the 12 species-site combinations—the exceptions occurred in the warmest



Table 1. Mean seedling diameter (measured at 5 cm above the root collar; D5) and height at the start (June 2014) and the end (September 2017) of the study in four dominant tree species growing in three temperature regimes in the Rocky Mountains.

Site	Diameter (mm) ( $\pm$ SE)		Height (cm) ( $\pm$ SE)		Cumulative survivorship (%)			
	2014	2017	2014	2017	2014	2015	2016	2017
Warmest								
Aspen	4.7 (0.1)	18.8 (0.8)	84.5 (1.6)	145.1 (3.7)	97.6	83.3	83.3	83.3
Lodgepole pine	6.0 (0.1)	18.4 (0.4)	41.5 (0.3)	81.4 (1.8)	97.6	90.5	88.1	71.4
Ponderosa pine	4.6 (0.1)	17.6 (0.4)	17.0 (0.3)	44.8 (1.2)	97.2	94.4	94.4	94.4
Subalpine fir	2.8 (0.1)	n/a	10.6 (0.2)	n/a	94.7	68.4	31.6	0
Intermediate								
Aspen	5.1 (0.1)	14.5 (1.3)	84.7 (1.6)	116.4 (6.0)	100	97.3	91.9	89.2
Lodgepole pine	6.5 (0.1)	11.9 (1.4)	43.3 (0.3)	52.9 (7.9)	97.6	47.5	30.0	30.0
Ponderosa pine	4.8 (0.1)	13.9 (0.5)	16.5 (0.3)	32.7 (1.0)	100	96.3	85.2	85.2
Subalpine fir	3.1 (0.1)	8.1 (0.5)	9.8 (0.2)	19.0 (1.2)	100	61.9	52.4	47.6
Coldest								
Aspen	5.0 (0.1)	10.5 (0.5)	88.6 (1.4)	106.6 (4.5)	89.5	86.8	81.6	78.9
Lodgepole pine	5.9 (0.1)	11.2 (0.7)	42.8 (0.3)	56.8 (2.8)	95.2	52.4	50.0	47.6
Ponderosa pine	4.8 (0.1)	10.3 (0.4)	15.7 (0.3)	26.0 (1.3)	100	91.4	91.4	91.4
Subalpine fir	3.0 (0.2)	7.5 (0.3)	10.1 (0.2)	22.3 (1.1)	100	85.7	85.7	85.7

Note: Cumulative survivorship (%) was calculated from the initial number of seedlings at the start of the study in early June 2014 to the end of each subsequent growing season in late September.

site where year-to-year survivorship was 81% for lodgepole pine and 0% for subalpine fir. Overall, lodgepole pine and ponderosa pine had their highest cumulative survivorship, and aspen its second highest cumulative survivorship, in the hottest site. The timing of these patterns suggest that the end of watering had a negligible effect on subalpine fir survivorship at the coldest and intermediate sites, but was coincident with a large decrease in survivorship at the warmest site; lodgepole pine had a small decrease in survivorship coincident with the end of watering at the warmest site; and aspen and ponderosa pine survivorship showed no coincident effects with changes in the watering regimen at any site.

Temperature across the sites and growth rate generally had significant effects on seedling survival (Cox model, Table 3). For the montane species, growing at the coldest site compared to the intermediate site significantly reduced the risk of mortality for aspen ( $P < 0.001$ ), lodgepole pine ( $P < 0.001$ ), and ponderosa pine ( $P < 0.001$ ), while moving from the intermediate to warmest site did not significantly change the risk of mortality for aspen and ponderosa pine but reduced it for lodgepole pine ( $P < 0.001$ ). Mortality risks between the warmest and coldest sites were insignificantly different for all three montane

species. For subalpine fir, growing at the coldest site compared to the intermediate site significantly reduced its risk of mortality ( $P < 0.001$ ), while growing at the warmest site compared to the intermediate and coldest sites significantly increased its risk of mortality (both  $P < 0.001$ ). For all species except lodgepole pine ( $P < 0.625$ ), faster-growing seedlings were significantly less likely to die compared to slower-growing seedlings, a ~3–10% reduction in annual mortality risk for each  $1 \text{ mm}^2 \text{ yr}^{-1}$  increase in growth rate compared to seedlings with little (i.e.,  $< 0.1 \text{ mm}^2 \text{ yr}^{-1}$ ) or no diameter growth (all  $P < 0.001$ ). Increases in height-to-basal area ratios in individual seedlings only significantly reduced the risk of mortality for ponderosa pine ( $P = 0.002$ ).

