Ecological Monographs, 89(1), 2019, e01340

Origins of abrupt change? Postfire subalpine conifer regeneration declines nonlinearly with warming and drying

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Citation: W. D. Hansen, and M. G. Turner. 2019. Origins of abrupt change? Postfire subalpine conifer regeneration declines nonlinearly with warming and drying. Ecological Monographs 89(1):e01340. 10.1002/ecm.1340

Abstract. Robust tree regeneration following high-severity wildfire is key to the resilience of subalpine and boreal forests, and 21st century climate could initiate abrupt change in forests if postfire temperature and soil moisture become less suitable for tree seedling establishment. Using two widespread conifer species, lodgepole pine (*Pinus contorta* var. *latifolia*) and Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), we conducted complementary experiments to ask (1) How will projected early- to mid-21st-century warming and drying affect postfire tree seedling establishment and mortality? (2) How does early seedling growth differ between species and vary with warming and drying? With a four-year in situ seed-planting experiment and a one growing season controlled-environment experiment, we explored effects of climate on tree seedling establishment, growth, and survival and identified nonlinear responses to temperature and soil moisture. In our field experiment, warmer and drier conditions, consistent with mid-21st-century projections, led to a 92% and 76% reduction in establishment of lodgepole pine and Douglas-fir. Within three years, all seedlings that established under warmer conditions died, as might be expected at lower elevations and lower latitudes of species' ranges. Seedling establishment and mortality also varied with aspect; approximately 1.7 times more seedlings established on mesic vs. xeric aspects, and fewer seedlings died. In the controlled-environment experiment, soil temperatures were 2.0°–5.5°C cooler than the field experiment, and warming led to increased tree seedling establishment, as might be expected at upper treeline or higher latitudes. Lodgepole pine grew taller than Douglas-fir and produced more needles with warming. Douglas-fir grew longer roots relative to shoots, compared with lodgepole pine, particularly in dry soils. Differences in early growth between species may mediate climate change effects on competitive interactions, successional trajectories, and species distributions. This study demonstrates that climate following high-severity fire exerts strong control over postfire tree regeneration in subalpine conifer forests. Climate change experiments, such as those reported here, hold great potential for identifying mechanisms that could underpin fundamental ecological change in 21st-century ecosystems.

Key words: alternative states; climate change; drought; ecological experiments; forest resilience; seedling establishment; seedling growth; succession; wildfire; Yellowstone National Park.

Introduction

The resilience of forests may erode with warming and increased natural disturbance during this century, which could cause them to change fundamentally (Gauthier et al. 2015, Ghazoul et al. 2015, Reyer et al. 2015, Trumbore et al. 2015, Johnstone et al. 2016, Ghazoul and Chazdon 2017). Resilience is the capacity of a system to absorb disturbances while retaining function, structure, feedbacks, and thus, identity (Walker et al. 2006), and if resilience is lost, transitions to alternate states can occur (e.g., conversion from forest to non-forest; Scheffer 2009, Ratajczak et al. 2018). There is tremendous interest in determining how and why regional forests may change because of the consequences for carbon storage (Bonan 2008, Seidl et al. 2014), climate regulation (Thom et al. 2017*a*), biodiversity (Thom et al. 2017*b*), and provision of ecosystem services (Turner et al. 2013, Seidl et al. 2016). However, changes in regional forests will likely emerge from aggregate effects of drivers acting on local processes, such as reproduction, seedling establishment, tree growth, and mortality (Allen and Starr 1982, Filotas et al. 2014, Messier et al. 2015, Rose et al. 2017). For example, early tree regeneration is critical to ensure forest resilience following large high-severity (stand-replacing) disturbances. Thus, research identifying and characterizing mechanisms that could initiate transitions in forests to alternate states with changing climate and disturbance is essential.

Manuscript received 7 June 2018; revised 5 September 2018; accepted 19 September 2018. Corresponding Editor: Scott L. Collins.

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Following a high-severity disturbance, transition to an alternate state first requires an origin mechanism, or an ecosystem process capable of producing fundamental change in a system when it is acted upon by a forcing driver (e.g., climate; Petraities and Latham 1999, Jackson 2006). Once the origin mechanism has initiated transition to the alternate state, positive feedbacks must stabilize it (Connell and Slatyer 1976, Connell and Sousa 1983). Identifying origin mechanisms is critical, as positive feedbacks are irrelevant if transitions are not initiated. State changes in forests are often difficult to identify because mature trees are long lived and tolerate a wide range of environmental conditions (Lloret et al. 2012). However, large severe disturbances can catalyze rapid reorganization (Crausbay et al. 2017, Hansen et al. 2018). In the Alaskan boreal forest, for example, increased severity of large stand-replacing fires (i.e., where all trees are killed) has caused regional transitions in postfire tree species composition from spruce to deciduous dominance (Johnstone et al. 2010, Mann et al. 2012).

The mechanisms underpinning tree seedling establishment following large severe wildfires are especially important in subalpine and boreal conifer forests of western North America. These systems are characterized by infrequent high-severity fires (Turner and Romme 1994) and are dominated by conifers, which must reestablish from seed. Early postfire tree seedling establishment shapes stand structure and species composition for decades (Turner et al. 1997, 2004, Kashian et al. 2005), making seedling establishment a critical determinant of postfire resilience (Donato et al. 2016, Hansen et al. 2018). Historically, subalpine forests followed an adaptive cycle (sensu Gunderson and Holling 2003) where forests burned, creating favorable conditions for seedling establishment, and succession led back to structurally and functionally similar mature forest (Romme 1982, Turner et al. 1994, Holling 2001, Johnstone et al. 2004, Allen et al. 2014; Fig. 1A). However, tree seedlings are very sensitive to temperature and soil moisture (Lotan 1964, Cochran and Berntsen 1973, Rochefort et al. 1994, Walck et al. 2011, Kueppers et al. 2017) and warmer and drier conditions following fires could initiate abrupt change in subalpine forests as conditions become less suitable for tree regeneration (Johnstone et al. 2010, Landhäusser et al. 2010, Harvey et al. 2016, Martínez-Vilalta and Lloret 2016, Liang et al. 2017; Fig. 1B,C).

If tree seedlings establish, interspecific variation in early growth can determine which individuals survive and thrive (Richter et al. 2012; Fig. 1D). Differences in growth patterns among species are often consistent with broader life history strategies and generally involve tradeoffs (e.g., prioritizing belowground growth over aboveground growth) that may confer advantage to some environmental conditions, while disadvantaging seedlings in other conditions (Eskelinen and Harrison 2015). These differences will likely mediate climate change effects on competitive interactions (Kunstler et al. 2016), successional trajectories, and tree species distributions (Salguero-Gómez et al. 2016).

Experiments are a valuable tool for understanding how postfire tree regeneration may respond to climate change because they are designed to reveal mechanisms and attribute causation (Carpenter 1998, Jentsch et al. 2007, Thompson et al. 2014, Nooten and Hughes 2017). Experiments are also useful for finding thresholds where incremental changes in environmental drivers cause nonlinear system responses (Groffman et al. 2006, Kreyling et al. 2013). However, designing climate change experiments can be challenging because multiple climate variables are projected to change simultaneously, making them difficult to untangle (Kreyling and Beier 2013, De Boeck et al. 2015). Further, there are inherent tradeoffs in experimental design between treatment realism and controlling for confounding abiotic and biotic factors. Finally, climate change effects can take years to manifest (Tilman 1989) and can play out over large spatial domains (Petraities and Latham 1999). Here, we present two seed planting experiments that were designed with these challenges in mind. The experiments encompass both in situ and controlled conditions and explore the multi-year effects of projected 21st-century warming and drying on postfire regeneration of two widespread conifers, lodgepole pine (*Pinus contorta* var. *latifolia*) and Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) in Yellowstone National Park (Wyoming, USA).

Yellowstone National Park is primarily an extensive central subalpine plateau, where lodgepole pine forests have experienced large stand-replacing fires every 100 to 300 yr during the Holocene (Romme 1982, Millspaugh et al. 2000, Power et al. 2011). Historically, dense carpets of lodgepole pine seedlings established soon after fires and trees grew rapidly during early succession (Turner et al. 2004, 2016). Lower montane forests of Yellowstone are composed of drought-tolerant Douglas-fir trees, which regenerate more slowly after fire (Donato et al. 2016), trading rapid aboveground growth for investment in deep root systems (Burns and Honkala 1990). Douglas-fir trees may be well suited to shift upslope with climate change (Hansen and Phillips 2015). Spring–summer temperature in Yellowstone could warm 4.5–5.5°C by the end of this century, while precipitation amount is not projected to change (Westerling et al. 2011). As a result, moisture deficit is widely expected to increase, fostering greater fire activity (Westerling et al. 2011). Thus, the importance of postfire tree seedling establishment to continued subalpine forest resilience is likely to only grow.

Our complementary experiments addressed two questions: (1) How will projected early- to mid-21st century warming and drying affect postfire tree seedling establishment and mortality? We hypothesized that projected warming and drying would reduce postfire lodgepole pine seedling establishment and enhance establishment of Douglas-fir seedlings. (2) How does initial seedling growth differ between species and vary with warming and drying? We expected lodgepole pine to grow taller and

FIG. 1. (A) Subalpine forests of western North America generally move through four phases of the adaptive cycle (Gunderson and Holling 2003): release (occurrence of severe wildfire), reorganization (initiation of successional trajectory), exploitation (succession back to mature forest), and conservation (mature forest). (B) During the reorganization phase, tree seedlings are sensitive to temperature and soil moisture and warming, drying conditions could initiate regeneration failure, causing transitions to alternate states (pictured, experimental pots of soil in which drought treatments have been implemented). (C) However, warming can also release seedlings from cold temperature limitation and enhance establishment (pictured, tree seedlings experiencing experimental warming). (D) If seedlings establish, interspecific variation in seedling growth may determine which individuals survive and thrive under warming and drying conditions (pictured, lodgepole pine seedling).

produce more needles with warming and we expected Douglas-fir to grow longer roots in response to drying.

