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ARTICLE

A field experiment informs expected patterns of conifer regeneration after disturbance under changing climate conditions

Monica T. Rother, Thomas T. Veblen, and Luke G. Furman

Abstract: Climate change may inhibit tree regeneration following disturbances such as wildfire, altering post-disturbance vegetation trajectories. We implemented a field experiment to examine the effects of manipulations of temperature and water on ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedlings planted in a low-elevation, recently disturbed setting of the Colorado Front Range. We implemented four treatments: warmed only (Wm), watered only (Wt), warmed and watered (WmWt), and control (Co). We found that measures of growth and survival varied significantly by treatment type. Average growth and survival was highest in the Wt plots, followed by the Co, WmWt, and Wm plots, respectively. This general trend was observed for both conifer species, although average growth and survival was generally higher in ponderosa pine than in Douglas-fir. Our findings suggest that warming temperatures and associated drought are likely to inhibit post-disturbance regeneration of ponderosa pine and Douglas-fir in low-elevation forests of the Colorado Front Range and that future vegetation composition and structure may differ notably from historic patterns in some areas. Our findings are relevant to other forested ecosystems in which a warming climate may similarly inhibit regeneration by dominant tree species.

Key words: field experiment, tree regeneration, climate change, wildfire, ponderosa pine, open-top chambers.

Résumé : Les changements climatiques pourraient inhiber la régénération des arbres à la suite de perturbations telles qu'un feu, ce qui modifierait les trajectoires de la végétation après une perturbation. Nous avons effectué une expérience de terrain pour étudier les effets de manipulations de la température et de l'eau sur la croissance et la survie des semis de pin ponderosa (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) et de douglas de Menzies (*Pseudotsuga menziesii* (Mirb.) Franco) plantés à faible altitude dans un milieu récemment perturbé du Colorado Front Range (CFR). Nous avons établi quatre traitements : réchauffement seulement (Wm), arrosage seulement (Wt), réchauffement et arrosage (WmWt) et témoin (Co). Nous avons observé que les mesures de croissance et de survie variaient significativement selon le traitement. La croissance et la survie étaient en moyenne les plus élevées dans les parcelles Wt suivies respectivement des parcelles Co, WmWt, et Wm. Cette tendance générale a été observée chez les deux espèces de conifère même si la croissance et la survie étaient en général meilleures chez le pin ponderosa que chez le douglas de Menzies. Nos résultats indiquent que l'augmentation de la température et la sécheresse qui y est associée vont probablement inhiber la régénération qui suit une perturbation chez le pin ponderosa et le douglas de Menzies dans les forêts du CFR situées à faible altitude et que la composition et la structure de la régénération pourraient dans le futur être très différentes de la configuration historique dans certaines régions. Bien que notre étude mette l'accent sur les forêts du CFR situées à faible altitude nos résultats sont pertinents pour d'autres écosystèmes forestiers où le réchauffement du climat peut de façon similaire inhiber la régénération des espèces dominantes. [Traduit par la Rédaction]

Mots-clés : expérience de terrain, régénération des arbres, changement climatique, feu de forêt, pin ponderosa, chambres à ciel ouvert.

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 postfire vegetation trajectories by inhibiting processes of conifer regeneration. In some dry ponderosa pine forests of the western United States (US), observations of limited postfire 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 in which seed availability is low (Dodson and Root 2013; Keyser et al. 2008; Roccaforte et al. 2012; Savage and Mast 2005). In the Colorado Front Range (CFR) and throughout the western US, more research is needed to document whether current patterns of postfire conifer regeneration are incongruous with historic patterns and what factors (e.g., increased temperatures and associated drought, wildfire severity, etc.) 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 rates and percent survival of ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedlings that were planted in a recently disturbed environment. Our research will allow land managers to better understand and prepare for changes in patterns of postfire conifer regeneration, including potential shifts from forest to nonforest vegetation.

