Seasonal temperature–moisture interactions limit seedling establishment at upper treeline in the Southern Rockies

SYDNEY N. BAILEY,1 GRANT P. ELLIOTT,1,† AND ERIN M. SCHLIEP2

1Department of Geography, University of Missouri, Columbia, Missouri 65211 USA
2Department of Statistics, University of Missouri, Columbia, Missouri 65211 USA

Citation: Bailey, S. N., G. P. Elliott, and E. M. Schliep. 2021. Seasonal temperature–moisture interactions limit seedling establishment at upper treeline in the Southern Rockies. Ecosphere 12(6):e03568. 10.1002/ecs2.3568

Abstract. Over recent decades, sharply rising temperatures without an accompanying increase in precipitation have created widespread heat-induced drought stress, or hotter drought. Tree-ring reconstructions have discovered significant declines in seedling establishment from hotter drought across montane and subalpine forest belts during this time, yet comparable studies at upper treeline are non-existent. In this study, we reconstruct annual patterns of seedling establishment at upper treeline in the Southern Rocky Mountains to test the hypotheses that establishment is governed by temperature–moisture interactions and that slope aspect mediates the influence of hotter drought. To test these hypotheses, we destructively sampled seedlings along a network of six study sites to reconstruct annual patterns of establishment on opposite north-facing and south-facing slopes. Results from this research can be summarized into two main points with respect to the influence of climate on seedling establishment at upper treeline over approximately the last three decades (1991–2019). First, temperature–moisture interactions throughout the year play a crucial role in facilitating successful seedling establishment. Second, and perhaps most striking, is the complete lack of establishment at all sites over the past decade. This could signify that a threshold has been surpassed and conditions are now beyond the climatic optimum for successful seedling establishment above treeline moving forward. These results expand upon similar findings from forests at lower elevations, introducing the likelihood that seedling establishment along the entire mountain forest belt of the Southern Rocky Mountains is being impacted by hotter drought. This means that any declines in the rate of seedling establishment across montane and subalpine forests will not be offset by increased recruitment at treeline.

Key words: climate change; Engelmann spruce; hotter drought; Rocky Mountain bristlecone pine; Sangre de Cristo; seedling establishment; southern Rocky Mountains; timberline; treeline; treeline dynamics.

Received 24 July 2020; revised 10 December 2020; accepted 2 February 2021; final version received 8 April 2021. Corresponding Editor: C. Jason Williams.

Copyright: © 2021 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
† E-mail: elliottg@missouri.edu

INTRODUCTION

Over the past few decades, amplified rates of warming produced the highest mean temperature for any century (1917–2016) of the past 11,000 yr (Marsicek et al. 2018). A temperature regime increasingly outside the natural range of variability for the Holocene raises the likelihood of threshold-induced switches affecting key ecological processes (Andersen et al. 2009). Arguably most important, sharply rising temperatures without an accompanying increase in precipitation have created widespread heat-induced drought stress, or hotter drought (Allen et al. 2015). This is particularly relevant for mountain regions because they are warming faster than lowland environments and this is expected to continue through the 21st century (Pepin et al.
research suggests that temperature (Harsch et al. 2009). Moreover, accumulating have documented treeline advance since 1900 only a slight majority of studies worldwide (52%)

 temperature-limited boundary (K
e et al. 2019). Although classically regarded as a from the emergent seedling phase (Brodersen

2019). A seedling becomes established when the first set of primary leaves replace the cotyledons from the emergent seedling phase (Brodersen et al. 2019). Although classically regarded as a temperature-limited boundary (Körner 2012), only a slight majority of studies worldwide (52%) have documented treeline advance since 1900 (Harsch et al. 2009). Moreover, accumulating research suggests that temperature–moisture interactions impact the spatiotemporal patterns of tree establishment within upper treeline ecotones (Hessl and Baker 1997; Lloyd and Graumlich 1997; Daniels and Veblen 2004; Morgan et al. 2014; Elliott and Cowell 2015; Moyes et al. 2015; Kueppers et al. 2017; Elliott and Petruccelli 2018; Sigdel et al. 2018; Lu et al. 2019, 2021; Elliott et al. 2021). Seedlings, with their relatively shallow root systems, are particularly susceptible to drought-induced mortality (Smithers et al. 2018).

As a result, it has been suggested that moisture limitations could now override cold temperature limitations for potential seedling establishment at or above treeline (Moyes et al. 2015, Loranger et al. 2016, Kueppers et al. 2017), particularly in continental climates, but broadscale examinations are lacking.

