FINAL REPORT

Title: Seedlings? The unexpected elders of understory trees

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Zoe Schapira

Colorado State University

Camille Stevens-Rumann

Colorado State University

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List of Abbreviations/Acronyms

VPD: Vapor pressure deficit

CWD: Climatic water deficit

Keywords: subalpine, regeneration, bark beetle, wildfire, disturbance ecology, climate

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Abstract

Over the past several decades, the impacts of climate change have threatened the health and functioning of forested ecosystems on a global scale. Warming and drying trends have altered disturbance regimes and have created significant uncertainty about tree regeneration and postdisturbance recovery in subalpine ecosystems. Aging seedlings is an important mechanism for ascertaining establishment dates of tree seedlings in disturbed stands, and when paired with long-term climate, can provide critical information on climatic drivers of subalpine tree establishment. In this study, we destructively sampled and aged 229 *Picea engelmannii* (Engelmann spruce) and *Abies lasiocarpa* (subalpine fir) seedlings from beetle-affected and postfire subalpine stands in northern Colorado and southern Wyoming. We modeled the relationship between nondestructive aging methods, including height class and terminal bud scar count, and seedling age to assess the accuracy of age proxies in predicting true age of seedlings from disturbed stands. We also compare climatic conditions in years of widespread tree establishment to years with no establishment to ascertain regional drivers of subalpine tree seedling recruitment. Both height and terminal bud scar counts were significant predictors of seedling age, although correlations were weaker in taller and older seedlings, and seedlings from beetle-affected stands that exhibited suppressed growth. Growing season minimum temperatures and precipitation, and annual vapor pressure and climatic water deficits were significantly correlated with spruce-fir establishment. Height and terminal bud scar counts do not accurately predict precise ages of subalpine tree establishment from beetle-affected stands; however, terminal bud scar counts provide more accuracy in postfire tree establishment. Average climate may provide suitable conditions for low-levels of semi-continuous tree establishment in beetle-affected stands. However, large spruce-fir establishment pulses occur in cooler and wetter growing years compared to the long-term average, posing significant uncertainty about post-disturbance subalpine recovery with continued drying and warming trends.

Objectives

The objectives of this project were to answer the following questions: 1) how does seedling age correspond to seedling height and non-destructive methods of aging following stand-replacing versus moderate severity disturbances? and 2) what is the effect of yearly climatic conditions on establishment dates? The first study question addressed the first two original objectives outlined in the task statement, which called for quantifying age distributions of Engelmann spruce and subalpine fir seedlings from spruce beetle affected stands and high-severity burn areas in subalpine forests. The second study question addressed the third objective from the original proposal, which called for the identification of drivers of tree seedling establishment and growth in disturbed subalpine forests.

Background

Over the past several decades, the impacts of climate change have created unprecedented risks to forests across the globe and will continue to threaten ecosystem health in future climate scenarios. Warmer and drier conditions associated with climate change have resulted in drought-induced tree mortality (van Mantgem et al. 2009), altered disturbance regimes (Johnstone et al.

2016; Thom et al. 2017), and harsher growing conditions that may threaten tree seedling survival (Hansen et al. 2018; Stevens-Rumann et al. 2018). Forests in the western United States have historically been shaped by climate-driven disturbance events such as wildfires and bark beetle outbreaks (Veblen et al. 1994; Veblen 2000). As the climate continues to warm and alter disturbance regimes, increases in disturbance extent, frequency, and interactions will result in widespread tree mortality (Abatzoglou & Williams 2016; Allen et al. 2015). Forest resilience to a high-severity disturbance is dependent on the ability of trees to regenerate and recover ecosystem functioning (Johnstone et al. 2016). Tree seedling germination and survival are particularly sensitive to climatic conditions; juvenile trees survive in narrower climatic conditions than those that support their adult counterparts (Dobrowski et al. 2015; Lazarus et al. 2017). Increased temperature and moisture stress associated with warming trends have resulted in tree regeneration failure in some forested ecosystems, particularly following high-severity wildfires (Flatley & Fulé 2016; Hansen et al. 2018; Stevens-Rumann et al. 2018; Kemp et al. 2019). Reduced tree regeneration can erode forest resilience to disturbances and a changing climate, and may result in shifts in species dominance, novel changes to forest structure, or state shifts to non-forested ecosystems (Harvey et al. 2016; Kemp et al. 2016; Stevens-Rumann et al. 2018; Coop et al. 2020).

In particular, climate change over the past several decades has impacted tree regeneration in Rocky Mountain subalpine forests. Rocky Mountain subalpine forests are characteristically cool and moist, with a persistent snowpack that provides moisture to the soil through late spring and early summer (Westerling et al. 2006; Lukas et al. 2014). These forests are particularly sensitive to warming conditions as earlier spring snowmelt results in drier soils and increased moisture stress during peak summer temperatures. Warm temperatures are positively correlated with episodic, infrequent seed production of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*), two dominant conifer species in the subalpine zone of the Rocky Mountains (Woodward et al. 1994; Buechling et al. 2016). At the same time, above-average snowpack and late season snowmelt provide significant soil moisture during warm summer months and are strongly correlated with successful subalpine seedling germination (Andrus et al. 2018; Hill et al. 2018). This requirement for the temporal alignment of high soil moisture for seed germination and warm temperatures for seed production makes the successful establishment of Engelmann spruce and subalpine fir seedlings an increasingly rare occurrence (Kroiss & HilleRisLambers 2015; Kueppers et al. 2017; Andrus et al. 2018).

