

Article

Climate Drives Episodic Conifer Establishment after Fire in Dry Ponderosa Pine Forests of the Colorado Front Range, USA

Monica T. Rother ^{1,2,*} and Thomas T. Veblen ¹

¹ Biogeography Lab, Department of Geography, University of Colorado, Boulder, CO 80309, USA; veblen@colorado.edu

² Tall Timbers Research Station & Land Conservancy, 13093 Henry Beadel Drive, Tallahassee, FL 32312, USA

* Correspondence: rother@colorado.edu or mrother@ttrs.org; Tel.: +1-541-908-2068

Academic Editor: Emanuele Lingua

Received: 1 March 2017; Accepted: 27 April 2017; Published: 8 May 2017

Abstract: In recent years, warming climate and increased fire activity have raised concern about post-fire recovery of western U.S. forests. We assessed relationships between climate variability and tree establishment after fire in dry ponderosa pine forests of the Colorado Front Range. We harvested and aged over 400 post-fire juvenile ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) trees using an improved tree-ring based approach that yielded annually-resolved dates and then assessed relationships between climate variability and pulses of tree establishment. We found that tree establishment was largely concentrated in years of above-average moisture availability in the growing season, including higher amounts of precipitation and more positive values of the Palmer Drought Severity Index. Under continued climate change, drier conditions associated with warming temperatures may limit forest recovery after fire, which could result in lower stand densities or shifts to non-forested vegetation in some areas.

Keywords: climate variability; regeneration dynamics; resilience; ponderosa pine; tree establishment; wildfire; tree rings; Colorado Front Range; dendrochronology; climate change

1. Introduction

In ecology, resiliency can be defined as the ability of an ecosystem to absorb disturbance without transitioning into a qualitatively different ecosystem type [1,2]. Western U.S. forests have historically exhibited high resiliency to fire, in that they have generally recovered in the decades following burning, rather than transforming into persistent alternative states such as grasslands, shrublands, or sparse woodlands [3]. However, recent studies have documented limited tree regeneration after fire, at least within portions of burns [4–10], which could be indicative of a trend toward lower resiliency to fire. These changes may be linked to climate change, altered wildfire regimes, low seed availability, or a combination of these and other factors.

In some forested ecosystems, increased temperature and associated drought may be important drivers of limited tree regeneration after fire [6,11–13]. Many species have a narrow regeneration niche under which new germination and establishment typically occurs. Given that climate change is resulting in hotter and drier conditions, some tree species may no longer be able to regenerate as successfully at sites that were previously suitable. Climate change is most likely to interfere with regeneration processes in forest types that are at the edges of where climate is optimal for the dominant tree species [14], such as at lower treeline or at lower latitudinal limits of species distributions. In these more vulnerable settings, fire can act as a catalyst to rapid changes that would otherwise occur more gradually. This is especially true following higher-severity fire which removes large numbers of live

trees and thus can accelerate shifts in tree species distributions predicted from differences between climatic tolerances of adult trees and climatic conditions necessary for successful establishment and survival of seedling populations [14–16].

Climate variability is known to be a key factor driving tree establishment in dry ponderosa pine forests, at least in the absence of recent fire. For example, many early papers attributed widespread ponderosa pine (*Pinus ponderosa*) regeneration in 1919 in Arizona to abundant summer precipitation following an excellent seed year [17–19]. Confidence in the role that interannual climate variability plays in driving patterns of ponderosa pine regeneration increased following improvements in methodologies of determining establishment dates. By dating the pith (i.e., innermost ring) at the root-shoot boundary, an annually-resolved estimate of tree establishment can be obtained [20,21]. In ponderosa pine forests of Arizona [22] and of the Colorado Front Range [23], annually-resolved establishment dates indicated that tree establishment occurred primarily in years of above-average moisture availability. More recently, researchers have addressed climate-establishment relationships in post-disturbance environments. Feddema et al. [11] and Savage et al. [12] examined the importance of climate variability in driving patterns of ponderosa pine regeneration in the Southwest and found that monthly to seasonal climate conditions associated with various developmental stages of ponderosa pine (e.g., germination, cone production, etc.) were important for predicting patterns of observed ponderosa pine establishment following fire. An acknowledged limitation of these studies is that tree establishment dates were based on estimates from increment cores and therefore annual resolution may not have been consistently achieved. Moreover, it is unclear whether patterns from the Southwest apply to other ponderosa pine forests, given differences in climate, topography, and forest composition and structure, among other factors. Although more research is needed, previous work suggests that regeneration in dry ponderosa pine forests requires above-average moisture conditions. Given that higher temperatures are generally associated with increased drought due to increased evapotranspiration, climate change may result in fewer occurrences of abundant ponderosa pine regeneration both before and after fire.

The possibility of climate-mediated shifts in post-fire vegetation patterns in western forests is especially important given increased wildfire activity in recent years. Both the numbers of large (>400 ha) forest wildfires and the areas burned by them exhibit a sustained increase since the mid-1980s across the U.S. West [24,25]. In the Southern Rockies (i.e., Wyoming and Colorado south of 42° N latitude) for the period from 2003 to 2012, the percent change over the 1973–1982 average in numbers of large wildfires and areas burned has been 256% and 331%, respectively [25]. Fire severity has also increased in some areas; data derived from satellite imagery for the Southern Rockies shows an increasing trend over the period 1984–2010 [26]. Increased fire severity is particularly of concern in systems where trees disperse seed by wind over relatively short distances. This is true of ponderosa pine forests, where recovery following high-severity fire is greatly delayed by slow dispersal by ponderosa pine and Douglas-fir (*Pseudotsuga menziesii*) into large openings [4,11,12]. The slow recovery in high-severity patches due to dispersal limitations is likely to be exacerbated by hotter, drier conditions that inhibit tree regeneration processes. Researchers continue to examine the drivers of increased wildfire activity, which vary across forest types. However, increased temperatures and associated drought, earlier spring snowmelt, and, in some areas, land-use history (especially fire exclusion), maybe linked to observed increases [24,25,27].

Retrospective studies using tree rings are an important source of information about historic forest recovery patterns after fire and can provide context for assessing present day conditions. However, in these types of studies it can be challenging to distinguish between the effects of past climate variability versus past fire on the age structure of the stand [28,29]. Pulses of establishment theoretically could be favored by short-lived favorable climatic conditions (e.g., pluvials) or by the occurrence of fires, which can create establishment opportunities by decreasing the shading effects from mature trees, exposing bare mineral soil, and reducing competition from understory species [30]. Distinguishing among the mechanisms responsible for pulses of establishment is particularly challenging when reconstructing tree ages in relatively closed canopy stands many

decades or more than a century following stand initiation and requires analytical procedures beyond simple graphical comparison of cohorts and potential drivers of tree establishment [28,29]. As a shade-intolerant species, regeneration of ponderosa pine is limited by light beneath dense or moderately dense forest canopies [18,19]. At more mesic sites where closed canopies can form, favorable climate conditions at an annual or even decadal scale are less likely to result in a major pulse of a shade-intolerant tree species such as ponderosa pine. Instead, pulses of regeneration at these sites have been linked to moderate or high severity burning that creates open patches in the main canopy, exposes bare mineral soil, and results in high light environments suitable for the regeneration of ponderosa pine [31–33]. The relative importance of stand-opening fires vs. climate variability on ponderosa pine regeneration is likely to vary across a topographically diverse landscape and uncertainty remains difficult to resolve. Feasibility of linking regeneration episodes to climatic variability is greatest in open habitats such as those created by recent fires where confounding competitive effects from mature trees are less notable [23].