Our current understanding of how annual climate variability influences seedling establishment at upper treeline is constrained by the temporal resolution of previous research methods and lags behind what we know for the rest of the mountain forest belt. At coarse timescales (century to millennia), for example, we know from tree rings (Lloyd and Graumlich 1997) and carbon dating (Morgan et al. 2014) that multi-decadal drought led to mortality-induced downward shifts in the elevation of upper tree-line in the Sierra Nevada and Wind River Range of the Central Rocky Mountains, respectively, between 950 and 550 yr BP. On decadal timescales, tree-ring reconstructions suggest a varying degree of influence of drought, from strongly limiting (Villalba and Veblen 1997) to triggering threshold increases in establishment (Elliott and Kipfmueller 2011). Field manipulation experiments have shown the critical role moisture availability plays in shaping annual patterns of seedling establishment, but are relatively limited in their period of observation, with five years or less (Brodersen et al. 2006, Moyes et al. 2015, Kueppers et al. 2017). Across montane and subalpine forests, however, tree-ring methods have recently been used to capture annual resolution over multiple decades, demonstrating that rates of seedling establishment are now lower within the context of hotter drought and contingent on isolated years with favorable moisture conditions (League and Veblen 2006, Andrus et al. 2018, Davis et al. 2019). Comparable research capable of evaluating annual variability in seedling establishment at decadal timescales is non-existent for upper treeline ecotones.

The specific objectives of this study were to (1) reconstruct annual variability of seedling establishment at upper treeline in the Sangre de Cristo Mountains within the Southern Rocky Mountain region and (2) examine how annual variability in seedling establishment is affected by seasonal climate conditions. Based on the evidence of intensifying hotter drought stress across western North America (e.g., Millar and Stephenson 2015), we hypothesized that annual seedling establishment would be governed by temperature–moisture interactions with warmer and drier conditions resulting in reduced seedling establishment. We also hypothesized that evidence for temperature–moisture interactions would be supported by the slope aspect mediation of hotter drought, with increased rates of establishment on more mesic north-facing slopes. This is in part based on our previous work that...
showed tree establishment was disproportionately favored on north-facing slopes during dry periods of the 20th century (Elliott and Cowell 2015). Considered together, the purpose of this research is to provide empirical evidence for whether hotter drought conditions are impacting seedling establishment along the highest upper treeline environments of the U.S. Rocky Mountains.

METHODS

Study area
Our study area extends approximately 400 km along the Sangre de Cristo (SDC) range in the South Rocky Mountain region of northern New Mexico and southern Colorado (Fig. 1a). The Southern Rocky Mountains contain the highest treeline ecotones along the spine of the Rocky Mountains and include the broadest expanse of climatically sensitive ecotones where subalpine forest borders alpine tundra capable of supporting seedling establishment upslope (Butler et al. 2007, Elliott and Petruccelli 2018). Pedogenic processes create shallow, infertile soils with a coarse texture, although higher elevations tend to have a deeper soil profile from increased weathering (Peet 2000). Annual soil water deficits are low (Elliott and Cowell 2015). Tree species composition at upper treeline is dominated by Engelmann spruce (Picea engelmannii), especially across north-facing slopes, with Rocky Mountain bristlecone pine (Pinus aristata) almost exclusively on south-facing slopes. Both species regenerate from seed rather than from vegetative root-sprouting and often form monospecific stands.

The precipitation regime of the SDC is bimodal, with both warm-season and cool-season regimes controlled by separate mechanisms (Coats et al. 2015). Within the Rocky Mountains, the SDC is unique in that they receive the majority of annual precipitation (57%) from the summer monsoon rather than cool-season snowfall (Elliott and Cowell 2015). The summer monsoon provides critical moisture that compensates for persistent cool-season droughts, which have become more common since trends of decreasing snowpack began in 1978 (Coats et al. 2015). Minimum temperature ($T_{min}$) has increased dramatically since the early 1990s to the point where it is now ~3–4°C above the mean from last century (Fig. 1b). Collectively, temperature increases coupled with decreases in precipitation suggest that drought stress could be intensifying across upper treeline in the SDC (Fig. 1b).

Field methods
During summer 2019, we re-visited six study sites at upper treeline in the SDC range to examine decadal-scale changes wrought by increasingly warm and dry conditions (Table 1; Fig. 1b). These sites were originally sampled in 2007 (see Elliott and Kipfmueller 2011). Initial site selection focused on identifying mountain peaks with climatic treelines to avoid human or natural disturbances, such as grazing, fire, and/or avalanches (Butler et al. 2007). We placed paired nested-belt transects on contrasting south-facing (azimuth 135°–225°) and north-facing (azimuth 315°–45°) slopes on three mountain peaks in the SDC ($n = 6$ transects). We systematically stratified study sites in this manner because mountain topography partitions broader scale climate into distinct topoclimates based on slope and aspect, with opposite temperature–moisture regimes on north- vs. south-facing slopes (Barry 2008). Transects were repeated from Elliott and Kipfmueller (2011) on each of these peaks, unless the original outpost tree (term after Paulsen et al. 2000) was harvested in 2007 or if regeneration extended farther upslope, then a new transect was placed. Transects began at the outpost tree, which was defined as the furthest upright seedling (<1 m in height) within the ecotone. At each site, a rectangular plot (40 m wide to timberline; maximum length of 150 m) was created along the transect on each of the six slopes. Timberline, or the forest line, was used to demarcate the uppermost extent of closed-canopy subalpine forest. We recorded detailed information for each of the transects including elevation, GPS coordinates of the outpost tree, slope aspect, and slope steepness (°). All seedlings inside the plots were sampled, and detailed conditions were collected for each one including height and species.