In Colorado, temperatures have risen almost universally across the state in recent decades and are expected to increase by an addi-

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tional 1.4–3.6 °C by 2050 (Lukas et al. 2014; Reclamation 2013). 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 (Lukas et al. 2014; Reclamation 2013). 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 (Cooper 1960; Pearson 1923). 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 a ponderosa pine forest in Arizona (Savage et al. 1996) and along a grassland–forest ecotone of the CFR (League and 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 postfire ponderosa pine regeneration. Further research is needed to document whether similar relationships between climate variability and postfire 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; Haire and McGarigal 2010; Shatford et al. 2007). Additionally, patches of high-severity wildfire can create altered microclimate conditions such as higher daily temperature ranges and reduced soil moisture levels due to blackened soil and absence of vegetation (Montes-Helu et al. 2009; Ulery and Graham 1993). However, abundant conifer regeneration following high-severity fire has been documented in ponderosa pine forests (Ehle and Baker 2003; Haire and McGarigal 2010; Savage and Mast 2005; Veblen and Lorenz 1986), 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 and Veblen 2007). Fire severity undoubtedly plays an important role in influencing postfire 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 play in influencing postdisturbance 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 rates and percent 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 (*i*) examine the effects of manipulations of temperature and water on the growth rates and percent survival of conifer seedlings, (*ii*) assess potential differences in aboveground vs. belowground biomass partitioning by conifer seedlings, and (*iii*) 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 rates and percent survival, whereas increased water would result in increased growth rates and percent survival. We hypothesized that ponderosa pine growth rates and percent survival may be higher than Douglas-fir growth rates and percent survival 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, nonconifer biomass was expected to vary in response to the experimental treatments; high total nonconifer biomass was expected to be associated with lower growth rates and percent survival of conifer seedlings due to increased competition for water.

Materials and methods

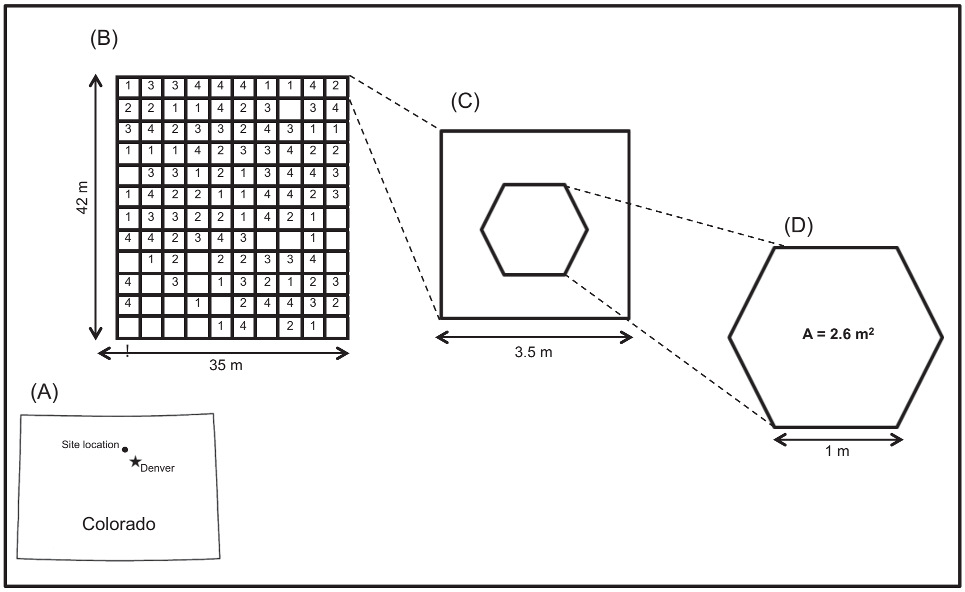
Study area

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 1960 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, 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.

Experimental design

Preparation for the field experiment began in the spring of 2012. A macro plot of 35 m × 42 m was divided into a grid of 120 cells of 3.5 m × 3.5 m (Fig. 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

Fig. 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, warmed only (Wm); 2, warmed and watered (WmWt); 3, watered only (Wt); 4, control (Co)), (C) cell, and the (D) micro plot within the cell in which experimental treatment was applied.



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 seedlings each) in a hexagonally shaped area of 2.6 m^2 within each cell, hereafter termed the micro plot. The seedlings were from a local genetic provenance and were approximately 1 year old at the time of planting. We regularly watered all of the seedlings for approximately 1 month prior to initiating experimental manipulations to help them acclimatize and minimize initial mortality. A fence that was c. 1.8 m tall 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.