In the current study, we examined temporal patterns of post-fire conifer establishment and survival for five areas that burned in the Colorado Front Range between 1988 and 2003. Our focus was on dry ponderosa pine forests of the lower montane zone, which is near the lower elevational limit of where climate is suitable for forested vegetation. The primary research objectives were to: (1) develop a record of annually-resolved establishment dates for ponderosa pine and Douglas-fir seedlings in recent burn areas, and (2) determine any influences of climate variability on temporal patterns of conifer establishment and survival following fire. We focused on tree establishment in open areas at sites burned within the previous c. 24 years (the earliest fire was in 1988, sampled in 2012) to increase the likelihood of being able to link establishment to annual or quasi-annual climate variability without the complicating factors related to long-term stand dynamics and development of light limitations beneath closed tree canopies. By examining the climate conditions under which past tree establishment occurred, the present study aims to provide insight into the potential effects of continued climate warming on the resilience of dry ponderosa pine forests in the face of recent and likely future wildfires.

2. Materials and Methods

2.1. Study Area

The study area is along the eastern slope of the Colorado Front Range, extending from a northernmost location in Boulder County to a southernmost location in Douglas County (Figure 1). The Colorado Front Range is along the eastern edge of the southern U.S. Rocky Mountains. In the lower montane zone where dry ponderosa pine forests occur [34,35], the long-term mean maximum January temperature is approximately 4.1 °C, mean maximum July temperature is approximately 26.4 °C, and annual mean precipitation is approximately 422 mm (Bailey Cooperative Observer Program (COOP) Station, 2360 m, period of record: 1901–2013). However, across Colorado, annually-averaged temperatures have been on a warming trajectory in recent decades, with consistently warmer than average temperatures since the mid-1990s [36]. A climate station in the lower montane zone centrally located in our study area shows a warming trend (0.15 °C/decade) in average yearly maxima temperatures over the period 1953–2008, which has steepened during the 1989–2008 period [37]. The most significant increases in monthly maxima temperatures have been in March and July, respectively, for these 56 and 20 year periods [37]. Additionally, regional average temperatures across Colorado are expected to rise by an additional 1.4–3.6 °C by 2050 [36]. In contrast, precipitation patterns have not changed significantly and it is uncertain if and how precipitation regimes may change in the future [36].

Throughout the Colorado Front Range, forest vegetation patterns are strongly influenced by moisture variability related to both elevation and aspect [35]. At the lower elevational range of the lower montane zone, ponderosa pine is dominant and forms relatively open stands. With increasing elevation

and moisture availability, stand density increases and Douglas-fir is often present or co-dominant [34]. The elevational range of the lower montane zone varies with latitude and microsite conditions, ranging from approximately 1675–2285 m in the northern Colorado Front Range and from approximately 1980–2590 m in the southern portion. Our study area is situated centrally, where the lower montane zone extends from approximately 1830–2440 m [34]. Below the lower montane zone is the lower ecotone where vegetation transitions from primarily forested to non-forested vegetation [38].

In ponderosa pine forests of the Colorado Front Range, the historic fire regime was mixed severity, meaning that fire effects varied both within stands and across the landscape and included low-, moderate-, and high-severity fire [30,32,34]. While historic fire regimes of exclusively low-severity were most common at the lowest elevations near lower treeline [27], higher severity fires that killed at least 70% of canopy trees also occurred even at low elevations [32,34,39]. Both ponderosa pine and Douglas-fir are non-serotinous and have seeds that are dispersed primarily by wind over relatively short distances [40–42].

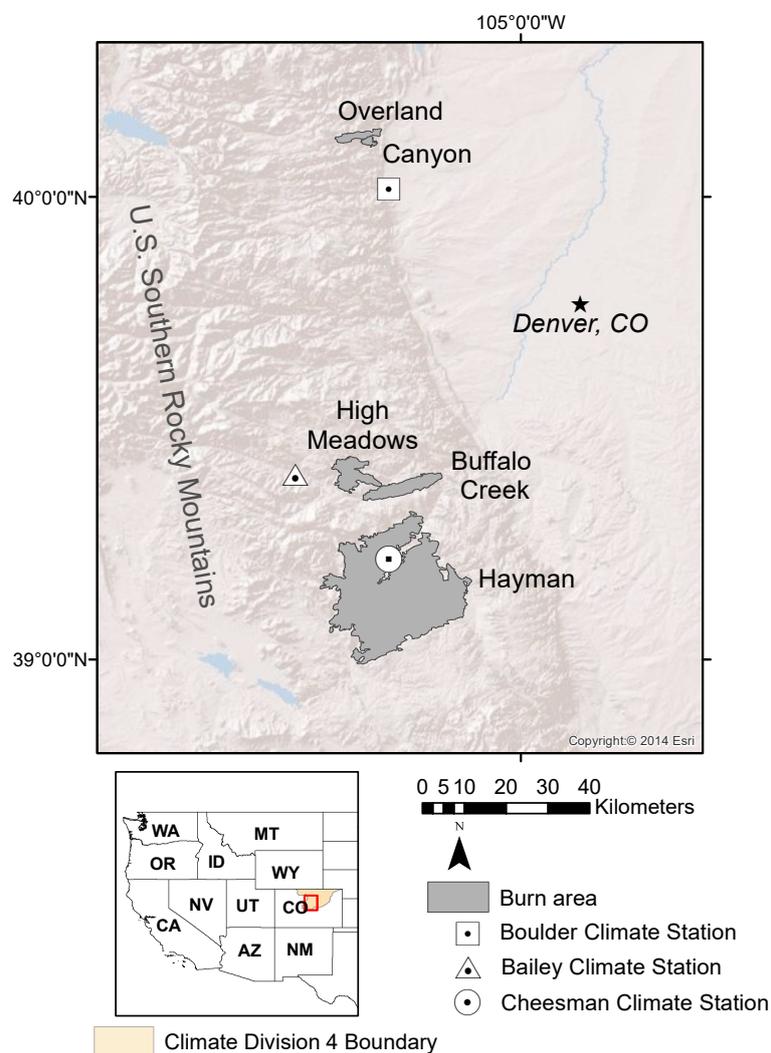


Figure 1. Locations of the five recently burned areas included in this study. All sites are within the lower montane zone of the Colorado Front Range, along the eastern edge of the U.S. Southern Rocky Mountains. All sites are characterized by dry ponderosa pine forests and are at elevations ranging between 1950 and 2230 m. The Boulder, Bailey, and Cheesman Cooperative Observer Program (COOP) climate stations and the boundary for the National Climatic Data Center (NCDC) Climate Division 4 for Colorado are also shown.

