Spring 1-1-2015

Conifer Regeneration After Wildfire in Low-Elevation Forests of the Colorado Front Range: Implications of a Warmer, Drier Climate

Monica T. Rother
University of Colorado Boulder, rother@colorado.edu

Follow this and additional works at: http://scholar.colorado.edu/geog_gradetds

Part of the Climate Commons, Forest Management Commons, Physical and Environmental Geography Commons, and the Terrestrial and Aquatic Ecology Commons

Recommended Citation
http://scholar.colorado.edu/geog_gradetds/88

This Dissertation is brought to you for free and open access by Geography at CU Scholar. It has been accepted for inclusion in Geography Graduate Theses & Dissertations by an authorized administrator of CU Scholar. For more information, please contact cuscholaradmin@colorado.edu.
CONIFER REGENERATION AFTER WILDFIRE IN LOW-ELEVATION FORESTS OF THE COLORADO FRONT RANGE: IMPLICATIONS OF A WARMER, DRIER CLIMATE

by

Monica T. Rother

B.A. Environmental Science, Willamette University – 2005
M.S. Geography, University of Tennessee – 2010

A thesis submitted to the Faculty of the Graduate School of the University of Colorado in partial fulfillment of the requirements for the degree of Doctor of Philosophy
Department of Geography
2015
This thesis entitled:

Conifer regeneration after wildfire in low-elevation forests of the Colorado Front Range:

Implications of a warmer, drier climate

written by Monica T. Rother

has been approved by the Department of Geography

_________________________________________
Thomas T. Veblen

_________________________________________
Holly Barnard

Date__________________

The final copy of this thesis has been examined by the signatories, and we find that both the content and the form meet acceptable presentation standards of scholarly work in the above mentioned discipline.
ABSTRACT

Rother, Monica T. (Ph.D., Geography)

CONIFER REGENERATION AFTER WILDFIRE IN LOW-ELEVATION FORESTS OF THE
COLORADO FRONT RANGE: IMPLICATIONS OF A WARMER, DRIER CLIMATE

Thesis directed by Full Professor Thomas T. Veblen

In recent years, concern has grown among researchers, land managers, and the public regarding potential shifts in forest resiliency to disturbances such as wildfire under warming climate conditions. We examined conifer regeneration after fire in low-elevation, ponderosa pine (Pinus ponderosa) forests of the Colorado Front Range (CFR). Given preliminary observations of limited post-fire conifer establishment, we developed the general hypothesis that warming temperatures and associated drought are less suitable for post-fire conifer regeneration. We surveyed juvenile conifer densities in six recently burned areas of the CFR and found that juvenile ponderosa pine and Douglas-fir (Pseudotsuga menziesii) densities were typically lower than needed for sufficient stocking levels. We also identified several site characteristics that were associated with conifer presence including higher elevation, more northerly aspect, and shorter distance to seed source. In addition to surveying post-fire conifer densities, we implemented a field experiment to examine the effects of microclimate manipulations on the growth and survival of ponderosa pine and Douglas-fir seedlings planted in a low-elevation, recently-disturbed setting. We found that average growth and survival was highest in the watered only plots, followed by the control, warmed + watered, and warmed plots, respectively. Lastly, we assessed past relationships between climate variability and post-fire conifer establishment. We dated 413
seedlings collected from five recently burned areas, using a dendrochronological method that yields annually-resolved estimates of tree age. We found that conifer establishment was concentrated in years of above-average precipitation and positive Palmer Drought Severity Index (PDSI) for the growing season (April-September).

Collectively, our findings suggest that warming temperatures and associated drought are likely to inhibit post-fire regeneration of ponderosa pine and Douglas-fir in low-elevation forests of the CFR, especially in xeric settings (i.e. at low elevations and on south-facing aspects). Future vegetation composition and structure may differ notably from historic patterns. In the absence of abundant conifer regeneration, some previously forested areas may be replaced by persistent grasslands or shrublands. We expect that similar changes are imminent or underway in other low-elevation forests where warmer climates may limit post-fire tree regeneration.
Dedication

This dissertation is dedicated to Della, Ryan, and my loving family.
ACKNOWLEDGEMENTS

Thank you to my advisor, Tom Veblen. I grew tremendously as a young scientist through Tom’s mentorship and feel very fortunate to have had the opportunity to be part of the Biogeography Lab at CU-Boulder. I am thankful to all of the lab members and visiting scholars that I overlapped with, including Juan Paritsis, Andres Holz, Jeremy Smith, Meredith Gartner, Teresa Chapman, Julia Hicks, Sarah Hart, Cameron Naficy, Robbie Andrus, Alessandra Bottero, Christian Temperli, Claudio Alvarez, and Anya Reid. I am also thankful to my dissertation committee members: Carol Wessman, Tim Seastedt, Holly Barnard, and William Travis.

I am grateful for the enormous amount of help I received with the field and laboratory components of this research. First, I want to thank Ryan Foster for the countless amount of time he spent with me in the field. From early reconnaissance in burn areas, to snapping numerous incredible photos, to firing up finicky water pumps and watering tree seedlings, Ryan helped me all along the way. I was also fortunate have the help of numerous undergraduate students. Thank you to: Emily Duncan, Luke Furman, Jeremy Arkin, Dana Goodwin, Steven Morigi, Lisa Trope, Michael Kirby, and Shea Lovato.

Funding for this research was provided by the National Science Foundation, the Colorado Mountain Club, the John W. Marr Ecology Fund, and Boulder County Parks and Open Space. With regard to the National Science Foundation, I was supported through the Graduate Research Fellowship Program, a Doctoral Dissertation Research Improvement Grant, and as a graduate researcher on WildFIRE PIRE. As part of WildFIRE PIRE, I had the opportunity to travel to New Zealand and Tasmania and interact with other fire ecologists both in the U.S. and abroad.

I feel fortunate to have been part of CU-Boulder’s Geography Department. The faculty and graduate students I encountered during my time as a PhD student inspired me to continually improve as a student and researcher. Sincere thanks also to three CU-Boulder
Geography staff members who helped me many times: Darla Shatto, Karen Weingarten, and Marcia Singer. Thank you to the dear friends I met while in the Geography Department and who provided endless amounts of encouragement and support, especially Julia Hicks and Leah Meromy. Finally, thank you my sweet and energetic dog, Della, for all of the ways in which she enriches my life.
CONTENTS

CHAPTER 1
INTRODUCTION ........................................................................................................................................... 1

1.1 Justification ....................................................................................................................................... 1

1.2 Background ....................................................................................................................................... 2

1.2.1 Low-elevation ponderosa pine forests of the CFR ................................................................. 2

1.2.2 Relationships between climate and conifer regeneration ....................................................... 3

1.2.3 Wildfire ecology ........................................................................................................................... 4

1.3 Research aims .................................................................................................................................. 5

CHAPTER 2
LIMITED CONIFER REGENERATION FOLLOWING WILDFIRES IN LOW-ELEVATION FORESTS OF
THE COLORADO FRONT RANGE ............................................................................................................. 6

2.1 Introduction ....................................................................................................................................... 6

2.2 Methods ........................................................................................................................................... 10

2.2.1 Overview .................................................................................................................................... 10

2.2.2 Study area ................................................................................................................................ 10

2.2.3 Site Selection and Field Sampling Methods ............................................................................. 12

2.2.4 Data Analyses ........................................................................................................................... 18

2.3. Results ............................................................................................................................................ 18

2.4. Discussion ...................................................................................................................................... 27

CHAPTER 3
A FIELD EXPERIMENT INFORMS EXPECTED PATTERNS OF CONIFER REGENERATION AFTER
DISTURBANCE UNDER CHANGING CLIMATE CONDITIONS ............................................................... 33

3.1 Introduction ..................................................................................................................................... 33

3.2 Methods ........................................................................................................................................... 36

3.2.1 Study area ................................................................................................................................ 36

3.2.2 Experimental design .................................................................................................................. 37

3.2.3 Data collection ........................................................................................................................... 40

3.2.4 Data analyses ............................................................................................................................ 40

3.3 Results ............................................................................................................................................. 41

3.3.1 Temperature and relative humidity data .................................................................................... 41

3.3.2 Ambient climate conditions ....................................................................................................... 44

3.3.3 Ponderosa pine growth and survival ......................................................................................... 46

3.3.4 Douglas-fir growth and survival ................................................................................................. 49

3.3.5 Non-conifer biomass ................................................................................................................. 49

3.4 Discussion ....................................................................................................................................... 52

3.4.1 Overview .................................................................................................................................... 52

3.4.2 Effects of experimental treatments on temperature and relative humidity ............................... 54
CHAPTER 4
CLIMATE DRIVES EPISODIC POST-FIRE CONIFER ESTABLISHMENT IN DRY PONDEROSA PINE FORESTS OF THE COLORADO FRONT RANGE ................................................................. 60

4.1 Introduction ..................................................................................................................... 60

4.2 Methods .......................................................................................................................... 63

4.2.1 Study area .................................................................................................................... 63

4.2.2 Site selection, field sampling, and sample processing ..................................................... 63

4.2.3 Climate-establishment analyses .....................................................................................70

4.3 Results ............................................................................................................................. 73

4.3.1 Annually-resolved establishment dates ......................................................................... 73

4.3.2 Climate-Establishment Analysis .................................................................................... 73

4.3.3 Seed production and conifer establishment ..................................................................... 77

4.4 Discussion ......................................................................................................................... 77

CHAPTER 5
SUMMARY AND CONCLUSIONS ............................................................................................. 85

5.1 Conifer regeneration after fire in low-elevation forests of the CFR ................................... 85

5.2 Management implications ................................................................................................. 88

5.3 Research Limitations and Future Needs ........................................................................... 89

REFERENCES ......................................................................................................................... 92
LIST OF TABLES

Table 2.1: Sample size of belt transects for each setting per burn area.................................15
Table 2.2: Summary of predictor variables used in the Random Forest analysis......................17
Table 2.3: Density of ponderosa pine, Douglas-fir, and combined conifer juveniles (stems/ha) in each of the six burn areas..................................................................................................................21
Table 3.1: Midday (10am–6pm) air temperature, relative humidity, and soil temperature by treatment type during the experimental period (June-Sept of 2012 and 2013).................................43
Table 3.2: Climate conditions during the experimental period vs. the long-term record (Boulder Station, 1893–2011, Western Regional Climate Center). .................................................................45
Table 3.3: GLMs of height growth rate and percent survival for ponderosa pine and Douglas-fir seedlings..................................................................................................................................................48
Table 3.4: Ratios of root to shoot biomass by treatment type..................................................51
Table 4.1: Description of the five fires included in this study.................................................65
Table 4.2: Description of the ten sampling sites included in this study. All sites are located in the lower montane zone of the Colorado Front Range (CFR). .................................................................66
Table 4.3: Sample sizes of juvenile ponderosa pine and Douglas-fir collected at each site......68
Table 4.4: COOP Climate stations used in the present study...............................................71
LIST OF FIGURES

Figure 2.1: Study area map including the name and year of the six burn areas...............11
Figure 2.2: Fire severity data for the mixed-severity burn areas included in the study........14
Figure 2.3: Percent of 10 m² quadrats sampled that contained no conifers ..................19
Figure 2.4: Mean density of conifer juveniles (trees/ha) for each of the six burn areas........22
Figure 2.5: Relationship between distance to seed source (m) and juvenile conifer density (tr/ha) for ponderosa pine and Douglas-fir seedlings in each of the six burn sites.........................23
Figure 2.6: Relationship between adjusted elevation and conifer regeneration ...............24
Figure 2.7: Proportion of juvenile conifers (trees/ha) occurring on north- and south-facing aspects. ........................................................................................................................................................................25
Figure 2.8: Proportion of juvenile conifers (trees/ha) occurring in low, moderate, and high-severity settings. ........................................................................................................................................................................................................26
Figure 2.9: Results from Random Forest (RF) analysis of (a) ponderosa pine and (b) Douglas-fir juvenile conifer presence for the combined dataset of all fires.................................................................28
Figure 2.10: Classification trees for (a) ponderosa pine and (b) Douglas-fir, produced with the top three predictor variables selected using the mean decrease in accuracy statistic in the Random Forest (RF) analysis. .............................................................................................................29
Figure 3.1: Plot design for the study including (a) site location within the Colorado Front Range ................................................................................................................................................................................................28
Figure 3.2: Mean air temperature (°C), relative humidity (%), and soil temperature (°C) by treatment type for (a) Year 1 (2012), and (b) Year 2 (2013) of the experiment.................................................42
Figure 3.3: Mean height growth rate (%) and survival (%) by treatment type for ponderosa pine and Douglas-fir seedlings for (a) Year 1 (2012) and (b) Year 2 (2013) of the experiment.........47
Figure 3.4: Shoot and root biomass (g/m²) by treatment type for (a) ponderosa pine and (b) Douglas-fir seedlings..................................................................................................................................................................50
Figure 3.5: Non-conifer biomass (g/m²) (i.e. grasses, forbs, and shrubs) by treatment type based on biomass harvesting completed at the end of year 2 (2013) of the experiment. ..............................53

Figure 4.1: Locations of the five recently burned areas of the Colorado Front Range included in this study. ..........................................................................................................................64

Figure 4.2: Images from the field and laboratory related to method in the present study. ........69

Figure 4.3: 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). ..............................................................................74

Figure 4.4: Monthly total precipitation (cm) for the growing season (April-September) during years of episodic establishment at each site. ..................................................................................75

Figure 4.5: Observed and expected frequencies of establishment by ponderosa pine and Douglas-fir seedlings occurring in years where one or more month in the growing season (April-September) had precipitation that exceeded the 90th percentile for the long-term record (1961-2010). ........................................................................................................................................76

Figure 4.6: Monthly Average Maximum Daily Temperature (°C) for the growing season (April-September) during years of episodic establishment at each site. ..................................................78

Figure 4.7: Comparison of (a) average April-September precipitation (cm), (b) average April-Sept temperature (°C), and (c) average April-September PDSI index values during establishment vs. non-establishment years for the combined dataset of all 5 study sites. .......79

Figure 4.8: Comparison of the frequency (%) of post-fire ponderosa pine and Douglas-fir establishment at the (a) Canyon (1988) and (b) Overland (2003) burn sites to average seed cone production per tree (n) at the Boulder Canyon seed cone-monitoring site during the period 1988–2009. .........................................................................................................................80
CHAPTER 1

INTRODUCTION

1.1 Justification

This research was motivated by preliminary observations of limited conifer regeneration in recently burned, low-elevation forests of the Colorado Front Range (CFR). These initial observations of minimal post-fire conifer establishment were concerning given evidence from retrospective studies that document abundant regeneration following burning in the 19th century and earlier in these same habitats (Veblen & Lorenz, 1986; Mast et al., 1998; Kaufmann et al., 2000; Ehle & Baker, 2003). In this dissertation, we set out to first determine whether the initial observations of limited conifer regeneration were valid, and then to determine what factors might explain this pattern. Building on previous research that has demonstrated the sensitivity of ponderosa pine regeneration to climate conditions (Savage et al., 1996, 2013; Mast et al., 1998; League & Veblen, 2006; Feddema et al., 2013), we developed the general hypothesis that warming temperatures and associated drought are less suitable for post-fire regeneration by ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*).

This research fits well into a broader theoretical conversation in ecology and physical geography concerning potential shifts in forest resiliency to disturbances such as wildfire. Few previous studies conducted in Colorado have examined how climate change may alter forest resiliency to disturbances (Buma & Wessman, 2011; Buma et al., 2013; Rocca et al., 2014), and this dissertation addresses the unanswered question of whether low-elevation forests of the CFR may be less resilient to wildfire given warmer, drier conditions. In the absence of disturbance, forests may appear stable under changing climate because mature trees are often able to survive conditions that are suboptimal (e.g. temperatures outside of their preferred range). However, following disturbance, vegetation change can be quite rapid because new establishment is generally more sensitive to climate conditions; the species more suited to the
current climate may establish more successfully than those that were favored previously.

The findings of this dissertation have important implications for managing and adapting to future changes in forested ecosystems, including, but not limited to, low-elevation forests of the CFR. Although these forests historically exhibited high resiliency to fire, warming climate may be limiting conifer regeneration following fire. Decision-making by land managers can be improved by better understanding of the factors that drive spatial and temporal variability in patterns of post-fire conifer regeneration.