STUDY AREA AND METHODS

Study area

Yellowstone National Park (Fig. 2A) spans ~9,000 km^2 at the corners of Wyoming, Idaho, and Montana. Elevation ranges from 1,600 to 3,400 m, with lower tree line at 1,800 m and upper tree line at 3,050 m (Despain 1990). At low elevations, current climate is relatively warm and dry with a mean July temperature of 17.5°C and 390 mm of annual precipitation (Western Regional Climate Center 2017*a*, *b*). Sagebrush grasslands transition to Douglas-fir forests, with some pockets of trembling aspen (*Populus tremuloides*; Romme et al. 1995). Dense stands of Douglas-fir are found on

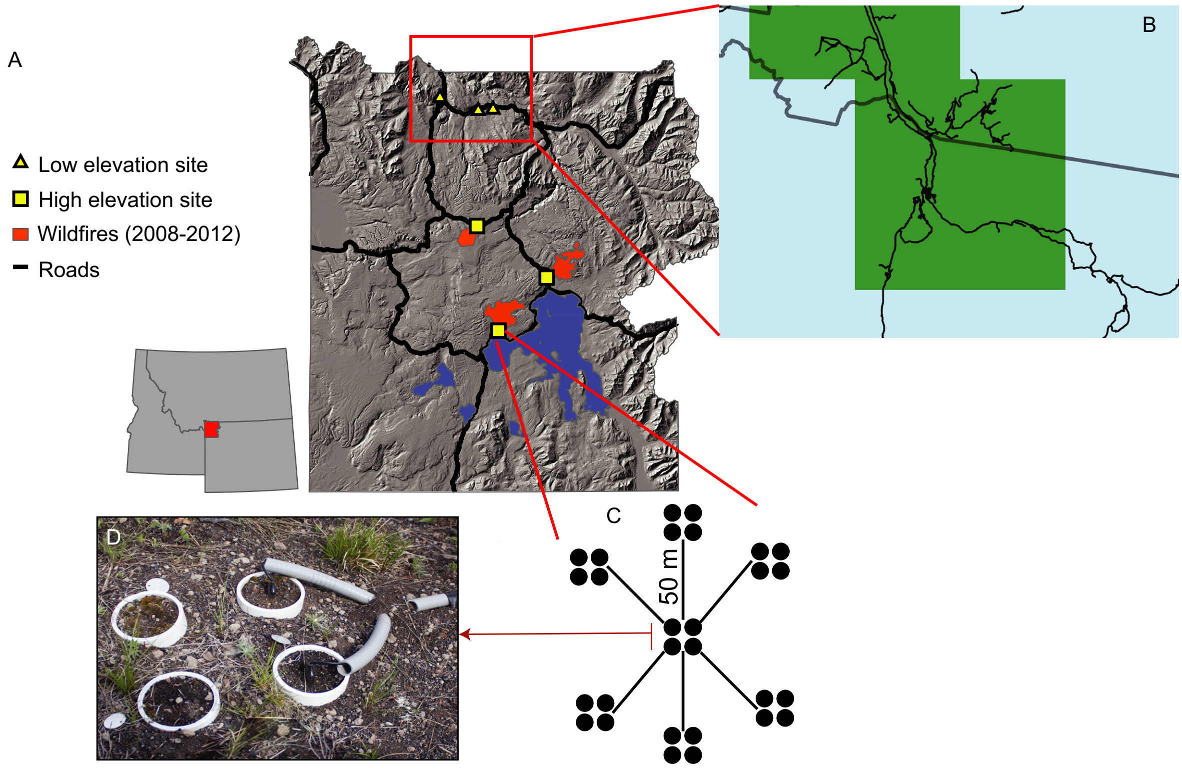

FIG. 2. (A) Map of Yellowstone National Park (Wyoming, USA) including the locations of field experiment sites. (B) Gridded climate showing the locations (green cells) in Yellowstone where recent moisture deficit (2002–2012) matches projected moisture deficit (2050–2060) in lodgepole pine forests. (C) Experimental plot layout. One plot was set up at each site in 2014 and another was set up at each site in 2015, separated from the first by >100 m. (D) A cluster of instrumented soil cores at the center of an experimental plot.

north facing mesic slopes and sparse, park-like stands occupy dry south-facing slopes (Donato et al. 2016). Climate is cooler and wetter at higher elevations on the central plateau, with a mean July temperature of 14°C and annual precipitation of 584 mm, most of which falls as snow during the winter (Western Regional Climate Center 2017*a*, *b*). Lodgepole pine trees dominate forests on the plateau. Historically, early postfire (<30-yr old) densities of lodgepole pine forests varied widely (0–555,000 stems/ha; Turner et al. 2004), determined primarily by level of prefire serotiny and fire severity (Turner et al. 1999).

Field experimental design

We conducted an in situ experiment in Yellowstone between August 2014 and August 2017 (Fig. 2). The experiment was a 2 × 2 factorial design with two climate treatments and two soil types. Climate treatments included current conditions in subalpine forests and warmer-drier conditions consistent with projected mid-21st-century climate in subalpine forests, which are found today at lower elevations. Soils vary across Yellowstone. Thus, we also used two soil types from areas that had recently burned to evaluate how differences in soils (e.g., soil texture) can mediate effects of climate on tree regeneration.

We located experimental sites representative of current subalpine climate in lodgepole pine forest (elevation = ~2,430 m) that had recently burned (between 2008 and 2012; Fig. 2A). To identify locations on the landscape where current climate is consistent with projected future conditions in the subalpine zone, we first characterized mid-21st-century climate in subalpine forests using gridded climate projections (12-km resolution) of moisture deficit (annual precipitation minus annual potential evapotranspiration) from the Fourth International Panel on Climate Change report (IPCC 2007; data *available online*).[2] We selected an ensemble product of three general circulation models (GCMs) that accurately represent historical conditions in Yellowstone, CCSM 3.0, CNRM CM3.0, and GFDL CM 2.1 (Westerling et al. 2011) forced with the A1B emissions scenario. We then calculated mean (±SD) growing season moisture deficit between 2050 and 2060 for grid cells within the current distribution of lodgepole pine. Finally, we identified grid cells at lower treeline (~2,000 m) where recent (2002–2012) moisture deficit was consistent with future projections for

[2] http://climatewizard.org/

lodgepole pine forest (Fig. 2B) and selected three experimental sites within these cells (Fig. 2A).

In summers 2014 and 2015, intact soil cores (10 cm diameter by 20 cm depth columns of soil in PVC tubes) were collected (n = 168 each summer, 336 total) from two recent fires (both burned in 2012). The first soil type was derived from rhyolite parent material and was a mixed superactive Dystric Cryochrept (hereafter, rhyolite-derived). It was collected from the Cygnet Fire (1,400 ha), which burned lodgepole pine-dominated forest. The second soil type was derived from sedimentary rocks and was a loamy-skeletal, mixed, superactive, Eutric Haplocryalf (hereafter, sedimentary-derived), which we collected from the Fontanelle Fire (19,000 ha) south of Yellowstone. Both fires were high severity and large patches burned as stand-replacing fires (i.e., all trees were killed), as is typical for forests in this region. Lodgepole pine was present before the Cygnet Fire and both lodgepole pine and Douglas-fir were present before the Fontanelle Fire. Flat soil collection sites were chosen within each fire perimeter to minimize aspect or topographic effects. At each soil collection site, two 50-m transects were established and soil cores were harvested at ~1-m increments on each side of the transect. Soil samples (10-cm depth) were also collected, sieved, and dried at 60°C for 24 h, and then were analyzed for soil texture (percent sand, silt, and clay), percent total soil N (micro Kjeldhal procedure), soil pH (measured in water), percent organic matter (determined using dry combustion), and available phosphorous (Bray P1 extract) by the University of Wisconsin Soil and Plant Analysis Laboratory, Madison, Wisconsin, USA (UWSPAL 2013). Soil cores were kept cool during transport and storage.

At each study site, one experimental plot was established in 2014 and 2015 (separated by >100 m) and 14 cores of rhyolite- and 14 cores of sedimentary-derived soils (n = 28 total) were installed by digging holes in the ground, placing soil cores (still in the PVC tubes) in the holes, and filling holes in until the upper rim of the PVC tubes were flush with surrounding soil (Fig. 2D). Cores were installed in clusters of four, with each cluster separated by 50 m (Fig. 2C). Plots were arranged in a hexagon with six clusters of soil cores on the outside surrounding a middle cluster (Fig. 2C). For each cluster, we recorded aspect (0–360°), which we later grouped into mesic (north and east directions) and xeric (south and west directions) categories. We also measured terrain shape (no slope, convex, or concave slope). Soil cores were not placed on slopes steeper than 30°. The middle cluster of soil cores was instrumented with one Decagon 5-TM volumetric soil moisture and temperature sensor Decagon, Pullman, WA, USA) in a core of each soil type and one sensor placed nearby in the surrounding soils (Fig. 2D). These sensors collected hourly data on soil surface temperature and volumetric soil moisture for the experiment duration (with some gaps due to damage by animals).