2.2. Data Collection and Sample Processing

We harvested and aged post-fire juvenile conifers in five recently burned areas in the lower montane zone in the Colorado Front Range (Figure 1, Table 1, and Supplementary Table S1). These burn areas were chosen using GIS data layers of recent fires from the Monitoring Trends in Burn Severity Program (MTBS). MTBS includes fire perimeter and severity data for all U.S. wildfires since 1984, except for small fires (fires <200–400 ha, depending on the region of the country). We generated a list of all wildfires over 400 hectares that occurred mostly or entirely within the lower montane zone of the Colorado Front Range between 1984 and 2003. More recent fires were not included because we wanted time since fire to be sufficient enough for post-fire regeneration to be underway. This generated a list of nine fires, of which six were chosen based on accessibility and presence of patches of abundant regeneration. The burns ranged in size from 443 to 52,368 ha (Supplementary Table S1). Time since fire ranged from 8–23 years.

Table 1. Description of the ten sampling sites included in this study. All sites are located in the lower montane zone of the Colorado Front Range.

Burn Area	Site Name	Latitude (Decimal Degrees)	Longitude (Decimal Degrees)	Elevation (m)	Aspect (Degrees)	Slope (Degrees)	Area (m ²)
Canyon	Can01	40.1195	−105.3255	2000	330	15	150 (10 × 15)
	Can02	40.1188	−105.3256	2030	340	15	50 (5 × 10)
Buffalo Creek	BFC01	39.3753	−105.2608	2190	350	5	1750 (35 × 50)
	BFC02	39.3733	−105.2722	2190	360	5	1875 (25 × 75)
High Meadows	HIM01	39.4097	−105.3667	2170	5	15	5625 (75 × 75)
	HIM02	39.4075	−105.3511	2130	5	20	250 (10 × 25)
Hayman	HAY01	39.1824	−105.1695	2220	40	15	750 (10 × 75)
	HAY02	39.1817	−105.1683	2230	30	20	875 (25 × 25)
Overland	OVL01	40.1428	−105.3167	1950	315	15	200 (10 × 20)
	OVL02	40.1353	−105.3228	1970	10	20	875 (25 × 25)

During the summers of 2011 and 2012, two sites were located in each of the five burn areas, for a total of ten sites (Table 1). At each site, areas of relatively abundant juvenile conifers were identified for sampling. We situated the plots in open areas; no mature trees were present within the plot boundaries. However, in all cases, an abundant seed source (i.e., at least five reproductively mature trees that could produce cones) was present within approximately 50 m of the plot center. Plot size varied to include a minimum of 50 juvenile trees (<150 cm tall). Elevation varied between 1950 and 2230 m and aspect was generally northerly (Table 1). The preferential sampling of the more mesic northerly aspect reflects the extreme scarcity of seedlings on xeric southerly aspects [9]; south-facing aspects with abundant seedlings are rare in the study area. Plots contained either exclusively ponderosa pine or a combination of ponderosa pine and Douglas-fir juveniles (Table 2). Within each plot, we recorded the species, height, and diameter at base height of each juvenile conifer. The juveniles were then harvested. Small juvenile conifers were uprooted by hand. For large juveniles, we first excavated an area around the roots with a shovel and then used a handsaw or clippers to remove a c. 15-cm long subsection, centered on the root collar (Figure 2).

In the laboratory, we determined the establishment year of the sampled juvenile conifers by dating the pith at the root-shoot boundary. To do so, we implemented an improved method of accurate tree aging, similar to that described by Telewski and Lynch [20] and Telewski [21]. We first divided each sample into several cross sections at 2.5 cm vertical intervals. The top surface of each cross section was then sanded with progressively finer sandpaper to reveal the cellular structure. As expected, ring counts typically increased from the uppermost cross section in the stem down toward the root collar. The appearance of a pith (characterized by dark, clustered parenchyma cells) is absent in the roots and thus the point at where pith no longer occurs was used to identify the location of the root-shoot boundary (Figure 2). For our samples, this transition typically occurred just below ground

level, but above the root collar. The establishment date assigned to each juvenile conifer was based on the number of rings present at the root-shoot boundary (i.e., last sample that still had pith before the roots) and also corresponded with a maximum ring count for the sample. Statistical crossdating is not feasible for juvenile trees due to the small number of total rings, but the outermost ring date was always known (2011 or 2012); in addition, we were able to identify marker rings from a regional ponderosa pine tree-ring chronology ([43], and updated by new sample collection in 2008) to assist with visual crossdating. Trees with unclear ring boundaries that could not be confidently counted were not included in the final dataset.

Table 2. Sample sizes of juvenile ponderosa pine and Douglas-fir collected at each site.

Burn Area	Site	Ponderosa Pine (<i>n</i>)	Douglas-Fir (<i>n</i>)	Total per Site (<i>n</i>)	Total per Burn (<i>n</i>)
Canyon	Can01	38	2	40	83
	Can02	37	6	43	
Buffalo Creek	BFC01	40	5	45	86
	BFC02	41	0	41	
High Meadows	HIM01	30	3	33	74
	HIM02	32	9	41	
Hayman	HAY01	28	4	32	79
	HAY02	40	7	47	
Overland	OVL01	47	1	48	91
	OVL02	39	4	43	
Overall Total		372	41		413



Figure 2. Images from the field and laboratory related to methods for dating juvenile trees in the present study. (A) A post-fire ponderosa pine seedling being harvested from a burn area; (B) collecting a subsample from the harvested seedling; (C) images from the stem portion of a sample, with the piths visible; (D) images from the root portion of a sample, with the pith no longer visible.

2.3. Analytical Methods

We began by assessing climate-establishment relationships in each of the individual burn areas. This phase of the analysis relied on COOP station data accessed from the Western Regional Climatic Center. The station nearest to the sample sites within each burn area was selected (Figure 1). This was the Cheesman Station (ID 051528-4, elevation 2097 m) for the Hayman sites, the Bailey Station (ID 050454-4, elevation 2356 m) for the High Meadow and Buffalo Creek sites, and the Boulder Station (ID 050848-4, elevation 1670 m) for the Overland and Canyon sites. We then examined whether years of episodic establishment by ponderosa pine and Douglas-fir coincided with years of anomalous precipitation and temperature patterns, compared to the long-term record (1961–2010). Three levels of episodic establishment were defined as years in which a minimum percentage (i.e., 5%, 10%, or 20%) of total tree establishment occurred at each site and for all sites combined. Based on initial assessment of the data, we noticed that years of episodic establishment tended to include one or more months in which precipitation was relatively high during the growing season (April–September). We then used a chi-square goodness of fit test to evaluate whether more establishment occurred in years with one or more months of exceptional precipitation (i.e., months where precipitation exceeded the 90th percentile based on the long-term record) than would be expected by chance.