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 (Hollister and Webber 2000; Marion et al. 1997; Tercero-Bucardo et al. 2007), which is reasonable given the 1.4–3.6 °C forecasted temperature increase expected by 2050 in Colorado (Lukas et al. 2014; Reclamation 2013). More uncertainty surrounds how precipitation regimes might change in Colorado (Lukas et al. 2014; Reclamation 2013), 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·$week^{-1}$ per micro plot. This method does not fully replicate precipitation, as natural precipitation falls more variably in terms of both the amount of water in a single rainfall event and the 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–September). 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 rates and percent survival across all treatment types than would otherwise be expected.

Data collection

We used HOBO automated data loggers (Onset Computer Corp., Bourne, Massachusetts) 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 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 min, whereas soil temperature data were recorded every 20 min (the highest allowable frequency given the data storage limitations of the devices). We monitored changes in ponderosa pine and Douglas-fir seedling growth rates and percent 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 (i.e., 2013), we harvested all biomass in a subset of the micro plots ($n = 80$) to calculate the aboveground and belowground biomass of conifer seedlings, as well as the aboveground herbaceous and shrub biomass (hereafter, "nonconifer biomass"). The nonconifer biomass data were collected to determine whether experimental treatments influenced nonconifer biomass and to assess whether competitive effects were important to conifer seedling growth rates and percent survival. All harvested biomass samples were weighed after they were dried in an oven at 70 °C to remove all water mass.

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–September) 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 with the long-term mean. To assess whether experimental treatments affected conifer seedling growth rates and percent 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 growing 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 percentage 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 generalized linear models (GLMs) with robust standard errors in Stata software (StataCorp 2015). Robust standard errors were used to account for clustering in the data due to nonindependence 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 nonconifer biomass, by treatment type, again using data pooled to the micro plot level, using 2×2 ANOVA.

Results

Temperature and relative humidity data

We observed that air temperature, relative humidity, and soil temperature varied among treatment types, particularly at midday (10:00 AM to 6:00 PM). Mean midday air temperature in Wm plots was 4.4 °C warmer than in Co plots in 2012 and 3.2 °C warmer than in Co plots in 2013 (Fig. 2; Table 1). In contrast, differences in mean air temperatures among the treatment types for the entire 24-hour day were less pronounced; we observed a 1.63 °C difference between Wm and Co in 2012 and a 1.38 °C difference between Wm and Co 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 (Fig. 2). Among treatment types, mean 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 standard deviations (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.

Ambient climate conditions

In both 2012 and 2013, there were periods during which the monthly air temperature or precipitation deviated substantially from the long-term mean (Table 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 2) is also evident in the air temperature data from the field experiment (Fig. 2; Table 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, whereas 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 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 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), which was approximately 13 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).

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 (Fig. 3). Generally, growth rates and percent survival were 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 with 15.5% in Wt plots, and in 2013, median height growth rates were 6.2% and 11.7% for Wm and Wt plots, respectively. Our GLMs revealed numerous significant relationships (Table 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 with the control ($P < 0.001$) and the Wt treatment resulted in significantly higher height growth rates compared with 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, whereas 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 ($P \leq 0.01$). In terms of year of experiment, we found significantly lower ponderosa pine height growth rates in 2013 vs. 2012 ($P < 0.001$) and significantly higher odds of ponderosa pine percent survival in 2013 vs. 2012 ($P < 0.001$). Finally, results from 2x2 ANOVA indicate that root to shoot ratios differed by treatment type ($F = 11.98$, $P < 0.001$). Root to shoot ratios were higher in Wm and WmWt plots than in Wt and Co plots (Fig. 4; Table 4).

Fig. 2. Mean air temperature, relative humidity, and soil temperature by treatment type for (A) year 1 (2012) and (B) year 2 (2013) of the experiment. Data were collected for June–September using HOBO data loggers placed in a subset of the plots. Different line types designate different treatment types: solid lines, warmed only (Wm), long-dashed lines, warmed and watered (WmWt), short-dashed lines, watered only (Wt), and dotted lines, control (Co).