1.2 Background

1.2.1 Low-elevation ponderosa pine forests of the CFR

In the CFR, vegetation composition and structure changes dramatically with elevation. The major vegetation zones of the CFR, in order of increasing elevation are: the plains grasslands zone, the lower ecotone zone, the lower montane zone, the upper montane zone, the subalpine zone, and the alpine zone (Kaufmann et al., 2006). We focus specifically on the lower montane zone where dry ponderosa pine forests occur. Although patterns of temperature and precipitation vary throughout the study area, data from a centrally-located climate station indicate that mean maximum January temperature is approximately 4.1 °C, mean maximum July temperature is approximately 26.4 °C, and annual mean precipitation is approximately 42.2 cm (Bailey COOP Station, 2360 m, period of record: 1901–2013). At the lower elevational range of the lower montane zone (i.e. closer to the lower ecotone), ponderosa pine is typically dominant and forms relatively open stands. With increasing elevation and moisture availability, stands become denser and Douglas-fir is often present or co-dominant. The elevational range of the lower montane zone varies with latitude and microsite conditions, ranging from c. 1675–2285 m (5500–7500 ft) in the northern CFR and from c. 1980–2590 m (6500–8500 ft) in the southern CFR (Kaufmann et al., 2006).
1.2.2 Relationships between climate and conifer regeneration

Land managers and researchers have long understood that climate variability is important for driving conifer regeneration patterns in dry ponderosa pine forests. For example, early accounts in the literature described 1919 as a year of abundant ponderosa pine regeneration in Arizona that coincided with high summer precipitation, following a good seed year (Pearson, 1923; Cooper, 1960; Schubert, 1974). In more recent years, these observations have been supported by the use of annually-resolved estimates of tree age in both Arizona (Savage et al., 1996) and the CFR (League & Veblen, 2006) that were used to identify strong relationships between high moisture availability and pulses of ponderosa pine establishment. These previous studies focused on environments that had not been recently disturbed. More recently, Feddema et al. (2013) and Savage et al. (2013) identified climate variability as also being a key driver of pulses of establishment in post-fire landscapes, where they found that monthly to seasonal climate conditions were important for predicting observed patterns of ponderosa pine regeneration in Arizona and New Mexico. A limitation of these post-fire studies is that tree establishment dates were estimated from increment cores and thus annual resolution may not have been consistently achieved. Additionally, it is uncertain whether patterns from the Southwest apply to the CFR, given significant differences in climate and associated vegetation and soil characteristics. Furthermore, controlling for seed availability has been challenging in all these studies, including the present one. Research indicates that abundant seed production occurs episodically in dry ponderosa pine forests. A study in Manitou Experimental Forest in the southern CFR (Shepperd et al., 2006) found that good seed years for ponderosa pine occurred only every 4 to 6 years, with little or no viable seed available in the time between. A subsequent study (Mooney et al., 2011) further examined seed production in ponderosa pine for Boulder County, while also incorporating the data from Manitou Experimental Forest (Shepperd et al., 2006). This study revealed that good seed years (i.e.
masting events) were synchronous within populations of ponderosa pine, but not at the regional level, and that the climate drivers of masting events differed among study sites.

1.2.3 Wildfire ecology

In ponderosa pine forests of the CFR, wildfire plays a central role in shaping vegetation composition and structure. Early research in ponderosa pine forests focused on their pattern and process in the Southwest (i.e. Arizona and New Mexico), but it is important to note that generalizations from the southwestern literature should not be applied to the CFR, as there are significant differences between these systems (Kaufmann et al., 2006). As a key example, in ponderosa pine forests of the CFR, low-severity fire did not play as central of a role as in the Southwest. Throughout the montane zone in the CFR, the historic wildfire regime was mixed severity, meaning that there was variability in wildfire severity between individual fires, and that most wildfires typically included a mixture of low-, moderate-, and high-severity fire (Sherriff & Veblen, 2007, 2008). Concerns regarding a potential shift toward higher-severity fire in the CFR have developed in part due to misconceptions about current wildfire severity, such as the assumption that higher-severity fire is unprecedented. Also contributing to the concern is that recent low-elevation fires have been more destructive than those of the past in terms of homes and lives lost. However, the expansion of the Wildland Urban Interface (WUI) (Theobald & Romme, 2007) has meant that more people are living in areas that are prone to fire, and thus the likelihood of catastrophic fires in terms of homes and/or lives lost has increased in recent years. Recent research has directly examined the question of whether wildfire severity has increased in the western US (Dillon et al., 2011), and specifically in the montane zone of the CFR (Sherriff et al., 2014). In the latter case, researchers compared historical (pre-fire suppression) and current fire potential and found that most (84%) montane forests of the CFR are not characterized by increased likelihood of crown fire (Sherriff et al., 2014).
Regardless of whether fire severity patterns have changed, fire severity is still understood to be an important factor driving post-fire vegetation patterns within any given burn. Ponderosa pine and Douglas-fir both disperse their seed via wind over relatively short distances (Bonnet et al., 2005; Shatford et al., 2007; Donato et al., 2009; Johnstone et al., 2010b). Thus high-severity fire that leaves behind few surviving trees can inhibit regeneration. Additionally, microclimate conditions in patches of high-severity fire can often be hotter and drier due to the presence of blackened soil and absence of vegetation (Ulery & Graham, 1993; Wondafrash et al., 2005; Moody et al., 2007; Montes-Helu et al., 2009). On the other hand, very low-severity fire can also limit regeneration because ponderosa pine establishment is favored by open light conditions with bare mineral soil (Cooper, 1960; Schubert, 1974).

1.3 Research aims

This dissertation aims to first determine whether recently burned forests of the CFR are characterized by limited conifer regeneration, and then to provide explanations for the patterns observed. In chapter two, we examined the spatial variability of regeneration by ponderosa pine and Douglas-fir in six burn areas of the CFR. We assessed the importance of fire severity, competition with herbaceous and woody species, distance to seed source, and topographic variables including elevation and aspect in explaining differences in conifer regeneration patterns across the study area. In chapter three, we used a field experiment to assess how differences in microclimate influenced the growth and survival of ponderosa pine and Douglas-fir seedlings. Our two-year study used a full factorial design of warming and watering treatments. In chapter four, we developed a dataset of annually-resolved tree ages for juvenile ponderosa pine and Douglas-fir that had established following recent wildfires in the CFR. We then examined relationships between climate variability and post-fire establishment. Collectively, this dissertation offers important insights into how climate change may alter the resiliency of low-elevation CFR forests to wildfire.
2.1 Introduction

An important concept in ecology is that of resilience, or the ability of an ecosystem to recover to a similar state following disturbance (Holling, 1973; Gunderson & Holling, 2002). Although wildfire has long played a central role in driving pattern and process in many forested ecosystems worldwide (Pausas & Keeley, 2009; Whitlock et al., 2015), it is uncertain whether forests that historically exhibited high resiliency to fire will continue to be as resilient under changing climate conditions. We examine this potential problem in low-elevation forests of the Colorado Front Range, where abundant conifer regeneration is well-documented following past wildfires (Veblen & Lorenz, 1986; Mast et al., 1998; Kaufmann et al., 2000; Ehle & Baker, 2003). We examine recently burned landscapes to determine whether vegetation patterns are consistent with regenerating forests similar to those that were present prior to fire. This study fits within a broader context of research concerning shifts in vegetation communities in response to climate change (Enright et al., 2015), and can provide valuable insights to land managers as they make decisions regarding how best to manage forests under warming climate conditions (Peterson et al., 2011).

In the absence of a facilitating disturbance such as fire or lethal insect outbreak, the effects of climate change on forested ecosystems occur gradually because mature trees can often survive through suboptimal climate conditions (e.g. temperatures outside the preferred range of the species), allowing vegetation communities to persist in apparent stability for long periods of time (Westman, 1978). In contrast, new tree establishment depends on a narrower range of requirements and can thus be highly responsive to subtle changes in climate (Hogg & Schwarz, 1997; Spittlehouse & Stewart, 2003; Johnstone et al., 2010a). In the case of dry ponderosa pine (Pinus ponderosa) forests, processes such as conifer seed production,
germination, and subsequent establishment and survival are associated with specific climate requirements (Savage et al., 1996, 2013; League & Veblen, 2006; Feddema et al., 2013). Following disturbance, new species assemblages may emerge as establishment and survival occurs most abundantly among species best suited to the current climate, rather than those favored previously (Hogg & Schwarz, 1997; Spittlehouse & Stewart, 2003; Johnstone et al., 2010a). In order to better anticipate where and when shifts in vegetation communities will occur, further research is needed to identify the conditions under which ecological resilience to fire may be inhibited.

Studies conducted on all forested continents show strong associations between climate variability and forest vegetation patterns have been well established through historical records and paleoecological studies using tree-rings and pollen (Prentice, 1986; Briffa et al., 2004). In the case of dry ponderosa pine forests, both historical records and tree-ring records have demonstrated links between pulses of tree establishment and climate variability. For example, many early papers attributed widespread ponderosa pine regeneration in 1919 in Arizona to abundant summer precipitation following an excellent seed year (Pearson, 1923; Cooper, 1960; Schubert, 1974). Confidence in the role that interannual climate variability plays in ponderosa pine regeneration has increased following improvements in methodologies of determining establishment dates. For example, in ponderosa pine forests of Arizona (Savage et al., 1996) and of the Colorado Front Range (CFR) (League & Veblen, 2006), annually resolved establishment dates indicate that tree establishment coincided with periods of above-average moisture availability. More recently, researchers have addressed climate-establishment relationships in post-disturbance environments. Feddema et al. (2013), and Savage et al. (2013) examined the importance of climate variability in driving patterns of ponderosa pine regeneration following wildfire by using a water balance modeling approach. They concluded 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. In the current study, we examine juvenile conifer densities across a variety of topographic settings that are associated with different microclimate conditions, including a range of elevations and aspects. Given that regeneration in dry ponderosa pine forests has historically coincided with wetter and/or cooler conditions both in the presence and absence of disturbance, current conditions may provide fewer opportunities for successful regeneration, except for in more favorable topographic settings.

The current study aims to improve understanding of expected vegetation trajectories given climate warming. Across Colorado, annually-averaged temperatures have been on a warming trajectory in recent decades, with consistently warmer than average temperatures since the mid-1990s. Average temperatures are expected to rise by an additional 1.4–3.6 °C by 2050 (Reclamation, 2013; Lukas et al., 2014). In contrast, precipitation patterns have not changed significantly and it is uncertain if and how precipitation regimes may change in the future (Reclamation, 2013; Lukas et al., 2014). In the absence of increased precipitation, higher temperatures are associated with increased occurrence of drought due to higher rates of evapotranspiration. These changes are expected to create increasingly fewer opportunities for abundant conifer regeneration in low-elevation forests of the CFR, especially near lower treeline.

In addition to climate change, increased fire severity has also been identified as a possible driver of changing vegetation patterns in the western US. It has been suggested that fire suppression has caused the drier forests of the western US to be susceptible to uncharacteristically severe fire (Covington, 2000; Williams, 2013), but these types of generalizations should be examined for particular landscapes and along elevation and moisture gradients within specific landscapes. In ponderosa pine forests of the CFR, the historic wildfire regime was of mixed severity, meaning that fire effects were varied both within stands and across the landscape and included low-, moderate- and high-severity fire (Sherriff & Veblen,
2007, 2008). Recent research comparing historical (pre-fire suppression) and current fire potential shows that most (84%) of montane forests of the CFR are not characterized by increased likelihood of crown fire (Sherriff et al., 2014). Although high severity fire per se does not preclude successful conifer regeneration, the effects of high severity fire potentially are important influences on patterns of post-fire regeneration within a given burn area. Most obviously, large patches of high severity fire are known to limit conifer regeneration by leaving behind fewer seed trees (Bonnet et al., 2005; Shatford et al., 2007; Haire & McGarigal, 2010). Additionally, edaphic changes as well as microclimatic effects of blackened soil and absence of vegetation may result in altered microclimate conditions such as higher daily temperature ranges and reduced soil moisture (Ulery & Graham, 1993; Wondafrash et al., 2005; Moody et al., 2007; Montes-Helu et al., 2009). In the present study, we assess conifer regeneration across a full range of fire severities to determine whether fire severity is an important predictor of conifer regeneration patterns.

Factors known to affect patterns of post-fire conifer establishment and survival include competition (primarily with herbaceous species), seed availability, and topographic characteristics. Previous research in the southwestern US demonstrated that competition with grasses inhibits establishment and survival of ponderosa pine by limiting moisture availability (Cooper, 1960; Schubert, 1974). In addition, the timing of seedfall, seed dispersal, and the abundance of seed can all affect new establishment in a given year (Schubert, 1974), and many empirical studies demonstrate strong relationships between distance to seed source and juvenile conifer density (Bonnet et al., 2005; Shatford et al., 2007; Donato et al., 2009; Johnstone et al., 2010b). Also, topographic variables including elevation and aspect can alter microclimate conditions and are well-known predictors of vegetation composition and structure in lower treeline Rocky Mountain forests (Peet, 1981; Baker, 2009). We examine the role that these and other ecological and topographic factors play in explaining spatial variability in conifer regeneration across the study area.
Our overall goal is to further understanding of how climate change may alter forest resiliency to wildfire. Our primary research objectives were to: (1) quantify post-fire conifer establishment and survival in dry ponderosa pine forests of the CFR, and (2) examine the spatial variability of juvenile conifer densities in relation to site factors such as fire severity (as indicated by canopy tree mortality), competition with herbaceous and woody species, distance to seed source, and topographic variables including elevation and aspect. Given the existing understanding of the climate requirements for regeneration by ponderosa pine and Douglas-fir (*Pseudotsuga menziesii*) (League & Veblen, 2006; Feddema et al., 2013; Savage et al., 2013), we hypothesized that current densities of conifer juveniles may be low, especially in hotter, drier settings such as at lower elevations and on south-facing aspects. We also expected distance to seed source to be important, given that both conifer species are wind dispersed.

### 2.2 Methods

#### 2.2.1 Overview

To target our objectives, we surveyed current vegetation patterns in six mixed-severity burn areas of the CFR. We used a stratified random sampling approach, whereby we situated belt transects in areas of varying aspects and fire severities. We then used Random Forests to first determine what variables were important predictors of ponderosa pine and Douglas-fir presence or absence and then constructed a classification tree using the top three predictors for each species. Current ponderosa pine and Douglas-fir densities were compared to historic stand densities to make inferences regarding the likely future forest composition and structure.

#### 2.2.2 Study area

The study area is in the lower montane zone (Kaufmann et al. 2006), along the eastern slope of the CFR, from a northernmost location in Boulder County to a southernmost location in Douglas County (Figure 2.1). In the lower montane zone where dry ponderosa pine forests
Figure 2.1: Study area map including the name and year of the six burn areas.
occur, mean maximum January temperature is approximately 4.1 °C, mean maximum July temperature is approximately 26.4 °C, and annual mean precipitation is approximately 42.2 cm (Bailey COOP Station, 2360 m, period of record: 1901–2013). Throughout the CFR, forest vegetation patterns are strongly influenced by moisture variability related to both elevation and aspect (Peet, 1981). 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 (Kaufmann et al., 2006). The elevational range of the lower montane zone varies with latitude and microsite conditions, ranging from c. 1675–2285 m (5500–7500 ft) in the northern CFR and from c. 1980–2590 m (6500–8500 ft) in the southern CFR (Kaufmann et al., 2006). These forests are characterized by frequent disturbances by fire and insect attack and are thus typified by varying stand ages and species compositions (Peet, 1981). A study of stand age structures for ponderosa pine forests of the CFR (including the lower and upper montane zones) indicated that stand densities ranged 39–3410 trees/hectare (Sherriff, 2004).

2.2.3 Site Selection and Field Sampling Methods

Potential study sites were identified 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 that have occurred since 1984, except for small fires (< 200–400 ha, depending on the region of the country). MTBS produces fire-severity data using the differenced Normalized Burn Ratio (dNBR), calculated from satellite imagery from LANDSAT. For this study, we generated a list of all wildfires of over 400 hectares that occurred mostly or entirely within the lower montane zone of the CFR between 1984 and 2003. Of the nine fires in this subset, we selected six fires to serve as study sites (Figure 2.1): the Buffalo Creek fire of 1996 (BC), the Bobcat Gulch fire of 2000 (BG), the Hayman fire of 2002 (HY), the High Meadows fire of 2000 (HI), the Overland fire of 2003 (OL), and the Walker Ranch fire of 2000 (WR). The other three
fires on the initial list were excluded due to limited access related to isolation and/or land ownership issues. We only included fires that occurred between 1988 and 2004 because we wanted time since fire to be sufficient enough so that post-fire conifer establishment should be well underway. Time since fire ranged from 8–15 years at time of survey, which is longer than average intervals of no or low seed production for ponderosa pine (Shepperd et al. 2006, Mooney et al. 2011). Fires ranged in size from c. 400–52,000 ha, and all fires included a mixture of low- to high-severity burn areas within their perimeters (Figure 2.2). The variability of vegetation cover (dominant understory and composition) along topographic and elevation gradients across the study area is well documented (Peet 1981, Kaufmann et al. 2006, Keith et al. 2010) and was used to guide the design of vegetation sampling. The diversity of site characteristics within and between fires is advantageous because it allows for comparison of post-fire vegetation patterns across varying settings and enables for inferences across relatively broad spatial and temporal scales.