Following our analysis at the site level, we combined all establishment data into one dataset to examine whether broader scale patterns were evident. Three levels of episodic establishment were defined as years in which a minimum percentage (i.e., 5%, 10%, or 20%) of total tree establishment occurred. This analysis relied on monthly divisional data from the National Climatic Data Center, which are averaged data that come from numerous Cooperative Observer Network (COOP) stations across each division. We used Division 4 data from Colorado because all of our study sites are included within that area. The variables we focused on were monthly total precipitation, monthly mean temperature, and monthly mean Palmer Drought Severity Index (PDSI) for years of episodic establishment vs. non-establishment years, averaged for the period April–September. PDSI is a measure of drought that uses positive values to indicate wetter than average conditions and negative values to indicate drier than average conditions. We assessed statistical differences between each climate variable in years of episodic establishment vs. non-episodic establishment using non-parametric Mann-Whitney tests at the $p < 0.05$ levels.

3. Results

3.1. Annually-Resolved Establishment Dates

Of the 562 post-fire conifer juveniles we collected, we successfully dated a total of 413 samples (73.5%, Table 2). To ensure high accuracy of our date estimates, only samples with clear ring boundaries were included in the final dataset. The majority of all samples dated were ponderosa pine (90% ponderosa pine, 10% Douglas-fir). Given that Douglas-fir seedlings were rare in our study sites ($n = 0-9$ Douglas-fir seedlings per site), we combined Douglas-fir and ponderosa pine in the analyses. Year of establishment ranged from 1992 to 2011 (Figure 3). At individual sites, establishment was generally concentrated within relatively few years. Some years of episodic establishment were common to multiple sites, such as 1998 (at Canyon and Buffalo Creek). For all sites combined using a criterion of 20% of the total establishment per site, three years stand out as accounting for much of the establishment: 1995, 1998, and 2009 (Figure 3f). Seedling establishment typically lagged behind wildfire by one to several years, although a pulse of establishment in the same year as fire was observed at the High Meadows site in 2000.

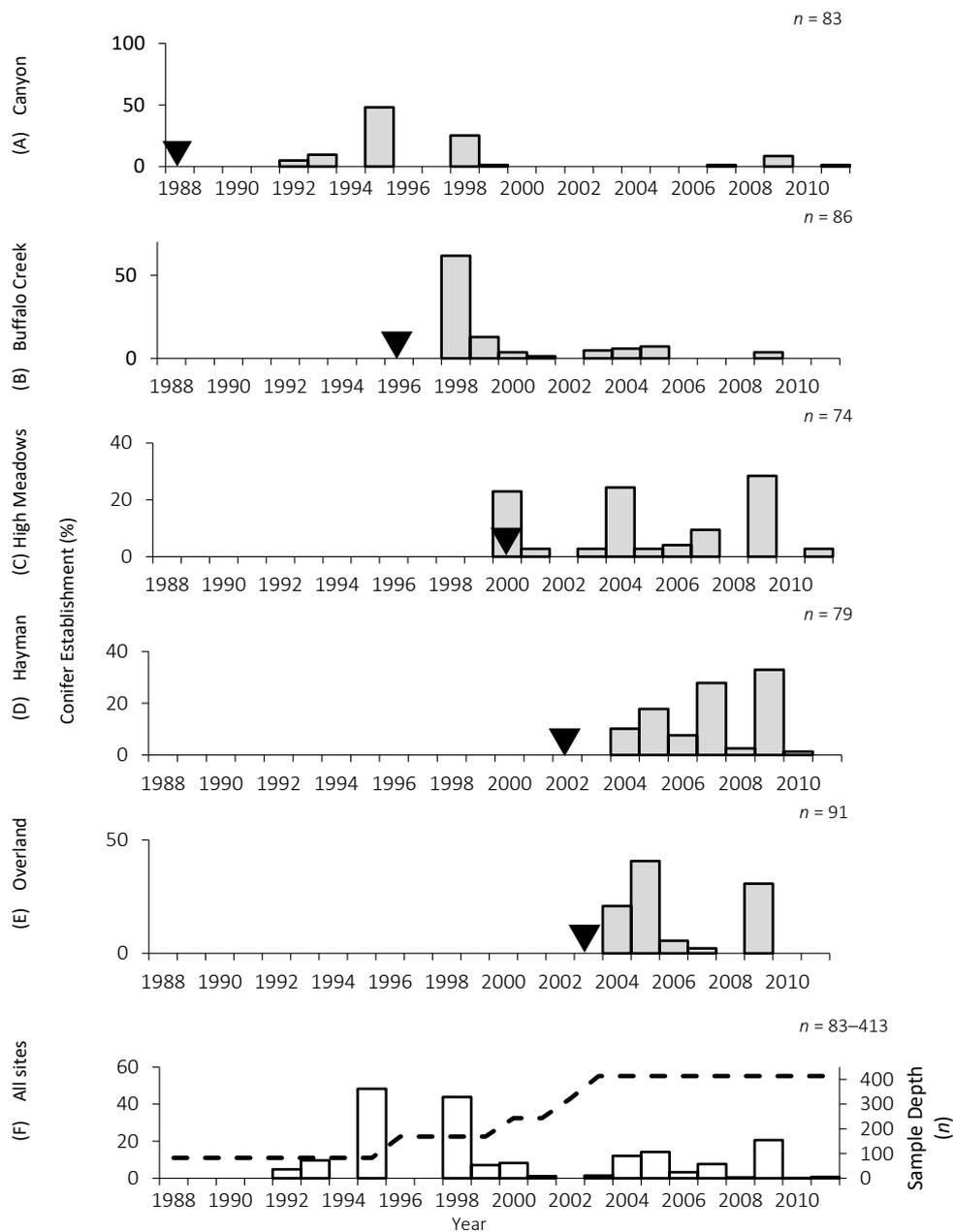


Figure 3. Percent establishment by ponderosa pine and Douglas-fir combined at each of the five sites (A–E) and for the full dataset of all five sites (F). The black triangles in parts (A–E) indicate the year of fire. The dashed line in part (F) indicates sample depth through time.

3.2. Climate-Establishment Analysis

At the individual site level, years of episodic establishment were generally characterized by above average precipitation during the growing season (Figure 4). The timing of wet periods was variable, with some years of episodic establishment being characterized by earlier wet periods (e.g., May in 1995 for the Canyon site) and others being characterized by later growing season wet periods (e.g., July in 1998 for both the Canyon and Buffalo Creek sites). Our assessment of whether ponderosa pine and Douglas-fir establishment was concentrated in years in which one or more month of the growing season experienced exceptionally high precipitation (i.e., exceeding the 90th percentile) revealed that differences between observed and expected patterns were statistically significant ($p < 0.05$) at all five sites. Relationships between temperature and ponderosa pine and Douglas-fir establishment

were less clear (Supplementary Figure S1). Temperatures in the growing season during years of episodic establishment did not depart greatly from the long-term average, but tended to be below the long-term average.