Twenty locally collected lodgepole pine or Douglas-fir seeds were planted just below the soil surface (~0.25 cm depth) to deter seed predation. Lodgepole pine seeds were collected from trees with serotinous cones at lower elevations of the species' range (~2050 m). Only cones that were >3 yr old were harvested to ensure seeds were mature. Serotinous cones were dried at 40°C for 12 h until they opened. Douglas-fir cones were collected in late August to late September from upper elevations of species' range (2,100–2,200 m). In 2014, Douglas-fir seeds were collected before cones were mature, leading to very low germination rates (<1% in the experiment). However, in 2015, Douglas-fir seed collection was more successful. Hardware mesh (0.6 cm openings) was then secured over the surface of the cores during the first season to deter granivory but still allow precipitation to fall unhindered. The mesh was removed once seedlings established so growth was not affected. During the experiment, all understory vegetation was regularly clipped around soil cores to minimize shading. At the end of each growing season (2015–2017), we measured tree seedling establishment, mortality, seedling heights, and seedling basal diameters.

To determine what percent of the collected seeds were viable under optimal conditions, we germinated seeds in the lab at 21°C in Petri dishes with filter paper kept constantly damp (Brown and Johnstone 2012). Overhead lights matched the daylength in Yellowstone during the growing season. The trials were run for one month. Lodgepole pine germination in 2014 was 43% and 62% in 2015. Douglas-fir germination in 2015 was 16%. In 2014, Douglas-fir germination was not tested due to lack of seeds (all were needed for experiment).

We also used data from nearby weather stations to better characterize differences in seasonal weather between low- and high-elevation experimental sites during the study period (2015–2017). We calculated daily growing season (May–August) air temperatures and cumulative precipitation (precipitation accumulation since 1 October of the previous year) for each year and we compared these values to the corresponding 30-yr average (1981–2010) daily growing season temperature or cumulative precipitation.

Controlled-environment experimental design

We also conducted a split-block design experiment in a controlled-environment facility at the University of Wisconsin, Madison to more precisely identify how combinations of temperature, soil moisture, and edaphic conditions affect postfire tree seedling establishment. This facility has rooms where environmental variables, including temperature and day length, can be precisely controlled at a very fine temporal grain (e.g., minutes). We replicated historical and future growing seasons (15 June 15–29 August) in Yellowstone, including three temperature treatments; a historical (1955–2005), mid-21st-century (2020–2050), and late-21st-century (2050–2080) period. Each temperature block was in a separate room and replicated three times (i.e., three rooms per temperature block, $n = 9$ rooms total). Within each replicate room, we applied five different precipitation treatments, representing wet to dry conditions. Eight 3.8 cm wide by 21 cm deep pots of rhyolite- and sedimentary-derived soils were assigned to each precipitation treatment. Pots received either 10 lodgepole pine or 10 Douglas-fir seeds. This yielded four replicate pots per temperature × precipitation × soil × tree species combination. The experiment ran for 75 days. For the first two weeks, soils were kept saturated to represent snow melt, and for the remainder of the experiment, precipitation treatments were implemented. After one month, pots from the three replicate rooms of each temperature block were consolidated into one room per temperature block, due to cost constraints.

Temperature.—Temperature treatments were developed based on gridded downscaled projections of current and future conditions from the IPCC Fifth Report (IPCC 2014). We selected the same GCMs used in the field experiment (albeit, the next generation of each model). General circulation models were forced with the representative concentration pathway 8.5 scenario, which assumes continued emissions increases through 2100 (Smith et al. 2016). General circulation models were downscaled to 6-km resolution using the Multivariate Adaptive Constructed Analogs approach (Abatzoglou and Brown 2012; data sets *available online*).[3] We selected historical and future climate data for grid cells that corresponded to our three high-elevation field experiment sites. Preliminary analysis suggested variance in temperature was orders of magnitude greater over time (i.e., year-to-year) than across space (between the three grid cells), so the three grid cells were pooled together.

For the pooled grid cells, we calculated the median daily minimum and maximum temperature between 15 June and 29 August for each period (Appendix S1). We then used linear trends fit to median minimum and maximum daily temperatures as the minimum and maximum daily temperatures for each temperature treatment. Pots of soil in the controlled-environment experiment were not insulated by surrounding soils like the soil cores in the field experiment. Thus, soil temperature more closely tracked air temperature and were on average a few degrees cooler than in the field experiment. This allowed us to quantify how warming influenced seedling establishment under relatively cool conditions, as might be experienced at the high-elevation edge of species' ranges.

Timing of daily minimum and maximum temperatures was calculated using hourly temperature data recorded at a SNOTEL weather station (Thumb Divide-816) located near our high-elevation field experiment sites between 1996 and 2015, the period for which data were available (data *available online*).[4] During the growing season, minimum and maximum daily temperatures most frequently occurred at 04:00 and 13:00, respectively. We set our minimum and maximum daily temperatures to occur at these times each day and linearly interpolated temperature between them. Day length was set using data from the Astronomical Applications Department of the U.S. Naval Observatory for West Yellowstone.

Precipitation.—The sum of growing season precipitation varied little between historical and future growing seasons in the gridded climate dataset. We set experimental precipitation treatments by calculating the median (95.7 mm), 40th (81.1 mm), 30th (76.9 mm), 20th (72.2 mm), and 10th (53.7 mm) percentile growing season precipitation totals during the historical climate period.

The number of precipitation events per growing season was determined using the instrumental record that we used for the timing of daily temperatures because precipitation was evenly distributed among days in the gridded climate data (Livneh et al. 2013). We first calculated the median number of rain events ($n = 14$) during growing seasons between 1988 and 2015. We then divided the sum of growing season precipitation by 14 and scheduled watering events to occur evenly spaced through the growing season (every 4–5 d). We multiplied the per-event precipitation amount in centimeters by the area of our pots (11.4 cm^2) to calculate how much water each pot should receive in milliliters. Each pot received 4.3 mL, 5.8 mL, 6.2 mL, 6.6 mL, or 7.8 mL of water with a pipette every four to five days.

Soils and seeds.—Rhyolite and sedimentary-derived soils were collected from the same recent fires where soil cores were taken for the field experiment. We harvested the top 20 cm of soil, passed it through a 2-mm sieve, and transported it to Madison, Wisconsin in sealed 5-gallon buckets (1 gallon = 3.79 L). Soils were kept cool until used in the experiment. The seeds used in this experiment were purchased from the U.S. Forest Service and collected in Greater Yellowstone. We selected seed stocks that were harvested at the same elevation as our low-elevation field experiment sites.

Experimental measurements.—During the experiment, soil temperature and water potential were measured in one pot per temperature × soil type combination for three of the five precipitation levels (driest, middle, wettest) every hour using Campbell Scientific 229 heat dissipation units (Logan, UT, USA). We measured soil water potential rather than volumetric soil moisture (as in the field experiment) to better characterize water balance that was physiologically meaningful to the tree seedlings. The sensors are capable of measuring soil water potential to −2 Mpa, which is lower than the threshold for lodgepole pine seedling emergence (Petrie et al. 2016). Thus, we could not characterize soil water potential for some treatments late in the experiment when water

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[3] http://climate.nkn.uidaho.edu/MACA/index.php

[4] https://www.wcc.nrcs.usda.gov/snow/

potential dropped below −2 Mpa. Every two to three weeks, we tallied seedling emergence and mortality and measured seedling heights. We defined emergence as any seedling with cotyledons that were visible above the soil and we measured it instead of establishment, because we could visit the controlled-environment facility often. At the end of the experiment, needles were counted, and root and shoot lengths were measured. Seedlings were then dried at 60°C for 24 h, and root and shoot biomass were measured.

Statistical analyses

Field experiment.—We used ANOVAs to identify factors (elevation, soil type, aspect, terrain shape, species) that influenced seedling establishment (percentage of planted seeds that established as seedlings; $n = 263$), mortality (percentage of established seedlings that died; $n = 111$), and size (height and basal diameter [mm]; $n = 61$) at the end of the experiment. Soil cores with Douglas-fir seeds from 2014 were excluded because of unsuccessful seed collection. Analyses of seedling mortality and size were conducted using high-elevation cores because all seedlings died at low elevations. The unit of analysis was the individual soil core (comparable cores were always ≥50 m apart). Establishment and mortality were logit transformed prior to analysis, and other response variables were log transformed as needed to meet analysis assumptions. For all response variables, we evaluated the need to use linear mixed effects models (LMMs) to control for experimental site and year planted (seedling cohort) as a random effect with a likelihood ratio test. All analyses were conducted with exhaustive model selection (Burnham and Anderson 2002) to identify variables with the most explanatory power. Means ± SE are presented in results. Analyses were conducted with R (R Development Core Team 2016) using the lme4 (Bates et al. 2015) and MuMIn (Barton 2016) packages.

Controlled-environment experiment.—ANOVAs were also used to determine what factors (temperature treatment, soil type, watering treatment, species, seedling density) explained seedling emergence (percentage of planted seeds that emerged as seedlings; $n = 180$), mortality ($n = 146$), height (mm; $n = 119$), needle number ($n = 119$), total biomass (mg; $n = 120$), root-to-shoot length ratios ($n = 120$), and root-to-shoot biomass ratios ($n = 120$). Here, the unit of analysis was the average response variable value across the four temperature × precipitation × soil type × tree species replicate pots. We tested whether LMMs were needed to control for experimental room as a random effect with a likelihood ratio test. Emergence and mortality were also logit transformed prior to analysis and other response variables were log transformed as needed. We again conducted exhaustive model selection.