## DISCUSSION

This study addresses the fundamental climate niche of Rocky Mountain tree seedlings across a wide range in temperature and modest fluctuations in interannual precipitation. In the montane species, the highest temperatures unambiguously increased cumulative and annual growth rates, with no attendant increases in mortality. In contrast, seedlings of subalpine fir showed no significant variation in growth as a function of

Table 2. Models of seedling growth as a function of climate and seedling size. Multiple linear regression models evaluated cumulative diameter growth from September 2014 to September 2017 as a function of growing-season temperature (GST), growing-season precipitation (GSP), and seedling size (D5).

Species	Parameter	$\beta \pm$ (SE)	<i>P</i> value	Partial $R^2$	df	<i>F</i>	<i>P</i> value	Model $R^2$
Cumulative growth—multiple linear regression models								
Aspen	Size	0.083 (0.480)	0.863	0.000	3,69	22.94	<0.001	0.50
	GST	3.902 (0.490)	<0.001	0.480				
	GSP	-0.060 (0.485)	0.902	0.000				
Lodgepole pine	Size	-0.359 (0.383)	0.341	0.019	3,49	30.59	<0.001	0.65
	GST	3.227 (0.393)	<0.001	0.579				
	GSP	-0.777 (0.402)	0.593	0.071				
Ponderosa pine	Size	-0.486 (0.258)	0.063	0.043	3,80	57.92	<0.001	0.69
	GST	3.171 (0.256)	<0.001	0.657				
	GSP	-0.011 (0.257)	0.967	0.000				
Subalpine fir	Size	-0.884 (0.195)	<0.001	0.261	3,58	8.797	<0.001	0.31
	GST	-0.064 (0.206)	0.759	0.002				
	GSP	0.522 (0.206)	0.014	0.099				
Annual growth—linear mixed-effects models								
Aspen	Size	-2.242 (0.13)	<0.001	0.333	1,162	303.39		0.47
	GST	2.144 (0.22)	<0.001	0.381	1,101	93.98		
	GSP	-0.229 (0.10)	0.019	0.007	1,144	5.63		
	GST $\times$ GSP	0.260 (0.08)	0.002	0.011	1,148	10.27		
Lodgepole pine	Size	-0.628 (0.11)	<0.001	0.151	1,132	52.99		0.49
	GST	1.224 (0.12)	<0.001	0.445	1,79	97.86		
	GSP	-0.569 (0.07)	<0.001	0.151	1,126	57.63		
	GST $\times$ GSP	-0.146 (0.07)	0.044	0.012	1,114	4.13		
Ponderosa pine	GST	0.848 (0.08)	<0.001	0.325	1,89	107.12		0.43
	GSP	-0.600 (0.08)	<0.001	0.197	1,180	65.64		
	GST $\times$ GSP	-0.098 (0.08)	0.228	0.005	1,172	1.47		

*Notes:* Linear mixed-effects models evaluated changes in annual seedling diameter growth from 2015 to 2017 and year-to-year variation at each site in growing-season temperature, growing-season precipitation, minimum annual temperature, cumulative winter precipitation, an interaction (GST  $\times$  GSP), and a seedling size term as a fixed effect. A random effect of individual seedling was included in these models to account for repeated measures of individual seedlings over time. The model shown here was selected using AIC.