Dendrochronology methods
To obtain annual resolution for the year of establishment, seedlings were destructively sampled and uprooted by removing the surrounding soil with a gardening shovel and retrieving the section of the stem containing the root-shoot
boundary. Larger samples were cut to extend at least 10 cm above and below the root-shoot boundary (Davis et al. 2019), while seedlings that were smaller were kept whole until we returned to the laboratory. In the laboratory, we cut the samples into at least four 1 cm successive cross sections from the root upward or until the pith appeared (League and Veblen 2006). The pith is

Fig. 1. (a) Study area map and (b) annual deviations from the 20th-century mean (1900–1999) for temperature and precipitation. Precipitation data plotted with a 10-yr running average. Data were obtained from each study site from PRISM climate grids and averaged together for a regional value (PRISM Group, Oregon State University, Corvallis, Oregon, USA).

Table 1. Study site characteristics.

| Site code | Elevation (m) | Aspect (°) | Slope (°) | Ecotone length (m) | No. seedlings sampled | Seedling density (no./ha) | Seedlings dated (%) | Species sampled (PIEN:PIAR) |
|-----------|---------------|------------|-----------|-------------------|-----------------------|--------------------------|---------------------|-----------------------------|
| DPS 3733  | 170           | 26         | 45        | 26                | 144.4                 | 88                       | 26:0                |                             |
| DPN 3716  | 313           | 21         | 28        | 25                | 223.2                 | 92                       | 25:0                |                             |
| GHS 3698  | 184           | 15         | 62        | 10                | 40.3                  | 100                      | 0:10                |                             |
| GHN 3680  | 340           | 10         | 148       | 34                | 57.4                  | 97                       | 33:1                |                             |
| TPS 3713  | 150           | 19         | 188       | 30                | 50.0                  | 97                       | 0:30                |                             |
| TPN 3660  | 310           | 23         | 68        | 110               | 404.4                 | 95                       | 100:10              |                             |

Notes: Ecotone length refers to the distance (m) between the uppermost seedling sampled on the slope and the timberline or forest line boundary. Seedlings were classified as being less than 1 m tall. Species data are listed as an abbreviation using the first two letters of the Latin binomial name: PIAR, Pinus aristata; PIEN, Picea engelmannii.
standardized precipitation-evapotranspiration index (SPEI) data to investigate the impact of drought on seedling establishment (http://spei.cosic.es/database.html). SPEI data combine temperature and precipitation values to produce a multiscalar drought index based on the environmental water balance (Vicente-Serrano et al. 2010).

To investigate possible seasonal impacts of climate, we considered the warm-season (WS; June–September) and cool-season (CS; October–May) \( T_{\text{min}} \) and maximum temperature \( (T_{\text{max}}) \) and precipitation separately. Principal component analysis (PCA) was done on groups of climate variables to mitigate issues of multicollinearity and to retain interpretability. First, we did PCA on the WS and CS \( T_{\text{min}} \) variables. Here, the first component captured 92% of the variation and provided a measure of overall \( T_{\text{min}} \) throughout the year, whereas the second created a contrast between WS and CS \( T_{\text{min}} \). Next, we did PCA on the WS and CS \( T_{\text{max}} \) variables. Again, the first principle component (66% of variation) provided a measure of overall \( T_{\text{max}} \) throughout the year, and the second created a contrast between WS and CS. Lastly, we did PCA on the variables relating to precipitation (i.e., WS precipitation, CS precipitation, and SWE_May1). Here, the first component (54% of variation) provided an average of the three variables, with more weight given to the cold season variables. The second component (33% of variation) provided a contrast between WS precipitation and CS precipitation, and the third component provided a contrast between annual (WS and CS) precipitation relative to SWE_May1. The resulting pairwise correlation across these components was low (<0.4). Each of the components was considered in the regression model below.

We modeled the counts of seedling establishment for each year, peak, and slope. We focused our analyses on the years 1991–2009 due to the seedling age-structure data (see below in Results). Species-level differences were not included in the model due to the stratification of species across slope aspects with 89% \( (n = 151/169) \) of Engelmann spruce confined to north-facing slopes, and 82% \( (n = 37/45) \) of bristlecone pine were relegated to south-facing slopes.

We used a generalized linear mixed model (GLMM) with Poisson distribution and log-link function (Stroup 2012) to model seedling
establishment, with a random effect for peak. In addition, we incorporated a temporal random effect with lag-1 autoregressive structure (AR(1)) to capture dependence between years not accounted for by the covariates. The temporal random effects were shared across sites. Climate variables and slope aspect (1 = north, 0 = south) were included as fixed effects. An interaction between slope aspect and each of the climate variables was also considered to capture potential differences in the impact of seasonal climate between north- and south-facing slopes (R Development Core Team 2017). Models were compared using Akaike information criteria (AIC) and Bayesian information criteria (BIC), and the model with the lowest value was chosen.

To further examine the patterns of seedling establishment, we quantified differences in treeline structure across north- and south-facing slopes. We used a two-sample Kolmogorov-Smirnov test to quantify differences in seedling age structure between slope aspects. To test for statistically significant differences in seedling age, we used a Mann-Whitney U-test since the data distribution deviated from normality.