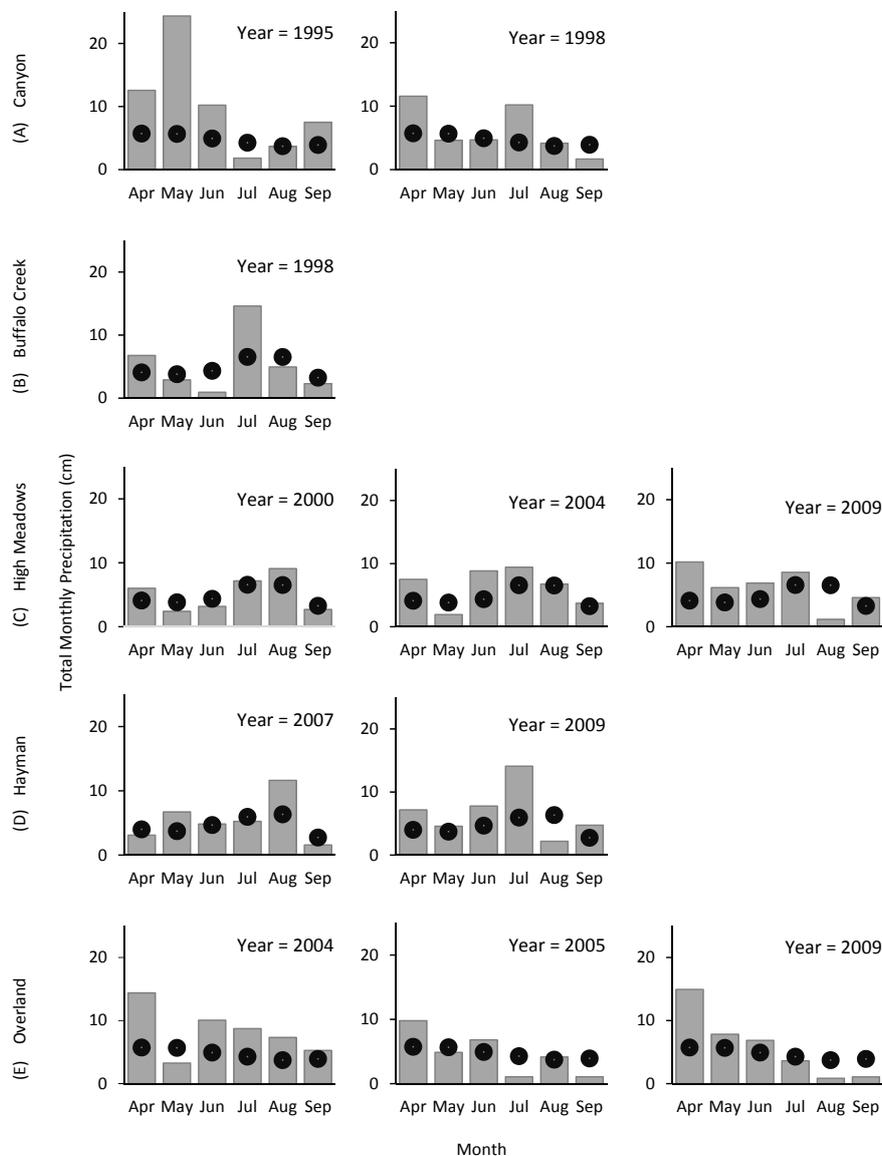


Figure 4. Total monthly precipitation (cm) for the growing season (April–September) during years of episodic establishment at each site (A–E). The dots over the bars represent the monthly mean for the long-term record (1961–2010), for comparison. Establishment years here are years in which a minimum of 20% of all ponderosa pine and Douglas-fir seedlings established.

We also examined relationships between climate conditions and ponderosa pine and Douglas-fir establishment for the combined dataset that included all five sites (Figure 5). Comparison of growing season precipitation, temperature, and PDSI during establishment and non-establishment years revealed statistically significant differences in the case of precipitation and PDSI. Episodic establishment years using a 10% filter and 20% filter were characterized by significantly higher precipitation than non-establishment years ($p < 0.05$). With regard to PDSI, episodic establishment years using the 20% filter were characterized by significantly higher PDSI values than non-establishment years ($p < 0.05$).

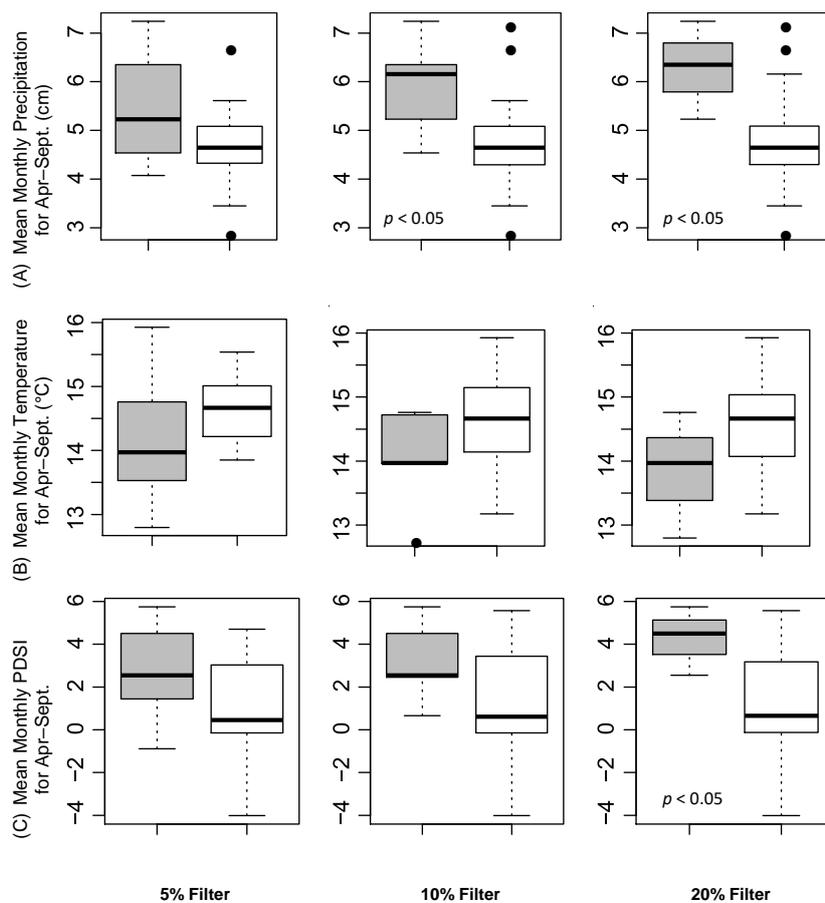


Figure 5. Comparison of (A) mean monthly precipitation (cm), (B) mean monthly temperature (°C), and (C) mean monthly Palmer Drought Severity Index (PDSI) index values during establishment years (gray boxes) versus non-establishment years (white boxes) for the combined dataset of all sites. Establishment years are defined as years in which a minimum percentage (5%, 10%, or 20%) of all ponderosa pine and Douglas-fir seedlings established. p -values are provided when differences are significant at the $p < 0.05$ level, according to Mann-Whitney tests. Climate data used are from the National Climatic Data Center (NCDC), Division 4 of Colorado.

