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Article *in* Ecological Applications · August 2022

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ARTICLE TITLE:	Forest restoration treatments increased growth and did not change survival of ponderosa pines in severe drought, Arizona
ARTICLE AUTHOR:	Fulé, Peter Z
VOLUME:	Ahead of Print
ISSUE:	
MONTH:	
YEAR:	2022
PAGES:	Ahead of Print
ISSN:	1051-0761
OCLC #:	

Processed by RapidX: 8/8/2022 5:28:22 PM

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Forest restoration treatments increased growth and did not change survival of ponderosa pines in severe drought, Arizona

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Open Research:

Tree data (Moore, et al. 2021) are available in the USDA Forest Service Research Data Archive at https://doi.org/10.2737/RDS-2021-0079. Tree-ring data are available in the International Tree-Ring Databank (ITRDB) at https://www.ncei.noaa.gov/access/paleo-search/study/36579.

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1002/eap.2717

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Abstract

We report on survival and growth of ponderosa pines (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) two decades after forest restoration treatments in the G. A. Pearson Natural Area, northern Arizona. Despite protection from harvest that conserved old trees, a dense forest susceptible to uncharacteristically severe disturbance had developed during more than a century of exclusion of the previous frequent surface-fire regime that ceased upon Euro-American settlement circa 1876. Trees were thinned in 1993 to emulate pre-fire-exclusion forest conditions, accumulated forest floor was removed, and surface fire was re-introduced at 4-year intervals (full restoration). There was also a partial restoration treatment consisting of thinning alone. Compared to untreated controls, mortality of old trees (mean age 243 yr, max 462 yr) differed by < 1 tree ha^{-1} and old tree survival was statistically indistinguishable between treatments (90.5% control, 92.3% full, 82.6% partial). Post-treatment growth as measured by basal area increment of both old (pre-1876) and young (post-1876) pines was significantly higher in both treatments than counterpart control trees for more than two decades following thinning. Drought meeting the definition of megadrought affected the region almost all the time since the onset of the experiment, including three severe dry years. Growth of all trees declined in the three driest years but old and young treated trees had significantly less decline. Association of tree growth with temperature (negative correlation) and precipitation (positive correlation) was much weaker in treated trees, indicating that they may experience less growth decline from warmer, drier conditions predicted in future decades. Overall, tree responses after the first two decades following treatment suggest that forest restoration treatments have led to substantial, sustained improvement in the growth of old and young ponderosa pines without affecting old tree survival, thereby improving resilience to warming climate.

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Keywords

Pinus ponderosa, ecological restoration, dendrochronology, Pearson Natural Area, Arizona

Introduction

Large-scale tree decline and mortality is a hallmark of warming climate worldwide (Allen et al. 2015). The multi-decadal megadrought currently impacting southwestern North America (Williams et al. 2021) is implicated in increasing tree mortality (Breshears et al. 2005, van Mantgem et al. 2009, Ganey et al. 2021). Reduced growth and decreased capacity for post-drought recovery constrain the resources needed for trees to produce defensive chemicals against herbivory (Kolb et al. 2016). Slowing growth is a strong predictor of impending tree mortality in angiosperms (Ireland et al. 2014, Rodríguez-Catón et al. 2019) and conifers (Ogle et al. 2000, Camarero et al. 2015). Old trees, typically the longest-lived and largest organisms in the forest ecosystem, are particularly at risk (Lindenmayer 2017). Old trees generally have substantial biomass, carbon storage and wildlife habitat value, contain valuable scientific information such as long-term genetic variability and tree-ring records, and have aesthetic value and cultural importance for people (Kolb et al. 2007). Past practices of heavy exploitation of timber resources removed the majority of old trees over vast areas (Covington et al. 1994). Contemporary forests are dense and dominated by abundant young trees, so old trees can suffer disproportionately from competition (Biondi 1996) and are highly vulnerable to severe wildfire due to dense ladder fuels and high canopy bulk density (Fulé et al. 2012). Drought and severe wildfires threaten forest sustainability, especially at the warmer, drier edges of species´ distributions (Camarero et al. 2013, Parks et al. 2019).