RESULTS

Field experiment

Temperature and moisture.—Between 2015 and 2017, daily growing season air temperature at high-elevation experimental sites ranged from −2.5°C to 19°C with a median of 10.6°C (Fig. 3A). Daily growing season soil surface temperature was generally warmer than air temperature (median = 15.1°C), with a wider range (0.4°–32°C; Fig. 3B). Median daily soil surface temperature in experimental cores closely matched surrounding soils. At the low-elevation sites, daily air and soil temperature was 2°–3°C warmer than at high elevations. Median daily air temperature was 13.1°C, ranging from −0.5°C to 22°C (Fig. 3A). Daily soil surface temperature was warmer than air temperature (median = 17.2°C) and ranged from 3.8°C to 25.2°C (Fig. 3B). Median daily soil surface temperature in experimental cores was 0.5°–1°C warmer than surrounding soils. At both elevations, growing season air temperature between 2015 and 2017 was consistent with the 30-yr average (1981–2010; Fig. 3A).

Cumulative water year (1 October to 30 September) precipitation at high-elevation experimental sites was 362 mm in 2015, 419 mm in 2016, and 724 mm in 2017 (Fig. 3C). Median daily growing season volumetric soil moisture at high-elevation experimental sites was 17.7% and ranged from 5% to 36% (Fig. 3D). Median daily volumetric soil moisture in experimental cores was four percentage points wetter than surrounding soils. Low-elevation sites received less precipitation than high-elevation sites during the water year (302 mm in 2015, 263 mm in 2016, and 319 mm in 2017; Fig. 3C) and daily volumetric soil moisture was on average eight percentage points drier than at high elevations (median = 11%, range = 3–23.5%; Fig. 3D). Experimental cores were 2.5 percentage points drier than surrounding soils. Precipitation in 2015 and 2016 was consistent with 30-yr averages at both elevations. In 2017, precipitation was 85% greater than the 30-yr average at high-elevation sites and 16% greater at low-elevation sites (Fig. 3C). However, precipitation anomalies in 2017 did not produce large differences in volumetric soil moisture (Fig. 3D).

Edaphic conditions.—Rhyolite-derived soils (texture = 38% sand, 43% silt, 19% clay) were less sandy than sedimentary-derived soils (texture = 70% sand, 19% silt, 11% clay). Rhyolite-derived soils were also more acidic (soil pH = 4.8 vs. 6.4), had more total N (0.11% vs. 0.08%), and had less available phosphorous (46 vs. 144 mg/kg), potassium (210 vs. 306 mg/kg), and calcium (772 vs. 1,542 mg/kg). Rhyolite and sedimentary-derived soils were similar in organic matter (3.0% vs. 2.5%), and magnesium (170 vs. 180 mg/kg).

Topographic conditions.—At high-elevation experimental sites, approximately one-half of the soil cores were planted on xeric aspects ($n = 80$), and one-quarter were

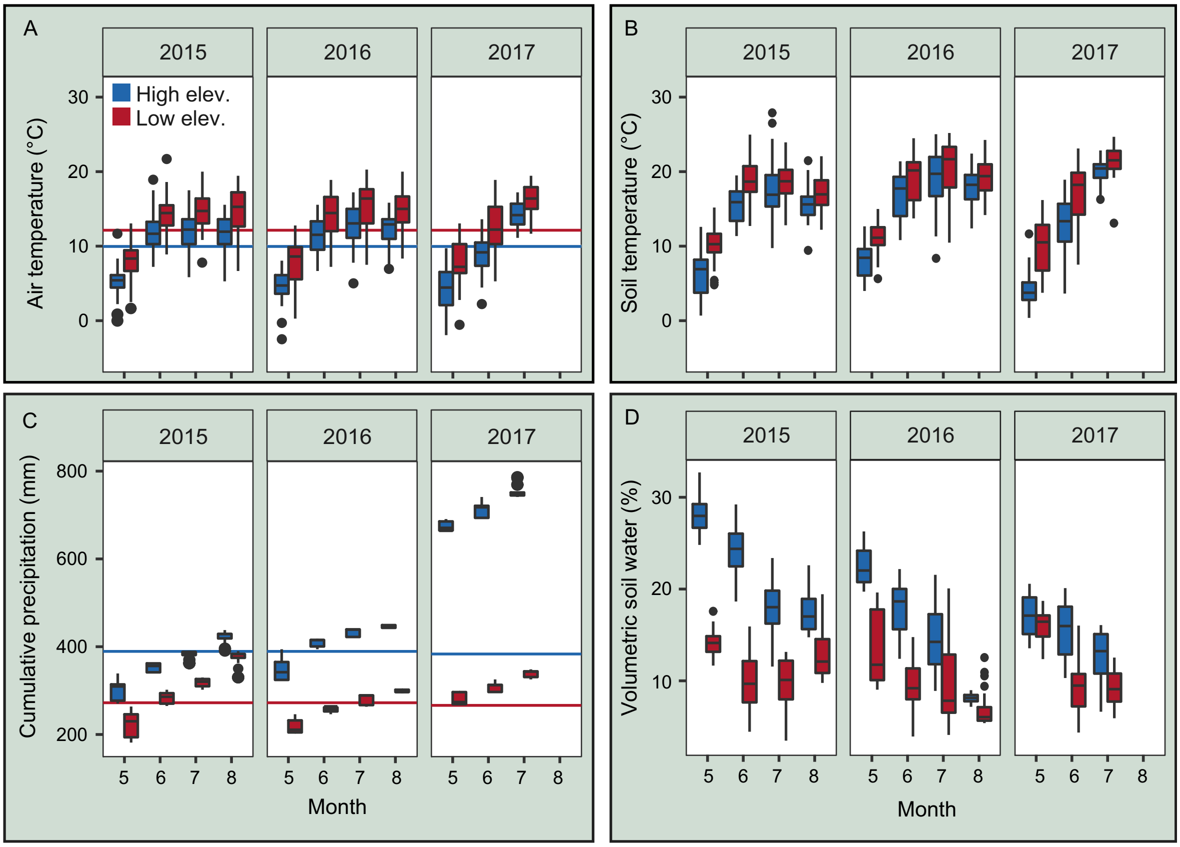

FIG. 3. (A) Daily air temperatures for each month during the growing season (May–August) from weather stations near high-elevation and low-elevation field experiment sites. The horizontal lines show 30-yr (1981–2010) average daily median growing season temperature at the high- and low-elevation weather stations. (B) Daily soil surface temperatures for each month during the growing season (May–August) at high-elevation and low-elevation field experiment sites. (C) Cumulative precipitation for each month during the growing season (May-August) recorded at weather stations near the high-elevation and low-elevation field experiment sites. The horizontal lines show thirty-year (1981–2010) average cumulative precipitation during the growing season at the high- and low-elevation weather stations. (D) Daily volumetric soil water content for each month during the growing season (May–August) at high-elevation and low-elevation field experiment sites. Values for the box plots are the median (middle line), interquartile range (box edges), observations within 1.5× the interquartile range (whiskers), and outliers (dots).

planted on mesic or flat aspects (n = 43 and 45, respectively). Of the soil cores planted on slopes, most were placed in convex positions (n = 60) and fewer were in concave positions (n = 24). At low elevations, 44% of cores were planted on flat aspects (n = 74), 29% on mesic aspects (n = 48), and the rest on xeric aspects (n = 44). Of the cores planted on slopes, one-half were located in convex positions and one-half in concave positions (n = 32 and 28, respectively).

Seedling establishment.—A total of 378 lodgepole pine seedlings (~11% of seeds) and 65 Douglas-fir seedlings (~4% of seeds) established. All seedling establishment occurred by the end of the first growing season following planting (2015 or 2016). Establishment rates in cores ranged from 0% to 55% of planted seeds. Variation in establishment was primarily explained by elevation (Table 1). On average, 12 times more lodgepole pine seedlings and 4 times more Douglas-fir seedlings established in cores at high elevations (mean lodgepole pine establishment = 19% ± 1.5%, mean Douglas-fir establishment = 5.4% ± 0.9%) compared to cores at low elevations (mean lodgepole pine establishment = 1.6%-± 0.4%, mean Douglas-fir establishment = 1.3%-± 0.5%; Fig. 4A). Lodgepole pine seedling establishment declined nonlinearly with warming temperature and reduced soil moisture; very little establishment occurred if average daily soil temperature was above 16°C (Fig. 4B) or soil moisture was below ~15%. Establishment also varied by aspect (Table 1). Fewer seedlings of both species established in cores located on flat or xeric aspects (mean establishment = 7.4% ± 1.1%) vs. mesic aspects (mean establishment = 12.4% ± 1.9%) (Fig. 5A). At low elevations, 92% of established seedlings were in cores located on mesic or flat aspects.

Seedling mortality.—By the end of the experiment, 201 (53%) of the lodgepole pine seedlings and 48 (73%) of

TABLE 1. ANOVA results for top models ($AIC_c < 2$) predicting establishment (%), mortality (%), seedling heights (mm), and basal diameters (mm) in the field experiment.