4. Discussion

Our study indicates that following wildfires of the late 1980s to early 2000s, ponderosa pine and Douglas-fir establishment in the lower montane zone of the Colorado Front Range was largely concentrated in years of above-average moisture availability. We observed this trend both at the individual site level and for our combined dataset that included all ten sites from all five fires. Growing season (April to September) precipitation tended to be above average in years of episodic establishment; at the site level, one or more growing season months were characterized by exceptional precipitation where total precipitation exceeded the 90th percentile for the long-term record. We found that the timing of these exceptionally wet periods varied from early (e.g., April) to late (e.g., July) in the growing season. Relationships with temperature and ponderosa pine and Douglas-fir establishment were less notable, although years of episodic establishment at individual sites were generally characterized by lower than average temperatures throughout the growing season. For the analysis of the combined dataset, again we observed that temperatures were cooler in establishment years vs. non-establishment years, but these differences were not statistically significant.

Our study provides the first annually-resolved dataset of post-fire tree establishment dates for the western United States. An earlier study in the Colorado Front Range [23] examined relationships

between climate variability and ponderosa pine establishment along forest-grassland ecotones, but included only sites that had not been recently affected by fire and thus it was uncertain whether the results were applicable to recently burned areas. Our findings along with the League and Veblen (2006) study indicate that conifer establishment in the Colorado Front Range is episodic and coincides with periods of above average moisture availability, both in the absence of recent fire and in the years following fire. Both our study and the League and Veblen (2006) study showed substantial variability of the specific months during the growing season that were characterized by above average moisture availability that coincided with episodes of tree establishment. Thus, adoption of a fixed single month or even a season of two or three months as a predictor of future climatic conditions limiting tree establishment is not warranted. Anomalously low moisture availability in any of several months may prove to be limiting to tree establishment.

Our study did not assess the role of seed availability in driving tree regeneration patterns. Ponderosa pine is a masting species that does not produce abundant seed crops most years [44–46]. Thus, seed availability, in addition to climate, is a limiting factor on successful tree regeneration in ponderosa pine forests. However, understanding of the drivers of masting events and their spatial and temporal variability is limited. Previous work in a study area similar to the present study [47] relied on a local dataset of ponderosa pine seed production [45] and did not find strong relationships between pulses of seed production and pulses of tree establishment, but this could be related to limitations of the data. The seed production monitoring site was approximately 10–15 km south of where seedlings were harvested, and masting by ponderosa pine can vary notably across relatively short distances [45]. Although the present study documented strong relationships between climate variability and tree establishment, it is likely that seed availability is one of several other factors that also constrain when abundant tree establishment can occur and may be relevant for differences in post-fire regeneration patterns among sites.

Our findings are especially relevant given increases in fire activity in recent decades. Recent research has documented that more large fires are occurring across the U.S. West, including in the Southern Rockies [24,25], and that fire severity in those burns has increased at least in some areas [26]. In the Colorado Front Range, numerous large wildfires with substantial amounts of higher-severity fire have occurred in the montane zone in recent years (e.g., 2002 Hayman fire—52,000 ha, 2012 High Park Fire—37,000 ha, 2012 Waldo Canyon Fire—8100 ha, 2013 Black Forest Fire—5800 ha) and land managers and the public are eager to understand what to expect in terms of future vegetation patterns in these areas.

Our findings clearly demonstrate the importance of favorable climate conditions in driving post-fire conifer regeneration. Tree establishment was disproportionately limited to a small number of anomalously moister years. Under projections of continued warming in Colorado of 1.4–3.6 °C by 2050 [36], drought is likely to increase. Nevertheless, uncertainty surrounds if and how precipitation regimes may change in the future [36]. Unless precipitation increases, higher temperatures will be associated with increased drought due to increased evapotranspiration. Our findings regarding the relationship between PDSI (a measure of drought) and ponderosa pine and Douglas-fir establishment indicate that increased temperatures may inhibit post-fire regeneration by these two species, particularly in the absence of increased precipitation. Although in previous years, establishment coincided with periods of abundant rainfall, under warmer future conditions, rainfall will be less available for uptake by plants due to higher rates of evapotranspiration. The expectation of more limited tree regeneration in the future is supported by parallel studies for the lower montane zone of the Colorado Front Range documenting the importance of climate in driving post-fire ponderosa pine regeneration patterns [9,48]. A field experiment that utilized warming and watering treatments on planted ponderosa pine and Douglas-fir seedlings in a recently disturbed setting (i.e., mimicking fire) found that seedling growth and survival was significantly lower in warmed plots, even in the presence of supplemental watering [48]. Additionally, an extensive survey of tree regeneration in six burns of the Colorado Front Range (including all the burns that are in the present study except

Canyon) found limited tree regeneration across the study area and also found that topo-climate (defined by slope aspect, elevation) along with seed availability were the strongest predictors of where seedlings occurred.

Although it is challenging to make predictions regarding the future given remaining uncertainties (e.g., regarding seed production and future precipitation patterns), existing insights from research including that provided by the present study indicate that post-fire conifer regeneration will be more limited in dry ponderosa pine forests under continued climate change. Forests provide many ecological and societal services including regulating water regimes and limiting flooding, storing carbon, and providing a place for recreation that can support local economies. One management intervention that can be taken to address limited post-fire forest recovery is to plant conifer seedlings in post-burn landscapes. However, plantings can be costly and are not always effective [49]. Our research suggests that targeting plantings around time periods that are expected to have higher moisture levels are most likely to be successful. Land managers could also target more mesic settings such as higher elevations and north-facing slopes. In some cases, land managers may decide the best path forward is to accept transitions toward lower density stands and/or some non-forested areas due to cost limitations or because there may be some benefits to limited forest recovery in certain areas, such as in Wildland Urban Interfaces where reoccurrence of forest fire is undesired or in forests that were previously overly dense.