Increasing summer temperatures observed in subalpine forests are typically associated with early season snowmelt, water deficits, and increased moisture stress on tree seedlings (Andreadis & Lettenmaier 2006). Drought-intolerant species in snow-dependent ecosystems are increasingly at risk of temperature-induced moisture stress (Harvey et al. 2016; Kueppers et al. 2017; Redmond & Kelsey 2018). Engelmann spruce and subalpine fir are particularly drought-sensitive during seedling establishment (Kueppers et al. 2017; Lazarus et al. 2017). As climatic conditions continue to warm and dry, there may be significant contractions in Engelmann spruce and subalpine fir ranges, resulting in novel changes to subalpine ecosystems (Conlisk et al. 2017; Kueppers et al. 2017).

Regeneration failures and changing disturbance regimes have raised concerns about understanding the processes that govern seedling establishment and post-disturbance recovery. An important mechanism for elucidating these processes is determining seedling establishment dates, which can provide information about stand age and drivers of recruitment. Counting bud scars is a common method for dating seedlings, as it is nondestructive, time-efficient, and can be implemented in the field (Urza & Sibold 2013; Hankin et al. 2018). However, this method may only act as a proxy for true age. Terminal bud scars can become indistinguishable as a seedling grows, and scar visibility can vary by species (Urza & Sibold 2013). Another method to achieve establishment dates is to destructively sample seedlings and count annual rings, although this kills the seedling and can be time-consuming (Telewski 1993; Rother & Veblen 2017; Andrus et al. 2018). However, this method provides improved accuracy and an annual resolution that helps understand the climatic drivers of seedling establishment (Hankin et al. 2018). Dendrochronological techniques are particularly useful in subalpine forests, where shade-tolerant species may remain suppressed in the understory and exhibit stunted growth for decades, making terminal bud scars imperceptible (Veblen 1986). Gaining insight into establishment dates is vital for understanding growth patterns and recovery dynamics of subalpine forests as climate change continues to create unprecedented disturbance regimes and hostile growing conditions.

Materials and Methods

We collected samples from 30 sites in subalpine forests from northern Colorado and southern Wyoming. Sites were located in the Arapaho-Roosevelt, Routt, and Medicine Bow National Forests, at elevations ranging from 2,649 to 3,326 m above sea level (Figure 1). Subalpine stands were co-dominated by Engelmann spruce and subalpine fir, and contained lesser proportions of lodgepole pine and quaking aspen (*Populus tremuloides*). Site locations in this study were a subset of study sites established in Schapira et al. (2020, *In Press*). We used Aerial Detection Survey (ADS) data of spruce beetle outbreaks that occurred from 1996 to 2017 in USFS Region 2 to identify areas with beetle caused mortality (collected by the USDA Forest Service, Forest Health Protection and its partners) (USFS 2017). We used Monitoring Trends in Burn Severity (MTBS) data on wildfires in spruce-fir forests (MTBS Data Access 2017). ArcMap (10.6) was used to generate random points within the outbreak and burn polygons. Outbreak plots were defined as >50% of stand basal area (m^2/ha) affected by spruce beetle. We used MTBS data to map high-severity fires since 1996. All plots were located at least 50 meters from any trail or road to minimize human impact on plot data.