Model	Elevation	Soil type	Aspect	Terrain shape	Species	Elevation × species	Aspect × species	Terrain shape × species	Obs
Establishment									263
Model 1	220.7*** (242.6, df = 2)		6.3** (13.8, df = 2)		27.8*** (30.6, df = 1)	27.1*** (29.8, df = 1)			
Mortality									111
Model 1			4.9** (99.7, df = 2)	2.4 (49.2, df = 2)	8.0** (81.6, df = 1)		3.2* (64.8, df = 2)		
Model 2			4.8* (99.7, df = 2)	2.4 (49.2, df = 2)	7.9** (81.6, df = 1)			2.6 (52.9, df = 2)	
Model 3				4.0* (85.1, df = 2)	6.7* (71.7, df = 1)			3.6* (77.3, df = 2)	
Model 4			4.7* (99.7, df = 2)		7.7** (81.6, df = 1)		2.4 (51.7, df = 2)		
Model 5			4.7* (99.7, df = 2)	2.3 (49.2, df = 2)	7.7** (81.6, df = 1)				
Height									61
Model 1					7.3** (0.5, df = 1)				
Model 2		1.2 (0.1, df = 1)			7.8** (0.5, df = 1)				
Basal diameter									61
Model 1				2.7 (0.4, df = 2)					
Model 2			2.2 (0.4, df = 2)						
Model 3				2.9 (0.5, df = 2)	1.3 (0.1, df = 1)				
Model 4			1.9 (0.3, df = 2)	2.3 (0.4, df = 2)					
Model 5					0.9 (0.08, df = 1)				

Notes: Establishment and mortality were logit transformed. *F* values (sum of squares) and significance levels are presented. df = degrees of freedom.
$^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

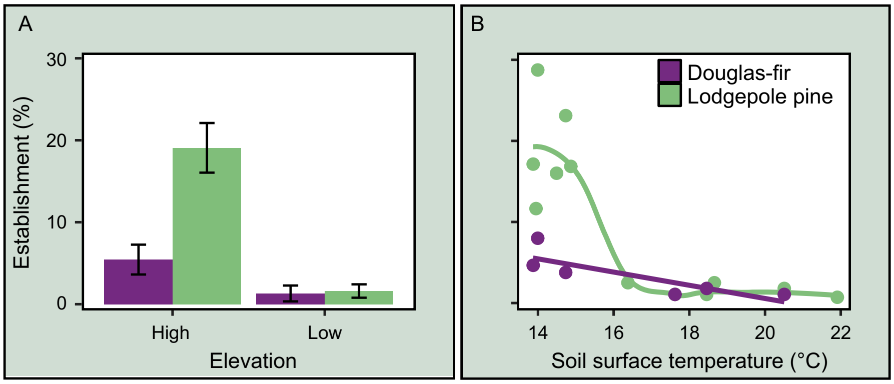

FIG. 4. (A) Establishment (%) of lodgepole pine seedlings and Douglas-fir seedlings in the field experiment as a function of elevation. Values are means ± 2SE. (B) Establishment (%) of lodgepole pine seedlings and Douglas-fir seedlings vs. site-level growing season soil surface temperature (°C) in the field experiment. Lines show a loess fit for lodgepole pine and a linear fit for Douglas-fir (for visualization purposes).

the Douglas-fir seedlings died. No low-elevation seedlings survived to the end of the experiment. However, some lodgepole pine seedlings planted on a north-facing aspect lived for three years at low elevations (Fig. 6A). At high elevations, percent mortality in cores ranged from 0% to 100% and varied primarily with species (Table 1). On average, 50% of lodgepole pine and 72% of Douglas-fir died (Fig. 6). Aspect was also influential (Table 1). High-elevation seedlings of both species were 1.75 times more likely to die in cores located on xeric or flat aspects (mean mortality = 65% ± 6%) relative to mesic aspects (mean mortality = 37% ± 7%; Fig. 5B).

Seedling size.—Where seedlings survived (at high-elevation sites), variation in height was explained only by species (Table 1). Lodgepole pine seedlings were taller than Douglas-fir seedlings (lodgepole pine mean height = 49 ± 1.3 mm, range = 19–112 mm; Douglas-fir mean height = 35.4 ± 2.9 mm, range 20–50 mm). Basal diameters did not differ by species and averaged 0.6 ± 0.4 mm (range 0.2–1.8 mm). No other variables explained variation in basal diameter (Table 1).

Controlled-environment experiment

Temperature and soil moisture.—Daily air temperature was coolest in the historical treatment, ranging from 10°C to 18°C (median = 11.5°C) and relative humidity varied between 59% and 81% (median = 74%). Temperature in the early-21st century treatment was approximately 2°C warmer than the historical treatment, with a median of 13.5°C, ranging from 9° to 20°C. Daily relative humidity varied from 42% to 77% (median = 69%). In the mid-21st century treatment, temperature was 4°C warmer than the historical (median air temperature = 15.8°C) and ranged from 13° to 23°C. Relative humidity ranged from 36% to 77% (median = 66%).

Soil surface temperature nearly matched air temperature in the controlled-environment experiment, likely because pots were narrow and not insulated from surrounding air. In the historical treatment, median soil surface temperature was 12.6°C and ranged from 10.6°C to 19.3°C. Median daily soil water potential was −0.37 Mpa and varied between −1.8 and −0.03 Mpa. In the early-21st-century treatment, soil surface temperatures were more than 2.5°C warmer than the historical treatment, with a median of 15.3°C and ranging between 13.5° and 19.3°C. However, daily soil water potential was similar to the historical treatment (median = −0.37 Mpa, range = −1.5 to −0.04 Mpa). In the mid-21st-century treatment, growing season soil surface temperature was warmer (median = 16.3°C, range = 14.3°–24.8°C). Daily soil water potential varied between −1.95 and −0.03 Mpa (median = −0.32 Mpa). Regardless of temperature treatment, soil type was a critical determinant of soil water potential. Rhyolite-derived soil was generally wetter (median = −0.31 Mpa) than sedimentary-derived soil (median = −0.49 Mpa).

Seedling emergence and mortality.—Five hundred forty-one lodgepole pine (~13% of seeds) and 366 Douglas-fir (~9% of seeds) emerged. Average percent emergence ranged from 0% to 40% among experimental replicates. Variation in emergence was primarily explained by soil type, with approximately three times more seedlings emerging in rhyolite-derived soil than sedimentary-derived soil (Table 2, Fig. 7A). Emergence also varied by species (Table 2) and was greater for lodgepole pine (mean = 12.8% ± 1.2%) than for Douglas-fir (mean = 8.7% ± 0.9%). Emergence of both lodgepole pine and Douglas-fir seedlings was also modestly enhanced in the mid-21st-century temperature treatment (Table 2, Fig. 7B), which was 2°–4°C warmer than historical and early-21st-century treatments and comparable to soil surface temperature in the high-elevation treatment of the field experiment (Fig. 3B). Watering treatment did not influence seedling emergence (Table 2).

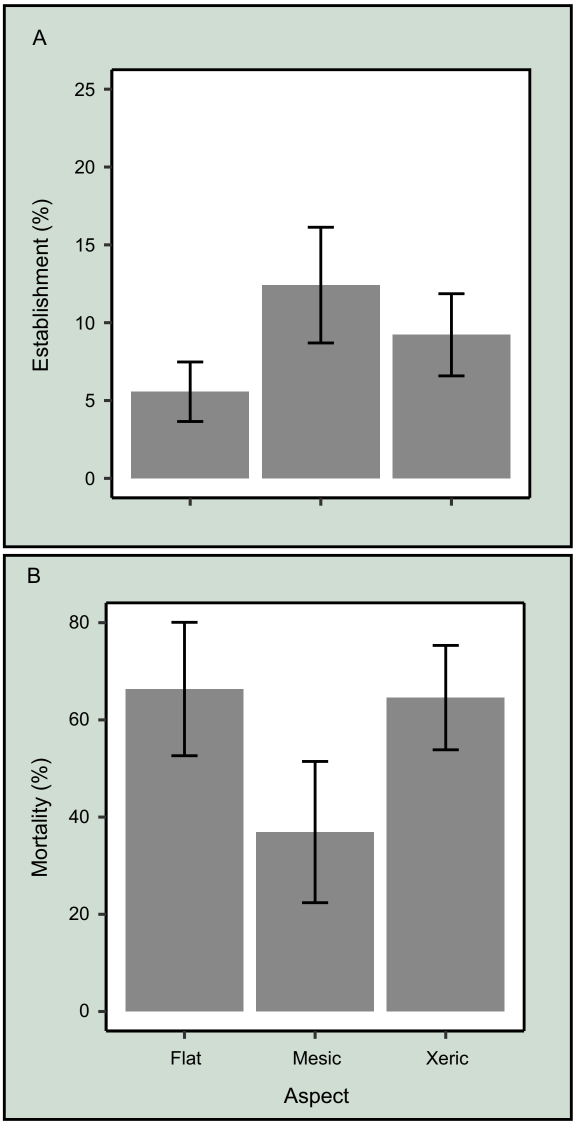

FIG. 5. (A) Establishment (%) and (B) mortality (%) of lodgepole pine and Douglas-fir seedlings in the field experiment as a function of aspect. Values are means ± 2SE.

By the end of the experiment, 182 (34%) lodgepole pine seedlings and 155 (42%) Douglas-fir seedlings died. Most variation in seedling mortality was explained by temperature treatment (Table 2). Few seedlings of both species died in the historical temperature treatment (mean mortality = 14.5% ± 2.5%), but percent mortality increased in the early-21st-century (mean mortality = 27.4%- ± 2.6%) and mid-21st-century (mean mortality = 29.7 ± 2.7%) treatments (Table 2, Fig. 7D). Mortality also varied with the density of seedlings in a pot (Table 2); greater mortality was observed in dense pots (Appendix S2). Percent mortality was similar between species (Douglas-fir mean = 26.7% ± 2.3%; lodgepole pine mean = 22.8% ± 2.2%) and did not differ with watering treatment or soil type (Table 2, Fig. 7C).

Seedling growth.—Lodgepole pine seedling height averaged 24.9 ± 0.7 mm (range = 12–45 mm) and Douglas-fir seedling height averaged 19.8 ± 0.5 mm (range = 11–28 mm) at experiment end. Variation in seedling height was largely due to species differences and the interaction of species with temperature (Table 2). Lodgepole pine seedlings grew taller in the mid-21st-century temperature treatment compared to the historical temperature treatment, whereas Douglas-fir height did not vary (Table 2, Fig. 8A).