To survey current vegetation patterns in each of the six burn areas, we used belt transects stratified by aspect and fire severity (Table 2.1). Sampling was stratified into a total of two aspect settings (north and south) and three fire-severity settings (low, moderate, and high). North-facing aspects were defined as ranging from 135–45° (NW to NE) while south-facing aspects ranged from 225–315° (SW to SE). We determined fire-severity classes by estimating percent canopy tree mortality for the stand in which the transect was situated, using three classes: low (0–20%), moderate (21–80%), and high (81–100%). Thus our survey work concentrated on six general fire severity/aspect settings: high-severity/north-facing (HN), high-severity/south-facing (HS), moderate-severity/north-facing (MN), moderate-severity/south-facing (MS), low-severity/north-facing (LN), and low-severity/south-facing (LS). In each burn, we collected 7-15 replicates of each setting, for a total of 49-90 transects per burn. Although the boundaries between aspect and fire-severity classes were subjectively set and are necessarily broad, we also recorded the precise aspect (degrees) and canopy mortality (%) for each
Figure 2.2: Fire severity data for the mixed-severity burn areas included in the study. The header for each fire includes the fire name, ignition date, and total size. Data are remotely sensed and are from the Monitoring Trends in Burn Severity Program (MTBS). Red areas indicate high severity, yellow areas indicate moderate severity, dark green areas indicate unburned to low severity, light green areas indicate low severity, bright green areas indicate increased greenness, and white areas indicate non-processing area mask. For the provided percentages of each fire-severity class above, low severity (light green) is combined with the unburned to low severity category (dark green).
Table 2.1: Sample size of belt transects for each setting per burn area.

<table>
<thead>
<tr>
<th>Burn Area</th>
<th>High Severity North (n)</th>
<th>High Severity South (n)</th>
<th>Mod. Severity North (n)</th>
<th>Mod. Severity South (n)</th>
<th>Low Severity North (n)</th>
<th>Low Severity South (n)</th>
<th>Total Per Burn (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Buffalo Creek</td>
<td>7</td>
<td>13</td>
<td>7</td>
<td>8</td>
<td>10</td>
<td>8</td>
<td>53</td>
</tr>
<tr>
<td>Bobcat Gulch</td>
<td>8</td>
<td>9</td>
<td>9</td>
<td>7</td>
<td>8</td>
<td>8</td>
<td>49</td>
</tr>
<tr>
<td>Hayman</td>
<td>15</td>
<td>15</td>
<td>15</td>
<td>15</td>
<td>15</td>
<td>15</td>
<td>90</td>
</tr>
<tr>
<td>High Meadows</td>
<td>7</td>
<td>10</td>
<td>10</td>
<td>7</td>
<td>9</td>
<td>7</td>
<td>50</td>
</tr>
<tr>
<td>Overland</td>
<td>9</td>
<td>8</td>
<td>11</td>
<td>8</td>
<td>13</td>
<td>11</td>
<td>60</td>
</tr>
<tr>
<td>Walker Ranch</td>
<td>8</td>
<td>8</td>
<td>8</td>
<td>10</td>
<td>8</td>
<td>8</td>
<td>50</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>8</strong></td>
<td><strong>8</strong></td>
<td><strong>8</strong></td>
<td><strong>10</strong></td>
<td><strong>8</strong></td>
<td><strong>8</strong></td>
<td><strong>352</strong></td>
</tr>
</tbody>
</table>
transect. Suitable areas for sampling within each burn area were first identified by viewing KMZ files of MTBS data in Google Earth. Specifically, we identified locations that were relatively uniform in terms of fire-severity and aspect. Then, in the field, we randomly situated midpoints for belt transects and then extended the transects parallel to the slope contour. Each transect measured 2 × 50 m and were divided into 10 quadrats (of 2 × 5 m each).

At the center of each transect, data collected included: elevation (m), aspect (°), canopy mortality (%), slope gradient (°), and GPS location. For comparison of sites, elevation was later adjusted to account for differences in latitude. The northernmost site (BG) was adjusted by adding 500 m to the elevation while the southernmost sites (HI, BC, HA) were adjusted by subtracting 500 m from the elevation. These adjustments were made to allow for more useful comparisons of elevation across the entire study area and were based on previous work defining the elevational ranges of the lower montane zone for the southern, central, and northern Front Range (Kaufmann et al., 2006). In each quadrat, we collected data on the number, height, and species of all post-fire juvenile conifers, the distance to nearest seed source (m), crown cover (%), as well as various substrate and vegetation cover data (Table 2.2). The substrate and vegetation cover data were collected using a modified Braun-Blanquet cover type approach. Cover classes were defined as: + = <1%; 1 = 1–4.99%, 2 = 5–24.99%, 3 = 25–49.99%, 4 = 50–74.99%, 5 = 75–100. Post-fire juvenile conifers were defined as trees of height < 1.4 m. Because it is not possible to be certain that an individual tree established pre- or post-fire, this may have led to slightly higher post-fire juvenile conifer counts, especially in low-severity settings where small trees could have survived the fire. However, the majority of juvenile conifer trees encountered were less than 0.3 m in height, which by size allows us to estimate their ages as within the post-fire time period (Veblen and Lorenz 1986, Kaufmann et al. 2000, Sherriff et al. 2006).
Table 2.2: Summary of predictor variables used in the Random Forest analysis.

<table>
<thead>
<tr>
<th>Variable Name</th>
<th>Expected Relationship</th>
<th>Variable definition</th>
<th>Significance for Conifer Regeneration</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dist. to Seed Source</td>
<td>−</td>
<td>Distance (m) from nearest mature, live ponderosa pine or Douglas-fir.</td>
<td>Both ponderosa pine and Douglas-fir are wind-dispersed over short distances.</td>
</tr>
<tr>
<td>Adjusted Elevation</td>
<td>+</td>
<td>Elevation (m) adjusted based on latitude (see text for details).</td>
<td>Moisture availability increases and temperature decreases with increasing elevation in the study area.</td>
</tr>
<tr>
<td>Aspect Variable</td>
<td>−</td>
<td>Absolute number of degrees away from North (0°).</td>
<td>North-facing slopes are cooler and more mesic than south-facing slopes.</td>
</tr>
<tr>
<td>Canopy Mortality</td>
<td>+ or −</td>
<td>Canopy mortality (%). Estimated based on the area immediate surrounding the transect (~25 m radius of transect center).</td>
<td>Canopy mortality is a measure of fire severity, with higher canopy mortality corresponding to higher fire severity. Low canopy mortality may create conditions that are too shady for conifer regeneration. High canopy mortality may create conditions that are too hot &amp; dry.</td>
</tr>
<tr>
<td>Crown Cover</td>
<td>+ or −</td>
<td>Crown cover (%) of the quadrat.</td>
<td>Crown cover corresponds to the amount of sunlight that reaches the forest floor. Low crown cover may create conditions that are too hot &amp; dry for conifer regeneration. High crown cover may create conditions that are too shady.</td>
</tr>
<tr>
<td>Slope Gradient</td>
<td>−</td>
<td>Slope gradient (°).</td>
<td>Steeper slopes retain less moisture and may be less suitable for conifer regeneration.</td>
</tr>
<tr>
<td>Bare Soil</td>
<td>+ or −</td>
<td>Cover class* of bare soil.</td>
<td>Bare soil provides a competition-free space for regeneration, but can also indicate hotter, drier microclimate conditions.</td>
</tr>
<tr>
<td>Litter</td>
<td>+ or −</td>
<td>Cover class* of litter.</td>
<td>Cover by litter is an indicator of crown cover.</td>
</tr>
<tr>
<td>C.W.D.</td>
<td>+</td>
<td>Cover class* of coarse woody debris.</td>
<td>Coarse woody debris can provide a 'safe site' for germination by increasing soil moisture and decreasing air/soil temperature.</td>
</tr>
<tr>
<td>Graminoids</td>
<td>−</td>
<td>Cover class* of graminoids.</td>
<td>High graminoid cover can create competition for conifer regeneration.</td>
</tr>
<tr>
<td>Forbs</td>
<td>−</td>
<td>Cover class* of forbs.</td>
<td>High forb cover can create competition for conifer regeneration.</td>
</tr>
<tr>
<td>Shrubs</td>
<td>−</td>
<td>Cover class* of woody understory vegetation.</td>
<td>High shrub cover can create competition for conifer regeneration.</td>
</tr>
<tr>
<td>Rocky</td>
<td>−</td>
<td>Cover class* of exposed rock.</td>
<td>Solid rock is unsuitable for conifer regeneration.</td>
</tr>
</tbody>
</table>

*Cover classes were defined as: + = <1%; 1 = 1–4.99%, 2 = 5–24.99%, 3 = 25–49.99%, 4 = 50–74.99%, 5 = 75–100.
2.2.4 Data Analyses

We used Random Forests (RF) to develop a model of the probability of juvenile conifer presence or absence, using the package randomForest (Liaw & Wiener, 2002) in R (R Development Core Team). RF is a method that is an approach of classification and regression tree (CART) analysis, whereby trees are constructed by repeatedly dividing the data into two mutually exclusive groups (Breiman, 2001). RF has been recognized as effectively identifying important ecological relationships (Cutler et al., 2007). Through RF, many trees are fit to the data and then later combined. The output allows the user to identify the variables that are most important for prediction, and has frequently been used to select a subset of variables for input into subsequent analyses. We used the mean decrease in accuracy statistic to select the top three variables. This statistic is a measure of how much the inclusion of the variable reduces classification error. We developed separate RF models for ponderosa pine and Douglas-fir, the two conifer species most commonly found in the study area. Our analysis included data from all six of the study areas combined. Because data were strongly zero-inflated (Figure 2.3), we first balanced the dataset to have equal sample size of empty and occupied quadrats (i.e. quadrats with zero juvenile conifers vs. quadrats with one or more juvenile conifers). The RF analysis includes the out-of-bag (OOB) error estimate. A lower OOB error estimate indicates a higher accuracy of classification (e.g. if the OOB error estimate = 30%, accurate classification occurred 70% of the time). Following our RF analysis, the top three predictor variables for each species (i.e. ponderosa pine and Douglas-fir) were then used to construct a classification tree in the rpart package in R.

2.3. Results

We collected data in 49–90 transects per burn, for a total of 352 transects (Table 2.1). In each burn, a relatively even number of transects were collected in each of the six settings of aspect and burn severity. The most striking pattern we observed in our data (Figure 2.3) was the virtual
Figure 2.3: Percent of 10 m² quadrats sampled that contained no conifers of any kind (dark gray), no Douglas-fir juveniles (medium gray), and no ponderosa pine juveniles (light gray) for each of the six burn areas. At all sites, the majority (71-97%) of quadrats did not contain any juvenile conifers.
absence of conifer juveniles across large areas in all six of the settings we sampled (HN, HS, MN, MS, LN, and LS) in all six of our burns, although juvenile conifer densities were somewhat higher at one site (HY). In all fires, the large majority (70–97%) of quadrats contained zero juvenile conifers and thus the median number of combined conifer juveniles per hectare is zero for all six burns (Figure 2.3). Mean density of conifer juveniles for ponderosa pine and Douglas-fir combined ranged from c. 50–1400 trees/ha, although all sites besides HY had mean densities of only c. 50 to 200 trees/ha (Table 2.3, Figure 2.4). At HY, many of the post-juvenile conifers were young and small (<10 cm height), and mean densities were notably lower (mean = 757 trees/ha) when the smallest height class was excluded (Table 2.3). In terms of tree species regenerating, we observed mostly ponderosa pine and Douglas-fir. A small number of aspen (Populus tremuloides), lodgepole pine (Pinus contorta), and Rocky Mountain Juniper (Juniperus scopulorum) were also observed, but due to low counts across the study area, these species were not included in the analysis.

Exploratory analysis of the data (i.e. graphically displaying the data) suggested that distance to seed source, elevation (adjusted by latitude), and aspect were strongly associated with juvenile conifer presence/absence and density (Figures 2.5, 2.6, and 2.7). For ponderosa pine and Douglas-fir, density of each species was greatest within close proximity (<50 m) of one or more remnant trees (i.e. the seed source), at higher elevations, and on north-facing slopes. With regard to fire severity, conifer regeneration was low across all fire severity settings (Figure 2.8). Although in some burn areas, conifer densities were somewhat higher in one or two of the settings, no clear patterns were observed across the six burn areas. Low-severity fire did not consistently correspond with higher seedling densities, and high-severity fire did not consistently correspond to lower seedling densities. However, in the field we observed that exceptionally large patches of very high severity fire (canopy mortality > 95%) were typically devoid of juvenile conifers.
Table 2.3: Density of ponderosa pine, Douglas-fir, and combined conifer juveniles (stems/ha) in each of the six burn areas. Height classes were defined as follows: Height Class One, height < 10 cm; Height Class Two, height 10–100 cm; Height Class Three, height > 100 cm. In addition to displaying data for all height classes combined, we display data for only height classes 2 + 3 because taller seedlings have a higher probability of long-term survival.

<table>
<thead>
<tr>
<th>Burn Area</th>
<th>All Height Classes</th>
<th>Height Classes 2+3</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean (SE)</td>
<td>Range</td>
</tr>
<tr>
<td></td>
<td>(stems/ha)</td>
<td></td>
</tr>
<tr>
<td>Buffalo Creek</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ponderosa pine</td>
<td>141.5 (20.2)</td>
<td>0-4000</td>
</tr>
<tr>
<td>Douglas-fir</td>
<td>49.1 (16.3)</td>
<td>0-7000</td>
</tr>
<tr>
<td>Combined</td>
<td>190.6 (26.3)</td>
<td>0–7000</td>
</tr>
<tr>
<td>Bobcat Gulch</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ponderosa pine</td>
<td>40.8 (11.0)</td>
<td>0-3000</td>
</tr>
<tr>
<td>Douglas-fir</td>
<td>6.1 (3.5)</td>
<td>0-1000</td>
</tr>
<tr>
<td>Combined</td>
<td>46.9 (12.9)</td>
<td>0–4000</td>
</tr>
<tr>
<td>Hayman</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ponderosa pine</td>
<td>924.2 (85.2)</td>
<td>0-23000</td>
</tr>
<tr>
<td>Douglas-fir</td>
<td>503.3 (78.9)</td>
<td>0-52000</td>
</tr>
<tr>
<td>Combined</td>
<td>1427.5 (120.6)</td>
<td>0–52000</td>
</tr>
<tr>
<td>High Meadows</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ponderosa pine</td>
<td>68.0 (14.7)</td>
<td>0-4000</td>
</tr>
<tr>
<td>Douglas-fir</td>
<td>142.0 (25.6)</td>
<td>0-5000</td>
</tr>
<tr>
<td>Combined</td>
<td>210.0 (30.9)</td>
<td>0–6000</td>
</tr>
<tr>
<td>Overland</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ponderosa pine</td>
<td>95.0 (17.8)</td>
<td>0-6000</td>
</tr>
<tr>
<td>Douglas-fir</td>
<td>21.7 (6.8)</td>
<td>0-2000</td>
</tr>
<tr>
<td>Combined</td>
<td>116.7 (20.0)</td>
<td>0–6000</td>
</tr>
<tr>
<td>Walker Ranch</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ponderosa pine</td>
<td>8.0 (4.0)</td>
<td>0-1000</td>
</tr>
<tr>
<td>Douglas-fir</td>
<td>38.0 (16.8)</td>
<td>0-7000</td>
</tr>
<tr>
<td>Combined</td>
<td>46.0 (17.2)</td>
<td>0–7000</td>
</tr>
</tbody>
</table>
Figure 2.4: Mean density of conifer juveniles (trees/ha) for each of the six burn areas. Ponderosa pine is displayed in black and Douglas-fir is displayed in white. WR = Walker Ranch, OL = Overland, HI = High Meadows, HY = Hayman, BG = Bobcat Gulch, BC = Buffalo Creek.
Figure 2.5: Relationship between distance to seed source (m) and juvenile conifer density (tr/ha) for ponderosa pine and Douglas-fir seedlings in each of the six burn sites.
Figure 2.6: Relationship between adjusted elevation and conifer regeneration. (a) Adjusted elevation for quadrats containing one or more conifer seedlings (present) vs. no conifer seedlings (absent). The bottom and top limits of each box are the lower and upper quartiles, respectively; the thick black line within the box is the median; error bars equal ±1.5 times the interquartile range; and empty circles denote outliers, values outside ±1.5 times the interquartile range. (b) Relationship between density of conifer seedlings (trees/ha) and adjusted elevation. Data presented are of all study sites combined. Actual elevations were adjusted by latitude to create the adjusted elevation variable, allowing for better comparisons among the burn areas.
Figure 2.7: Proportion of juvenile conifers (trees/ha) occurring on north- and south-facing aspects. N = north-facing, S = south-facing. North-facing aspects were defined as ranging from 135–45° (NW to NE) while south-facing aspects ranged from 225–315° (SW to SE).
Figure 2.8: Proportion of juvenile conifers (trees/ha) occurring in low, moderate, and high-severity settings. L = low severity, M = moderate severity, and H = high severity. Fire-severity classes were determined by estimating percent canopy tree mortality for the stand in which the transect was situated, using 3 classes: low (0–20%), moderate (21–80%), and high (81–100%).
Our RF analysis supported our exploratory analysis; elevation, aspect, and distance to seed source were identified as the most important variables for ponderosa pine as well as for Douglas-fir (Figure 2.9). In the case of ponderosa pine, the top three predictor variables in order of descending importance were: (1) adjusted elevation, (2) distance to seed source, and (3) the aspect variable, while in the case of Douglas-fir, the top predictor variables were: (1) the aspect variable, (2) adjusted elevation, and (3) distance to seed source (see left-side panel of Figure 2.9). Canopy mortality and crown cover (both indicators of fire severity) were lower in importance, as were the substrate and vegetation cover variables. The general association between conifer presence and adjusted elevation was positive (increased elevation = higher probability of juvenile conifer presence), while relationships with distance to seed source and the aspect variable were negative (greater distance from seed source and more southerly aspect, farther from north = lower probability of juvenile conifers), although relationships were not linear (see right-side panels of Figure 2.9). The out-of-bag (OOB) error estimate was 23% in the ponderosa pine model and 24% in the Douglas-fir model, indicating that accurate classification occurred 77% and 76% of the time, respectively. Our RF analysis allowed for the construction of useful classification trees for the presence of ponderosa pine and Douglas-fir juveniles (Figure 2.10).