temperature and experienced complete mortality at the highest temperatures by the fourth year in the study. In the montane species, we observed faster rates of growth at higher temperatures when moisture was comparatively high due to higher precipitation and watering, and when moisture was comparatively low due to lower precipitation and no watering (Figs. 2 and 3). Likewise, faster growth occurred even though the warmer sites had consistently lower soil moisture (Fig. 2), mostly likely due to higher evaporative demand from higher ambient temperatures. Growth continued to accelerate at the warmest site for two of the montane species over the length of the study. Overall, the results clearly indicate that under these conditions (e.g., average precipitation), the temperature increases

in our study (+3°C MAT for aspen and lodgepole pine, +1°C MAT for ponderosa pine) do not exceed the thermal growth thresholds of the montane species, and suggest that predicted increases in temperature over the next century may be insufficient alone to induce a negative growth switch even in seedlings of these species, which show evidence of higher sensitivity to ongoing regional change than adult-sized trees (e.g., Bell et al. 2014, but see Copenhaver-Parry et al. 2020). The montane species also exhibited a wide range in growth plasticity to temperature, both within and between species. The within-species plasticity is notable as the seedlings were all propagated from a single population and hence are likely to have limited differences in local adaptation to climate between individuals.

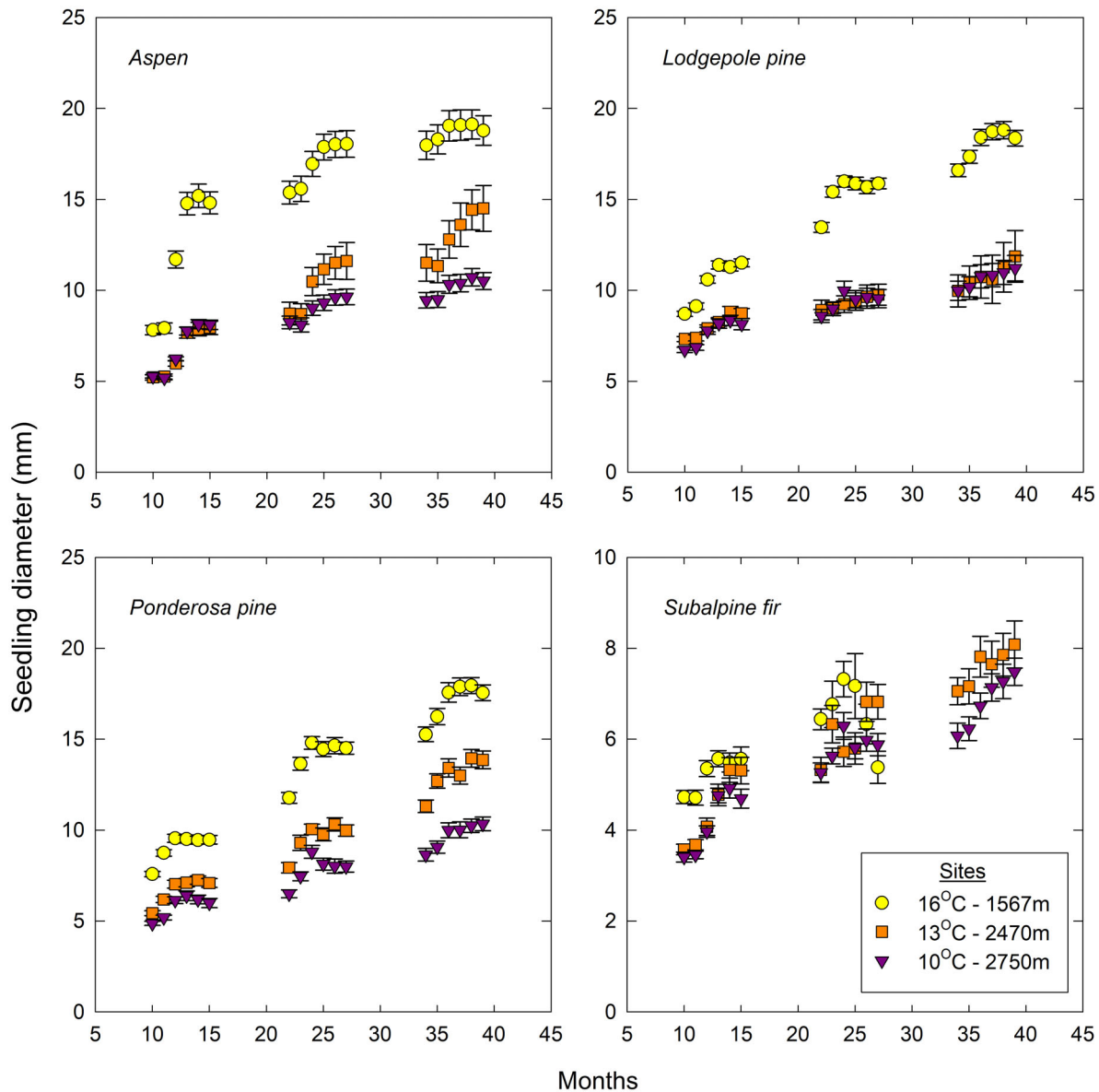


Fig. 3. Change in seedling diameter (measured at 5 cm above the ground) over time in 1-year-old seedlings of four tree species transplanted in experimental gardens on a 6°C gradient in mean annual temperature in the Rocky Mountains. Growth was measured monthly, and the x-axis shows growth by time beginning in June 2015 (10 months after planting) to the end of the study in month 40 (September 2017). Growth data from the first growing season (2014) were excluded from the analysis to avoid the effects transplant shock. Mean values of D5 ( $\pm 1$  SE) in each site are shown at each sampling date. Site temperatures (10°C, 13°C, 16°C) are the mean growing-season temperatures for each site during the study. Note the different scales on y-axes.