Variation in needle number was largely explained by temperature treatment (Table 2). In the historical temperature treatment, lodgepole pine and Douglas-fir seedlings produced a similar number of needles (6.0 ± 0.4). In the mid-21st-century temperature treatment, lodgepole pine produced more needles than Douglas-fir seedlings (16.2 ± 0.9 vs. 10.9 ± 0.6; Table 2, Fig. 8B).

Total biomass ranged from 2.6–40.6 mg and did not differ by species (mean = 13.8 ± 1.1 mg) (Table 2). Total biomass increased with warming, from 7.8 ± 0.8 mg in the historical temperature treatment, to 10.6 ± 0.9 mg in the early-21st-century temperature treatment and 20.0 ± 1.1 mg in mid-21st century temperature treatment (Table 2, Fig. 8C). There was a slight effect of watering on Douglas-fir seedling biomass but not for lodgepole pine (Table 2). Total biomass also did not differ with soil type (Table 2, Fig. 8C).

Root-to-shoot biomass ratio did not differ between species (Table 2) but increased with warming, averaging 0.4 ± 0.02 in the historical temperature treatment and 0.7 ± 0.06 in the early-21st-century and mid-21st-century temperature treatments (Table 2, Fig. 8D). Root-to-shoot biomass ratio did not differ between soil types (Table 2, Fig. 8D).

Root-to-shoot length ratio differed between species and was smaller for lodgepole pine (mean = 1.6 ± 0.1) than Douglas-fir (2.1 ± 0.2; Table 2). However, most variation in root-to-shoot length ratio was explained by temperature. The ratio was close to one in the historical temperature treatment (Douglas-fir mean = 1.3 ± 0.3, lodgepole pine mean = 0.9 ± 0.2), increased modestly in the early-21st-century temperature treatment (Douglas-fir mean = 1.8 ± 0.3, lodgepole pine mean = 1.3 ± 0.2), and more than doubled in the mid-21st-century temperature treatment (Douglas-fir mean = 2.9 ± 0.3, lodgepole pine mean = 2.1 ± 0.1) (Table 2, Fig. 8E). The root-to-shoot length ratio of both species was also nearly twice as large on sedimentary vs. rhyolite-derived soil (Table 2 Fig. 8E). Watering had no effect.

DISCUSSION

These experiments provide mechanistic insights into climate change effects on postfire tree regeneration, a critical life history stage for the resilience of subalpine forests. In our field experiment, an increase of just 2°C in median daily soil temperature (from 15.1° to 17.2°C) and a seven-percentage-point decrease in median daily

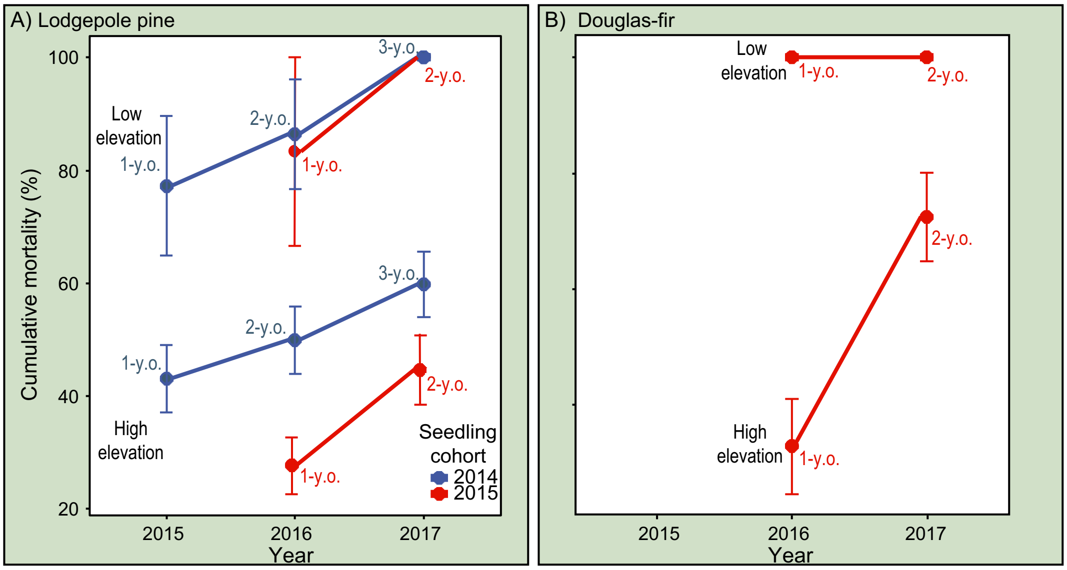

Fig. 6. Cumulative mortality (%) of (A) lodgepole pine and (B) Douglas-fir during the field experiment broken out by elevation (low or high) and seedling cohort (2014 or 2015). Values are means ± 1SE (for visualization purposes) and the age of seedlings are provided for each data point. The abbreviation "y.o." stands for "year old".

soil moisture (from 18% to 11%) caused enormous declines in seedling establishment for lodgepole pine and Douglas-fir. Further, no seedlings survived three growing seasons at experimental sites where conditions were consistent with 21st-century projections for subalpine forests. In our controlled-environment experiment, daily soil surface temperature was cooler than in the field experiment (11.5°–15.7°C), and warming led to increased tree seedling establishment, as might be expected at upper treeline. Integrating results from both experiments, the range of median daily growing season temperature in which seedling establishment occurred (approximately 5.5°C) was surprisingly narrow (Fig. 9). At the warm end, thresholds were crossed where drying reduced seedling densities nonlinearly. At the cool end, warming led to increased seedling densities. In both experiments, seedling establishment was also influenced by topo-edaphic heterogeneity, especially in soils and aspect. Clearly, climate following severe stand-replacing fire can exert strong control over a key mechanism associated with 21st-century subalpine forest resilience.

By focusing on changes in average climate conditions, we did not account for shorter-term variability or extreme events (Reichstein et al. 2013). Climate variability and extremes are expected to change during this century (Easterling et al. 2000) and could be important drivers of forest demographics, including tree regeneration (Uriarte et al. 2016). Quantifying how mean climate trends and shorter-term variability may jointly influence subalpine tree regeneration is an important research direction (Thompson et al. 2013). However, it was not logistically feasible to account for both in this study. We also did not consider effects of elevated CO_2, which could influence seedling carbon balance and ameliorate some 21st-century drought impacts. However, increased CO_2 effects on tree growth remain poorly understood (Dusenge et al. 2018) and may be less important for seedlings than mature trees (Johnson et al. 2011).

Climate thresholds of tree regeneration

We identified a threshold of average growing season (May–August) temperature (~16°C) associated with nonlinear decreases in postfire establishment of subalpine conifer seedlings. Seedling establishment and survival are colimited by cold temperature and soil moisture, which declines with hot temperatures in subalpine forests. The effects of climate change on postfire tree regeneration will thus emerge from complex tradeoffs between warming and drying at fine spatial and temporal scales (Anderson-Teixeira et al. 2013, Kroiss and HilleRisLambers 2015, Kueppers et al. 2017, Lazarus et al. 2018). Initially, tree seedlings must establish and survive with little accumulated carbon − there is small margin for error (Johnson et al. 2011). Warming can enhance carbon gain by increasing photosynthesis and reducing frost damage on leaf and root tissues (Inouye 2000, Walck et al. 2011). Conversely, drying can reduce carbon assimilation by causing stomatal closure and hydraulic failure (Moyes et al. 2013, Reinhardt et al. 2015). The relative importance of these factors may change over a single growing season. In Colorado, for example, cold temperature and soil moisture both limited carbon assimilation in limber pine seedlings, but cold temperature was important in early summer, and soil moisture was important in mid to late summer (Moyes et al. 2015).

TABLE 2. ANOVA results for top models ($AIC_c < 2$) predicting emergence (%), mortality (%), heights (mm), needle number, total biomass (mg), root-to-shoot biomass ratio, and root-to-shoot length ratio in the controlled-environment experiment.

Model	Temp. period	Soil type	Seedling density	Watering	Species	Temp. × species	Temp × soil type	Temp × seedling density	Emerg. × soil type	Seedling density × species	Species × watering	Species × soil type	Obs
Emergence													180
Model 1	9.5** (9.8, df = 2)	219.0*** (112.6, df = 1)			20.2** (10.4, df = 1)		6.1** (6.2, df = 2)						
Mortality													146
Model 1	14.5*** (60.1, df = 2)		7.5** (15.5, df = 1)		1.2 (2.6, df = 1)								
Model 2	15.0*** (60.1, df = 2)		7.7** (15.5, df = 1)	2.1 (17.1, df = 4)	1.3 (2.6, df = 1)								
Model 3	14.3*** (60.1, df = 2)		6.2* (12.9, df = 1)										
Model 4	14.6*** (60.1, df = 2)	2.6 (5.3, df = 1)	3.8 (7.8, df = 1)						4.1* (8.4, df = 1)				
Model 5	14.6*** (60.1, df = 2)		7.5** (15.5, df = 1)		1.2 (2.6, df = 1)					1.7 (3.5, df = 2)			
Model 6	14.7*** (60.1, df = 2)		7.6** (15.5, df = 1)		1.2 (2.6, df = 1			1.9 (7.6, df = 2)					
Model 7	14.8*** (60.1, df = 2)		6.4* (12.9, df = 1)	2.1 (17.1, df = 4)									
Model 8	14.6*** (60.1, df = 2)		7.5** (15.5, df = 1)		1.2 (2.6, df = 1)	1.6 (6.4, df = 2)							
Model 9	14.4*** (60.1, df = 2)		6.2* (12.9, df = 1)					1.4 (6.0, df = 2)					
Height													119
Model 1	5.2* (170.5, df = 2)	4.7* (78.0, df = 1)			43.8*** (721.7, df = 1)	5.7** (188.2, df = 2)							
Model 2	4.1 (139.5, df = 2)		4.2* (71.3, df = 1)		35.1*** (590.9, df = 1)	4.4* (147.4, df = 2)							
Needle number													119
Model 1	64.9*** (1425.3, df = 2)	5.2* (57.1, df = 1)			8.2** (89.9, df = 1)	12.4*** (271.5, df = 2)							
Model 2	64.6*** (1425.3, df = 2)		0.03 (0.3, df = 1)		10.6** (116.5, df = 1)	13.4*** (295.6, df = 2)							
Model 3	63.6*** (1425.3, df = 2)				10.3** (115.0, df = 1)	11.9*** (266.5, df = 2)							
Total biomass													120
Model 1	18.4*** (7.1, df = 2)			2.6* (2.0, df = 4)	0.3 (0.1, df = 1)						4.2** (3.2, df = 4)		
Root-to-shoot biomass													120
Model 1	24.5*** (19.8, df = 2)												
Model 2	25.8*** (20.1, df = 2)				4.3* (1.7, df = 1)								
Model 3	19.9*** (13.6, df = 2)	16.9*** (5.8, df = 1)			8.2** (2.8, df = 1)								