RESULTS

Seedling establishment
A total of 235 seedlings were collected from six treeline sites in the SDC range (Table 1). The year of establishment was successfully determined for 223 samples (95% of total). These seedlings were relatively young, with 96% (n = 214) established since 1991 (Fig. 2). From 2003 to 2006, there was an abrupt peak across both aspects that contained over 67% of seedling establishment (mean = 37.5 seedlings/yr; Fig. 2). There was no evidence of establishment since 2010 (Fig. 2). Overall age-structure patterns were not significantly different across slope aspects (P > 0.05), yet seedling age was significantly younger (P < 0.05) on north-facing slopes (Fig. 3).

Climate effects
Overall, model results suggest that annual patterns of seedling establishment were driven by temperature-moisture interactions throughout the year (Table 2). Rising annual $T_{\text{min}}$ had a significant negative relationship (P = 0.017) with seedling establishment. The influence of $T_{\text{max}}$ was more contingent on seasonal differences. For example, annual increases in $T_{\text{max}}$ during both cool and warm seasons showed a significant positive relationship (P = 0.002) with annual establishment, but if rising $T_{\text{max}}$ was confined to the warm season, then there was a significant negative impact on seedling establishment (P = 0.011; Table 2). High precipitation totals from both snow and summer monsoon rain had a positive relationship with seedling establishment (P = 0.149) and were highly significant when accompanied by low 1 May SWE (P < 0.001; Table 2).

Model results also identified the importance of slope aspect, with significantly higher rates of seedling establishment on north-facing slopes compared with south-facing slopes (P < 0.001; Table 2). In addition, the influence of $T_{\text{max}}$ and precipitation on seedling establishment were mediated by slope aspect. High $T_{\text{max}}$ had a significantly stronger and positive influence on establishment across south-facing slopes relative to north-facing slopes (P = 0.005; Table 2). Years with both high annual precipitation and 1 May SWE significantly reduced establishment on north-facing slopes in comparison with south-facing slopes (P = 0.014; Table 2).

DISCUSSION

Results from this research in the Southern Rocky Mountain region can be summarized into two main points with respect to the influence of climate on seedling establishment at upper treeline over approximately the last three decades (1991–2019). First, temperature-moisture interactions throughout the year play a crucial role in facilitating successful seedling establishment. Second, and perhaps most striking, is the complete lack of establishment at all sites over the past decade. This could signify that a threshold has been surpassed and conditions are now beyond the climatic optimum for successful seedling establishment above treeline moving forward (sensu Lu et al. 2019). To our knowledge, this study represents the first reconstruction of annually resolved data to examine the influence of climate on seedling establishment at upper treeline across a landscape scale.

Multiple lines of evidence suggest that drought stress during the growing season limits
seedling establishment at upper treeline in the SDC. For example, the annual alignment of high precipitation totals with lower $T_{\text{min}}$ and lower warm-season $T_{\text{max}}$ in years with high recruitment underscores the critical role of sufficient moisture availability in concert with reduced evaporative demand during the growing season. Increased moisture availability during the growing season has been shown to serve as a critical counterbalance to offset the negative impacts of sharply rising temperatures during the summer (Moyes et al. 2015, Kueppers et al. 2017). These findings also align with recent work at upper treeline in the Himalayas, where moisture-mediated responses were reported in response to rising temperatures (Sigdel et al. 2018, Lu et al. 2019). Taken together, drought stress governing seedling establishment at upper treeline suggests that hotter drought may already be engulfing forests not previously considered moisture-limited, which offers empirical support for previous projections (Allen et al. 2015).

Fig. 2. Seedling age-structure data (1991–2019) by species for (a) south-facing slopes, (b) north-facing slopes, and (c) all sites combined. Spruce is Engelmann spruce (Picea engelmannii), and pine is Rocky Mountain bristlecone (Pinus aristata).
Comparing patterns of seedling establishment across opposite north-facing and south-facing slopes provides further evidence that drought stress is likely limiting establishment. The fact that seedlings are considerably more dense and significantly younger on north-facing slopes provides empirical evidence that recent establishment is more prolific on mesic slopes. In addition, model results strongly support the suitability of north-facing slopes for seedling establishment, except within the context of higher warm-season \( T_{\text{max}} \), when pine-dominated south-facing slopes responded more favorably than spruce-dominated north-facing slopes. Collectively, the dramatic differences in rates of seedling establishment across opposite slope aspects demonstrate the pivotal role of heat-induced drought stress at upper treeline in the SDC. Previous studies have reported similar results, where seedling establishment was more common on north-facing slopes (Weisberg and Baker 1995, Germino et al. 2002, Gill et al. 2015, Millar et al. 2015, Elliott and Petruccelli 2018). Furthermore, experimental evidence from a southwest-facing treeline site in the Colorado Front Range found that seedling establishment was limited by growing season drought stress (Moyes et al. 2015, Kueppers et al. 2017). Reconstructed patterns of seedling establishment from this research support the idea that this is occurring more broadly throughout the Southern Rocky Mountain region.