2.4. Discussion

Our findings indicate that at a broad scale, current densities of juvenile ponderosa pine and Douglas-fir are insufficient to regenerate forests similar to those that were present prior to disturbance. In all fires, the large majority of quadrats contained no juvenile conifers and thus the median number of combined conifer juveniles per hectare is zero for all six burns. Mean density of conifer juveniles for ponderosa pine and Douglas-fir combined ranged from c. 50–1400 trees/ha. The differences between the medians and the means reflect the patchiness of conifer regeneration in these burns. In general, most areas are devoid or nearly devoid of
Figure 2.9: Results from Random Forest (RF) analysis of (a) ponderosa pine and (b) Douglas-fir juvenile conifer presence for the combined dataset of all fires. Variable importance plots (far left panel) rank variables using mean decrease in accuracy. Mean decrease in accuracy is the normalized difference of the accuracy of the classification when the data for that variable are included vs. when they have been randomly permuted. Higher values indicate variables that were more important to the RF analysis. Partial dependence plots (right three panels) show the dependence of the probability of juvenile conifer occurrence on one predictor after the effects of the other predictor variables are averaged out. The out-of-bag (OOB) error estimate was 23% in the ponderosa pine model and 24% in the Douglas-fir model, indicating that accurate classification occurred 77% and 76% of the time, respectively.
Figure 2.10: Classification trees for (a) ponderosa pine and (b) Douglas-fir, produced with the top three predictor variables selected using the mean decrease in accuracy statistic in the Random Forest (RF) analysis. At each terminal node, information presented includes: (i) the predicted condition (presence or absence of juvenile conifers), (ii) the probability ($P$) that the predicted response will occur given the path leading to the node, and (iii) the percentage of observations.
juvenile conifers, with only small areas of higher densities occurring. Guidelines for stocking
levels in the Front Range of the Central Rocky Mountains (which is centered on the CFR),
suggests that post-logged stands should have at least c. 710 seedlings and saplings per
hectare, with a minimum of c. 120 seedlings per hectare in the smallest size class assessed
(Alexander, 1986). Although some areas we sampled had juvenile conifer densities that met or
exceeded this requirement, generally current stocking levels are insufficient to maintain the
lower montane vegetation type.

Although there are some areas that are regenerating abundantly (especially at HY), in
many cases, the seedlings are currently young and small, and thus survival into adulthood is
highly uncertain. Climate conditions are expected to continue to warm in recent years, making
conditions even less suitable for conifer regeneration, especially in hotter/drier topographic
settings such as south-facing aspects and low elevations. In the absence of abundant conifer
regeneration in future years, we expect that areas that burned at high severity will persist as
grasslands, with only sparse remnant trees. In areas where canopy tree mortality was relatively
low (i.e. in low-severity and moderate-severity burn areas), the forested vegetation type will
likely persist into the future. However, even these areas could face an eventual transition to
non-forested vegetation as mature trees senesce, or as additional disturbances (e.g. another
fire, beetle outbreak, etc.) occur, unless regeneration patterns change in the future.

The early successional patterns in montane forests of the CFR are understood to be
generally representative of future vegetation composition. Earlier work in montane forests of the
CFR relied on repeat photography and age structure analysis to examine vegetation patterns
following 19th century logging and burning (Veblen & Lorenz, 1986). This study demonstrated
that an initial floristic pattern (Egler, 1954) was typical in most areas, whereby both early and
late successional species established more or less synchronously. An initial floristic pattern
should also be expected for our study sites, and thus ponderosa pine and Douglas-fir should emerge on the post-fire landscape relatively soon after fire.

Although we expect ponderosa pine and Douglas-fir establishment to occur soon after fire, it is uncertain exactly how quickly abundant establishment should occur in this forest type. Several studies have found that establishment was historically concentrated soon after fire. In the Veblen and Lorenz (1986) study, tree core estimates of age indicated that establishment by ponderosa pine and Douglas-fir was concentrated in the first few decades after fire. Another study in the CFR focused on the pine/grassland ecotone (Mast et al., 1998), indicated that establishment at some sites was concentrated 0-3 decades after fire. Additionally, work by Ehle and Baker (2003) in ponderosa pine forests of Rocky Mountain National Park demonstrated that abundant tree establishment was concentrated 0-20 years after fire where canopy mortality was high. Additionally, good seed years occur every 4-6 years in the case of ponderosa pine (Shepperd et al., 2006). Collectively, these studies suggest that establishment by ponderosa pine and Douglas-fir should begin immediately or soon after fire. Our expectation for the burn areas included in the present study is that both ponderosa pine and Douglas-fir establishment should already be well underway at our burn sites, where time since fire ranged from 8-15 years. Although additional conifer establishment is likely to occur in future years, the lack of bare soil in most areas due to the current dominance of herbaceous species will provide fewer opportunities for new establishment moving forward. Moreover, expectations of continued climate warming may also limit new conifer establishment in future years and result in mortality of existing seedlings, which are vulnerable to climate stress.

Through our RF analysis, we identified higher elevations, more northerly aspects, and shorter distances to seed source to be associated with higher probability of presence of juvenile ponderosa pine and Douglas-fir. In contrast, south-facing slopes at lower elevations were typically devoid of juvenile conifers, especially where distance to seed source was high (> c. 50
m). Our findings regarding the benefit of higher elevations and more northerly aspects for conifer regeneration are consistent with our expectation that warming climate conditions are playing a key role in limited post-fire regeneration patterns in the study area. As climate continues to warm, we anticipate increasingly limited post-fire regeneration in hotter/drier settings. In the future, the lower elevational extent of ponderosa pine forests may shift upslope, and this shift will be especially rapid under the catalyst of wildfire or other disturbances. We expect that similar changes are underway or eminent in many low-elevation forests where warmer climates may inhibit post-fire tree regeneration processes.

ACKNOWLEDGEMENTS

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. Thank you especially to N. Stremel, E. Duncan, L. Furman and W. Foster for assistance with project planning, fieldwork, and/or lab work.
CHAPTER 3

A FIELD EXPERIMENT INFORMSEXPECTED PATTERNS OF CONIFER REGENERATION AFTER DISTURBANCE UNDER CHANGING CLIMATE CONDITIONS

3.1 Introduction

Recent studies of vegetation patterns following wildfire have been motivated by concern that climate change and/or potential increases in wildfire severity may alter post-fire vegetation trajectories by inhibiting processes of conifer regeneration. In some dry ponderosa pine forests of the western US, observations of limited post-fire conifer regeneration have led to the hypothesis that forested stands may be replaced by persistent grasslands or shrublands following fire, at least within portions of burns where seed availability is low (Savage & Mast, 2005; Keyser et al., 2008; Roccaforte et al., 2012; Dodson & Root, 2013). In the Colorado Front Range (CFR) and throughout the US West, more research is needed to document whether current patterns of post-fire conifer regeneration are incongruous with historic patterns and whether climate change (i.e. increased air temperature and associated drought) and/or potential changes in wildfire severity explain any significant deviation from the past. We tackle part of this complicated issue through a field experiment that assesses the role that variability in temperature and water plays in influencing the growth and survival of ponderosa pine (Pinus ponderosa) and Douglas-fir (Pseudotsuga menziesii) seedlings planted in a recently disturbed environment. Our research will allow land managers to better understand and prepare for changes in patterns of post-fire conifer regeneration including potential shifts from forest to non-forest vegetation.

In Colorado, temperatures have risen almost universally across the state in recent decades and are expected to increase by an additional 1.4–3.6 °C by 2050 (Reclamation, 2013; Lukas et al., 2014). Unlike predictions of changing temperature, uncertainty surrounds how precipitation regimes might change, and over the last several decades, there has been no clear trend across the state (Reclamation, 2013; Lukas et al., 2014). In the absence of increased precipitation, higher temperatures are associated with an increased occurrence of drought due to higher rates of
evapotranspiration. Increased drought has already resulted in ecological change in many forested communities including higher background tree mortality rates (van Mantgem et al., 2009; Williams et al., 2013). Researchers have linked tree mortality to carbon starvation, hydraulic failure, or a combination of the two, along with other drought-mediated factors such as insect attack and disease (McDowell et al., 2011; Sevanto et al., 2014). Trees that do survive climate stress may acclimate in a variety of ways such as through biomass partitioning (Turner, 1997). A number of studies have shown that conifers allocate more carbon to roots and/or sapwood under conditions of elevated temperature, water stress, or both (Callaway et al., 1994; Delucia et al., 2000; Olszyk et al., 2003). Although this strategy may improve the likelihood of survival by increasing water access, it may also increase the probability of death by limiting plant height and increasing susceptibility to mortality by factors such as wildfire, herbivory, and competition for light.

Land managers and researchers have long recognized the importance of climate variability in driving patterns of conifer regeneration in dry ponderosa pine forests. For example, many early papers identified 1919 as an astonishing year for widespread ponderosa pine regeneration in Arizona, due to high levels of summer precipitation that followed an excellent seed year (Pearson, 1923; Cooper, 1960). This observational evidence of infrequent years of abundant regeneration coinciding with favorable weather was supported in later years through the development of large datasets of annually resolved establishment dates in ponderosa pine forest in Arizona (Savage et al., 1996) and along a grassland/forest ecotone of the CFR (League & Veblen, 2006). These studies both concluded that in environments lacking recent disturbance, establishment by ponderosa pine occurs episodically in association with high moisture availability. More recently, researchers examined relationships between climate variability and ponderosa pine regeneration following wildfire (Feddema et al., 2013; Savage et al., 2013) and found that monthly to seasonal climate conditions associated with multiple developmental stages of ponderosa pine (e.g. cone production, germination, etc.) were important for predicting patterns of observed post-fire ponderosa pine regeneration. Further research is needed to
document whether similar relationships between climate variability and post-fire ponderosa pine regeneration hold true in the CFR, given significant differences between the two areas (e.g. climate regimes, soil characteristics, understory composition, genetic provenance of species, etc.).

In addition to climate conditions, fire severity may also influence patterns of conifer regeneration in dry ponderosa pine forests. Within a given burn, large patches of high-severity fire can limit regeneration by ponderosa pine and Douglas-fir because these species disperse seed primarily by wind over relatively short distances of c. 200 m or less (Bonnet et al., 2005; Shatford et al., 2007; Haire & McGarigal, 2010). Additionally, patches of high-severity wildfire can create altered microclimate conditions such as higher daily temperature ranges and reduced soil moisture due to blackened soil and absence of vegetation (Ulery & Graham, 1993; Montes-Helu et al., 2009). However, abundant conifer regeneration following high-severity fire has been documented in ponderosa pine forests (Veblen & Lorenz, 1986; Ehle & Baker, 2003; Savage & Mast, 2005; Haire & McGarigal, 2010), indicating that high-severity fire does not universally result in regeneration failure. Additionally, in the ponderosa pine zone in the CFR, the historic wildfire regime was mixed severity, meaning that fire effects were varied both within stands and across the landscape and included low-, moderate- and high-severity fire (Sherriff & Veblen, 2007; 2008). Fire severity undoubtedly plays an important role in influencing post-fire vegetation trajectories in dry ponderosa pine forests, but it is unlikely to be the sole factor explaining observations of limited conifer regeneration following recent wildfires.

In the present study, we focused on the role that differences in air temperature and water availability plays in influencing post-disturbance conifer regeneration in low-elevation forests of the CFR. We employed open-top chambers and watering treatments to assess how altered temperature and water availability influenced growth and survival of ponderosa pine and Douglas-fir seedlings at a site where the aerial biomass was scraped off to expose bare mineral soil, simulating fire (i.e. “scalping” sensu Kayes et al., (2010)). Our primary objectives were to: (1) examine the effects of
manipulations of temperature and water on the growth and survival of conifer seedlings, (2) assess potential differences in aboveground vs. belowground biomass partitioning by conifer seedlings, and (3) determine whether conifer seedling growth and survival were dependent on herbaceous and shrub groundcover. We hypothesized that experimental treatments would result in significant differences in growth and survival patterns of both ponderosa pine and Douglas-fir. Given the semi-arid, low-elevation setting for the experiment, we expected that increased air temperature would result in decreased growth and survival, while increased water would result in increased growth and survival. We hypothesized that ponderosa pine growth and survival may be higher than for Douglas-fir given that the latter species tends to occupy relatively cooler and more mesic sites, although significant overlap of the two species occurs. Partitioning among aboveground vs. belowground biomass of the conifer seedlings was also expected to vary; we hypothesized that allocation to belowground biomass, as opposed to aboveground biomass, would be greater under conditions of higher water stress. Finally, non-conifer biomass was expected to vary in response to the experimental treatments; high total non-conifer biomass was expected to be associated with lower growth and survival of conifer seedlings due to increased competition for water.

3.2 Methods

3.2.1 Study area

We installed the experiment on a closed section of Heil Valley Ranch Open Space in Boulder County, Colorado. The research site was located at 40.15 °, -105.32° at an elevation of 1,960 m, within the lower montane zone of the CFR. The experimental plot was situated on a slope with a north-northeast aspect and a gentle gradient and is surrounded by dry ponderosa pine forest. Several juvenile ponderosa pine trees were present in the plot prior to experimentation, indicating that the site was suitable for conifer regeneration. Data from a nearby weather station (Boulder Station, 1893–2013, Western Regional Climate Center, 39.99 °, -105.27 °) show that the mean maximum January
temperature for the area is c. 7.2 °C and mean maximum July temperature is c. 30.2 °C. Total annual precipitation is c. 476 mm. Precipitation patterns vary significantly over the course of the year as well as interannually. In typical years, peak precipitation occurs in spring and summer months.

3.2.2 Experimental design

Preparation for the field experiment began in the spring of 2012. A macro plot of 35 x 42 m was divided into a grid of 120 cells of 3.5 × 3.5 m (Figure 3.1). Due to excessively rocky or uneven surfaces in portions of the macro plot, only 100 of the cells were selected for use in the experiment. In each of the 100 cells, burning was simulated by killing all aerial biomass through scraping away of the vegetation to expose bare mineral soil (i.e. “scalping” sensu Kayes et al., (2010)). Prescribed fire was not a viable option because a statewide burn ban was in place at the time. Although the effects of scalping are not identical to those of burning, an advantage of this approach for field experiments is that it creates a more uniform disturbance than the patchier effect of prescribed fire. After scalping was completed, we obtained 700 ponderosa pine and 700 Douglas-fir seedlings from the Colorado State Forest Service Seedling Tree Program. We then planted fourteen seedlings of ponderosa pine and Douglas-fir (seven each) in a hexagonally shaped area of 2.6 m² within each cell, hereafter termed the micro plot. The seedlings were from a local genetic provenance and were approximately one year old at the time of planting. We regularly watered all of the seedlings for approximately one month prior to initiating experimental manipulations to help them acclimatize and minimize initial mortality. A c. 1.8 meter tall fence was installed around the perimeter of the macro plot to deter entry and subsequent trampling and/or herbivory by large mammals such as elk and deer. Following site preparation and the acclimation period, one of the following four treatments was assigned randomly to each micro plot: i) warmed only (Wm), (ii) watered only (Wt) (iii) warmed and watered (WmWt), and (iv) control (Co). Treatment types were assigned following a restricted random protocol to ensure that minor variability in soil characteristics, slope, ground cover, and light availability within the macro plot did not confound the study’s outcomes.
Figure 3.1: Plot design for the study including (a) site location within the Colorado Front Range, (b) layout of randomly located experimental treatments within the macro-plot (1 = Wm, 2 = WmWt, 3 = Wt, 4 = Co), (c) cell (d) micro-plot within cell in which experimental treatment was applied.
For micro plots designated to be warmed (Wm and WmWt), hexagonal open-top chambers (OTCs) were constructed and installed following the methods outlined by (Marion et al., 1997). The OTCs were expected to increase air temperature by c. 1–2 °C (Marion et al., 1997; Hollister & Webber, 2000; Tercero-Bucardo et al., 2007), which is reasonable given the 1.4–3.6 °C forecasted temperature increase expected by 2050 in Colorado (Reclamation, 2013; Lukas et al., 2014). More uncertainty surrounds how precipitation regimes might change in Colorado (Reclamation, 2013; Lukas et al., 2014), and over the last several decades there has been no clear trend (Lukas et al., 2014). In this study, we simulated increased precipitation through watering treatments. For micro plots designated to be watered (Wt and WmWt), weekly watering treatments were implemented to roughly approximate the upper quartile for total monthly precipitation, based on local instrumental climate data (Boulder Station, 1893-2010, Western Regional Climate Center). To do so, the difference between the long-term median and upper quartile for monthly total precipitation was first calculated. Then, we determined what additional volume of water would be required to raise the median value to the upper quartile, based on the surface area to be watered. This calculation led to varying weekly watering requirements for each month (June = 9.8 L, July = 9.1 L, August = 6.1 L, September = 9.8 L). However, for feasibility purposes related to water delivery to the site and the manual implementation of the watering treatments, we used a consistent watering treatment of 7.6 L per week per micro plot. This method does not fully replicate precipitation since natural precipitation falls more variably in terms of both the amount of water in a single rainfall event and time between rainfall events. However, we assumed that our watering efforts would effectively alter moisture availability in similar ways as natural rainfall (i.e. through increased soil moisture). Both warming and watering treatments occurred only during the growing season (June–Sept). During excessively dry periods, additional watering was occasionally delivered to all 100 micro plots to compensate for excessive drought that could lead to widespread mortality of seedlings across all treatment types. It is important to note that growing season precipitation patterns in the study area are highly variable, and that excessively dry periods are
not uncommon. Thus supplemental watering during those periods may have resulted in higher growth and survival across all treatment types than would otherwise be expected.