TABLE 2. (Continued)

Model	Temp. period	Soil type	Seedling density	Watering	Species	Temp. × species	Temp × soil type	Temp × seedling density	Emerg. × soil type	Seedling density × species	Species × watering	Species × soil type	Obs
Root-to-shoot length													119
Model 1	28.1*** (19.8, df = 2)	13.2*** (4.6, df = 1)			8.0** (2.8, df = 1)							2.7 (0.9, df = 1)	
Model 2	27.8*** (19.8, df = 2)	13.0*** (4.6, df = 1)			7.9** (2.8, df = 1)								

Notes: Establishment and mortality were logit transformed and root-to-shoot length ratio was log transformed. *F* values (sum of squares) and significance levels are presented. df = degrees of freedom.

$^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

Effects of warming and drying on establishment of individuals can also alter broader scale patterns of forest structure and tree species composition. Warming in Yellowstone since 1988 enhanced survival of aspen that had previously established from seed at elevations far above their prefire distribution (Turner et al. 2003, Hansen et al. 2016). Following the 1988 fires, postfire regeneration of lower montane Douglas-fir was also greatly reduced on south-facing slopes (Donato et al. 2016), likely because temperature and soil moisture thresholds were crossed.

Threshold responses to environmental drivers have been observed at multiple scales in forests (Lenton et al. 2008, Hirota et al. 2011, Staver et al. 2011, Scheffer et al. 2012, Savage et al. 2013, Enright et al. 2014, 2015, van Nes et al. 2018). However, nonlinear responses can be extremely difficult to anticipate before thresholds are crossed because trees are long lived, which can mask the signal of impending change (Lloret et al. 2012, Hughes et al. 2013, Connell and Ghedini 2015). In subalpine forests, reduced tree regeneration could signal slowing recovery rates after disturbance and serve as a measurable indicator of declining resilience (Dakos and Bascompte 2014, Allen et al. 2016, van de Leemput et al. 2018). However, recovery rates are system specific, and long-term studies of early post-disturbance succession under contemporary conditions are necessary to provide baselines for comparison with future recovery (Turner et al. 1997, 2004, 2016).

Warming and drying effects on early seedling growth

When seedlings survived, lodgepole pine and Douglas-fir responded to warming and drying by differentially allocating resources to roots, shoots, or needles, following patterns consistent with broader life history strategies (Franks et al. 2014, Smith et al. 2017). Seedlings generally produced more biomass and needles with warming, and root-to-shoot length ratios increased, with Douglas-fir increasing more than lodgepole pine. However, only lodgepole pine seedlings grew taller. Understanding early growth differences between and within species in response to climate change will better resolve where species may flourish or be disadvantaged, helping to identify climate mismatches, locations where climate is no longer suitable for particular species (Kerr et al. 2015, Münzbergová et al. 2017). Further, growth differences at the seedling stage can shape growth and survival during later life history stages (Tobner et al. 2013), thus, influencing population- and community-level processes (Felton and Smith 2017). For example, Douglas-fir seedlings produced longer roots than lodgepole pine in our experiments. This may allow Douglas-fir to better survive 21st-century postfire droughts in Yellowstone and promote change in relative species abundances.

Given sufficient water, lodgepole pine seedlings allocated resources to height growth and needle production with warming, helping maximize light exposure under optimal conditions. Following fire, lodgepole pine

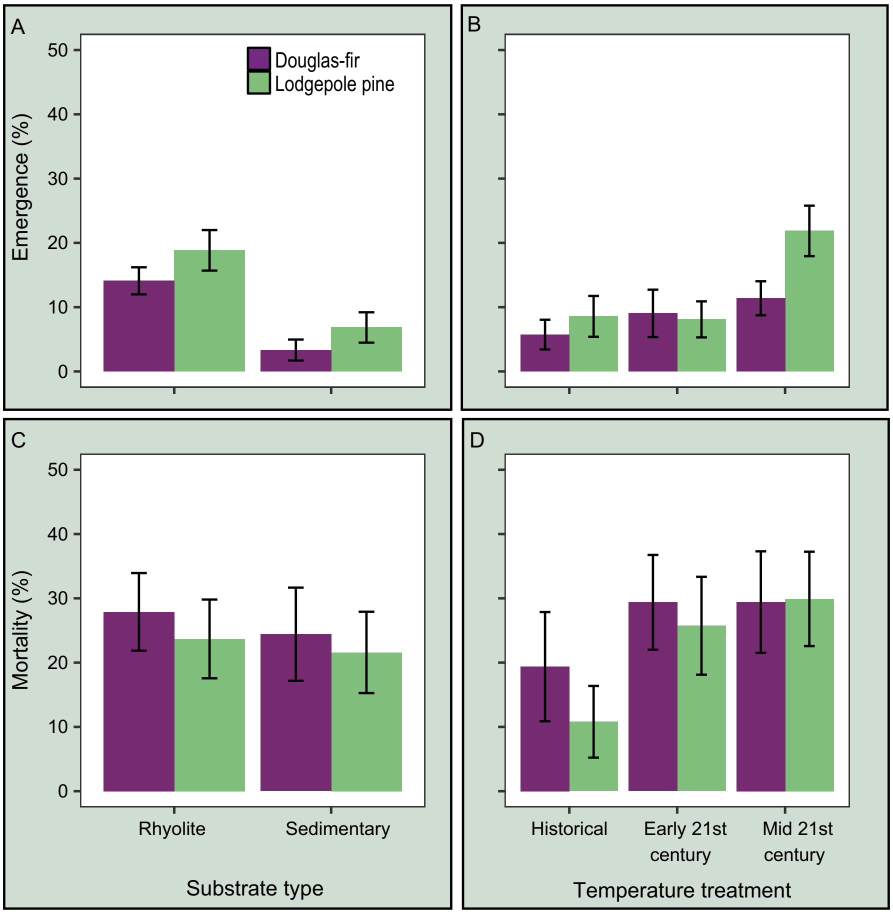

FIG. 7. Top panels show seedling emergence (%) of lodgepole pine and Douglas-fir in the controlled-environment experiment vs. (A) soil type and (B) temperature treatment. Bottom panels show seedling mortality (%) by the end of the experiment vs. (C) soil type and (D) temperature treatment. Values are means ± 2SE.

establish and grow very quickly (Turner et al. 2004), prioritizing height growth (Coates 2000). As fires become more frequent at higher elevations in Yellowstone, these traits may confer advantage to lodgepole pine over other high-elevation conifer species because lodgepole pine could rapidly colonize burns and dominate early succession (Loehle 1998, Ettinger and HilleRisLambers 2017). However, producing more needles during the seedling stage also increases transpiration demands (Moran et al. 2017) and prioritizing height growth appears to come at the expense of root length, both of which may disadvantage lodgepole pine seedlings as drought increases within their current distribution.

In contrast, Douglas-fir seedlings allocated resources to root length at the expense of height growth. Douglas-fir had larger root-to-shoot length ratios than lodgepole pine and the differences between species increased with soil drying and on sedimentary-derived soil with poor water-holding capacity. Increasing root lengths and reduced needle number could help Douglas-fir seedlings tolerate drying conditions (Olmo et al. 2014), if they can establish. Douglas-fir also produce relatively large seeds, compared to lodgepole pine, which provides seedlings with greater carbohydrate reserves (Moles and Westoby 2004, Lazarus et al. 2018).