We emphasize, however, that the increased growth for the montane species under higher temperatures in our study occurred in conditions of generally average precipitation and perhaps

slightly above-average soil moisture (due to watering), and that these patterns could reverse in drier years. Others have also found that trees can grow markedly faster in warmer temperatures

Table 3. Cox proportional hazards models of seedling survivorship, contrasting mortality patterns between low (warm), intermediate (moderate), and high (cold) elevation sites.

Species	Site contrast	$\beta \pm$ (SE)	z score	P value	Hazard Ratio
Aspen	Intermediate vs. low	-0.864 (0.466)	-1.854	0.064	0.421
	Intermediate vs. high	-1.153 (0.317)	-3.641	<0.001	0.316
	Low vs. high	-0.289 (0.522)	-0.555	0.579	0.749
	Diameter growth	-0.447 (0.131)	-3.418	<0.001	0.640
	Allocation ratio	-0.040 (0.076)	-0.531	0.595	0.960
Lodgepole pine	Intermediate vs. low	-1.842 (0.396)	-4.606	<0.001	0.161
	Intermediate vs. high	-1.020 (0.276)	-3.680	<0.001	0.361
	Low vs. high	0.806 (0.436)	1.850	0.064	2.240
	Diameter growth	-0.048 (0.098)	-0.488	0.625	0.953
	Allocation ratio	0.099 (0.197)	0.506	0.612	1.105
Ponderosa pine	Intermediate vs. low	-0.858 (0.688)	-1.246	0.213	0.424
	Intermediate vs. high	-1.816 (0.536)	-3.390	<0.001	0.163
	Low vs. high	-0.958(0.840)	-1.142	0.254	0.383
	Diameter growth	-1.108 (0.278)	-3.982	<0.001	0.330
	Allocation ratio	-1.656 (0.548)	-3.020	0.002	0.191
Subalpine fir	Intermediate vs. low	1.434 (0.287)	5.000	<0.001	4.200
	Intermediate vs. high	-1.494 (0.449)	-3.327	<0.001	0.224
	Low vs. high	-2.928 (0.053)	-6.555	<0.001	0.053
	Diameter growth	-0.730 (0.178)	-4.179	<0.001	0.175
	Allocation ratio	-0.360 (0.255)	-1.411	0.158	0.698

Note: Probability of mortality of a seedling was modeled as a function of site (i.e., temperature), change in diameter growth (at D5), and change in allocation ratio (height:basal area) at annual time-steps.

when precipitation is normal or high (e.g., Carroll et al. 2014, Sillett et al. 2015), but caution that growth subsequently declines in the same species during drought conditions (Sillett et al. 2019).