Model results indicate that snowpack dynamics should also be considered as a significant control on seedling establishment at upper treeline, particularly during the transition from spring into the growing season. More specifically, high snowfall totals increase seedling establishment when coupled with a low 1 May SWE. Snowpack has proven critical for seedling establishment at upper treeline throughout the Northern Hemisphere because it provides thermal protection and prevents physical damage (Hättenschwiler and Smith 1999, Hagedorn et al. 2014, Davis and Gedalof 2018, Elliott and Petruccelli 2018). In the Rocky Mountains, extremely low cool-season...

---

**Table 2. Results from generalized linear mixed model (GLMM) with Poisson distribution and log-link function to model seedling establishment.**

| Variable                  | Coef. Estimate | SE  | z    | P     |
|---------------------------|----------------|-----|------|-------|
| Intercept                 | -1.318         | 1.113 | -1.184 | 0.236  |
| North Face                | 0.930          | 0.164 | 5.659 | <0.001 |
| \( T_{\text{min}} \) (PC1) | -0.652         | 0.272 | -2.395 | 0.017  |
| \( T_{\text{max}} \) (PC1) | 0.699          | 0.227 | 3.075 | 0.002  |
| \( T_{\text{max}} \) (PC2) | -0.478         | 0.188 | -2.543 | 0.011  |
| Precipitation (PC1)       | 0.247          | 0.171 | 1.444 | 0.149  |
| Precipitation (PC3)       | 0.933          | 0.275 | 3.398 | <0.001 |
| North Face \( \times T_{\text{max}} \) (PC1) | -0.508 | 0.182 | -2.785 | 0.005  |
| North Face \( \times \) Precipitation (PC1) | -0.339 | 0.138 | -2.452 | 0.014  |

Notes: Principal component analysis (PCA) was done on groups of predictor variables (\( T_{\text{min}}, T_{\text{max}}, \) and precipitation) to mitigate issues of multicollinearity and to retain interpretability. The first principal component (PC1) in each analysis represents the overall or annual level of the variable. The second principal component (PC2) captures WS relative to the CS. For example, \( T_{\text{max}} \) (PC2) is large when \( T_{\text{max}} \) during the WS is high and \( T_{\text{max}} \) during the CS is low. The third principal component (PC3) for the precipitation variables captures WS and CS relative to SWE, meaning precipitation (PC3) is large when WS and CS precipitation levels are high yet SWE is low.
temperatures facilitate the formation of abrasive ice crystals that can limit establishment by physically damaging trees (Smith et al. 2003). This is most common in mountain ranges east of the Continental Divide, such as the SDC, because they are exposed to exceptionally cold and dry arctic air masses during the cool season (Barry 2008). Yet high snowpack that persists beyond late spring can limit seedling establishment by reducing the length of the growing season and increasing susceptibility to fungal infections (Holtmeier and Broll 2007, Tomback and Resler 2007, Lu et al. 2021). We therefore interpret the significance of low 1 May SWE to signify the importance of a relatively early snowmelt, especially on north-facing slopes (Table 2). Moreover, the significance of high annual precipitation paired with a low 1 May SWE in the model highlights the crucial role monsoon rainfall from mid- to late summer plays in facilitating seedling establishment at upper treeline across the SDC in the Southern Rocky Mountains.

The fact that reconstructed dates of seedling establishment end in 2009 across all six sites, regardless of slope aspect, raises the question of whether climate over the past decade has exceeded critical thresholds and is at the point where it is too hot and dry for establishment? This seems plausible considering the strong negative relationship between seedling establishment and rising $T_{min}$, which, on average, has been $3^\circ \pm 0.8^\circ C$ ($\pm$SD) warmer than last century since 2010 (Fig. 4). Warming-induced drought limitations have been reported for shrub establishment along treeline in the Himalayas since the 1940s (Lu et al. 2019). In addition, drought during the 1980s precluded seedling establishment in northern Patagonia (Villalba and Veblen 1997). By contrast, and more recently, prolific pine regeneration was observed from 2013 to 2018 at treeline in the Swedish Scandes, with the total population size increasing by 150% from previous decades (Kullman 2018). Although a decade presents limitations to understanding tree demography, the last year with seedling establishment at each site was 2007 and there was no establishment after 2009 at any sites along an approximate 400 km latitudinal gradient. Taken together, this supports the idea that the absence of seedling establishment is most likely driven by changes in climate.

Although results from this research provide evidence that establishment is shaping the patterns observed during this study, the influence of seed production and mortality merits consideration. For example, seed production in Engelmann spruce is enhanced by consecutive years of relatively high summer temperatures and reduced spring snowfall, but over the past decade, there is evidence that temperatures have warmed beyond a threshold creating possible negative effects from moisture stress (Buechling et al. 2016). Specific requirements for seed production in bristlecone pine are less clear, but it typically takes 50–70 yr for seedlings to reach reproductive maturity (Schoettle et al. 2012), so we cannot rule out that poor seed production at treeline is contributing to this trend. In addition, we cannot discount the possibility that severe drought conditions killed several consecutive cohorts of seedlings, even though it is impossible to reconstruct rates of seedling mortality because of how quickly evidence disappears from the landscape. In particular, the drought of 2002 could have led to the very low levels of establishment recorded from 1997 to 2002 (Figs. 2 and 4). Drought and drying soil have been linked to high rates of seedling mortality at upper treeline (Dolanc et al. 2014, Moyes et al. 2015). Hotter drought-induced mortality could have also contributed to the lack of seedling establishment reconstructed for the past decade, despite only observing a single dead seedling during our fieldwork.