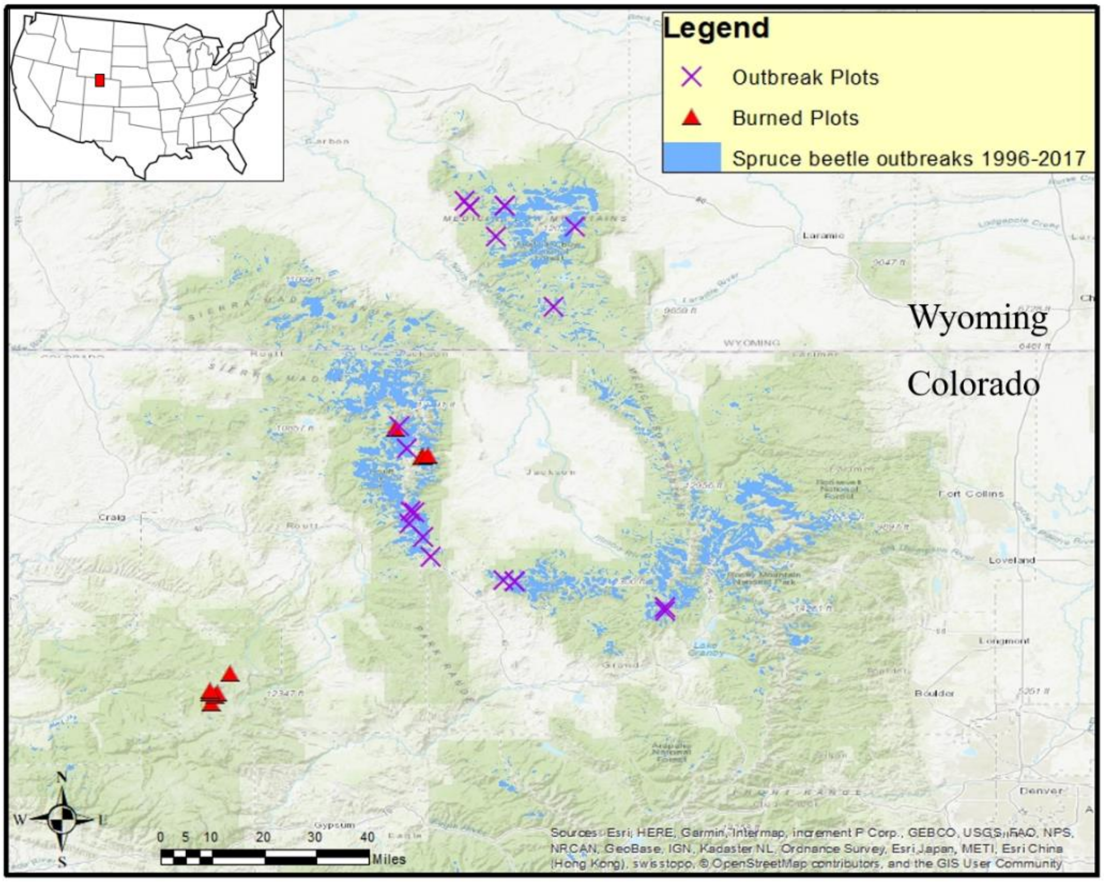

Figure 1: Map of site locations in Northern Colorado and Southern Wyoming.

Seedling samples were collected from a subset of fixed-area plots established by Schapira et al. (2020, *In Press)* (design adapted from Ott et al. 2018). Five circular subplots (0.004-ha (3.6m radius)) were established within the fixed-area plot to count tree regeneration. Seedling samples were collected from regeneration subplots. The first two seedlings of differing height classes encountered in each subplot were selected for destructive sampling. After height measurements and terminal bud scar counts (Urza & Sibold 2013), each sample was excavated to approximately 10 cm below the root collar and cut to obtain the root-shoot boundary. We collected 229 tree seedling samples across 30 sites. Ninety-three subalpine fir and 89 Engelmann spruce seedlings (182 samples) were collected across a range of height classes from 20 spruce beetle outbreak sites. Additionally, 22 subalpine fir and 25 Engelmann spruce (47 samples) were collected across a range of height classes from 10 burned sites, with approximately equal proportions from burned only and post-outbreak burned sites. Seedlings were only collected from plots with 2,500 seedlings/ha or more to limit the impact on site recovery.

Establishment dates were determined from the maximum count of annual rings on cross-section cuts from each tree seedling (Telewski 1993; League & Veblen 2006; Rother & Veblen 2017). Seedling samples were cut into at least three cross-sections at 2.5cm intervals beginning below the estimated root-shoot boundary (typically below ground level, above root collar). Each cross-section's top surface was sanded with progressively finer sandpaper (i.e., from 120 to 3000 grit) and examined under a microscope for the presence of pith; pith is not present in roots but is visible in the shoot of the tree (Telewski 1993). The first cross-section cut with the presence of pith is indicative of the oldest tissue, or the sample with the maximum ring count. We counted annual rings from the outer ring to the center pith. Half of the samples were photographed with an AxioCam color camera on a stereomicroscope (up to 50x zoom), and rings were subsequently counted. The other half of the samples were counted in real-time under a stereomicroscope (30x zoom). The maximum annual ring count was recorded as the age for that sample if it corresponded with the first appearance of pith; if not, the ring count in the cross-section cut with the first appearance of pith was used. A subset of samples was randomly selected for recount and age verification. A third count was performed to achieve a final age if there were discrepancies in annual ring counts. Seedlings with unclear ring boundaries were not included in analyses.

Statistics and graphics were completed in RStudio 1.3 (R Core Team 2019). Graphics were created using the ggplot2 package (Wickham 2016). A threshold of α=0.05 was used to designate statistical significance. Simple linear models were used to determine correlations between height and bud scar counts to true age. Significant predictors (height, disturbance type, and bud scar count) were incorporated into a generalized linear model (GLM) to assess correlations with the response variable (seedling age); outbreak sites were used as the baseline category in GLM analyses. The difference between bud scar count and seedling age ($count - age$) was used to quantify error from using bud scar counts as a proxy for age for both species. Seedling age and height were used as predictor variables to assess correlations with bud scar count errors in simple linear models. Accuracy of bud scar counts was calculated as the percentage of samples of which bud scars predicted the exact age. Simple and general linear models were performed using the base R package.