Genecological studies have regularly demonstrated steep genetic clines in the cold adaptation traits of tree species on temperature gradients (e.g., Rehfeldt et al. 1999, Howe et al. 2003), and generally show populations of species are best adapted to the net effects of their local climate. This optimization generally creates a negative trade-off between growth potential and survivorship traits related to adaptation to low temperatures (i.e., cold hardiness and growth phenology; Loehle 1998, Rehfeldt et al. 1999, Aitken et al. 2008). The need for species to optimize their life-history strategies to the local climate raises the question why the montane species in our study experienced improved fitness—via accelerated growth coupled with high survivorship—in temperatures higher than currently found in their local distributions. The answer is likely that this growth-survivorship trade-off does not directly constrain acclimation and adaptation to warmer climates (Aitken et al. 2008). Indeed, numerous provenance trials have demonstrated that most

tree species have a strong acclimation potential to temperatures higher than found in their current range, and that their southern range limits are constrained not by excessive temperatures but by interspecific competition with warm-adapted species with faster growth rates in higher temperatures (Loehle 1998). However, strong acclimation to warmer temperatures may come at the expense of cold temperature survivorship (Loehle 1998).

#### Temperature and growth

There may now be sufficient evidence to generally expect faster growth in many woody species in higher temperatures—as found in our study—as several large meta-analyses report substantial increases in mean aboveground woody biomass in warming experiments: +26% (Lin et al. 2010), +27% (Wu et al. 2011), and +22% (Yuan et al. 2018). Such results have important implications for the productivity of forest ecosystems which appears likely to increase, at least until any temperature thresholds are exceeded. An increase in productivity should help buffer forest structure and composition to changes produced by warming temperatures, hopefully until warm-adapted

species arrive via migration (Loehle 1998). Except for subalpine fir, our results also conform with the pattern where tree species from montane ecosystems generally respond positively to warming (Way and Oren 2010).

These trends are not universal, however, and many studies stress that the effects of higher temperatures are often species- and site-specific. In a meta-analysis by Rustad et al. (2001), forest growth had both positive and negative responses to warming with a net response of  $\sim 0$ , and other studies report higher latitude tree species can experience reduced growth in higher temperatures, based on to (a) the form of the species (deciduous vs. evergreen, with evergreens more often showing negative effects; Way and Oren 2010); (b) when the species is growing near its warm range limit (Reich et al. 2015); (c) when soil fertility is insufficient to support faster growth (Ryan 2013); and (d) when warming is combined with reduced precipitation (Wu et al. 2011, Rodgers et al. 2018). These contrasting results demonstrate the need for more study.

The interspecific patterns in our study were surprisingly similar overall between the montane trees. Nevertheless, there were some notable differences between the species. We expected the lowest elevation species (ponderosa pine) and highest elevation species (subalpine fir) to show inverse growth and survivorship patterns at the hottest and coldest sites, but ponderosa pine survivorship was surprisingly insensitive to cold temperatures. In our study, aspen grew marginally faster in higher temperatures in relative and absolute diameter and dramatically faster in absolute height compared to the other species (Fig. 3, Table 1). This is consistent with other studies of aspen; for example, its seedlings grew taller, had larger stem diameters, and attained 59% total more biomass when grown in higher temperatures (Way et al. 2013). Ponderosa pine and lodgepole pine had similar rates of diameter growth across the study (Appendix S1: Table S4), but lodgepole pine grew substantially faster in absolute height compared to ponderosa pine in the warmest conditions (Table 1). Recent increases in temperature and associated increases in water deficit also increased growth in juveniles of ponderosa pine in the northern Rockies, although these factors were associated with decreased growth in the past (Hankin et al.

2019). For shade-intolerant species like aspen, ponderosa pine, and lodgepole pine, absolute height growth in juveniles is important in closed-canopy forests, as taller individuals receive more light and are more likely to occupy a spot in the upper tier once the canopy closes during stand development (e.g., Martin and Marks 2006). Unlike the montane species, diameter and height growth rates of subalpine fir were very uniform across the range in temperatures. Subalpine fir was the only shade-tolerant species in the study, however, and the high light levels in the gardens may have negatively interacted with the effects of higher temperatures on this species. Given wide variation in understory light levels in forests with different structure and composition (Canham et al. 1999), the role of shade in mediating species-specific responses to warming should be included in future studies, as variation in local conditions may strongly interact with the effects of climate change (Clark et al. 2011).