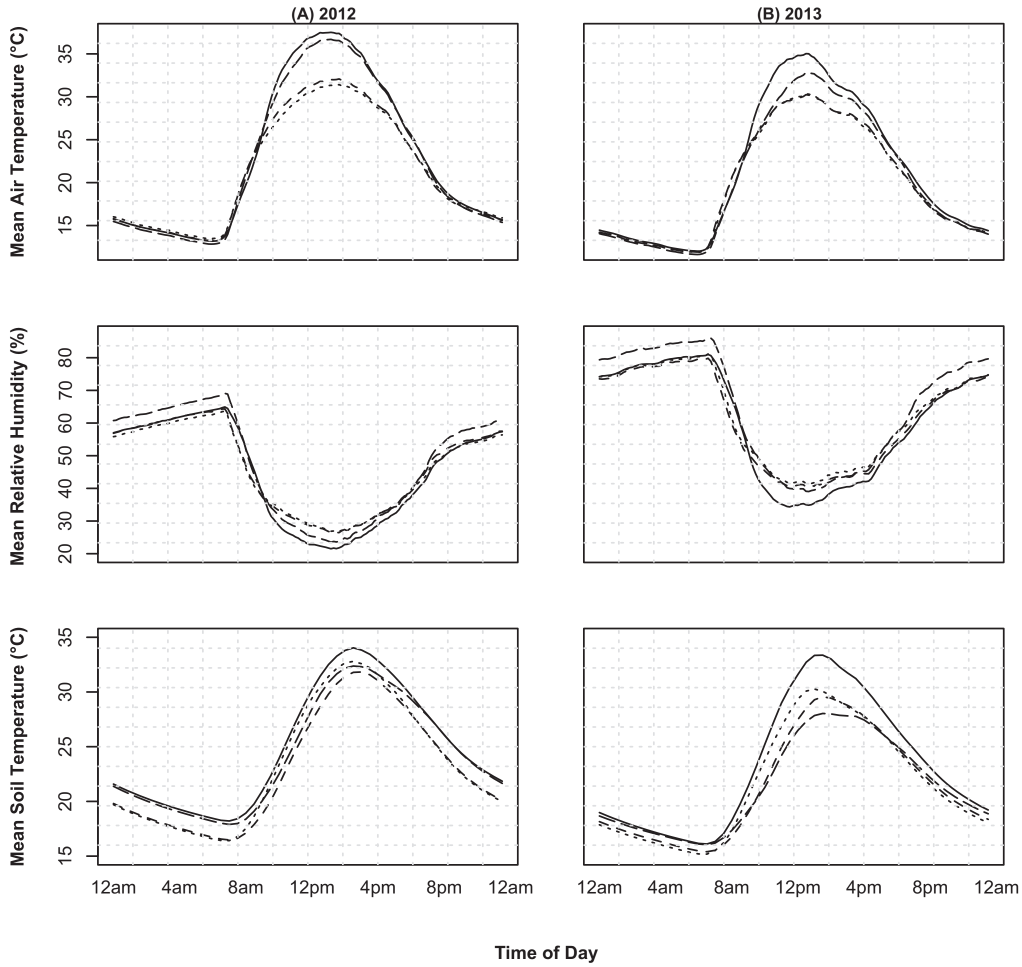


Table 1. Midday (10 AM – 6 PM) air temperature, relative humidity, and soil temperature by treatment type during the experimental period (June–September of 2012 and 2013).

	Air temperature (°C)			Relative humidity (%)			Soil temperature (°C)		
	Mean	Median	SD	Mean	Median	SD	Mean	Median	SD
2012									
Wm	33.2	34.6	4.2	27.4	25.8	5.4	30.7	31.4	3.0
WmWt	32.6	33.6	3.8	29.7	28.4	5.3	29.4	30.3	3.0
Wt	29.3	30.1	2.7	31.5	30.4	4.4	28.5	29.2	3.1
Co	28.8	29.5	2.5	31.6	30.6	4.1	29.6	30.3	2.8
2013									
Wm	30.4	31.2	4.0	41.1	39.9	6.3	29.9	30.4	2.7
WmWt	28.8	29.7	3.2	45.4	43.6	6.0	26.3	26.7	1.7
Wt	27.3	28.0	2.7	45.0	43.5	4.7	26.9	27.3	2.1
Co	27.2	27.9	2.8	46.5	45.0	5.1	27.5	27.9	2.2

Note: SD, standard deviation. Treatment types: Wm, warmed only; WmWt, warmed and watered; Wt, watered only; Co, control.

Douglas-fir growth and survival

We observed that Douglas-fir growth rates and percent survival were typically highest in the Wt plots followed by the Co, WmWt, and Wm plots, respectively (Fig. 3). This general pattern is the same as what we observed for ponderosa pine. However, for Douglas-fir, 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 with 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 (Fig. 3). In contrast, Wt plots had median percent

Table 2. Climate conditions during the experimental period (2012 and 2013) vs. the long-term record.