5. Conclusions

Our analysis of a dataset of annually-resolved establishment dates of over 400 post-fire juvenile ponderosa pine and Douglas-fir trees revealed that tree establishment was disproportionately concentrated in years of above-average moisture availability in the growing season, including higher amounts of precipitation and more positive values of the Palmer Drought Severity Index. Our study builds upon previous studies that demonstrated that tree regeneration in dry ponderosa pine forests requires above-average moisture conditions, both in the absence of recent fire [17–19,22,23] and following fire [11,12,48]. Under continued warming and associated drought, there may be fewer occurrences of climate conditions that are optimal for tree regeneration in these forests, which occur near the lower treeline. If limited tree regeneration occurs after fire, decreased forest density or transitions to non-forested vegetation are expected, especially in areas of higher-severity fire where few mature trees remain.

Supplementary Materials: The following are available online at www.mdpi.com/1999-4907/8/5/159/s1. Table S1: Ignition date and size of the five fires included in this study. Figure S1: Monthly average maximum daily temperature (°C) for the growing season (April–September) during years of episodic establishment at each site (A–E). The dots over the bars represent the 4 monthly mean for the long-term record (1961–2010), for comparison. Establishment years here are years 5 in which a minimum of 20% of all ponderosa pine and Douglas-fir seedlings established.

Acknowledgments: This research was supported by the National Science Foundation (awards No. 1232997 and 0966472, and the Graduate Research Fellowship Program). Boulder County Parks and Open Space (BCPOS) also provided financial and staff support. We thank N. Stremel, E. Duncan, L. Furman, and W. Foster for assistance with project planning, fieldwork, and lab work.

Author Contributions: Monica T. Rother and Thomas T. Veblen conceived and designed the study; Monica T. Rother performed the study and analyzed the data; Monica T. Rother and Thomas T. Veblen wrote the paper.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Holling, C.S. Resilience and stability of ecological systems. *Annu. Rev. Ecol. Syst.* **1973**, *4*, 1–23. [CrossRef]
2. Walker, B.; Holling, C.S.; Carpenter, S.; Kinzig, A. Resilience, adaptability and transformability in social–ecological systems. *Ecol. Soc.* **2004**, *9*, 5. [CrossRef]
3. Baker, W.L. *Fire Ecology in Rocky Mountain Landscapes*; Island Press: Washington DC, USA, 2009.

4. Chambers, M.E.; Fornwalt, P.J.; Malone, S.L.; Battaglia, M.A. Patterns of conifer regeneration following high severity wildfire in ponderosa pine-dominated forests of the Colorado Front Range. *For. Ecol. Manag.* **2016**, *378*, 57–67. [[CrossRef](#)]
5. Dodson, E.K.; Root, H.T. Conifer regeneration following stand-replacing wildfire varies along an elevation gradient in a ponderosa pine forest, Oregon, USA. *For. Ecol. Manag.* **2013**, *302*, 163–170. [[CrossRef](#)]
6. Harvey, B.J.; Donato, D.C.; Turner, M.G. High and dry: Post-fire tree seedling establishment in subalpine forests decreases with post-fire drought and large stand-replacing burn patches. *Glob. Ecol. Biogeogr.* **2016**, *25*, 655–669. [[CrossRef](#)]
7. Keyser, T.L.; Lentile, L.B.; Smith, F.W.; Shepperd, W.D. Changes in forest structure after a large, mixed-severity wildfire in ponderosa pine forests of the Black Hills, South Dakota, USA. *For. Sci.* **2008**, *54*, 328–338.
8. Roccaforte, J.P.; Fulé, P.Z.; Chancellor, W.W.; Laughlin, D.C. Woody debris and tree regeneration dynamics following severe wildfires in Arizona ponderosa pine forests. *Can. J. For. Res.* **2012**, *42*, 593–604. [[CrossRef](#)]
9. Rother, M.T.; Veblen, T.T. Limited conifer regeneration following wildfires in dry ponderosa pine forests of the Colorado Front Range. *Ecosphere* **2016**, *7*, 1–17. [[CrossRef](#)]
10. Savage, M.; Mast, J.N. How resilient are southwestern ponderosa pine forests after crown fires? *Can. J. For. Res.* **2005**, *35*, 967–977. [[CrossRef](#)]
11. Feddema, J.J.; Mast, J.N.; Savage, M. Modeling high-severity fire, drought and climate change impacts on ponderosa pine regeneration. *Ecol. Model.* **2013**, *253*, 56–69. [[CrossRef](#)]
12. Savage, M.; Mast, J.N.; Feddema, J.J. Double whammy: High-severity fire and drought in ponderosa pine forests of the Southwest. *Can. J. For. Res.* **2013**, *43*, 570–583. [[CrossRef](#)]
13. Vose, J.M.; Miniati, C.F.; Luce, C.H.; Asbjornsen, H.; Caldwell, P.V.; Campbell, J.L.; Grant, G.E.; Isaak, D.J.; Loheide, S.P.; Sun, G. Ecohydrological implications of drought for forests in the United States. *For. Ecol. Manag.* **2016**, *380*, 335–345. [[CrossRef](#)]
14. Bell, D.M.; Bradford, J.B.; Lauenroth, W.K. Early indicators of change: Divergent climate envelopes between tree life stages imply range shifts in the western United States. *Glob. Ecol. Biogeogr.* **2014**, *23*, 168–180. [[CrossRef](#)]
15. Dobrowski, S.Z.; Swanson, A.K.; Abatzoglou, J.T.; Holden, Z.A.; Safford, H.D.; Schwartz, M.K.; Gavin, D.G. Forest structure and species traits mediate projected recruitment declines in western US tree species. *Glob. Ecol. Biogeogr.* **2015**, *24*, 917–927. [[CrossRef](#)]
16. Turner, M.G. Disturbance and landscape dynamics in a changing world. *Ecology* **2010**, *91*, 2833–2849. [[CrossRef](#)] [[PubMed](#)]
17. Pearson, G.A. *Natural reproduction of western yellow pine in the Southwest, Forest Service Bulletin, Number 1105*; U.S. Department of Agriculture: Washington, DC, USA, 1923.
18. Cooper, C.F. Changes in vegetation, structure, and growth of southwestern pine forests since white settlement. *Ecol. Monogr.* **1960**, *30*, 129–164. [[CrossRef](#)]
19. Schubert, G.H. *Silviculture of southwestern ponderosa pine: the status of our knowledge*; United States Department of Agriculture, Forest Service, RM-123: Fort Collins, CO, USA, 1974.
20. Telewski, F.W.; Lynch, A.M. Measuring growth and development of stems. In *Techniques and Approaches in Forest Tree Ecophysiology*; CRC Press: Boca Raton, FL, USA, 1991; pp. 505–555.
21. Telewski, F.W. Determining the germination date of woody plants: A proposed method for locating the root/shoot interface. *Tree-Ring Bull.* **1993**, *53*, 13–16.
22. Savage, M.; Brown, P.M.; Feddema, J. The role of climate in a pine forest regeneration pulse in the southwestern United States. *Ecoscience* **1996**, *3*, 310–318. [[CrossRef](#)]
23. League, K.; Veblen, T. Climatic variability and episodic *Pinus ponderosa* establishment along the forest-grassland ecotones of Colorado. *For. Ecol. Manag.* **2006**, *228*, 98–107. [[CrossRef](#)]
24. Dennison, P.E.; Brewer, S.C.; Arnold, J.D.; Moritz, M.A. Large wildfire trends in the western United States, 1984–2011. *Geophys. Res. Lett.* **2014**, *41*, 2014GL059576. [[CrossRef](#)]
25. Westerling, A.L. Increasing western US forest wildfire activity: sensitivity to changes in the timing of spring. *Philos. Trans. R. Soc. B* **2016**, *371*, 20150178. [[CrossRef](#)] [[PubMed](#)]
26. Picotte, J.J.; Peterson, B.; Meier, G.; Howard, S.M. 1984–2010 trends in fire burn severity and area for the conterminous US. *Int. J. Wildland Fire* **2016**, *25*, 413–420. [[CrossRef](#)]