Climate data for each plot from 1958 to 2019 was used to identify drivers of seedling establishment (Abatzoglou et al. 2018). Growing season maximum temperature (°C), minimum temperature (°C), precipitation (mm), and soil moisture (mm) were used in analyses (monthly values averaged over May-September for each year). Average annual values of vapor pressure deficit (VPD, in kPa) and climatic water deficit (CWD, in mm) were used in analyses. VPD describes the amount of water vapor in the air at a given temperature, independent of precipitation or soil moisture, and is used as a metric of the atmospheric water demand for plants (Yuan et al. 2019). CWD is defined as the evaporative demand that exceeds available soil moisture, integrating solar radiation, precipitation, and evapotranspiration at a given air temperature (Stephenson 1998). CWD is different from VPD in that it is directly affected by snowpack and precipitation; CWD is used as a metric for drought stress on soils and plants (Stephenson 1998; McCullough et al. 2016). Twenty-seven seedlings were established before 1958 and consequently were not included in the climate variable analyses.

Z-scores were calculated for each climate variable for each site in order to standardize comparisons across sites. Each variable's long-term average is in the 50^{th} percentile of data and has a z-score of 0. Establishment pulses were identified as years with abundant seedling establishment across sites. Years in which cross-site establishment occurred were used to identify broad-scale climatic drivers of establishment pulses. Seedling establishment was grouped by the percentage of all seedlings (229) established per year. Four establishment pulse thresholds were defined as years in which 5%, 2%, $<2\%$, and 0% of total seedlings (229) were established in that year (methods adapted from Hankin et al. (2019)). Each climate variable was averaged across sites during years of establishment pulses for each species and threshold group. Kruskal Wallis tests were used to identify if significant differences were present in climate variable z-scores between threshold groups for each species. Dunn's Test was used to compare groups and identify statistically different groups using the dunn.test R package (Dinno 2017).

Results and Discussion

Results

All GLM predictors (height, disturbance type, and bud scar) were significant and explained 82% variability in Engelmann spruce seedling age and 80% variability in subalpine fir seedling age. Seedling height was a significant predictor of age for both species from both disturbances ($P<0.02$; $R^2>0.24$). However, correlations between height and age were weaker with taller seedlings.

Terminal bud scar counts were significant predictors of seedling age for both species from both disturbances (Figure 2). On average, bud scars underestimated the true age of seedlings from outbreak sites by 11.1 years, although estimates ranged from underestimates of 76 years to overestimates of 12 years. Conversely, the average bud scar estimate of post-fire seedling age was an underestimate by 1 year. Age estimates of post-fire seedlings ranged from underestimates of 3 years to overestimates of 7 years.

The error of bud scar predictions of true age increased with increasing age for both species ($P<0.0001$; $R^2>0.84$). Bud scar counts of Engelmann spruce seedlings from beetle-affected stands over ~30 years old started to deviate from the fitted regression line (Figure 2b). Similarly, the accuracy of bud scar counts on subalpine fir seedlings from beetle-affected stands older than ~28 years decreased substantially (Figure 2a). Bud scar counts as a proxy for true age did not differ with age in post-fire seedlings (Figures 2c and 2d). The error rate of bud scar predictions of true age increased with increasing height for both species ($R^2>0.3$); however, the relationship was relatively weak compared to the strong correlation between seedling age and bud scar count error (Figure 2). Table 1 shows the difference in errors and accuracy for subalpine fir and Engelmann spruce from beetle-affected stands and high-severity burn areas in subalpine forests.