21st-century tree regeneration and forest resilience

This study offers insights into how patterns of postfire tree regeneration may shift in subalpine forests of western North America. As climate changes in the short term, it seems likely that the importance of climate variability over space and time will grow (Fig. 9; Davis et al. 2018*a*). Tree regeneration may be increasingly limited to mesic landscape positions (e.g., underlain by soils with higher water-holding capacity, on north-facing aspects, or at higher elevations). Establishment events might also become limited to unusually cool-wet years (e.g., Urza and Sibold 2017, Andrus et al. 2018). Landscape variability in soil moisture would result in patchy forest cover and a coarsening of forest heterogeneity, with more xeric sites decreasing in stand density or transitioning to non-forest. Aspect exerted a secondary but meaningful influence on tree regeneration in our field

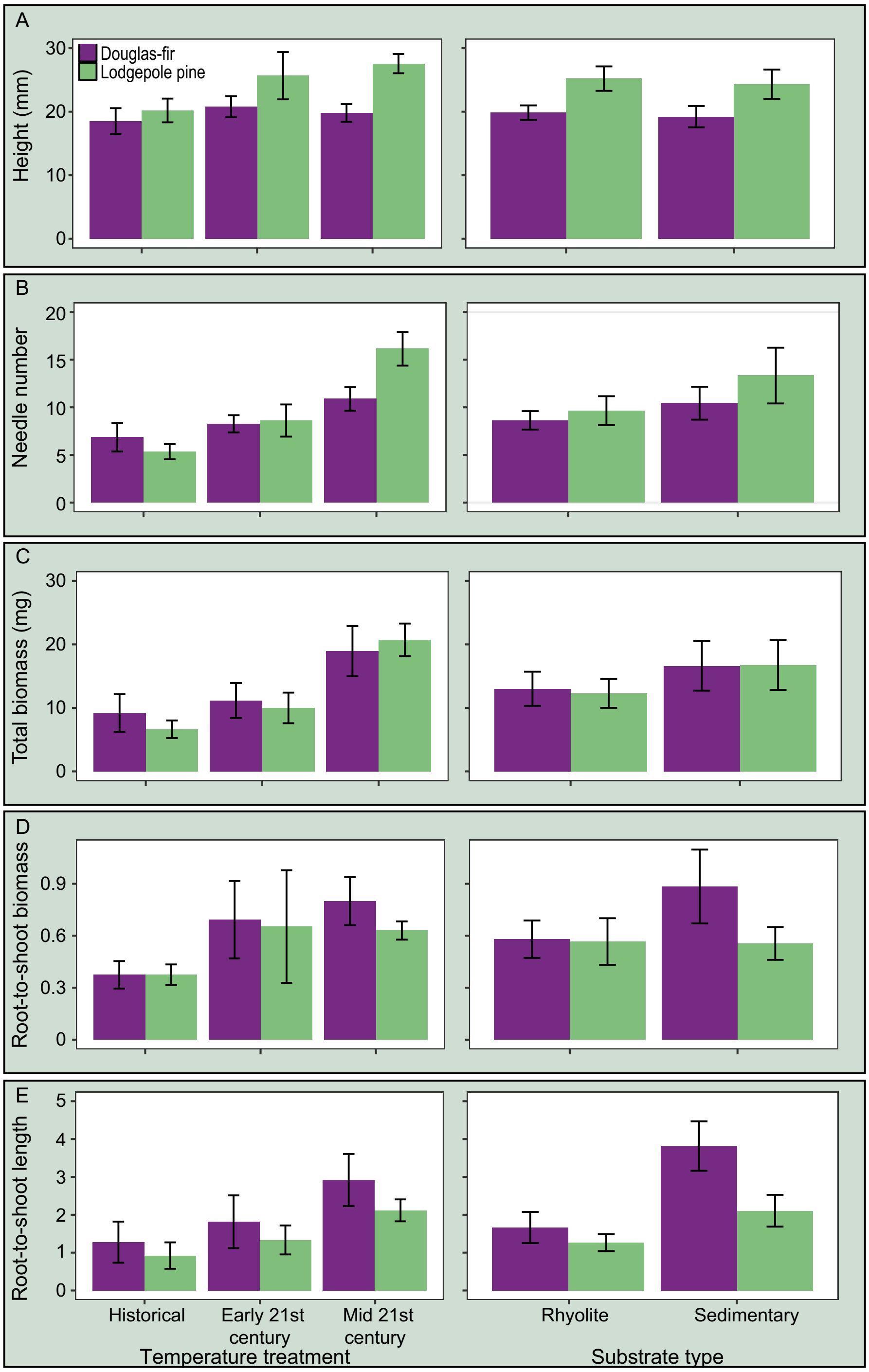

FIG. 8. Lodgepole pine and Douglas-fir (A) seedling height, (B) needle number, (C) total biomass, (D) root-to shoot biomass ratio, and (E) root-to shoot length ratio as a function of temperature treatment and soil type in the controlled-environment experiment. Values are means ± 2SE.

experiment, and soil type was the primary determinant of establishment and mortality in the controlled-environment experiment. How the spatial distribution of soil moisture will mediate effects of climate change and future postfire tree regeneration needs further investigation, and field-based experimentation is a promising approach.

In the longer term, it appears plausible that climate mismatches will occur where conditions in mid-21st-century subalpine forests become incompatible with continued postfire establishment of the current suite of conifer species (Fig. 9; Kueppers et al. 2017, Davis et al. 2018*b*, Stevens-Rumann et al. 2018). This is largely consistent with species distribution models in Yellowstone that project upslope migration of lodgepole pine and Douglas-fir and decreases in suitable habitat (Crookston et al. 2010, Coops and Waring 2011, Gray and Hamann 2013, Hansen and Phillips 2015, Piekielek et al. 2015). Our results further suggest that both species could be well suited to shift their ranges upslope, which is also supported by evidence from the fossil pollen record, particularly for Douglas-fir. During the early- to mid-Holocene, when conditions were warmer and drier than today, Douglas-fir occupied areas at higher elevations than their current distribution (Whitlock 1993). However, Douglas-fir pollen was not observed in sediment cores from lakes surrounded by rhyolite-derived soils, suggesting that edaphic conditions may have constrained the species' distribution. We found that Douglas-fir established better on rhyolite-derived soils than on sedimentary-derived soils where the species is present. Perhaps negative effects of rhyolite-derived soils on Douglas-fir manifest during later life history stages (e.g., reduced nitrogen availability). Other factors, such as competition with lodgepole pine, dispersal limitations, and seed predation, could also influence longer-term persistence of Douglas-fir on rhyolite-derived soils in Yellowstone. To understand how Douglas-fir distributions may shift with climate change, it will be critical to determine what mediates Douglas-fir persistence and growth.

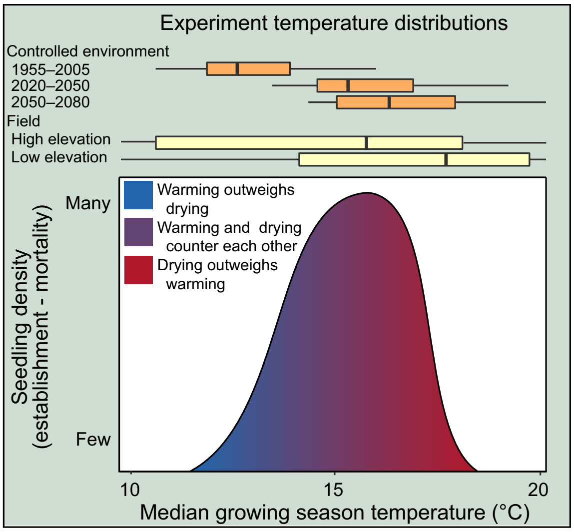

FIG. 9. The range of growing season temperatures in which lodgepole pine and Douglas-fir seedling establishment occurs in Yellowstone. In the blue zone warming temperatures cause increased seedling density. In the purple zone warming and drying counter one another and secondary variables such as aspect are particularly important determinants of seedling density. In the red zone, drying outweighs warming and seedling density declines quickly. Above, the temperature distributions from the field and controlled environment (CE) experiments are provided for context.

CONCLUSION

Warming and drying trends are projected to continue over coming decades and may initiate abrupt change in forests following disturbances (Williams et al. 2013, Clark et al. 2016). We found the range of median daily growing season temperature in which seedling establishment occurs (approximately 5.5°C) was surprisingly narrow. At the warm end, thresholds were crossed where drying reduced seedling densities nonlinearly. At the cool end, warming led to increased seedling densities. Our approach demonstrates the value of experiments for identifying mechanisms that could cause ecosystems to change fundamentally. Further, the results illustrate how climate change in this century could severely constrain tree seedling establishment, growth, and survival following stand-replacing fires in subalpine forests of western North America.

ACKNOWLEDGMENTS

W. D. Hansen and M. G. Turner designed the study, W. D. Hansen conducted the study and analyzed the data, and W. D. Hansen and M. G. Turner wrote the manuscript. This research was conducted under permits from Yellowstone National Park under permit numbers (YELL-2014-SCI-5238, YELL-2015-SCI-5238, YELL-2016-SCI-5238, and YELL-2017-SCI-5238). We thank William Romme for help designing the study. We acknowledge Stephen Carpenter, Kate McCulloh, Kristin Braziunas, Tyler Hoecker, and two anonymous reviewers for valuable comments on earlier drafts of this paper. We acknowledge Stacey Sigler, Sarah Haas, and Roy Renkin at Yellowstone National Park; Eric Winter, Rob Hoelscher, and Don Dranendonk from the Bridger Teton National Forest; and Bjorn Karlsson and Jacob Schoville at the UW-Madison Biotron for logistical support. Field and greenhouse assistance was provided by Tim Whitby, Catherine Frock, Kari Forseth, Aisha Ba, Matthew Norman, Kristin Braziunas, Ryan Fitzsimmons, Ann Olsson, and Tyler Hoecker. Funding for this research was provided by an NSF GRFP (DGE-1242789), and NSF DDIG (DEB-1600716) to W. D. Hansen, the Joint Fire Science Program (16-3-01-4), and the University of Wisconsin-Madison Vilas Research Trust.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecm.1340/full

Data Availability

Data available from the EDI Data Portal: controlled-environment experiment data https://doi.org/10.6073/pasta/0fdb3ec8957f2a68575c32afc87be03d; field experiment data https://doi.org/10.6073/pasta/87228301512ef3007ba3daff8d002e23.