27. Sherriff, R.L.; Platt, R.V.; Veblen, T.T.; Schoennagel, T.L.; Gartner, M.H. Historical, observed, and modeled wildfire severity in montane forests of the Colorado Front Range. *PLoS ONE* **2014**, *9*, e106971. [[CrossRef](#)] [[PubMed](#)]
28. Dugan, A.J.; Baker, W.L. Sequentially contingent fires, droughts and pluvials structured a historical dry forest landscape and suggest future contingencies. *J. Veg. Sci.* **2015**, *26*, 697–710. [[CrossRef](#)]
29. Tepley, A.J.; Veblen, T.T. Spatiotemporal fire dynamics in mixed-conifer and aspen forests in the San Juan Mountains of southwestern Colorado, USA. *Ecol. Monogr.* **2015**, *85*, 583–603. [[CrossRef](#)]
30. Baker, W.L.; Veblen, T.T.; Sherriff, R.L. Fire, fuels and restoration of ponderosa pine-Douglas fir forests in the Rocky Mountains, USA. *J. Biogeogr.* **2007**, *34*, 251–269. [[CrossRef](#)]
31. Ehle, D.S.; Baker, W.L. Disturbance and stand dynamics in ponderosa pine forests in Rocky Mountain National Park, USA. *Ecol. Monogr.* **2003**, *73*, 543–566. [[CrossRef](#)]
32. Sherriff, R.L.; Veblen, T.T. Ecological effects of changes in fire regimes in *Pinus ponderosa* ecosystems in the Colorado Front Range. *J. Veg. Sci.* **2006**, *17*, 705–718. [[CrossRef](#)]
33. Schoennagel, T.; Sherriff, R.; Veblen, T. Fire history and tree recruitment in the Colorado Front Range upper montane zone: implications for forest restoration. *Ecol. Appl.* **2011**, *21*, 2210–2222. [[CrossRef](#)] [[PubMed](#)]
34. Kaufmann, M.R.; Veblen, T.T.; Romme, W.H. *Historical Fire Regimes in Ponderosa Pine Forests of the Colorado Front Range, and Recommendations for Ecological Restoration and Fuels Management*; Front Range Fuels Treatment Partnership Roundtable, findings of the Ecological Workgroup: Fort Collins, CO, USA, 2006.
35. Peet, R.K. Forest vegetation of the Colorado Front Range. *Plant Ecol.* **1981**, *45*, 3–75. [[CrossRef](#)]
36. Lukas, J.; Barsugli, J.; Doesken, N.; Rangwala, I.; Wolter, K. *Climate change in Colorado: A synthesis to support water resources management and adaptation*; University of Colorado: Boulder, CO, USA, 2014.
37. McGuire, C.R.; Nufio, C.R.; Bowers, M.D.; Guralnick, R.P. Elevation-dependent temperature trends in the Rocky Mountain Front Range: Changes over a 56-and 20-year record. *PLoS ONE* **2012**, *7*, e44370. [[CrossRef](#)] [[PubMed](#)]
38. Kaufmann, M.R.; Regan, C.M.; Brown, P.M. Heterogeneity in ponderosa pine/Douglas-fir forests: Age and size structure in unlogged and logged landscapes of central Colorado. *Can. J. For. Res.* **2000**, *30*, 698–711. [[CrossRef](#)]
39. Veblen, T.T.; Lorenz, D.C. Anthropogenic disturbance and recovery patterns in montane forests, Colorado Front Range. *Phys. Geogr.* **1986**, *7*, 1–24.
40. Bonnet, V.H.; Schoettle, A.W.; Shepperd, W.D. Postfire environmental conditions influence the spatial pattern of regeneration for *Pinus ponderosa*. *Can. J. For. Res.* **2005**, *35*, 37–47. [[CrossRef](#)]
41. Shatford, J.P.A.; Hibbs, D.E.; Puettmann, K.J. Conifer regeneration after forest fire in the Klamath-Siskiyou: How much, how soon? *J. For.* **2007**, *105*, 139–146.
42. Haire, S.L.; McGarigal, K. Effects of landscape patterns of fire severity on regenerating ponderosa pine forests (*Pinus ponderosa*) in New Mexico and Arizona, USA. *Landsc. Ecol.* **2010**, *25*, 1055–1069. [[CrossRef](#)]
43. Veblen, T.T.; Kitzberger, T.; Donnegan, J. Climatic and human influences on fire regimes in ponderosa pine forests in the Colorado Front Range. *Ecol. Appl.* **2000**, *10*, 1178–1195. [[CrossRef](#)]
44. Keyes, C.R.; González, R.M. Climate-influenced ponderosa pine (*Pinus ponderosa*) seed masting trends in western Montana, USA. *For. Syst.* **2015**, *24*, 021. [[CrossRef](#)]
45. Mooney, K.A.; Linhart, Y.B.; Snyder, M.A. Masting in ponderosa pine: comparisons of pollen and seed over space and time. *Oecologia* **2011**, *165*, 651–661. [[CrossRef](#)] [[PubMed](#)]
46. Shepperd, W.D.; Edminster, C.B.; Mata, S.A. Long-term seedfall, establishment, survival, and growth of natural and planted ponderosa pine in the Colorado front range. *West. J. Appl. For.* **2006**, *21*, 19–26.
47. Rother, M.T. *Conifer Regeneration after Wildfire in Low-elevation Forests of the Colorado Front Range: Implications of a Warmer, Drier Climate*; ProQuest Dissertations Publishing: Boulder, CO, USA, 2015.
48. Rother, M.T.; Veblen, T.T.; Furman, L.G. A field experiment informs expected patterns of conifer regeneration after disturbance under changing climate conditions. *Can. J. For. Res.* **2015**, *45*, 1607–1616. [[CrossRef](#)]
49. Ouzts, J.; Kolb, T.; Huffman, D.; Meador, A.S. Post-fire ponderosa pine regeneration with and without planting in Arizona and New Mexico. *For. Ecol. Manag.* **2015**, *354*, 281–290. [[CrossRef](#)]