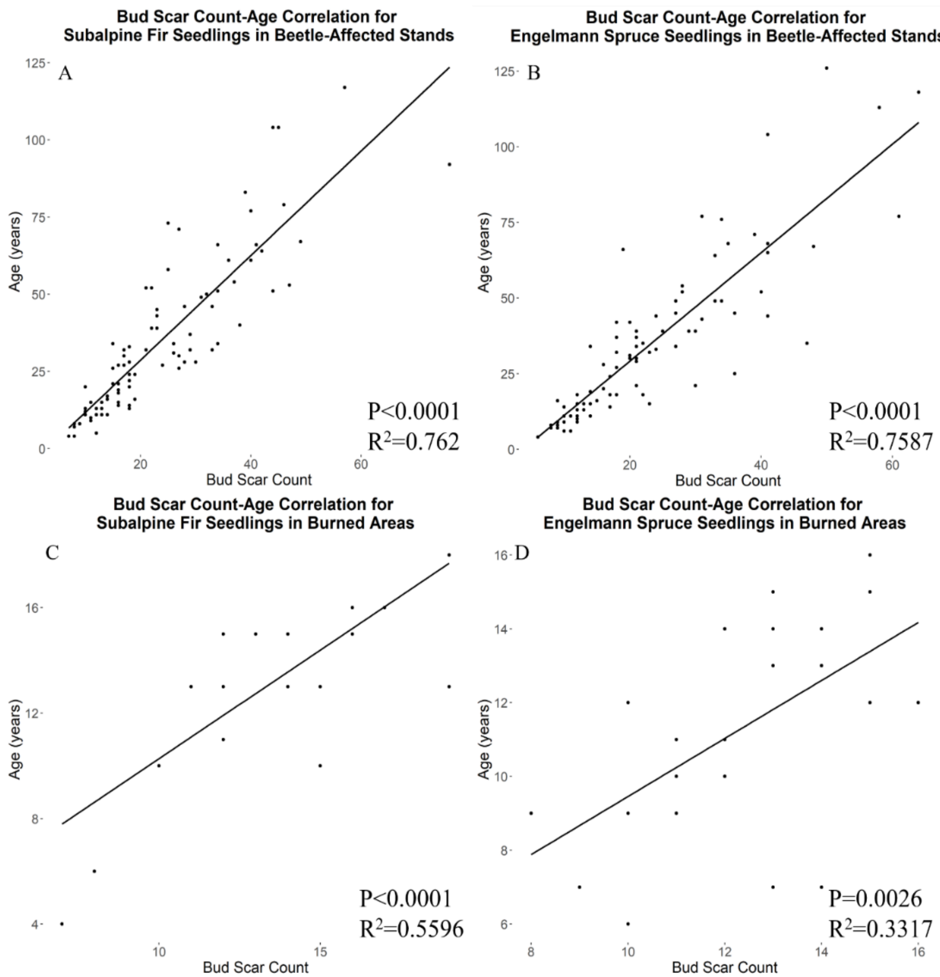

Figure 2: Correlation between terminal bud scar count and true age for A) subalpine fir in beetle-affected stands, B) Engelmann spruce seedlings in beetle-affected stands, C) subalpine fir in burned stands, and D) Engelmann spruce in burned stands.

Comparisons of climate variable z-scores yielded significant differences between years with large establishment pulses (5% group) and years with no establishment. Growing season temperature minimums, precipitation, annual VPD, and annual CWD were significantly different between years of >5% total seedling establishment and years with no establishment. In years with low levels of establishment (<2% and 2% establishment threshold groups), there were not significant differences between climatic variables, and climatic variable z-scores fell in between extreme z-score values that occurred in years of no establishment and years with >5% seedling establishment (Figure 3). These low-level establishment groups occurred in years that represented mean conditions of study sites over the last 61 years. During years of establishment pulses for both subalpine tree species, growing season maximum temperatures ($P>0.1$) and growing season soil moisture ($P>0.3$) did not exhibit significant correlations with threshold groups. Large establishment pulses were synchronous across sites, and many were consistent among both species.

Growing season minimum temperatures were significantly lower in years with abundant establishment (5% threshold group) compared to years with less or no establishment of both subalpine fir ($P<0.03$) and Engelmann spruce ($P<0.0001$) (Figure 3a). Precipitation was significantly different among establishment threshold groups for both species ($P<0.0001$) (Figure 3b). Years with no establishment had the lowest growing season precipitation z-scores of any establishment group, and large Engelmann spruce and subalpine fir seedling establishment pulses occurred in years with above average precipitation (Figure 3b). Years with no seedling establishment (0% group) had the highest VPD values of all establishment groups and higher mean VPD than the long-term average (z-score=0.4727; 68th percentile); large pulses of subalpine fir and Engelmann spruce seedling establishment occurred in years with below average VPD (Figure 3c). Large establishment pulses of both tree seedlings occurred in years with below average CWD, while years of no establishment had the highest CWD values of all establishment groups (Figure 3d).