CONCLUSION

Results from this research support our first hypothesis regarding the overriding influence of temperature–moisture interactions in governing patterns of seedling establishment at upper treeline in the Southern Rocky Mountains. Further, these results also support our second hypothesis that the impacts of hotter drought will be more apparent on warmer and drier aspects. Perhaps what is most compelling to consider for the future is that these results reconstruct seedling establishment along some of the highest upper treeline ecotones in the Rocky Mountains and from a mountain range where the majority of annual precipitation falls as rain, which helps offset drought stress during the growing season. Consequently, these results introduce the
likelihood that limitations from drought stress are overriding the possible benefits of sharply rising temperatures at upper treeline across the Rocky Mountains.

Projections for future climate scenarios point to intensified hotter drought conditions (Lukas et al. 2014), which will perpetuate moisture stress and continue to limit seedling establishment along the uppermost extent of the mountain forest belt. As a result, establishment will likely become confined to isolated years with favorable temperature–moisture interactions, expanding upon similar findings from subalpine forests below (Andrus et al. 2018). This means that seedling establishment along the entire mountain forest belt of the Southern Rocky Mountains is being impacted by hotter drought conditions and that any declines across montane and subalpine forests will not be offset by increased recruitment at treeline.

ACKNOWLEDGMENTS

We thank Steve Cardinal for providing valuable assistance in the field and Cyd Smith for help in the laboratory. We also thank various members of Carson, San Isabel, and Santa Fe US National Forest Service offices for permission to destructively sample seedlings.

---

Fig. 4. Annual temperature and precipitation data (1991–2009) shown as annual deviations from the 20th-century mean (1900–1999) for (a) cool season (October–May) and (b) warm season (June–September). Dashed line denotes the beginning of the period with no reconstructed establishment (2010–2019).
LITERATURE CITED

Allen, C. D., D. D. Breshears, and N. G. McDowell. 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere 6:art129.

Andersen, T., J. Carstensen, E. Hernández-García, and C. M. Duarte. 2009. Ecological thresholds and regime shifts: approaches to identification. Trends in Ecology & Evolution 24:49–57.

Andrus, R. A., B. J. Harvey, K. C. Rodman, S. J. Hart, and T. T. Veblen. 2018. Moisture availability limits subalpine tree establishment. Ecology 99:567–575.

Barry, R. G. 2008. Mountain weather and climate. Second edition. Cambridge University Press, Cambridge, UK.

Brodersen, C. R., et al. 2019. Seedling survival at timberline is critical to conifer mountain forest elevation and extent. Frontiers in Forests and Global Change 2:9.

Brodersen, C. R., M. J. Germino, and W. K. Smith. 2006. Photosynthesis during an episodic drought in *Abies lasiocarpa* and *Picea engelmannii* across an alpine treeline. Arctic, Antarctic, and Alpine Research 38:34–41.

Buechling, A., P. H. Martin, C. D. Canham, W. D. Sheppard, and M. A. Battaglia. 2016. Climate drivers of seed production in *Picea engelmannii* and response to warming temperatures in the southern Rocky Mountains. Journal of Ecology 104:1051–1062.

Butler, D. R., G. P. Malanson, S. J. Walsh, and D. B. Fagre. 2007. Influences of geomorphology and geology on alpine treeline in the American West—more important than climatic influences? Physical Geography 28:434–450.

Camarero, J. J., J. M. García-Ruiz, G. Sangüesa-Barreda, J. D. Galván, A. Q. Allá, Y. Sanjuán, S. Beguería, and E. Gutiérrez. 2015. Recent and intense dynamics in a formerly static Pyrenean treeline. Arctic, Antarctic, and Alpine Research 47:773–783.

Coats, S., J. E. Smerdon, R. Seager, D. Griffin, and B. I. Cook. 2015. Winter-to-summer precipitation phasing in southwestern North America: a multicentury perspective from paleoclimatic model-data comparisons. Journal of Geophysical Research: Atmospheres 120:8052–8064.

Daly, C., M. Halbleib, J. I. Smith, W. P. Gibson, M. K. Doggett, G. H. Taylor, J. Curtis, and P. P. Pasteris. 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. International Journal of Climatology 28:2031–2064.

Danby, R. K., and D. S. Hik. 2007. Variability, contingency and rapid change in recent subarctic alpine tree line dynamics. Journal of Ecology 95:352–363.

Daniels, L. D., and T. T. Veblen. 2004. Spatiotemporal influences of climate on altitudinal treeline in northern Patagonia. Ecology 85:1284–1296.

Davis, E. L., and Z. E. Gedalof. 2018. Limited prospects for future alpine treeline advance in the Canadian Rocky Mountains. Global Change Biology 24:4489–4504.