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Ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson), with two recognized varieties (*scopulorum* and *ponderosa*), has the most widespread distribution of any North American conifer, ranging from the US-Mexico border into southwestern Canada in pure and mixed-conifer stands. Prior to abrupt cessation of the frequent, predominantly surface-fire regime associated with Euro-American settlement in the second half of the 19th century (Fulé et al. 1997), ponderosa forests were relatively open and dominated by patchy groups of large, old trees that reached several hundred years in age (White et al. 1985); the oldest on record exceeded 900 years[1]. Contemporary forests typically have dense contiguous stands that support severe, stand-replacing wildfires (Singleton et al. 2019, Coop et al. 2020) exacerbated by increasingly arid climate (Mueller et al. 2020). Ponderosa pines are well-adapted to drought and fire intensities short of crown fire behavior (Stevens et al. 2020), but the small number of remaining old trees growing in dense conditions suffer disproportionately from competition with younger trees (Biondi 1996) and from pathogens (Negrón et al. 2009, Aflitto et al. 2015).

Ecological restoration and related treatments are designed to reduce forest vulnerability to disturbance from fire and pathogens (Allen et al. 2002, Stephens et al. 2012) and have been widely tested over the range of ponderosa pine and associated species (e.g., *Pseudotsuga menziesii*, *Pinus jeffreyi*). Treatments typically include retention of old trees, thinning of young trees, and reintroduction of surface fire through prescribed burning (Fulé et al. 2012). Restoration of key characteristics of the pre-fire-exclusion ecosystem has been a specific goal in southwestern USA ponderosa forests (Covington and Moore 1994), where treatments have included removal of accumulated forest floor fuels prior to burning (Covington et al. 1997),

[1] OLDLIST, http://www.rmtrr.org/oldlist.htm, visited 22 April 2020.

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attention to spatial pattern of retained trees (Sánchez Meador et al. 2009), and understory community reestablishment (Laughlin et al. 2017).

Old ponderosa pine trees have shown positive short-term responses to restoration treatments, such as rapid significant increases of resin flow (related to bark beetle defense), foliar nitrogen content, and foliar toughness (foliovore defense) in the first two years post-treatment (Covington et al. 1997, Feeney et al. 1998). Skov et al. (2005) found no significant increase in old tree radial growth in the first three years following treatment, perhaps due to a lag in the ability of trees to allocate new resources to radial growth (Latham and Tappeiner 2002). However, decadal-scale studies at an intensively measured study site (Kolb et al. 2007) as well as at the landscape scale (Erickson and Waring 2013) showed significant and sustained post-treatment growth increases in trees averaging over 200 years in age. Similar results were reported in central Oregon by McDowell et al. (2003) and for old ponderosa and Jeffrey pines in northern California by Hood et al. (2018a). Crown dieback was also reduced in old trees post-treatment compared to controls (Kolb et al. 2007). Drought reduced old tree growth in Arizona, but trees in treated forests declined less and recovered more quickly than trees in controls (Kolb et al. 2007).

Warming climate and concurrent drying were less well appreciated at the onset of forest treatments aimed explicitly at ecological restoration in the 1980s and 1990s, when ecological restoration principles were focused on historical reference conditions to guide interventions (Society for Ecological Restoration 2002). Profound drought conditions and associated tree death in the southwestern U.S. since the mid-1990s (Breshears et al. 2018), coupled with better understanding of historical drought (Steiger et al. 2019) and the implications of future climate projections on native forests (Williams et al. 2012, Yazzie et al. 2019) have drawn attention to

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the interaction of treatments and climate. We took advantage of the longest-standing intensively measured forest restoration study site in the southwestern U.S., at the G.A. Pearson Natural Area (hereafter "Pearson Natural Area") in Arizona, to investigate long-term impacts of restoration treatments on both young and old ponderosa pine trees during an ongoing megadrought. The site has a high density of old trees (Avery et al. 1976). Young trees were thinned in 1992-93 and prescribed fire was applied on a 4-year cycle in half of the thinned area beginning in 1994 (Covington et al. 1997). Prescribed fires were carried out in autumn, a standard practice in the region, resulting in low burn severity (Covington et al. 1997).