	2012	2013	Long-term record Mean	SD
Mean temperature (°C)				
June	23.4	21.1	19.3	1.7
July	23.8	22.3	22.5	1.5
August	22.9	22.3	21.7	2.3
September	18.9	18.4	17.2	1.3
Total precipitation (cm)				
June	1.0	1.5	4.9	3.4
July	12.7	2.6	4.7	3.0
August	0.9	3.6	4.1	3.0
September	5.8	46.1	3.9	3.2

Note: Data are from the Boulder Station, 1893–2011, Western Regional Climate Center. SD, standard deviation.

survivals 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 ($P < 0.05$) treatments. With regard to year of experiment, we found significantly higher Douglas-fir height growth rates in 2013 vs. 2012 ($P < 0.001$) and significantly higher Douglas-fir percent survival in 2013 vs. 2012 ($P < 0.001$). Lastly, in terms of aboveground and belowground biomass, results from 2×2 ANOVA indicate that root to shoot ratios varied by treatment type ($F = 16.17$, $P < 0.001$). Root to shoot ratios were higher in Wm and WmWt plots than in Wt and Co plots.

Nonconifer biomass

By the end of the second experimental year (i.e., 2013), most plots had substantial cover by nonconifer biomass, mostly by grasses and forbs. Among all 100 micro plots, total nonconifer biomass varied widely from 12.9 $g \cdot m^{-2}$ to 98.3 $g \cdot m^{-2}$, with an average of 43.3 ± 17.8 $g \cdot m^{-2}$ (mean ± SD). Some plots still had substantial amounts of bare soil at the end of 2013, whereas other plots were completely vegetated. Although nonconifer biomass varied substantially across the entire macro plot, no statistically significant relationships were found through our 2×2 ANOVA (Fig. 5), indicating that the experimental treatments did not explain the observed differences.

Discussion

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 postfire regeneration of ponderosa pine and Douglas-fir in low-elevation forests of the CFR and that future postfire 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 rates and percent 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 the changing climate may affect seed production. The experimental treatment in our study that is most similar to what is expected for the future in the study area is the Wm treatment, in which temperatures are elevated but the 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 that the Wm scenario most closely resembles future climate conditions based on model projections (Lukas et al. 2014; Reclamation 2013), 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 rates and percent survival may still be relatively limited, as indicated by the difference between WmWt and Co treatment types. Changes in patterns of postfire conifer regeneration in lower montane forests of the CFR have important management implications given the ecological, social, and economic benefits these forests provide (e.g., carbon storage, habitat, recreation, timber, etc.).

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 that used OTCs (Hollister and Webber 2000; Marion et al. 1997; Tercero-Bucardo et al. 2007) and is reasonable given expectations of an increase of 1.4–3.6 °C in Colorado in future years (Lukas et al. 2014; Reclamation 2013). 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 daytime and nighttime. This is a notable limitation given that warmer nighttime temperatures may have significant effects on plant growth rates and percent 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 had drier air 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 than in Co plots. Regarding soil temperatures, we observed relatively small differences in soil temperatures among treatment types, suggesting that air temperature, relative humidity, and soil moisture were more important than soil temperature in driving differences in the growth rates and percent survival of ponderosa pine and Douglas-fir seedlings.

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 generally resulted in lower average percent survival and height growth rates for both ponderosa pine and Douglas-fir seedlings, whereas increased water resulted in higher average percent survival and height growth rates for both ponderosa pine and Douglas-fir seedlings. 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 root to shoot 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 car-

Fig. 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 dots indicate any outliers. Treatment types: Wm, warmed only; WmWt, warmed and watered; Wt, watered only; Co, control.