3.2.3 Data collection

We used HOBO® automated data loggers (Onset Computer Corp., Bourne, MA) to monitor how the experimental treatments influenced air temperature, relative humidity, and soil temperature. We used restricted random methods to identify eight micro plots (two of each treatment type) for monitoring. In each of these micro plots, we placed: (i) one data logger for air temperature and relative humidity situated at 20 cm aboveground, near the seedling canopy, and (ii) two data loggers for soil temperature, buried at a depth of 5 cm. Air temperature and relative humidity data were recorded every 30 minutes, while soil temperature data were recorded every 20 minutes (the highest allowable frequency given the data storage limitations of the devices). We monitored changes in ponderosa pine and Douglas-fir seedling growth and survival over the 2-year period. Data collection of seedling stem height and status as dead or living occurred at the start and end of both growing seasons (2012 and 2013), for a total of four data collection periods. A seedling was considered dead if no green needles remained. At the end of the second growing season (2013), we harvested all biomass in a subset of the micro plots (n = 80) to calculate aboveground and belowground biomass of conifer seedlings as well as aboveground herbaceous and shrub biomass (hereafter, ‘non-conifer biomass’). The non-conifer biomass data were collected to determine whether experimental treatments influenced non-conifer biomass and to assess whether competitive effects were important to conifer seedling growth and survival. All harvested biomass samples were weighed after they were dried in an oven at 70 °C to remove all water weight.

3.2.4 Data analyses

We analyzed the data from the data loggers to determine how the experimental treatments influenced air temperature, relative humidity, and soil temperature. We calculated mean air temperature, relative humidity, and soil temperature for each time step (e.g. 12:00 am, 12:30 am, 1:00
am) over the course of a day for the full experimental period (June–Sept.) in both 2012 and 2013. We also assessed ambient conditions in 2012 and 2013 using local climate data (Boulder Station, 1893–2011, Western Regional Climate Center) to compare conditions in those years to the long-term average. To assess whether experimental treatments affected conifer seedling growth and survival, we pooled individual tree seedling stem height and survivorship data to the micro plot level and calculated mean height growth rates and percent survival for the 2012 and 2013 seasons. Height growth rates were calculated as the mean percent increase in seedling stem height that occurred from the start to the end of each growing season, averaged for each micro plot, for each species. Percent survival was calculated as the percent of seedlings of each species in a micro plot that survived from the start to the end of each growing season. Height growth rates and percent survival for each of the four treatment types were then assessed using GLMs (Generalized Linear Models) with robust standard errors in Stata software (StataCorp, 2015). Robust standard errors were used to account for clustering in the data due to non-independence of plots between years (Baum, 2006). With regard to our height growth rate data, log transformations were applied to data for Douglas-fir to address issues of non-normality. In the case of the percent survival data, the GLMs applied a logit link function with a binomial family specified. We also assessed differences in ratios of root to shoot biomass as well as non-conifer biomass by treatment type, again using data pooled to the micro plot level, using 2X2 ANOVA.

3.3 Results

3.3.1 Temperature and relative humidity data

We observed that air temperature, relative humidity, and soil temperature varied among treatment types, particularly at midday (10 am to 6 pm). Mean midday air temperature in Wm plots was 4.4 °C warmer than in Co plots in 2012, and 3.2 °C warmer in 2013 (Figure 3.2, Table 3.1). In contrast, differences in mean air temperatures among the treatment types for the entire 24-hr day were less pronounced; we observed a 1.63 °C difference between Wm and Co in 2012 and a 1.38 °C
Figure 3.2: Mean air temperature (°C), relative humidity (%), and soil temperature (°C) by treatment type for (a) Year 1 (2012), and (b) Year 2 (2013) of the experiment. Data were collected for June–Sept. using HOBO data loggers placed in a subset of the plots. Different line types designate different treatment types: solid lines = Wm, long-dashed lines = WmWt, short-dashed lines = Wt, and dotted lines = Co.
Table 3.1: Midday (10am–6pm) air temperature, relative humidity, and soil temperature by treatment type during the experimental period (June-Sept of 2012 and 2013).

<table>
<thead>
<tr>
<th></th>
<th>Air Temperature (°C)</th>
<th>Relative Humidity (%)</th>
<th>Soil Temperature (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>Median</td>
<td>SD</td>
</tr>
<tr>
<td><strong>2012</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Warmed Only</td>
<td>33.2</td>
<td>34.6</td>
<td>4.2</td>
</tr>
<tr>
<td>Warmed + Watered</td>
<td>32.6</td>
<td>33.6</td>
<td>3.8</td>
</tr>
<tr>
<td>Watered Only</td>
<td>29.3</td>
<td>30.1</td>
<td>2.7</td>
</tr>
<tr>
<td>Control</td>
<td>28.8</td>
<td>29.5</td>
<td>2.5</td>
</tr>
<tr>
<td><strong>2013</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Warmed Only</td>
<td>30.4</td>
<td>31.2</td>
<td>4.0</td>
</tr>
<tr>
<td>Warmed + Watered</td>
<td>28.8</td>
<td>29.7</td>
<td>3.2</td>
</tr>
<tr>
<td>Watered Only</td>
<td>27.3</td>
<td>28.0</td>
<td>2.7</td>
</tr>
<tr>
<td>Control</td>
<td>27.2</td>
<td>27.9</td>
<td>2.8</td>
</tr>
</tbody>
</table>
difference in 2013. With regard to relative humidity, results were consistent with expectations that over
the course of a day, relative humidity would typically be lowest at midday, when temperatures were
highest (Figure 3.2). Among treatment types, median midday relative humidity was lowest in Wm plots
in both years. Additionally, we observed that both mean midday air temperature and mean midday
relative humidity were more variable in Wm and WmWt plots than in Wt and Co plots in both years, as
indicated by the relatively high SDs associated with those treatment types. Finally, we observed that
differences in soil temperature were less pronounced than differences in air temperature and relative
humidity, although the Wm plots were associated with higher soil temperatures.

3.3.2 Ambient climate conditions

In both 2012 and 2013, there were periods during which monthly air temperature and/or
precipitation deviated substantially from the long-term average (Table 3.2). Regarding air temperature,
all but one month during the experimental period (July 2013) was hotter than the long-term mean
(1893–2012). Months in which average temperatures were especially high included June 2012,
September 2012, and June 2013. Mean temperatures during those months exceeded the long-term
mean by more than 1 SD. Additionally, 2012 and 2013 were notably different from each other, with
higher mean monthly temperatures occurring in 2012 than in 2013. This general pattern of higher
temperatures in 2012 than in 2013 documented by the climate station data (Table 3.2) is also evident
in the air temperature data from the field experiment (Figure 3.2, Table 3.1). Mean and median air
temperatures in all four treatment types were warmer in 2012 than in 2013. With regard to
precipitation, some monthly totals during the experimental period were exceptionally low while others
were exceptionally high. June 2012, August 2012, and June 2013 had total precipitation amounts that
were more than 1 SD lower than the long-term mean (Table 3.2). These were months during which
supplemental water was applied to the entire experimental plot to compensate for lack of natural
rainfall. In terms of wet periods, July 2012 and September 2013 had total precipitation amounts that
were more than 1 SD above the long-term mean. September 2013 is especially remarkable as during
Table 3.2: Climate conditions during the experimental period vs. the long-term record (Boulder Station, 1893–2011, Western Regional Climate Center).

<table>
<thead>
<tr>
<th></th>
<th>2012</th>
<th>2013</th>
<th>Long-Term Record</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SD</td>
<td>Mean</td>
</tr>
<tr>
<td><strong>Mean Temp. (°C)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>June</td>
<td>23.4</td>
<td>21.1</td>
<td>19.3</td>
</tr>
<tr>
<td>July</td>
<td>23.8</td>
<td>22.3</td>
<td>22.5</td>
</tr>
<tr>
<td>August</td>
<td>22.9</td>
<td>22.3</td>
<td>21.7</td>
</tr>
<tr>
<td>September</td>
<td>18.9</td>
<td>18.4</td>
<td>17.2</td>
</tr>
<tr>
<td><strong>Total Precip. (cm)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>June</td>
<td>1.0</td>
<td>1.5</td>
<td>4.9</td>
</tr>
<tr>
<td>July</td>
<td>12.7</td>
<td>2.6</td>
<td>4.7</td>
</tr>
<tr>
<td>August</td>
<td>0.9</td>
<td>3.6</td>
<td>4.1</td>
</tr>
<tr>
<td>September</td>
<td>5.8</td>
<td>46.1</td>
<td>3.9</td>
</tr>
</tbody>
</table>
part of that month, flood conditions occurred in Boulder and across a broad stretch of the CFR. Total monthly precipitation was 46.1 cm (Boulder Station, Western Regional Climate Center), approximately 14 SDs above the long-term mean. The experiment was terminated approximately 2 weeks after this event, as soon as access was feasible. Although the study site received an enormous amount of precipitation in September, no significant changes were observed (e.g. no major erosion, no damage to OTCs or monitoring equipment, and no significant changes in seedling survival or growth).

3.3.3 Ponderosa pine growth and survival

In both 2012 and 2013, we observed that measurements of growth and survival for ponderosa pine seedlings varied among treatment types (Figure 3.3). Generally, growth and survival was highest in the Wt plots and lower in the Co, WmWt, and Wm plots, in that order. Differences between Wm and Wt were especially large. In 2012, the median height growth rate was 5.6% in Wm plots compared to 15.5% in Wt plots and in 2013, medians were 6.2% and 11.7% for Wm and Wt plots, respectively. Our GLMs revealed numerous significant relationships (Table 3.3). In the case of our ponderosa pine height growth rate GLM, our findings indicate that the Wm treatment resulted in significantly lower height growth rates compared to the control (P < 0.001) and the Wt treatment resulted in significantly higher height growth rates compared to the control (P < 0.05). Regarding the survival of ponderosa pine seedlings, median percent survival in Wm plots in 2012 and 2013 were 42.9% and 66.7%, respectively, while in both years the median percent survival in Wt plots was 100%. With regard to the ponderosa pine survival GLM, we found significantly lower odds of survival for plots with the Wm and WmWt treatment (P < 0.001), and significantly higher odds of survival for plots with the Wt treatment (P ≤ 0.01). In terms of year of experiment, we found significantly lower ponderosa pine height growth rates in year 2 vs. 1 (P < 0.001) and significantly higher odds of ponderosa pine percent survival in year 2 vs. 1 (P < 0.001). Finally, results from 2X2 ANOVA indicate that the warming treatment (Wm and WmWt) had a significant effect on root to shoot ratios for ponderosa pine (F = 11.98, P < 0.001).
Figure 3.3: Mean height growth rate (%) and survival (%) by treatment type for ponderosa pine and Douglas-fir seedlings for (a) Year 1 (2012) and (b) Year 2 (2013) of the experiment. The thick black line inside the box indicates the median, the lines at the outer edges of the box indicate the upper and lower quartiles, and the lines at the end of vertical dashed lines indicate the maximum and minimum values. The hollow dots indicate any outliers.
Table 3.3: GLMs of height growth rate and percent survival for ponderosa pine and Douglas-fir seedlings. Models are based on the combined dataset for both years. Standard errors are robust standard errors. Asterisks indicate statistical significance (* = P < 0.05, ** = P < 0.01, *** = P < 0.001).

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Ponderosa pine height model</th>
<th>In Douglas-fir height model</th>
<th>Ponderosa pine survival model</th>
<th>Douglas-fir survival model</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Coefficient (SE)</td>
<td>Coefficient (SE)</td>
<td>Odds ratio (SE)</td>
<td>Odds ratio (SE)</td>
</tr>
<tr>
<td>Warmed</td>
<td>-4.78 (0.95)***</td>
<td>-0.11 (.18)</td>
<td>0.16 (0.04)***</td>
<td>0.16 (0.05)***</td>
</tr>
<tr>
<td>Watered</td>
<td>2.41 (0.97)*</td>
<td>0.41 (0.17)*</td>
<td>4.69 (2.10)**</td>
<td>1.77 (0.52)</td>
</tr>
<tr>
<td>Warmed *</td>
<td>-1.71 (1.11)</td>
<td>0.15 (0.17)</td>
<td>0.31 (0.09)***</td>
<td>0.49 (0.14)*</td>
</tr>
<tr>
<td>Year</td>
<td>-3.04 (0.62)***</td>
<td>0.81 (0.16)***</td>
<td>2.74 (0.49)***</td>
<td>2.09 (0.42)***</td>
</tr>
<tr>
<td>Constant</td>
<td>12.87 (0.87)</td>
<td>0.70 (0.13)</td>
<td>5.49 (1.27)</td>
<td>2.25 (0.52)</td>
</tr>
</tbody>
</table>
Root to shoot ratios were significantly higher in Wm and WmWt plots than in Wt and Co plots (Figure 3.4, Table 3.4).

3.3.4 Douglas-fir growth and survival

Generally, the pattern for Douglas-fir growth and survival was similar to the pattern for ponderosa pine; growth and survival was highest in the Wt plots followed by the Co, WmWt, and Wm plots, respectively (Figure 3.3). However, for Douglas-fir, fewer statistically significant relationships were found and both height growth rates and percent survival were lower than for ponderosa pine regardless of treatment type. In 2012, for all treatment types, the median height growth rate of Douglas-fir seedlings was less than 4%; this is even lower than the lowest median height growth rate for ponderosa pine that year (5.6% in Wm plots). The Douglas-fir height growth rate GLM indicated that the watering treatment resulted in significantly higher height growth rates compared to control (P < 0.05). In terms of survival of Douglas-fir seedlings, percent survival in both 2012 and 2013 were lowest in Wm plots, with medians of 28.6% and 16.7%, respectively (Figure 3.3). In contrast, Wt plots had median percent survival of 85.7% and 100% for 2012 and 2013, respectively. Our Douglas-fir survival model revealed significantly lower odds of survival for plots with the Wm (P < 0.001) and WmWt (P < 0.05) treatment. With regard to year of experiment, we found significantly higher Douglas-fir height growth rates in year 2 vs. 1 (P < 0.001) and significantly higher Douglas-fir percent survival in year 2 vs. 1 (P < 0.001). Lastly, in terms of above- and belowground biomass, results from 2X2 ANOVA indicate that the warming treatment (Wm and WmWt) had a significant effect on root to shoot ratios (F = 16.17, P < 0.001). Root to shoot ratios were higher in Wm and WmWt plots than in Wt and Co plots.

3.3.5 Non-conifer biomass

By the end of the second experimental year (2013), most plots had substantial cover by non-conifer biomass, mostly by grasses and forbs. Among all 100 micro plots, total non-conifer biomass varied widely from 12.9 g/m$^2$ to 98.3 g/m$^2$, with an average of 43.3 g/m$^2$ ± 17.8 (mean ± SD). Some plots still had substantial amounts of bare soil at the end of 2013, while others plots were completely
Figure 3.4: Shoot and root biomass (g/m²) by treatment type for (a) ponderosa pine and (b) Douglas-fir seedlings. Biomass harvesting was completed at the end of year 2 (2013) of the experiment.
Table 3.4: Ratios of root to shoot biomass by treatment type. Data were collected for both ponderosa pine and Douglas-fir after two years of experimental treatment. Results from 2×2 ANOVA indicate that the warming treatment (Wm and WmWt) had a significant effect on root to shoot ratios for both ponderosa pine ($F = 11.98, P < 0.001$) and Douglas-fir ($F = 16.17, P < 0.001$).