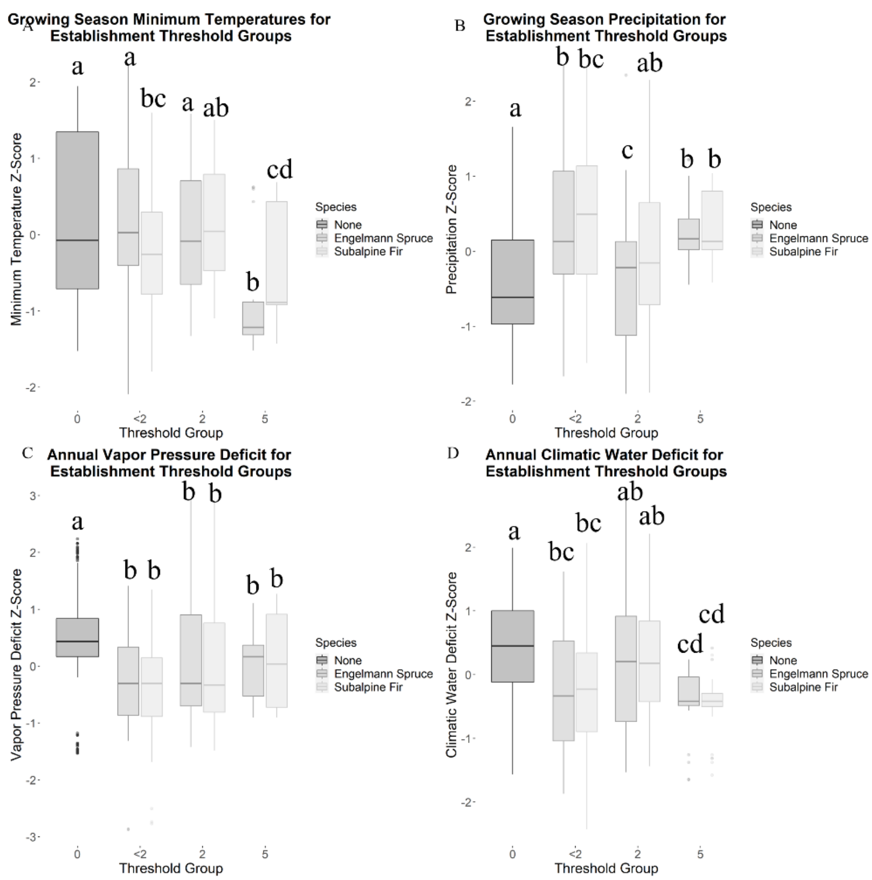

Figure 3: Boxplots of differences of climate variable z-scores between establishment threshold groups: A) growing season temperature minimums, B) growing season precipitation, C) annual vapor pressure deficit, D) annual climatic water deficit. Green boxes and text represent Engelmann spruce seedlings; blue boxes and text represent subalpine fir seedlings. <2% and 2% threshold groups represent long-term mean conditions. Different letters above groups indicate statistical significance using Kruskal-Wallis tests to detect differences, and Dunn's tests to compare same species groups with years of no establishment ($\alpha=0.05$).

Discussion

Height and terminal bud scar counts were both significant predictors of seedling age for both species. However, the strength of correlation decreased as seedling height and age increase. Climate drives broad-scale tree seedling establishment in dominant subalpine species. Growing season temperature and precipitation, annual VPD, and CWD were limiting factors to subalpine tree establishment. The age distribution of post-disturbance regeneration indicates low levels of semi-continuous establishment pre- and post-spruce beetle outbreaks during years of suitable climatic conditions. However, large Engelmann spruce and subalpine fir establishment pulses occur in growing years with cooler and wetter conditions than the long-term average, which may warrant concern with continued drying and warming climatic trends.

Subalpine fir and Engelmann spruce are both shade-tolerant species that can remain suppressed in the understory or subcanopy for decades to centuries. Because of this growth trait, height classes are not accurate proxies for the true age of either subalpine tree species. For example, a 15-year-old seedling and a 52-year-old seedling were both 10.8cm tall, and thus these seedlings are counted in the same height class and assumed to be the same age. Although there is a strong positive relationship between height and age (older trees *tend* to be taller), there can be exceptions to this correlation. Seedlings in subalpine stands tend to be multi-aged with variable growth rates; classification based solely on height as a proxy for relative age does not provide sufficient information to assess post-disturbance recovery dynamics.

A greater age-height slope coefficient in outbreak stands compared to burned stands indicates the older age distribution of seedlings typical in spruce-fir forests (Figure 4). Establishment dates from beetle-affected stands range from 1893 to 2015, given closed-canopy conditions that permit prolonged suppressed growth. On the other hand, the lower age-height slope coefficient in burned stands relative to beetle-affected stands indicates the younger age distribution of post-fire seedlings (Figure 4). Post-fire seedlings established in 2001 or later, resulting in a younger cohort of seedlings from burned areas. Subalpine species are fire-sensitive, and wildfires are often stand replacing in subalpine forests; without canopy cover and dense understory vegetation, Engelmann spruce and subalpine fir grow quickly over short temporal scales given high light levels (Veblen 1986). Compared to outbreak sites with suppressed growing conditions, seedlings of a given age are generally taller in burn areas than in beetle-affected stands. Moderate severity, biotic disturbances allow for continuous establishment both pre- and post-disturbance, compared to stand-replacing, abiotic disturbances that truncate the age distribution of seedlings.