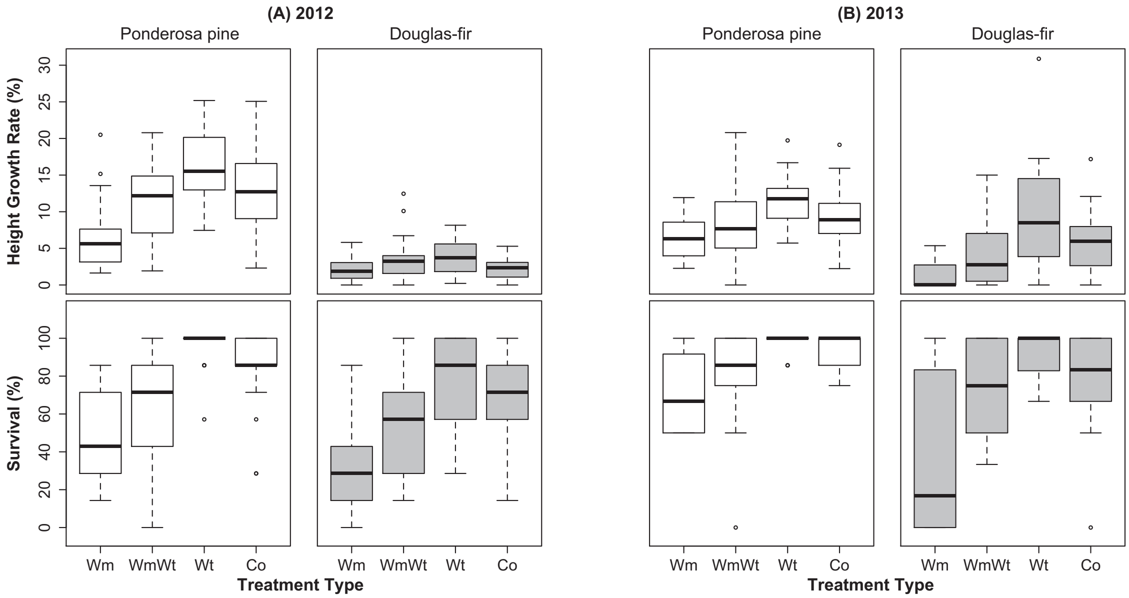


Table 3. Generalized linear models (GLMs) of height growth rate and percent survival for ponderosa pine and Douglas-fir seedlings.

	Coefficient (SE)		Odds ratio (SE)	
	Ponderosa pine growth model	ln Douglas-fir growth model	Ponderosa pine survival model	Douglas-fir survival model
Wm	–4.78 (0.95)***	–0.11 (0.18)	0.16 (0.04)***	0.16 (0.05)***
Wt	2.41 (0.97)*	0.41 (0.17)*	4.69 (2.10)**	1.77 (0.52)
Wm × Wt	–1.71 (1.11)	0.15 (0.17)	0.31 (0.09)***	0.49 (0.14)*
Year	–3.04 (0.62)***	0.81 (0.16)***	2.74 (0.49)***	2.09 (0.42)***
Constant	12.87 (0.87)	0.70 (0.13)	5.49 (1.27)	2.25 (0.52)

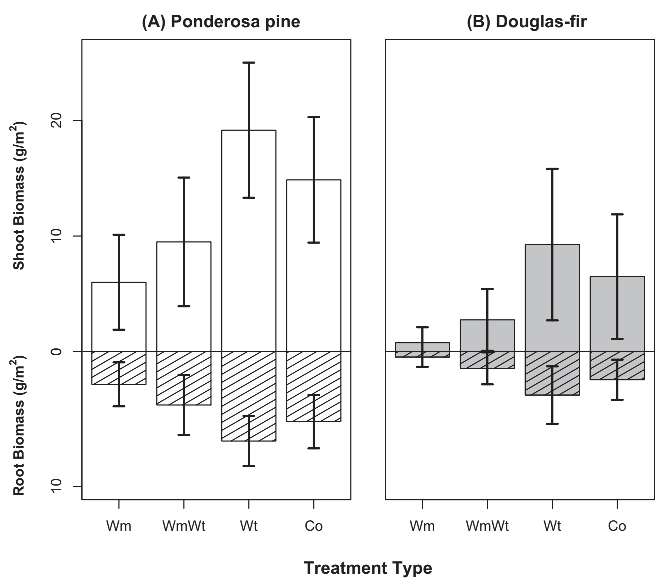
Note: Models are based on the combined dataset for both years. Standard errors (SE) are robust standard errors. Asterisks indicate statistical significance: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. Treatment types: Wm, warmed only; Wt, watered only.

bon to their roots 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 rates and percent survival for Douglas-fir was universally lower than for ponderosa pine. This finding suggests that Douglas-fir seedlings were more stressed than ponderosa pine seedlings. 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 with Douglas-fir (Kaufmann et al. 2006; Peet 1981), 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).