There are several reasons why warming could cause higher growth in the montane tree species, including higher net photosynthesis ( $P_n$ ) rates, a longer growing season, or improved soil fertility via higher N mineralization and decomposition of soil organic matter (SOM; Rustad et al. 2001). We expect that any changes in fertility were minor at our sites given the generally low SOM and total N in these soils. Likewise, Carroll et al. (2017) working in the same gardens, found inconsistent effects for how temperature altered  $P_n$  rates of the 3 montane species: at the temperatures typical for a site (i.e., its mean growing-season daytime temperatures), the average  $P_n$  rate of ponderosa pine showed no variation between sites, aspen had its highest  $P_n$  rate at the intermediate site and lodgepole pine its highest  $P_n$  rate at the coldest site. Rather, by providing a longer period for carbon accumulation and biomass gain, changes in phenology—all species had significantly earlier bud break at higher temperatures in these gardens, due in part to variation in snowpack duration among sites (Carroll et al. 2017)—appears the most likely explanation for the montane seedlings' higher growth rates in warmer conditions.

#### *Precipitation and growth*

Surprisingly, subalpine fir was the only species which had a significant and positive growth response to higher precipitation (Table 2). For the

montane species, we found little evidence of any change in growth rates in response to periods with higher precipitation, either in the growing season or in the winter, and growth rates in the montane species were actually negatively associated with higher growing-season precipitation, but these negative effects were minimal. To a degree, this is to be expected given the similar intra-annual growing-season precipitation levels between sites, but the lack of any substantial influences of inter-annual variation in precipitation is noteworthy. Likewise, differences in winter precipitation in these years played little direct role in growth rates in our models, although it may have played an indirect role by shortening the growing season at higher elevations via a deeper snowpack, which can limit growth and reproduction in adult-sized individuals of tree species in the Colorado Rockies (Buechling et al. 2016). We speculate this weak influence of precipitation, especially winter precipitation, is partially a function of the shallow root systems of young seedlings. A deep snowpack, and the associated deep recharge of soil moisture by snowmelt, is likely to mostly benefit large trees with deep, well-developed root systems (e.g., Canham et al. 2018). Indeed, the lack of any strong precipitation signal on seedlings of the montane species in our study is in contrast to an observational study of adult-sized trees in the region which found growth of montane and subalpine tree species responded positively to increases in annual precipitation, up to a threshold level (Buechling et al. 2017); this growth data, however, was collected over much wider gradients in precipitation than in our study, and we expect seedling growth would respond positively to a wider range in precipitation as well.

#### *Seedling survivorship*

The effects of warming temperatures on tree survivorship are likely to be as important as growth in influencing forest dynamics, and the montane species showed surprisingly robust survivorship in the high temperatures at the lowest elevation site. Higher temperatures can have direct effects (e.g., heat stress, higher respiration) and indirect effects (e.g., increased water stress) on survivorship. In contrast to growth, survivorship rates for the montane species were generally insensitive to the net effects of warming—survivorship was consistently high across the range

in temperature and soil moisture conditions, and remained high after supplemental watering ended and through large interannual fluctuations in ambient precipitation. Given the low mortality rates in the montane species, it is unsurprisingly that our analysis with Cox Proportional Hazard models found only small changes in the risk of mortality due to temperature in these species (Table 3). Growth rates often have strong relationships with survivorship patterns (e.g., Martin et al. 2010), and growth did have modest effects in these seedlings with an increased risk of mortality in slower-growing individuals. If widespread, this pattern suggests faster growth in higher temperatures may counteract some of the risk of higher mortality expected for regeneration in the Rocky Mountains under climate change (e.g., Kemp et al. 2019), at least in the short term.

Our study only found strong effects of temperature on survivorship for subalpine fir, as warming of +3°C led to fairly low survivorship of 47.5% by year four and +6°C led to 100% mortality by year three even with watering, highlighting this species' sensitivity to increasing temperatures. Our results suggest subalpine fir survivorship is sensitive to soil moisture as well, as its survivorship dropped markedly in the warmest site from 2015 to 2016 (Table 1), coincident with reductions in supplemental water and precipitation inputs, as the low elevation site received ~35% less precipitation than the long-term average in 2016 (Fig. 2). Indeed, the combined direct and indirect effects of warming are thought to be threatening subalpine fir's persistence in the southern Rocky Mountains entirely (Hansen and Philips 2015).