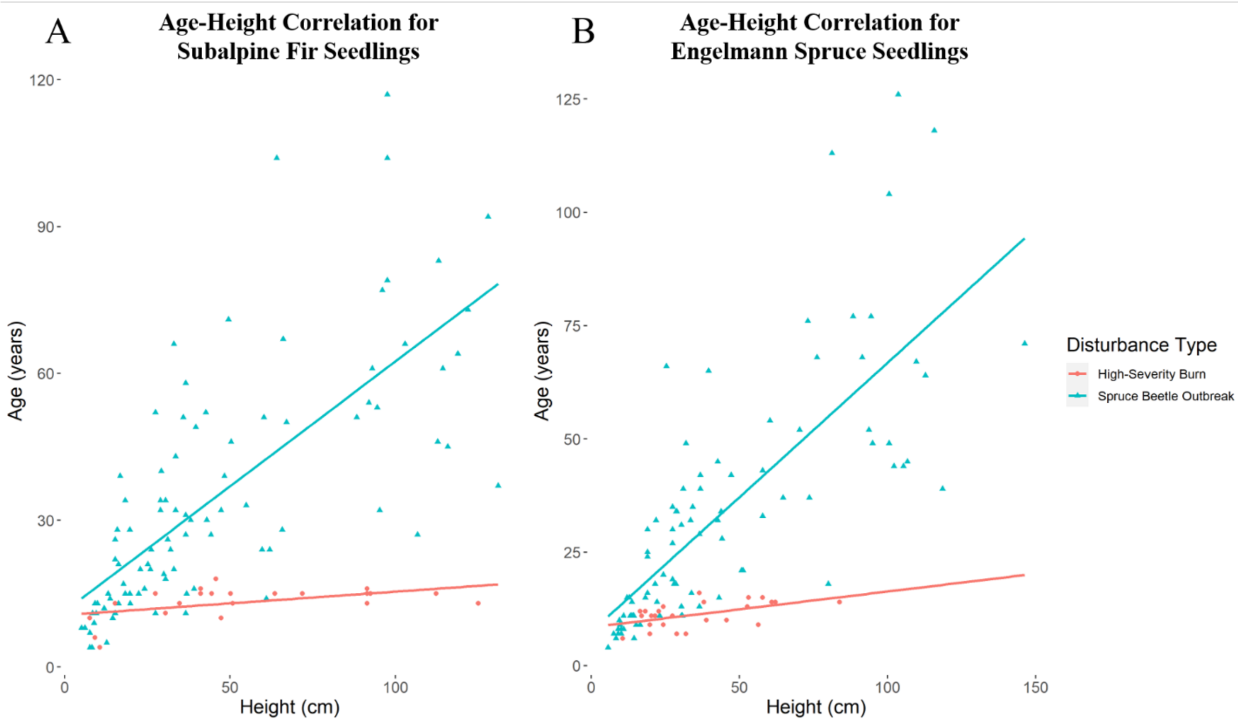

Figure 4: Age-height relationships for A) subalpine fir and B) Engelmann spruce seedlings from high-severity burn areas (red points and lines) and beetle-affected stands (blue points and lines).

For both Engelmann spruce and subalpine fir, the error between bud scar counts and true age becomes increased in older seedlings; terminal bud scar counts consistently underestimate long-lived seedlings. This trend could be due to the slow growth exhibited by older seedlings in suppressed settings. Using terminal bud scar counts may be limited in slow-growing species such as suppressed subalpine fir and Engelmann spruce due to extremely small growth increments between bud scars and the potential for radial growth in older seedlings to obscure bud scars (Urza & Sibold 2013). We found greater accuracy of terminal bud scar counts in predicting ages of young seedlings. Aside from differences in sample size, greater accuracy of bud scar counts in predicting postfire seedling age could be due to high growth rates and younger ages of seedlings from burned areas compared to seedlings from closed canopy stands, negating the difficulty of discerning narrow growth increments. Relatively fast growth rates in postfire seedlings compared to suppressed seedlings from beetle-affected stands may result in greater visibility of bud scars, leading to more accurate age predictions in postfire tree establishment than establishment from closed canopy stands, supported by the findings of Urza and Sibold (2013).

Subalpine fir and Engelmann spruce establishment pulses were correlated with low minimum temperatures and high precipitation levels in the spring and summer months. Abundant subalpine fir and Engelmann spruce seedling establishment occurred in years with average growing season minimum temperatures below -0.1°C and -0.38°C of the mean minimum site temperature, respectively. Low spring temperature minimums may contribute to the persistence of winter snowpack late into the growing season; snowpack levels were directly correlated with successful subalpine fir and Engelmann spruce establishment in other studies (Buechling et al.

2016; Andrus et al. 2018; Carlson et al. 2020). Late season snowmelt provides soil moisture as evaporative demand increases with increasing temperature in the summer months (Stephenson 1998; Redmond & Kelsey 2018; Hill et al. 2018); soil moisture is critical for establishing seedlings as it is a major contributor of temperature-induced moisture stress (Brodersen et al. 2006). Below-average temperature minimums with above-average precipitation creates cool and moist growing season conditions that are optimal for subalpine tree species (Gill et al. 2015; Andrus et al. 2018; Hill et al. 2018). First-year subalpine tree germinants have high turgor loss points, indicative of high drought sensitivity (Lazarus et al. 2017); thus, subalpine seedlings require abundant growing season moisture in the first year of growth as we observed in high-level establishment years. Our results indicate that subalpine fir and Engelmann spruce establishment events are highly correlated with lower-than-average VPD and CWD. Low deficit values correspond with cooler temperatures on subalpine tree seedlings, supporting our findings of preferential establishment in cooler growing conditions. This finding of cool temperatures favoring subalpine tree establishment is supported by other studies in this forest type (Lutz et al. 2010; Kueppers et al. 2017; Andrus et al. 2018; Hill et al. 2018). The correlation of both temperature and moisture with deficit values underscores the importance of cool *and* moist growing conditions for the establishment and survival of subalpine tree species.