<table>
<thead>
<tr>
<th></th>
<th>Mean</th>
<th>Median</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Ponderosa pine</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Warmed Only</td>
<td>0.43</td>
<td>0.43</td>
<td>0.10</td>
</tr>
<tr>
<td>Warmed + Watered</td>
<td>0.43</td>
<td>0.42</td>
<td>0.11</td>
</tr>
<tr>
<td>Watered Only</td>
<td>0.36</td>
<td>0.34</td>
<td>0.09</td>
</tr>
<tr>
<td>Control</td>
<td>0.35</td>
<td>0.36</td>
<td>0.07</td>
</tr>
<tr>
<td><strong>Douglas-fir</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Warmed Only</td>
<td>0.52</td>
<td>0.52</td>
<td>0.09</td>
</tr>
<tr>
<td>Warmed + Watered</td>
<td>0.46</td>
<td>0.45</td>
<td>0.08</td>
</tr>
<tr>
<td>Watered Only</td>
<td>0.38</td>
<td>0.36</td>
<td>0.10</td>
</tr>
<tr>
<td>Control</td>
<td>0.36</td>
<td>0.34</td>
<td>0.10</td>
</tr>
</tbody>
</table>
vegetated. Although non-conifer biomass varied substantially across the entire macro plot, no statistically significant relationships were found through our 2X2 ANOVA (Figure 3.5), indicating that the experimental treatments did not explain observed differences.

3.4 Discussion

3.4.1 Overview

Our study provides significant insight regarding the effects of climate change on post-disturbance vegetation patterns. Our findings suggest that warming temperatures and associated drought are likely to inhibit post-fire regeneration of ponderosa pine and Douglas-fir in low-elevation forests of the Colorado Front Range and that future post-fire vegetation composition and structure may differ notably from historic patterns in some areas. Because we planted tree seedlings, our experiment focuses specifically on the growth and survival of conifer seedlings in the absence of seed limitation. Masting by ponderosa pine in the CFR is known to be sensitive to climate (Mooney et al. 2011), and thus research is needed to investigate how changing climate may affect seed production. The experimental treatment in our study most similar to what is expected for the future in the study area is the $Wm$ treatment, in which temperatures are elevated but amount of precipitation does not significantly change. Height growth rates and percent survival for both ponderosa pine and Douglas-fir seedlings in $Wm$ plots were much lower than in other treatment types. Although we think the $Wm$ scenario most closely resembles future climate conditions based on model projections (Reclamation, 2013; Lukas et al., 2014), there is considerable uncertainty about how precipitation regimes may change in the CFR. It is possible that elevated temperatures will be accompanied by increased precipitation (like the $WmWt$ treatment) or reduced precipitation (not examined in this study). However, even if precipitation is to increase in the future, our findings indicate that ponderosa pine and Douglas-fir growth and survival may still be relatively limited, as indicated by the difference between $WmWt$ and $Co$ treatment types. Changes in patterns of post-fire conifer regeneration in lower montane forests of
Figure 3.5: Non-conifer biomass (g/m²) (i.e. grasses, forbs, and shrubs) by treatment type based on biomass harvesting completed at the end of year 2 (2013) of the experiment. The thick black line inside the box indicates the median, the lines at the outer edges of the box indicate the upper and lower quartiles, and the lines at the end of vertical dashed lines indicate the maximum and minimum values. The hollow dots indicate any outliers. Results of 2X2 ANOVA indicate that means are statistically equal.
the CFR have important management implications given the ecological, social, and economic benefits these forests provide (e.g. carbon storage, habitat, recreation, timber, etc.).

3.4.2 Effects of experimental treatments on temperature and relative humidity

The experimental treatments we implemented effectively altered conditions in the plots. With regard to air temperature, the average increased temperature we achieved was similar to the c. 1–2 °C documented in other studies using similar OTCs (Marion et al., 1997; Hollister & Webber, 2000; Tercero-Bucardo et al., 2007) and is reasonable given expectations of an increase of 1.4–3.6 °C in Colorado in future years (Reclamation, 2013; Lukas et al., 2014). Also similar to other studies, temperature differences between experimental treatments were most pronounced during midday (Marion et al., 1997; Tercero-Bucardo et al., 2007). The similarity in air temperature among experimental treatments outside of the midday hours indicates that the OTCs did not create uniform warming through time, but instead resulted in amplified temperatures only when incoming solar radiation was present. Trapped heat was largely or completely lost from the OTCs at night. In contrast, warming conditions associated with human-induced climate change result in elevated temperatures during both day and nighttime. This is a notable limitation given that warmer nighttime temperatures may have significant effects on plant growth and survival (Turnball et al., 2002).

In addition to air temperature differences, we also observed differences in relative humidity among treatment types. Findings indicated that warmed plots were drier than plots that did not receive a warming treatment. Soil moisture was not monitored, but we assume that soil moisture varied by treatment type because height growth rates and percent survival of ponderosa pine and Douglas-fir seedlings were higher in Wt plots compared to Co plots. Regarding soil temperatures, we observed relatively small differences in soil temperatures among treatment types, suggesting that air temperature and soil moisture were more important than soil temperature in driving differences in the growth and survival of ponderosa pine and Douglas-fir seedlings.
3.4.3 Growth and survival of ponderosa pine and Douglas-fir seedlings

Our experiment was situated in the lower montane zone of the CFR, where moisture limits tree growth. As hypothesized, we found that increased temperatures resulted in lower average percent survival and height growth rates for both ponderosa pine and Douglas-fir seedlings, while increased water resulted in higher average percent survival and height growth rates. We interpret lower percent survival and height growth rates in warmed plots (Wm and WmWt) to be a consequence of lower moisture availability in those treatment types, due to increased evapotranspiration. However, we did not monitor plant physiological responses and thus cannot be certain what mechanisms drove the plant responses we observed; further study to that end would be beneficial. With regard to root to shoot ratios, we found that the warming treatment (Wm and WmWt) had a significant effect on mean root to shoot ratios, with higher ratios in plots that were warmed. Previous studies of conifer biomass partitioning (Callaway et al., 1994; Delucia et al., 2000; Olszyk et al., 2003) indicate that water-stressed conifers tend to allocate more carbon to their roots in order to increase their ability to access soil water. This strategy may reduce the probability of mortality due to water stress, but increase the likelihood of death by drivers where height is beneficial (e.g. wildfire, herbivory, and competition for light). Although many trends were similar for ponderosa pine and Douglas-fir, we observed that growth and survival for Douglas-fir was universally lower than ponderosa pine. This finding suggests that Douglas-fir seedlings were more stressed than ponderosa pine. Both ponderosa pine and Douglas-fir can tolerate dry conditions, but where the two species co-occur, ponderosa pine is more common in relatively xeric topographic settings (i.e. low-elevation south-facing aspects) compared to Douglas-fir (Peet, 1981; Kaufmann et al., 2006) and our findings are also consistent with experimental work that demonstrated that Douglas-fir may be more vulnerable to drought stress than ponderosa pine (Cleary, 1970).
3.4.4 Non-conifer biomass

We did not observe significant differences in non-conifer biomass among treatment types, suggesting that altered temperature and water did not influence the growth and survival of forbs, grasses, and shrubs. This indicates that these understory plants were less sensitive to the experimental treatments we implemented than the ponderosa pine and Douglas-fir seedlings and thus may be less affected by future climate change in the lower montane zone. Although there was significant variability in total non-conifer biomass among the micro plots, this variability did not correspond to differences in-seedling growth and survival. We interpret this finding to indicate that competitive effects between non-conifer plant species and ponderosa pine and Douglas-fir seedlings were not significant in our study. The differences in temperature and relative humidity created by the experimental treatments, not variability in non-conifer biomass, was the key driver of patterns of ponderosa pine and Douglas-fir growth and survival.

3.4.5 Forest management in the context of climate change

Disturbances such as wildfire can act as catalysts of rapid transformation of forested ecosystems, particularly under changing climate conditions. Although mature trees often survive through suboptimal environments such as temperatures outside the preferred range of the species, new germination and establishment depends on a relatively narrow range of requirements and can be highly responsive to subtle changes in climate (Hogg & Schwarz, 1997; Spittlehouse & Stewart, 2003). A general hypothesis of rapid post-disturbance shifts in vegetation patterns in the context of changing climate has previously been put forward by numerous researchers (e.g. Enright et al., 2015; Hogg and Schwarz, 1997; Johnstone et al., 2010a; Spittlehouse and Stewart, 2003; Turner, 2010), yet few studies have tested this expectation (but see: Overpeck et al., 1990; Landhausser & Wein, 1993; Hogg & Schwarz, 1997; Tercero-Bucardo et al., 2007; Johnstone et al., 2010b; Moser et al., 2010; Dodson & Root, 2013; Feddema et al., 2013; Savage et al., 2013). Our field experiment directly assessed how temperature and water availability influence tree
seedling growth and survival after disturbance and contributes to the growing understanding that in the context of climate change, disturbances such as wildfires may result in vegetation patterns inconsistent with pre-disturbance patterns.

We demonstrated that ponderosa pine and Douglas-fir seedling growth and survival following disturbance was inhibited by warmer temperatures, but that non-conifer biomass (i.e. grasses, forbs, and some shrubs) was unaffected by the experimental treatments. Historically, conifer regeneration in dry ponderosa pine forests nearby and in the CFR was abundant after fire, as indicated by tree-ring retrospective studies that document ponderosa pine and Douglas-fir establishment following wildfires in the 19th century and earlier (Veblen & Lorenz, 1986; Mast et al., 1998; Ehle & Baker, 2003). Our findings suggest that future post-fire vegetation trajectories in lower montane ponderosa pine forests of the CFR may differ notably from historic patterns. In the absence of abundant regeneration by ponderosa pine and Douglas-fir, some previously forested areas may be replaced by persistent grasslands or shrublands, particularly at lower elevations near the ecotone, where water stress is highest. Where conifer regeneration does occur, our findings suggest that ponderosa pine may be more common than Douglas-fir. Given that our study does not account for seed limitation (removed by planting seedlings) or periods of extreme drought (removed by supplemental watering in periods without rainfall), our findings are conservative, and may underestimate the consequences of warmed climate on ponderosa pine and Douglas-fir regeneration. Land managers in the CFR should be prepared for post-fire vegetation trajectories that are incongruent with historic patterns. Difficult decisions will be required concerning how to manage recently burned, lower montane forests given expectations of less abundant regeneration by ponderosa pine and Douglas-fir. For high priority areas, land managers may choose to adopt resistance strategies (Millar et al., 2007) to forestall major vegetation changes. Given that wildfire has the potential to drive rapid vegetation change, fire mitigation practices such as installing fuel breaks, thinning stands, or use of prescribed burning may be appropriate. However, management strategies such as these can be expensive, time-intensive,
and of variable efficacy (Roccaforte et al., 2010; Graham et al., 2012) and are therefore only viable at relatively small spatial scales. Land managers may also opt for strategies that promote resiliency of forests to wildfire. Resilient forests are described as those that return to a similar prior condition after disturbance (Holling, 1973; Millar et al., 2007). Intensive management of the post-fire landscape to promote resiliency may include tree plantings. Our study suggests that plantings should occur on cooler, wetter microsites such as north-facing aspects. Additionally, plantings that are timed around cooler, wetter periods (such as during El Niño conditions in the CFR) are likely to be most successful. Ultimately, response strategies that accept the transition of post-fire landscapes to new vegetation assemblages may be most feasible and practical at broad scales. Such largely passive response strategies may be ideal for both remote areas where access is limited and costs of active management are high. One of the most significant impacts of localized climate-induced transitions from forest to non-forest vegetation is likely to be on water quantity and quality, which should be an area of priority research (Ebel & Mirus, 2014).

In conclusion, the results of our study suggest that under projected climate change scenarios, post-disturbance regeneration of ponderosa pine and Douglas-fir may be limited in lower montane forests of the CFR. Different species assemblages are expected to emerge as regeneration occurs most abundantly among the species best suited to the current climate, rather than those favored previously. In recently burned areas of high tree mortality, conifer regeneration may be restricted to areas that provide suitable microclimate conditions such as higher elevations and north-facing slopes. It is possible that a transition to grasslands or shrublands may occur in some areas following wildfire. Although our study focused on low-elevation forests of the CFR, our findings are relevant to other forested ecosystems where increased temperatures and associated drought may similarly inhibit post-disturbance regeneration by the dominant tree species. We expect that many forests worldwide are currently vulnerable to post-disturbance shifts in vegetation patterns due to climate change, as supported by research in northern Patagonia (Tercero-Bucardo et al., 2007), the Central Alps.
(Moser et al., 2010), the eastern U.S. (Overpeck et al., 1990), the western U.S. (Dodson & Root, 2013; Feddema et al., 2013; Savage et al., 2013), and portions of Canada (Landhausser & Wein, 1993; Hogg & Schwarz, 1997; Johnstone et al., 2010b). In areas where climate-mediated shifts in vegetation following disturbance are anticipated, land managers will need to act quickly to prioritize areas where they would like to forestall loss of forested cover following fire, versus areas where the persistence of alternative vegetation communities is acceptable or desired.

ACKNOWLEDGEMENTS

This research was supported by the National Science Foundation (grant #1232997 & #0966472, and the Graduate Research Fellowship Program). Boulder County Parks and Open Space (BCPOS) also provided financial and staff support in implementing and monitoring the experiment. Thank you especially to N. Stremel, E. Duncan, and W. Foster for project planning and fieldwork assistance and to Philip Pendergast for advice regarding statistical analyses. Also thank you to the anonymous reviewers whose suggestions significantly improved the manuscript.
CHAPTER 4

CLIMATE DRIVES EPISODIC POST-FIRE CONIFER ESTABLISHMENT IN DRY PONDEROSA PINE FORESTS OF THE COLORADO FRONT RANGE

4.1 Introduction

Disturbances such as wildfire can serve as catalysts of rapid transformation in forested ecosystems, particularly in the context of climate change or other environmental changes (Turner, 2010). Following disturbance, different ecological communities may emerge as establishment occurs most abundantly among species best suited to the current conditions rather than those favored previously (Hogg & Schwarz, 1997; Spittlehouse & Stewart, 2003). Although mature trees often survive through suboptimal conditions (e.g. temperatures outside the preferred range of the species), the narrow regeneration niche of many tree species means that new germination and establishment may not occur if climate conditions are not favorable. In the western U.S., a number of recent studies have documented post-fire shifts from forested vegetation to grasslands or shrublands, at least in areas where seed availability is limited (Savage & Mast, 2005; Keyser et al., 2008; Roccaforte et al., 2012; Dodson & Root, 2013). However, uncertainty surrounds whether these shifts are being driven by changes in wildfire severity, climate change, or a combination of these factors as well as whether observed transitions will be fleeting or persistent.

It has long been understood that climate variability is a key factor driving patterns of conifer regeneration in dry ponderosa pine (Pinus ponderosa) forests. As an example, many early papers attributed widespread ponderosa pine regeneration in 1919 in Arizona to abundant summer precipitation following an excellent seed year (Pearson, 1923; Cooper, 1960; Schubert, 1974). Confidence in the role that interannual climate variability plays in 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 (Telewski & Lynch, 1991; Telewski, 1993). In ponderosa pine forests of Arizona (Savage et al., 1996) and of the Colorado Front Range (CFR) (League & Veblen, 2006), annually resolved establishment dates indicate that tree establishment was strongly coincident with above-average moisture availability. More recently, researchers have addressed climate-establishment relationships in post-disturbance environments. Feddema et al. (2013), and Savage et al. (2013) examined the importance of climate variability in driving patterns of ponderosa pine regeneration following wildfire by using a water balance modeling approach. They concluded 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. A limitation of these post-fire 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 the CFR, given significant differences in climate and associated vegetation and soil characteristics. Further research is needed to clarify the role that climate plays in driving post-fire regeneration in dry ponderosa pine forests of the CFR.

In retrospective studies of ponderosa pine regeneration, it can be challenging to distinguish between the effects of past climate variability and past fire on the age structure of the stand. Pulses of establishment theoretically could be favored by short-lived favorable climatic conditions or by the high light levels, bare mineral soil, and reduced competition favorable to establishment of a shade intolerant tree species (Baker et al., 2007). Associating climate with regeneration is most feasible in open areas such as along grassland ecotones or in woodlands (League & Veblen, 2006). Ponderosa pine is a shade-intolerant species that is limited by light in dense or moderately dense forest canopies (Cooper, 1960; Schubert, 1974). 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 (Ehle & Baker, 2003; Sherriff & Veblen, 2006; Schoennagel et al., 2011). 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.