Davis, K. T., S. Z. Dobrowski, P. E. Higuera, Z. A. Holden, T. T. Veblen, M. T. Rother, S. A. Parks, A. Sala, and M. P. Maneta. 2019. Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration. Proceedings of the National Academy of Sciences of the United States of America 116:6193–6198.

Dolanc, C. R., H. D. Safford, J. H. Thorne, and S. Z. Dobrowski. 2014. Changing forest structure across the landscape of the Sierra Nevada, CA, USA, since the 1930s. Ecosphere 5:art101.

Elliot, G. P. 2012. Extrinsic regime shifts drive abrupt changes in regeneration dynamics at upper treeline in the Rocky Mountains, USA. Ecology 93:1614–1625.

Elliot, G. P., S. N. Bailey, and S. J. Cardinal. 2021. Hotter drought as a disturbance at upper treeline in the Southern Rocky Mountains. Annals of the American Association of Geographers 111:756–770.

Elliot, G. P., and C. M. Cowell. 2015. Slope aspect mediates fine-scale tree establishment patterns at upper treeline during wet and dry periods of the 20th Century. Arctic, Antarctic, and Alpine Research 47:681–692.

Elliot, G. P., and K. F. Kipfmueller. 2011. Multiscale influences of climate on upper treeline dynamics in the Southern Rocky Mountains, USA: evidence of intraregional variability and bioclimatic thresholds in response to twentieth-century warming. Annals of the Association of American Geographers 101:1181–1203.

Elliot, G. P., and C. A. Petruccelli. 2018. Tree recruitment at the treeline across the Continental Divide in the Northern Rocky Mountains, USA: the role of spring snow and autumn climate. Plant Ecology & Diversity 11:319–333.

Germino, M. J., W. K. Smith, and A. C. Resor. 2002. Conifer seedling distribution and survival in an alpine-treeline ecotone. Plant Ecology 162:157–168.

Gill, R. A., C. S. Campbell, and S. M. Karlinsky. 2015. Soil moisture controls Engelmann spruce (*Picea engelmannii*) seedling carbon balance and survivorship at timberline in Utah, USA. Canadian Journal of Forest Research 45:1845–1852.
Hagedorn, F., et al. 2014. Treeline advances along the Urals mountain range – driven by improved winter conditions? Global Change Biology 20:3530–3543.
Harsch, M. A., P. E. Hulme, M. S. Mcglone, and R. P. Duncan. 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. Ecology Letters 12:1040–1049.
Hättenschwiler, S., and W. K. Smith. 1999. Seedling occurrence in alpine tree species: a case study from the Central Rocky Mountains, USA. Acta Oecologica 20:219–224.
Hessl, A. E., and W. L. Baker. 1997. Spruce and fir regeneration and climate in the forest-tundra ecotone of Rocky Mountain National Park, Colorado, USA. Arctic and Alpine Research 29:173–183.
Holtmeier, F., and G. Broll. 2007. Treeline advance or regression: a case study from the central Rocky Mountains, USA. Acta Oecologica 20:219–224.
Kueppers, L. M., E. Conlisk, C. Castanha, A. B. Moyes, M. J. Germino, P. D. Valpine, M. S. Torn, and J. B. Mitton. 2017. Warming and provenance limit tree recruitment across and beyond the elevation range of subalpine forest. Global Change Biology 23:2383–2395.
Kullman, L. 2018. A recent and distinct pine (Pinus sylvestris L.) reproduction upsurge at the treeline in the Swedish Scandes. International Journal of Research in Geography 4:39–52.
Körner, C. 2012. Alpine treelines: functional ecology of the global high elevation tree limits. Springer, Basel, Switzerland.
Kueppers, L. M., E. Conlisk, C. Castanha, A. B. Moyes, M. J. Germino, P. D. Valpine, M. S. Torn, and J. B. Mitton. 2017. Warming and provenance limit tree recruitment across and beyond the elevation range of subalpine forest. Global Change Biology 23:2383–2395.
Kullman, L. 2018. A recent and distinct pine (Pinus sylvestris L.) reproduction upsurge at the treeline in the Swedish Scandes. International Journal of Research in Geography 4:39–52.
League, K., and T. T. Veblen. 2006. Climatic variability and episodic Pinus ponderosa establishment along the forest-grassland ecotones of Colorado. Forest Ecology and Management 228:98–107.
Lloyd, A. H., and L. J. Graumlich. 1997. Holocene dynamics of treeline forests in the Sierra Nevada. Ecology 78:1199–1210.
Loranger, H., G. Zotz, and M. Y. Bader. 2016. Early establishment of trees at the alpine treeline: idiosyncratic species responses to temperature-moisture interactions. AoB Plants 8(plw053).
Lu, X., E. Liang, Y. Wang, F. Babst, and J. J. Camarero. 2021. Mountain treelines climb slowly despite rapid climate warming. Global Ecology and Biogeography 30:305–315.
Lu, X., E. Liang, Y. Wang, F. Babst, S. Leavitt, and J. J. Camarero. 2019. Past the climate optimum: Recruitment is declining at the world’s highest juniper shrublines on the Tibetan Plateau. Ecology 100:e01497.
Lukas, J., J. Barsugli, N. Doesken, I. Rangwala, and K. Wolter. 2014. Climate change in Colorado: a synthesis to support water resources management and adaptation. Pages 1–114 in A report for the Colorado water conservation board. University of Colorado-Boulder, Western Water Assessment, Cooperative Institute for Research in Environmental Sciences (CIRES), Boulder, Colorado, USA.
Malanson, G. P., D. G. Brown, D. R. Butler, D. M. Cairns, D. B. Fagre, and S. J. Walsh. 2009. Ecotone dynamics: invasibility of alpine tundra by tree species from the subalpine forest. Pages 35–61 in D. R. Butler, G. P. Malanson, S. J. Walsh, and D. B. Fagre, editors. The changing alpine treeline: the example of Glacier National Park, MT, USA. Elsevier, Amsterdam, The Netherlands.
Marsicek, J., B. N. Shuman, P. J. Bartlein, S. L. Shafer, and S. Brewer. 2018. Reconciling divergent trends and millennial variations in Holocene temperatures. Nature 554:92–96.
Martínez-Vilalta, J., and F. Lloret. 2016. Drought-induced vegetation shifts in terrestrial ecosystems: the key role of regeneration dynamics. Global and Planetary Change 144:94–108.
Millar, C. I., and N. L. Stephenson. 2015. Temperate forest health in an era of emerging megadisturbance. Science 349:823–826.
Millar, C. I., R. D. Westfall, D. L. Delany, A. L. Flint, and L. E. Flint. 2015. Recruitment patterns and growth of high-elevation pines in response to climatic variability (1883–2013), in the western Great Basin, USA. Canadian Journal of Forest Research 45:1299–1312.
Morgan, C., A. Losey, and L. Trout. 2014. Late-Holocene paleoclimate and treeline fluctuation in Wyoming’s Wind River Range, USA. The Holocene 24:209–219.
Moyes, A. B., M. J. Germino, and L. M. Kueppers. 2015. Moisture rivals temperature in limiting photosynthesis by trees establishing beyond their cold-edge range limit under ambient and warmed conditions. New Phytologist 207:1005–1014.
Paulsen, J., U. M. Weber, and C. Körner. 2000. Tree growth near treeline: Abrupt or gradual reduction with altitude? Arctic, Antarctic, and Alpine Research 32:14–20.
Peet, R. K. 2000. Forests and meadows of the Rocky Mountains. Pages 75–122 in M. G. Barbour, and W. D. Billings, editors. North American terrestrial vegetation. Cambridge University Press, Cambridge, UK.
Pepin, N., R. S. Bradley, H. F. Diaz, and M. Baraer. 2015. Elevation-dependent warming in mountain regions of the world. Nature Climate Change 5:424–430.
R Development Core Team. 2017. R: a Language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
Rangwala, I., and J. R. Miller. 2012. Climate change in mountains: a review of elevation-dependent warming and its possible causes. Climatic Change 114:527–547.