Years with large establishment pulses of both species (>5% total seedlings established across all sites) were strongly correlated with the climate variables detailed above. Many of the pulse events were synchronous across sites and species, indicating broad-scale drivers of seedling establishment. Some years with low levels of spruce-fir establishment had climatic conditions that were closer to the long-term average than years with large establishment pulses. However, these years were significantly different from years of no establishment which had hostile growing conditions compared to long-term climatic averages. This could be indicative of low levels of establishment that require suitable climatic conditions (but not anomalous from long-term mean) in addition to site-specific conditions, such as overstory facilitation or microclimate (Kroiss & HilleRisLambers 2015). Our finding of steady, yet low density, seedling establishment in subalpine forests is consistent with Woodward et al. (1995). Although site-specific conditions may encourage low levels of seedling establishment during moderately suitable growing years, regional conditions anomalous to long-term climate promoted broad-scale establishment events as seen with our data.

Science Delivery

The findings of this study have been delivered through oral presentations over zoom in a graduate master’s thesis defense and a webinar for JFSP Southern Rockies Fire Science Network to a diverse audience including forestry professionals, students, and the general public. As this study was necessitated as an addendum to the original thesis project, the results from the original project were delivered through an oral presentation at the 8th International Fire Ecology and Management Congress hosted by the Association for Fire Ecology in Tucson, AZ. This study will be submitted to the *Journal of Vegetation Science* for publication by the end of 2020.

Conclusions

This project is one of few studies to assess annual climatic drivers of subalpine tree establishment. Our results corroborate the strong correlation between cool and moist growing conditions with successful subalpine tree establishment previously established in the scientific literature. Our findings suggest that favorable, broad-scale anomalous climatic conditions act as regional drivers of establishment pulses, while suitable regional climate and site-specific conditions may facilitate low-levels of establishment on short temporal scales. The use of terminal bud scar counts and height classes to predict the age of suppressed seedlings lacks a high degree of accuracy, especially in older seedlings. However, greater accuracy can be obtained in postfire establishment due to distinguishable bud scars resulting from rapid growth that is unimpeded by light availability. This is an important consideration for managers when assessing post-disturbance recovery. The critical role of first-year climate in seedling survival in conjunction with projected increases in moisture stress contribute to significant uncertainty about subalpine forests' resilience against altered disturbance regimes and changing climatic conditions. Our findings also suggest that in the absence of high-severity disturbances such as fire, shade tolerant species have established and remained in the understory for over 100 years, indicating that recruitment predates bark beetle outbreaks in these stands; long-lived cohorts in the understory may prime these landscapes for rapid recovery to similar forest structures given suitable climate for growth.

Research Limitations

In this study, we tried to encapsulate regional drivers of establishment within one forest type and incorporating fine-scale spatial variability into analyses was beyond the scope of this project, but important for future research. There could be a potential scale mismatch between remote sensing derived site variables, such as soil moisture, and actual site conditions that vary over narrow spatial and temporal scales. Additionally, the sample size of seedlings from burned areas was relatively small in comparison to the number of seedlings from beetle-affected stands, potentially introducing bias when comparing the two groups. Seedlings from burned areas have only established over the last two decades, while seedlings from beetle-affected stands date back to the late 19th century. This shorter window of establishment in burned areas prevents observations of long-term growth trends of post-fire recruitment. Additional samples and samples from older fires could increase the power of future analyses.

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Appendix A

Zoe Schapira- zhschapi@colostate.edu

Camille Stevens-Rumann- c.stevens-rumann@colostate.edu

Appendix B

- This study will be submitted to *Journal of Vegetation Science* by December 30, 2020 as:

  Schapira, Z.S., Stevens-Rumann, C.S., and Shorrock, D. 2020. Seedlings? The unexpected elders of understory trees. *Journal of Vegetation Science*.

- Once this publication is complete, all data will be made available on the USFS Research Data Archive.
- The MS thesis was successfully defended on October 30, 2020.
- The findings of this study were presented at a webinar for JFSP Southern Rockies Fire Science Network on November 6, 2020. http://www.southernrockiesfirescience.org/research-publications-1/2020/11/13/webinar-ecological-effects-of-multiple-disturbances-on-subalpine-forest-structure-and-recovery-in-a-changing-climate
- This study, in combination with the other chapter of the MS thesis will be made into a research brief for the SRFSN in January 2021.
- The findings of the preceding publication were presented at the 8th International Fire Ecology and Management Congress hosted by the Association for Fire Ecology in Tucson, AZ on November 18, 2019. This publication can be found in the **Other Products** tab.

Appendix C

The data collected from this project include maximum ring counts as seedling age, height and terminal bud scar counts of seedlings. Establishment dates of seedlings were calculated from seedling age. Other data used in this study include TerraClimate monthly climate variables from 1958-2017. The data used in this project did not deviate from the original data management plan. Metadata can be accessed at the USFS Research Data Archive.