By focusing on study sites situated in relatively open forest conditions and by examining post-fire establishment pulses across a range of study sites that burned at different time periods, we will reduce ambiguity in climate vs. disturbance driven pulses in establishment.

In the current study, we examine temporal patterns of post-fire conifer establishment and survival for five areas that burned in the CFR between 1988 and 2003. The primary research objectives were to: (1) develop a record of annually resolved establishment dates for ponderosa pine and Douglas-fir (*Pseudotsuga menziesii*) seedlings in recent burn areas, and (2) determine the influences of climate variability on temporal patterns of post-fire conifer establishment and survival. This research should improve understanding of expected vegetation trajectories given climate warming. Across Colorado, annually-averaged temperatures have been on a warming trajectory in recent decades, with consistently warmer than average temperatures since the mid-1990s. Additionally, average temperatures are expected to rise by an additional 1.4–3.6 °C by 2050 (Reclamation, 2013; Lukas et al., 2014). In contrast, precipitation patterns have not changed significantly and it is uncertain if and how precipitation regimes may change in the future (Reclamation, 2013; Lukas et al., 2014). In the absence of increased precipitation, higher temperatures are associated with increased occurrence of drought due to higher rates of evapotranspiration. The present study provides valuable insight with regard to the potential
effects of increased temperature and/or altered precipitation regimes on post-fire vegetation patterns in dry ponderosa pine forests of the CFR.

4.2 Methods

4.2.1 Study area

The study area is along the eastern slope of the CFR, from a northernmost location in Boulder County to a southernmost location in Douglas County (Figure 4.1). In the lower montane zone where dry ponderosa pine forests occur, mean maximum January temperature is approximately 4.1 °C, mean maximum July temperature is approximately 26.4 °C, and annual mean precipitation is approximately 42.2 cm (Bailey COOP Station, 2360 m, period of record: 1901–2013).

Throughout the CFR, forest vegetation patterns are strongly influenced by moisture variability related to both elevation and aspect (Peet, 1981). 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 (Kaufmann et al., 2006). The elevational range of the lower montane zone varies with latitude and microsite conditions, ranging from c. 1675–2285 m (5500–7500 ft) in the northern CFR and from c. 1980–2590 m (6500–8500 ft) in the southern CFR. Our study area is situated within the central CFR, where the lower montane zone extends from c. 1830–2440 m (Kaufmann et al., 2006).

4.2.2 Site selection, field sampling, and sample processing

We harvested and aged post-fire juvenile conifers in five recently burned areas in the lower montane zone in the CFR (Figure 4.1, Table 4.1). During the summers of 2011 and 2012, two sites were situated in each of the five burn areas, for a total of ten sites (Table 4.2). At each site, areas of relatively abundant juvenile conifers were identified for sampling. All plots were
Figure 4.1: Locations of the five recently burned areas of the Colorado Front Range included in this study. For each burn, the name and year of fire are provided. The boundary for the National Climatic Data Center (NCDC)'s Climate Division 4 for Colorado is also shown.
Table 4.1: Description of the five fires included in this study.

<table>
<thead>
<tr>
<th>Fire name</th>
<th>Date of ignition</th>
<th>Size (ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>LH Canyon</td>
<td>September, 1988</td>
<td>443</td>
</tr>
<tr>
<td>Buffalo Creek</td>
<td>May, 1996</td>
<td>3962</td>
</tr>
<tr>
<td>High Meadows</td>
<td>June, 2000</td>
<td>3889</td>
</tr>
<tr>
<td>Hayman</td>
<td>June, 2002</td>
<td>52368</td>
</tr>
<tr>
<td>Overland</td>
<td>October, 2003</td>
<td>1308</td>
</tr>
</tbody>
</table>
Table 4.2: Description of the ten sampling sites included in this study. All sites are located in the lower montane zone of the Colorado Front Range (CFR).

<table>
<thead>
<tr>
<th>Burn Area</th>
<th>Site Name</th>
<th>Latitude (DD)</th>
<th>Longitude (DD)</th>
<th>Elevation (m)</th>
<th>Aspect (degrees)</th>
<th>Slope (degrees)</th>
<th>Area (m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>LH Canyon</td>
<td>LHC01</td>
<td>40.1195</td>
<td>-105.3255</td>
<td>2000</td>
<td>330</td>
<td>15</td>
<td>150 (10 x 15)</td>
</tr>
<tr>
<td></td>
<td>LHC02</td>
<td>40.1188</td>
<td>-105.3256</td>
<td>2030</td>
<td>340</td>
<td>15</td>
<td>50 (5 x 10)</td>
</tr>
<tr>
<td>Buffalo Creek</td>
<td>BFC01</td>
<td>39.3753</td>
<td>-105.2608</td>
<td>2190</td>
<td>350</td>
<td>5</td>
<td>1750 (35 x 50)</td>
</tr>
<tr>
<td></td>
<td>BFC02</td>
<td>39.3733</td>
<td>-105.2722</td>
<td>2190</td>
<td>360</td>
<td>5</td>
<td>1875 (25 x 75)</td>
</tr>
<tr>
<td>High Meadows</td>
<td>HIM01</td>
<td>39.4097</td>
<td>-105.3667</td>
<td>2170</td>
<td>5</td>
<td>15</td>
<td>5625 (75 x 75)</td>
</tr>
<tr>
<td></td>
<td>HIM02</td>
<td>39.4075</td>
<td>-105.3511</td>
<td>2130</td>
<td>5</td>
<td>20</td>
<td>250 (10 x 25)</td>
</tr>
<tr>
<td>Hayman</td>
<td>HAY01</td>
<td>39.1824</td>
<td>-105.1695</td>
<td>2220</td>
<td>40</td>
<td>15</td>
<td>750 (10 x 75)</td>
</tr>
<tr>
<td></td>
<td>HAY02</td>
<td>39.1817</td>
<td>-105.1683</td>
<td>2230</td>
<td>30</td>
<td>20</td>
<td>875 (25 x 25)</td>
</tr>
<tr>
<td>Overland</td>
<td>OVL01</td>
<td>40.1428</td>
<td>-105.3167</td>
<td>1950</td>
<td>315</td>
<td>15</td>
<td>200 (10 x 20)</td>
</tr>
<tr>
<td></td>
<td>OVL02</td>
<td>40.1353</td>
<td>-105.3228</td>
<td>1970</td>
<td>10</td>
<td>20</td>
<td>875 (25 x 25)</td>
</tr>
</tbody>
</table>
located in moderate to high-severity burn patches. No mature trees occurred within the plots, but in all cases, an abundant seed source was present within c. 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 4.2). Plots contained either exclusively ponderosa pine or a combination of ponderosa pine and Douglas-fir juveniles (Table 4.3). Within each plot, we recorded the species, height, and diameter at base height of each juvenile conifer. The juveniles were then harvested. In the case of small juvenile conifers that could be easily uprooted by hand, we collected the entire specimen for laboratory analysis. In the case of larger juveniles, we first excavated an area around the roots and then used a handsaw to remove a c. 15-centimeter long subsection, centered on the root collar (Figure 4.2).

In the laboratory, we determined the establishment dates 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 (1991) and Telewski (1993). We first divided each sample into several 2.5 cm cross sections. We documented which cross sections corresponded with ground level and which cross sections corresponded with the root collar. The top surface of each cross section was then sanded with progressively fine sandpaper to reveal the cellular structure. Next, we determined a ring count for each cross section under a microscope. Statistical crossdating is not feasible for juvenile trees due to the small number of total rings, but we were able to use marker rings from a regional ponderosa pine tree-ring chronology (Veblen et al., 2000, and updated by new sample collection in 2008) to assist with visual crossdating. 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 presence or absence of pith was used to identify the exact location of the root-shoot boundary (Figure 4.2). This transition typically occurred below ground level, but above the root collar.
Table 4.3: Sample sizes of juvenile ponderosa pine and Douglas-fir collected at each site.

<table>
<thead>
<tr>
<th>Burn Area</th>
<th>Site</th>
<th>Ponderosa pine (n)</th>
<th>Douglas-fir (n)</th>
<th>Total per site (n)</th>
<th>Total per burn (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>LH Canyon</td>
<td>LHC01</td>
<td>38</td>
<td>2</td>
<td>40</td>
<td>83</td>
</tr>
<tr>
<td></td>
<td>LHC02</td>
<td>37</td>
<td>6</td>
<td>43</td>
<td></td>
</tr>
<tr>
<td>Buffalo Creek</td>
<td>BFC01</td>
<td>40</td>
<td>5</td>
<td>45</td>
<td>86</td>
</tr>
<tr>
<td></td>
<td>BFC02</td>
<td>41</td>
<td>0</td>
<td>41</td>
<td></td>
</tr>
<tr>
<td>High Meadows</td>
<td>HIM01</td>
<td>30</td>
<td>3</td>
<td>33</td>
<td>74</td>
</tr>
<tr>
<td></td>
<td>HIM02</td>
<td>32</td>
<td>9</td>
<td>41</td>
<td></td>
</tr>
<tr>
<td>Hayman</td>
<td>HAY01</td>
<td>28</td>
<td>4</td>
<td>32</td>
<td>79</td>
</tr>
<tr>
<td></td>
<td>HAY02</td>
<td>40</td>
<td>7</td>
<td>47</td>
<td></td>
</tr>
<tr>
<td>Overland</td>
<td>OVL01</td>
<td>47</td>
<td>1</td>
<td>48</td>
<td>91</td>
</tr>
<tr>
<td></td>
<td>OVL02</td>
<td>39</td>
<td>4</td>
<td>43</td>
<td></td>
</tr>
<tr>
<td>Overall Total</td>
<td></td>
<td>372</td>
<td>41</td>
<td>413</td>
<td></td>
</tr>
</tbody>
</table>
Figure 4.2: Images from the field and laboratory related to method in the present study. (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.
The establishment date assigned to each juvenile conifer was based on the number of rings present at the root-shoot boundary and also corresponded with a maximum ring count for the entire sample.

4.2.3 Climate-establishment analyses

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 (http://www.wrcc.dri.edu/). The station nearest to the sample sites within each burn area was selected (Table 4.4). We then examined whether years of episodic establishment by ponderosa pine and Douglas-fir coincided with years of atypical 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 atypically high during the growing season (April-September). We thus 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. This analysis relied on Divisional Data from the National Climatic Data Center. We used Division 4 data from Colorado because all of our study sites are included within this division. We compared median April-Sept. total precipitation, daily maximum temperature, and the Palmer Drought Severity Index (PDSI) for years of episodic establishment vs. non-establishment years. Measures of precipitation, temperature, and measures of drought have all been previously linked to ponderosa pine
Table 4.4: COOP Climate stations used in the present study. For each site, the nearest climate station with a sufficient period of record was chosen. Data were accessed from the Western Regional Climate Center.

<table>
<thead>
<tr>
<th>Station Name</th>
<th>Station ID</th>
<th>Elevation (m)</th>
<th>Study Sites</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cheesman</td>
<td>051528-4</td>
<td>2097</td>
<td>HAY01 + 02</td>
</tr>
<tr>
<td>Bailey</td>
<td>050454-4</td>
<td>2356</td>
<td>HIM01 + 02, BFC01 + 02</td>
</tr>
<tr>
<td>Boulder</td>
<td>050848-4</td>
<td>1670</td>
<td>OVL01 + 02, LHC01 + 02</td>
</tr>
</tbody>
</table>
establishment (Savage et al., 1996, 2013; League & Veblen, 2006; Feddema et al., 2013). 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. Establishment years were again defined as years in which a minimum percentage (5%, 10%, or 20%) of all ponderosa pine and Douglas-fir seedlings established. We assessed statistical differences between medians of each climate variable in years of episodic vs. non-episodic establishment using Mann-Whitney tests at the P < 0.05 levels.

Finally, we examined whether seed production data collected in a previous study (Mooney et al., 2011) was related to patterns of establishment by ponderosa pine and Douglas-fir seen in the present study. This portion of the analysis focused on only two of our burn areas (Overland and LH Canyon), as seed production data were not available for the other study sites. The seed production data we used from Mooney et al. came from their Boulder Canyon site, which is located 10-15 km south of the locations where we harvested the seedlings for the present study. This Mooney et al. site was chosen not only for its proximity to our sample sites, but also because it has the greatest temporal overlap with our data. However, as emphasized by Mooney et al., masting by ponderosa pine can vary notably across relatively short distances, and thus the seed data do not directly correspond to seed availability at our study sites. We graphically displayed seed production data against tree establishment data and used Spearman’s correlation to examine potential associations between seed production and conifer establishment. For both the graphical display and Spearman’s correlations, seed cone years were adjusted +1 year to account for the lag between seed production and germination and subsequent establishment.
4.3 Results

4.3.1 Annually-resolved establishment dates

Of the 562 post-fire conifer juveniles we collected, we dated a total of 413 samples (73.5%, Table 4.3). The majority of all samples dated were ponderosa pine (90% ponderosa pine, 10% Douglas-fir). Given that Douglas-fir was rare in our study sites (n = 0–9 Douglas-fir samples per site), we combined Douglas-fir and ponderosa pine for our analyses. To ensure high accuracy of our dating estimates, only samples with clear ring boundaries were included in the final dataset. Year of establishment ranged from 1992 to 2011 (Figure 4.3). At individual sites, establishment was generally concentrated within relatively few years. Some years of episodic establishment occurred across sites, such as 1998 (at LH 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 4.3f). Seedling establishment typically lagged behind wildfire by one or more years, although a pulse of establishment in the same year as fire was observed at the High Meadows site in 2000.

4.3.2 Climate-Establishment Analysis

At the individual site level, graphical display of precipitation during years of episodic establishment revealed that conditions were generally wetter than average throughout the growing season (Figure 4.4). 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 LH Canyon site) and others being characterized by later growing season wet periods (e.g. July in 1998 for both the LH 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 very high precipitation (exceeding the 90th percentile) revealed that differences between observed and expected patterns were statistically significant (P < 0.05) at all five sites (Figure 4.5). Relationships between monthly average maximum temperature and
Figure 4.3: 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 size through time.
Figure 4.4: Monthly total precipitation (cm) for the growing season (April-September) during years of episodic establishment at each site. The horizontal line is the monthly mean for the long-term record (1961-2010). Establishment years are defined as years in which a minimum of 20% of all ponderosa pine and Douglas-fir seedlings established.
Figure 4.5: Observed and expected frequencies of establishment by ponderosa pine and Douglas-fir seedlings occurring in years where one or more month in the growing season (April-September) had precipitation that exceeded the 90th percentile for the long-term record (1961-2010). Differences between observed and expected frequencies were statistically significant in all cases, according to chi-square goodness of fit tests (P < 0.001).
ponderosa pine and Douglas-fir establishment were less clear (Figure 4.6). 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.

We also examined patterns between climate conditions and ponderosa pine and Douglas-fir establishment for the combined dataset that included all five sites (Figure 4.7). Comparison of median growing season precipitation, temperature, and PDSI during establishment and non-establishment years revealed statistically significant differences in the case of precipitation and PDSI. With regard to precipitation, episodic establishment years using a 10% filter and 20% filter were characterized by significantly higher precipitation than non-establishment years. With regard to PDSI, episodic establishment years using the 20% filter were characterized by significantly higher PDSI values than non-establishment years.

4.3.3 Seed production and conifer establishment

Finally, we observed only weak associations between seed production data and establishment by ponderosa pine and Douglas-fir (Figure 4.8). Analysis was focused only on the Overland and LH Canyon burns and relied on only one nearby site of seed production data (Mooney et al., 2011), as that was all that was appropriate given the available data. Of the years of episodic establishment for which seed production data were available (using a 20% filter; 1995, 1998, 2005, and 2009), moderate to high seed production occurred in the year prior. Although at least some years of episodic establishment appeared to correspond with seed production in the previous year, Spearman’s correlation analysis between average seed cones per tree (in year t-1) and frequency of establishment (in year t=0) at the two sites revealed no statistically significant relationships at the P < 0.05 level.