Some caution is warranted in applying the high survivorship rates of the montane species in our study to expectations for natural regeneration, as watering may have increased the fitness and hence survivorship of the seedlings even after watering ended. For example, Castanha et al. (2013) found higher survivorship of watered seedling transplants compared to natural unwatered germinants after watering was ended, although the one-year-old seedlings used in our study are likely to be less sensitive to moisture than the new germinants studied by Castanha et al. (2013). Likewise, exogenous events like episodic droughts or disturbances—which are common in forests on both temperate

(e.g., Veblen et al. 2003) and tropical mountains (Crausbay and Martin 2016), and are interconnected with warming temperatures in the western USA, as recent increases in heat- and drought-triggered mortality demonstrate (van Mantgem et al. 2009)—could quickly counteract the high survivorship of the montane species in hotter temperatures found in our study.

#### *Climate and seedling dynamics*

Our results indicate that climate, and temperature in particular, should have strong effects on structure and dynamics of established seedlings in Rocky Mountain forests, controlling the vigor and abundance of these species. In particular, we expect that strong growth and survivorship rates of the montane species in warmer temperatures would lead to higher seedling abundances as temperatures increase in the region. This pattern, however, was not found in other recent studies which found that the ranges of established seedlings of these species are contracting (Bell et al. 2014) and that seedling abundance is poorly explained by climate in general in western forests (Kroiss and HilleRisLambers 2015, Dallas and Hastings 2018, Redmond and Kelsey 2018, Copenhagen-Parry et al. 2020). Likewise, a study of the climate distributions of Rocky Mountain tree species found no increase in patch frequency nor abundance of saplings toward the hotter end of the regional temperature gradient (Martin and Canham 2020).

Ongoing climate change is likely to further complicate the connections between seedling growth and survivorship and changing temperature regimes. Distributions of tree species in the Rockies are likely to shift in response to climate change particularly in the drier and hotter ends of their distributions (e.g., Savage et al. 2013, Martin and Canham 2020). As noted, Bell et al. (2014) report an ongoing niche divergence between adult and established seedlings in the region's tree species, as adult tree distributions have not yet changed in response recent climate change but seedling distributions of the same species have contracted. When considered with the generally positive response to warming in our study, the seedling range contractions detected by Bell et al. (2014) suggest that the earliest stages of seed ecology, that is, fecundity (Buechling et al. 2016), germination, and first-year survivorship, may be playing an important

role in ongoing changes to seedling recruitment patterns or that other components of climate change not in our study (e.g., increased severe drought frequency) are causing seedling ranges to contract. Changes in seed availability and suitable microsites for germination have been found to constrain tree species' responses to climate change, especially at and beyond range limits (Kroiss and HilleRisLambers 2015). Temporal fluctuations in seedling and canopy recruitment dynamics are also likely to accompany ongoing changes in climate, as periods of favorable conditions (e.g., high precipitation) can lead to pulsed seedling establishment in the Rockies in montane (Brown and Wu 2005) and subalpine communities (Andrus et al. 2018).

Given these contrasting patterns, longer studies of seedlings dynamics, which include all stages of recruitment over a range in climate, are needed to determine if increased seedling growth rates at higher temperatures are sustained and how interspecific changes in demography feedback on the abundance of juveniles in Rocky Mountain forests. Future studies should expand on research to date to include temperature interactions with other conditions, including wider variation in precipitation, nutrient availability, fluctuations in the timing and duration of warming, and increases in atmospheric CO<sub>2</sub>. While relationships between germinant success and climate are receiving ongoing attention in some Rocky Mountain tree species (Kueppers et al. 2017b), there is need for more studies focused on the earliest life stages of tree species in the region (see Petrie et al. 2016), and the role functional traits and belowground allocation patterns play in the viability of tree regeneration in a warming world.

#### ACKNOWLEDGMENTS

We thank Dr. Catherine Durso (University of Denver) for assistance with the statistical analysis, and the Colorado Forest Restoration Institute, Colorado State University, and the Colorado State Forest Service for helping to make this work possible.

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