Nonconifer biomass

We did not observe significant differences in nonconifer biomass among treatment types, suggesting that altered temperature and water did not influence the growth rates and percent survival of forbs, grasses, and shrubs. This indicates that these understory plants were less sensitive to the experimental treat-

Fig. 4. Shoot and root biomass (g·m^{-2}) 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. Treatment types: Wm, warmed only; WmWt, warmed and watered; Wt, watered only; Co, control.



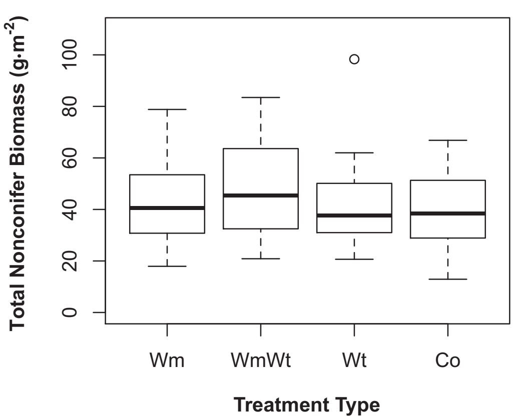
ments we implemented than the ponderosa pine and Douglas-fir seedlings and thus may be less affected by future climate change in the lower montane zone. Although there was significant variability in total nonconifer biomass among the micro plots, this variability did not correspond to differences in seedling growth rates and percent survival. We interpret this finding to indicate that competitive effects between nonconifer 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 nonconifer biomass, was the

Table 4. Ratios of root to shoot biomass by treatment type.

	Mean	Median	SD
Ponderosa pine			
Wm	0.43	0.43	0.10
WmWt	0.43	0.42	0.11
Wt	0.36	0.34	0.09
Co	0.35	0.36	0.07
Douglas-fir			
Wm	0.52	0.52	0.09
WmWt	0.46	0.45	0.08
Wt	0.38	0.36	0.10
Co	0.36	0.34	0.10

Note: Data were collected for both ponderosa pine and Douglas-fir after 2 years of experimental treatment. Results from 2x2 ANOVA indicate that root to shoot ratios differed by treatment type for both ponderosa pine ($F = 11.98$, $P < 0.001$) and Douglas-fir ($F = 16.17$, $P < 0.001$). SD, standard deviation. Treatment types: Wm, warmed only; WmWt, warmed and watered; Wt, watered only; Co, control.

Fig. 5. Total nonconifer biomass (g·m^{-2}) (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 circle indicates an outlier. Results of 2×2 ANOVA indicate that means are statistically equal. Treatment types: Wm, warmed only; WmWt, warmed and watered; Wt, watered only; Co, control.



key driver of patterns of ponderosa pine and Douglas-fir growth rates and percent survival.

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 and Schwarz 1997; Spittlehouse and 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. 2010*a*; Spittlehouse and Stewart 2003; Turner 2010), yet few studies have tested this expectation (but see Dodson and Root 2013; Feddema et al. 2013; Hogg and Schwarz 1997; Johnstone et al. 2010*b*; Landhausser and Wein 1993; Moser et al. 2010; Overpeck et al. 1990; Savage et al. 2013; Tercero-Bucardo et al. 2007). Our field experiment directly assessed how temperature and water availability influence tree seedling growth rates and percent 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 predisturbance patterns.

We demonstrated that ponderosa pine and Douglas-fir seedling growth rates and percent survival following disturbance was inhibited by warmer temperatures but that nonconifer 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 (Ehle and Baker 2003; Mast et al. 1998; Veblen and Lorenz 1986). Our findings suggest that future postfire 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 postfire 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 using prescribed burning may be appropriate. However, management strategies such as these can be expensive, time intensive, and of variable efficacy (Graham et al. 2012; Roccaforte et al. 2010) 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 postfire 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 postfire landscapes to new vegetation assemblages may be most feasible and practical at broad scales. Such largely passive response strategies may be ideal for 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 nonforest vegetation is likely to be on water quantity and quality, which should be an area of priority research (Ebel and 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 in which 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 US (Overpeck et al. 1990), the western US (Dodson and Root 2013; Feddema et al. 2013; Johnstone et al. 2010*b*; Savage et al. 2013), and portions of Canada (Hogg and Schwarz 1997; Landhausser and Wein 1993). 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 vs. areas where the persistence of alternative vegetation communities is acceptable or desired.

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