4.4 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 CFR was typically
Figure 4.6: Monthly Average Maximum Daily Temperature (°C) for the growing season (April-September) during years of episodic establishment at each site. The horizontal line is the monthly mean for the long-term record (1961-2010). Years of episodic establishment were defined as years in which at least 20% of the total establishment at a site occurred.
Figure 4.7: Comparison of (a) average April-September precipitation (cm), (b) average April-Sept temperature (°C), and (c) average April-September PDSI index values during establishment vs. non-establishment years for the combined dataset of all 5 study sites. Positive values of PDSI correspond with wetter conditions while negative values correspond with drought. Establishment years are defined as years in which a minimum percentage (5%, 10%, or 20%) of all ponderosa pine and Douglas-fir seedlings established. Establishment years are in grey and non-establishment years are in white. P-values are provided when differences between medians 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 (see Figure 4.1 for Division 4 location).
Figure 4.8: Comparison of the frequency (%) of post-fire conifer establishment at the (a) Canyon (1988) and (b) Overland (2003) burn sites to average ponderosa pine seed cone production per tree (n) at the Boulder Canyon seed cone-monitoring site during the period 1988–2009. Seed cone years are adjusted +1 year to account for the lag between seed production and germination (e.g. seed cones produced in 1987 are graphed as 1988, the expected year of germination and subsequent establishment). Seed cone data are from Mooney et al., 2011. No seed cone data were collected in 2004. The upside-down black triangles along the top of the figure indicate the year of the two fires included (LH Canyon, 1988 and Overland, 2003).
concentrated in years of above-average moisture availability (i.e. high precipitation and positive values of PDSI). We observed this trend both at the individual site level and for our combined dataset that included all ten sites from all five fires. We found that growing season (April to September) precipitation tended to be above average in years of episodic establishment, and that the growing season often included one or more months of 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 maximum 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 ponderosa pine and Douglas-fir in the CFR. An earlier study in the CFR (League & Veblen, 2006) examined relationships between climate variability and ponderosa pine establishment along forest-grassland ecotones, but included only sites that had not been recently disturbed. In terms of post-disturbance establishment, a previous study in the CFR did examine climate-establishment relationships, but resolution was decadal and thus not very conclusive. Annually resolved dating of tree establishment is most feasible with younger juveniles, as destructive sampling is required and it can become more difficult to extract a sample from the root-shoot boundary with larger trees. Additionally, the inability to use statistical crossdating methods with juvenile trees due to low ring counts means that missing or false rings can throw off age estimates. We used a conservative approach in the present study and only dated samples with clear ring boundaries. Future studies that validate the aging of trees via the
methods used in this paper (and based on Telewski and Lynch (1991) and Telewski (1993)) are still needed.

Colorado is expected to see a temperature increase of 1.4–3.6 °C by 2050. In contrast, uncertainty surrounds if and how precipitation regimes may change in the future (Reclamation, 2013; Lukas et al., 2014). However, unless precipitation increases, higher temperatures will be associated with increased drought. Our findings regarding the relationship between PDSI 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 hotter conditions, rainfall will be less available for uptake by plants due to higher rates of evapotranspiration.

We found only weak associations between seed production data and establishment by ponderosa pine and Douglas-fir. Given the limited data available, it is unclear whether the relationship between seed cone production and conifer establishment is weak, or whether the data available are unable to capture meaningful relationships. Seed production data were for only one site, and were used for assessment of only 2 burn areas that were located 10-15 km south of 2 burn sites. To our knowledge, better data are not available to improve this analysis. Despite the limitations, we did observe that most years of episodic establishment (20% filter) were preceded by a year of moderate to abundant seed production. However, correlations between seed production and juvenile tree establishment were not statistically significant. Additional studies that examine the relationship between climate, seed production, and conifer establishment are still needed.

Recent studies of vegetation patterns following wildfire have been motivated by concern that climate change and/or potential increases in wildfire severity may alter post-fire vegetation trajectories by inhibiting processes of conifer regeneration (e.g. Savage & Mast, 2005; Feddema
et al., 2013; Savage et al., 2013). These two drivers are not mutually exclusive, and it is likely that both fire severity and recent climate conditions have played key roles in influencing current patterns of vegetation recovery after fire in the CFR and throughout the West. Blackened soil and absence of vegetation may result in altered microclimate conditions such as higher daily temperature ranges and reduced soil moisture (Ulery & Graham, 1993; Wondafrash et al., 2005; Moody et al., 2007; Montes-Helu et al., 2009). Additionally, ponderosa pine and Douglas-fir both disperse their seed via wind over relatively short distances of approximately 200 m or less (Bonnet et al., 2005; Shatford et al., 2007; Haire & McGarigal, 2010), so high percent tree mortality can result in limited seed availability. Despite these potential disadvantages, abundant conifer regeneration following high-severity fire has been documented in ponderosa pine forests (Veblen & Lorenz, 1986; Ehle & Baker, 2003; Savage & Mast, 2005; Haire & McGarigal, 2010) and thus high-severity fire does not necessarily inhibit conifer establishment and survival. Additionally, in the ponderosa pine zone in the CFR, the historic wildfire regime was of mixed severity, meaning that fire effects were varied both within stands and across the landscape and included low-, moderate- and high-severity fire (Sherriff & Veblen, 2007, 2008). Although it has been suggested that fire suppression has caused the drier forests of the U.S. West to be susceptible to uncharacteristically severe fire (Covington, 2000; Williams, 2013), such generalizations need to be examined for particular landscapes and along elevation and moisture gradients within specific landscapes. Recent research comparing historical (pre-fire suppression) and current fire potential shows that most (84%) of montane forests of the CFR are not characterized by increased likelihood of crown fire (Sherriff et al., 2014). Our current understanding of fire severity and conifer regeneration in dry ponderosa pine forests strongly suggests that although fire severity undoubtedly plays an important role in influencing post-fire vegetation patterns, it is unlikely to be the only factor explaining observations of limited conifer regeneration following recent wildfires.
Our findings clearly demonstrate the importance of favorable climate conditions in driving post-fire conifer regeneration. The montane zone of the CFR has experienced numerous large wildfires in recent years (e.g. 2012 High Park Fire – 37,000 ha, 2012 Waldo Canyon Fire – 8,100 ha), and land managers and the public are eager to understand what to expect in terms of future vegetation patterns in these areas. Our study, along with previous experimental work regarding the climate requirements of ponderosa pine and Douglas-fir (Rother et al., under review), suggests that some previously forested areas that have recently burned may be replaced by persistent grasslands or shrublands under current and future climate conditions.

ACKNOWLEDGEMENTS
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. Thank you especially to N. Stremel, E. Duncan, L. Furman and W. Foster for assistance with project planning, fieldwork, and/or lab work. Also thank you to K.A. Mooney, Y.B. Linhart, and M.A. Snyder for the use of seed production data from Mooney et al. (2011).
SUMMARY AND CONCLUSIONS

5.1 Conifer regeneration after fire in low-elevation forests of the CFR

Although ponderosa pine forests of the CFR have historically demonstrated high resiliency to wildfire (Veblen & Lorenz, 1986; Mast et al., 1998), it is uncertain whether these forests will exhibit similar resiliency under changing climate conditions. In some western ponderosa pine forests, previous research documented significant shifts toward non-forested vegetation (i.e. grasslands or shrublands) after fire, at least in portions of burns where seed availability is low (Savage & Mast, 2005; Keyser et al., 2008; Roccaforte et al., 2012; Dodson & Root, 2013). These studies have attributed observed changes to high-severity fire, low seed availability, climate change, or a combination of factors. Through this dissertation, we aimed to determine whether similar patterns of limited conifer regeneration were present in recently burned lower montane forests of the CFR (chapter 2). We then examined what role factors such as climate change, fire severity, seed availability, understory composition, and topography played in explaining current patterns (chapter 2, 3, and 4).

To accomplish our objective of assessing current post-fire conifer regeneration patterns, we surveyed six burn areas of the CFR. At a broad scale, we observed that current densities of juvenile ponderosa pine and Douglas-fir were generally low throughout the study area, regardless of local factors such as topography, fire severity, and understory composition. However, we did identify some settings as being associated with a higher probability of successful conifer establishment. The probability of seedling presence was higher for north-facing slopes, at higher elevations, and where distance to seed source was lower. Importantly, we did not observe strong relationships between fire severity and post-fire conifer regeneration. This finding is consistent with understanding of historic wildfire regimes of the study area. Ponderosa pine forests of the CFR were historically characterized by mixed-severity wildfire,
meaning that burns included a combination of low-, moderate-, and high-severity fire (Sherriff & Veblen, 2007, 2008). Misperceptions regarding the historical range of variation (HRV) for these forests have led to concerns that the wildfire regime has dramatically shifted toward higher-severity fire (Veblen et al., 2012), but research indicates that these concerns are largely unfounded (Sherriff et al., 2014). We should not expect that higher-severity fire will necessarily inhibit conifer regeneration given that higher-severity fire is part of the HRV and that abundant establishment after higher-severity fire has occurred historically in these same habitats (Veblen & Lorenz, 1986; Mast et al., 1998; Kaufmann et al., 2000; Ehle & Baker, 2003). The strong relationships we identified between conifer regeneration and aspect and elevation suggest the importance of moisture availability in driving patterns within a given burn area. North-facing slopes and higher elevations are both associated with cooler, moister conditions. Thus this finding is consistent with previous research that demonstrates a strong link between climate and regeneration in ponderosa pine forests (Savage et al., 1996, 2013; League & Veblen, 2006; Feddema et al., 2013).

We further examined the importance of climate in driving post-fire regeneration patterns using a field experiment (chapter 3) and a tree-ring study of climate-establishment relationships (chapter 4). In the field experiment, we examined the effects of microclimate manipulations of temperature and water on changes in stem height, above- and belowground biomass, and survival of 700 ponderosa pine and 700 Douglas-fir seedlings planted in a low-elevation, recently disturbed setting of the CFR. We followed a full factorial design of four experimental treatments of warming and watering (warmed only, watered only, warmed and watered, and control). We found that measures of survival and growth for both conifer species varied significantly by treatment type. Average growth and survival rates were highest in watered only plots and lowest in warmed only plots. This finding is consistent with our expectation that ponderosa pine and Douglas-fir regeneration is favored by relatively cool and wet conditions.
and is inhibited by hotter and drier conditions. Our findings also suggest that the window of favorable climate necessary to allow for successful regeneration extends beyond the time of germination because subsequent growth and survival are also sensitive to climate conditions.

We sought further evidence for the importance of climate in driving post-fire regeneration patterns through a tree-ring study that examined whether pulses of ponderosa pine and Douglas-fir establishment were synchronous with certain climate conditions. We began by building a large dataset (n = 413) of post-fire establishment dates for ponderosa pine and Douglas-fir seedlings that we harvested from five recently burned areas of the CFR. We used an accurate method of aging trees that involves dating the pith at the root-shoot boundary (Telewski & Lynch, 1991; Telewski, 1993), in order to achieve annually-resolved tree establishment dates. We found that conifer regeneration was concentrated in relatively few years, and that those years were characterized by high growing season precipitation and positive values of PDSI (i.e. cooler, wetter conditions). Moreover, the driest and hottest years following fire were characterized by virtually no tree establishment by either species.

As a whole, the three studies in this dissertation (chapters 2, 3, and 4) identify climate as a key driver of conifer regeneration patterns in low-elevation forests of the CFR. We conclude that warming temperatures and associated drought have already begun to inhibit regeneration processes in lower montane forests, and that future warming is likely to exacerbate current trends. In the absence of abundant regeneration by ponderosa pine and Douglas-fir, persistent grasslands or shrublands may replace some previously forested areas. The extent of dry ponderosa pine forests is likely to decline near lower treeline. If significant upslope expansion of this forest type occurs (as is expected when climate conditions alone are considered to drive plant distributions) the total area of lower montane forest has the potential to expand (Shafer et al., 2001; Rehfeldt et al., 2006). However, expectations for the future based on climate
envelopes alone are limited because they do not take into account factors such as feedbacks involving natural disturbances and current upslope vegetation (Enright, et al., 2015).

5.2 Management implications

Our research suggests that land managers should prepare for post-fire shifts in vegetation type in low-elevation forests of the CFR, at least in some areas. Current densities of ponderosa pine and Douglas-fir seedlings are generally low across the burn areas we surveyed. Looking forward, continued warming is expected to limit the amount of additional germination and establishment, as conditions will become even less suitable, particularly at lower elevations and on south-facing aspects. In areas where few surviving trees remain on the landscape, a transition to non-forested vegetation type is already underway. In contrast, in areas where canopy tree mortality was lower (i.e. in low- to moderate-severity areas), surviving trees have allowed the forested vegetation type to persist. However, the lack of notable conifer regeneration in these areas suggests that they too are vulnerable to future transitions in vegetation type following additional disturbance and/or the senescence of the surviving trees. Forest openings (i.e. areas within forests that are non-forested) have always been present in CFR ponderosa pine forests and have sometimes persisted for long periods of time (Kaufmann et al., 2000; Dickinson, 2014). However, landscape-scale conversion to non-forested vegetation and a general upslope shift in lower treeline in the CFR is unprecedented in the historical record (i.e. in the last few hundred years).

An important question for land managers will be whether to try and forestall major vegetation changes. Given that wildfire can serve as a catalyst for rapid change (Turner 2010), one option might be to mitigate wildfire occurrence through strategies such as mechanical thinning and prescribed burning. In the CFR, these types of efforts are currently being implemented, with a focus on creating heterogeneous forest conditions (e.g. variable stand density) that are also consistent with forest restoration goals (Underhill et al., 2014). However,
these types of management strategies are typically time intensive, costly, and not universally effective (Roccaforte et al., 2010; Graham et al., 2012), and therefore are only a reasonable option for high-priority areas. Another option for forestalling vegetation changes is to plant tree seedlings in recently burned areas. Similar limitations arise with tree plantings in terms of cost, time, and the effectiveness of those efforts. Findings from our field experiment suggest that survival of planted seedlings is likely to be low under warmer, drier conditions. Plantings that are targeted during relatively wet and cool periods as well as in wetter and cooler topographic settings (n-facing aspects, higher elevations) are likely to be most successful. At broad scales, response strategies that accept the transition of post-fire landscapes to new vegetation assemblages are likely to be most feasible.

5.3 Research Limitations and Future Needs

This dissertation provides important insights regarding conifer regeneration after wildfire in low-elevation forests of the CFR, and is an important contribution to understanding how climate change may alter the resiliency of these forests to wildfire. The combination of field survey, a field experiment, and a tree-ring study provides multiple lines of evidence that climate warming may inhibit post-fire conifer regeneration in the study area. However, this dissertation does include several limitations, and further research is still needed.

One limitation is the incomplete control of seed availability. In our survey of juvenile conifer densities across burn areas, we used distance to seed source as a proxy for seed availability, but were unable to account for the spatial and temporal variability in seed production by individual trees or tree populations. A nearby tree is not truly a seed source if it does not produce seed. The strong relationships we found between distance to seed source and conifer establishment indicate that distance is indeed important, but we cannot be certain that seed production was sufficient in the years following fire across our study area, nor do we know what role climate variability may have played in driving patterns of seed production. Resolving this
uncertainty requires more studies that assess seed production (Shepperd et al., 2006; Mooney et al., 2011). Given that climate variability has been associated with masting by ponderosa pine (Mooney et al., 2011), it will also be necessary to examine whether changing climate conditions are altering the timing and/or frequency of seed production.

Another limitation of this study is that it is difficult to contextualize our current findings against historic patterns of post-fire conifer regeneration because previous studies leave uncertainty regarding the timing and abundance of conifer establishment following 19th century and earlier fires (Veblen & Lorenz, 1986; Mast et al., 1998; Kaufmann et al., 2000; Ehle & Baker, 2003). These retrospective studies relied on tree-ring reconstructions of tree establishment, and can only provide estimates of the length of past recruitment periods. Additionally, these studies (along with the present study) are unable to account for tree mortality that occurred between the fire events and data collection period. Although these earlier studies indicated that conifer establishment in ponderosa pine forests was pulsed and occurred most abundantly relatively soon after fire (Veblen & Lorenz, 1986; Mast et al., 1998; Kaufmann et al., 2000; Ehle & Baker, 2003), we cannot fully rule out the possibility that not enough time has passed in the current study (time since fire 8-15 years) to expect sufficient regeneration to occur. Continued monitoring of regeneration in these burns is recommended. However, given results of this dissertation, we do not expect future climate conditions to be conducive to significant new conifer establishment. Moreover, competition with non-conifer species (especially grasses) is likely to deter future widespread tree establishment. Finally, an increased frequency of disturbances has the potential to narrow the temporal window for successful post-fire regeneration (Enright, N.J. et al., 2015).

Our research demonstrated that elevation is associated with increased conifer regeneration for both ponderosa pine and Douglas-fir. This finding raises the interesting question of whether similar patterns of limited conifer regeneration are present at elevations
higher than those included in the present study. We hypothesize that in the upper montane zone, where conditions are notably wetter and cooler than in the lower montane zone, we may observe significantly higher post-fire juvenile conifer densities. The Hayman fire (HY in this study) provides a unique opportunity to compare regeneration patterns in the lower montane zone to those in the upper montane zone because the burn includes large areas within both zones. Although we have already observed patterns with elevation in the lower montane zone, expanding research into the upper montane would strengthen our argument that current patterns of limited regeneration in the lower montane zone are climate driven. A CU-undergraduate student (Jeremy Arkin) has collected juvenile conifer density data in the upper montane zone, and we plan to collaborate to analyze our combined datasets in the future. Research is also needed that begins to synthesize findings from various parts of the western US, including the Rocky Mountain region. Differences in data collection methods complicate efforts to draw broadscale conclusions, yet this type of research is vital. We are currently in conversations with other researchers regarding future collaboration. Finally, research is needed to determine what impacts shifts in vegetation patterns may have on carbon storage, water quantity and quality, habitat, and other ecosystem services that vary strongly with vegetation type (Rocca et al., 2014).
REFERENCES