Schoettle, A. W., B. A. Goodrich, V. Hipkins, C. Richards, and J. Kray. 2012. Geographic patterns of genetic variation and population structure in Pinus aristata, Rocky Mountain bristlecone pine. Canadian Journal of Forest Research 42:23–37.

Sigdel, S. R., Y. Wang, J. J. Camarero, H. Zhu, E. Liang, and J. Peñuelas. 2018. Moisture-mediated responsiveness of treeline shifts to global warming in the Himalayas. Global Change Biology 24:5549–5559.

Smith, W. K., M. J. Germino, T. E. Hancock, and D. M. Johnson. 2003. Another perspective on altitudinal limits of alpine timberlines. Tree Physiology 23:1101–1112.

Smithers, B. V., M. P. North, C. I. Millar, and A. M. Latimer. 2018. Leap frog in slow motion: divergent responses of tree species and life stages to climatic warming in Great Basin subalpine forests. Global Change Biology 24:e442–e457.

Stroup, W. W. 2012. Generalized linear mixed models: modern concepts, methods and applications. CRC Press, Boca Raton, Florida, USA.

Telewski, F. W. 1993. Determining the germination date of woody plants: a proposed method for locating the root/shoot interface. Tree-Ring Bulletin 53:13–16.

Tomback, D. F., and L. M. Resler. 2007. Invasive pathogens at alpine treeline: consequences for treeline dynamics. Physical Geography 28:397–418.

Vicente-Serrano, S. M., S. Beguería, and J. I. López-Moreno. 2010. A multiscalar drought index sensitive to global warming: the Standardized Precipitation Evapotranspiration Index. Journal of Climate 23:1696–1718.

Villalba, R., and T. T. Veblen. 1997. Regional patterns of tree population age structures in northern Patagonia: climatic and disturbance influences. Journal of Ecology 85:113–124.

Weisberg, P. J., and W. L. Baker. 1995. Spatial variation in tree regeneration in the forest-tundra ecotone, Rocky Mountain National Park, Colorado. Canadian Journal of Forest Research 25:1326–1339.