Using tree measurements and tree-ring data from 1992-2016 (25 years), we address research questions centered on survival of old trees, tree growth changes in the treated sites affecting old and young trees, and climate-growth interactions. Our hypotheses were H_1: Survival of old trees would be higher in treated areas than control areas. H_2: Tree growth would respond positively to thinning, with younger trees growing relatively faster than older trees. H_3: Drought would reduce tree growth, but both old and young treated trees would experience less drought impact on growth than control trees. H4: fine-scale (monthly) influence of climatic factors would be attenuated for treated trees.

Methods

Study Area. The study area is located in the Fort Valley Experimental Forest, the oldest such forest in the USDA Forest Service system, within the G.A. Pearson Natural Area (GPNA), located approximately 10 km northwest of Flagstaff, Arizona. The area comprises approximately 4.3-ha, of which the southern two-thirds were decommissioned from Natural Area status in 1988 to permit tree cutting due to concern about the high fuel hazard threatening historic Forest

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Service buildings. The decommissioned area became the site for the ecological restoration treatments with an adjacent portion of the Natural Area serving as the control. Fifteen ≈ 0.28-ha plots were established and assigned to three treatments: control, thinning restoration, and composite restoration. The control plots with no treatments remained in the designated Natural Area, forming a contiguous portion of the study (shaded grey in the northwestern portion of the study area map, Figure 1). The area for treatments (colored in Figure 1), comprising the southern to eastern portion of the site, was officially decommissioned from Natural Area designation. The ten treatment plots were randomly assigned to Full or Partial restoration treatments. Two areas at the southwestern and eastern edges of the site were excluded from the experiment (Figure 1).

The study site is approximately 2200 m in elevation, with flat to gently rolling topography. Soils are derived from Tertiary basalt flows and cinders, and are classified as a Brolliar stony clay loam, and a complex of fine, smectitic Typic Argiborolls and Mollic Eutroboralfs (National Cooperative Soil Survey 2006). The average annual temperature is 7.8 °C and average annual precipitation is approximately 540 mm, with a bimodal distribution in winter and summer (monsoon) (Flagstaff Airport weather station, 1950-2016). Ponderosa pine (*Pinus ponderosa* Laws.) forms a monospecific, uneven-aged forest (White 1985). A few large trees were selectively harvested from GPNA in 1894 but then the area was set aside as a control site since the early days of the Fort Valley Experimental Forest and was considered “virgin forest” (Avery et al. 1976). The frequent surface fire regime ended in 1876 (Dieterich 1976), followed by massive pine regeneration in 1914 and especially 1919 (Savage et al. 1996) that grew into a dense midstory.

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Forest Restoration Experiment. The forest restoration experiment was described in detail by Covington et al. (1997) and other authors (e.g., Kaye et al. 2005, Laughlin et al. 2017); it is summarized here. As stated above, the 4.3 ha study site was divided three 1.4-ha areas and then further subdivided into 15 0.28-ha plots (N = 5 per treatment). All trees above 1.37 m in height were stem-mapped and measured for condition and diameter at breast height (DBH, 1.37 m) in 1992. Treatments were carried out in the decommissioned area and the experimental control was the adjacent portion of the Natural Area. Treatments were "full" and "partial" restoration. Both treatments had the same guidelines for trees: all old trees were retained. Old trees were those present prior to the exclusion of fire after 1876 and were provisionally defined in the field as those having DBH $\geq$ 37.5 cm and/or yellowed bark, a sign of age (White 1985). Tree ages were confirmed with tree-ring sampling (Mast et al. 1997). Most young trees were thinned in 1993, with a small percentage retained near places where evidence of formerly living trees such as snags, logs, or stumps were present. In the full restoration treatment, accumulated forest floor material was removed by hand. Litter and mown native grasses were scattered back over the forest floor to emulate a natural fuelbed for the first fire only. The full treatment was burned with a prescribed surface fire using strip headfires under cool autumn conditions in 1994 and every 4 four years thereafter: 1998, 2002, 2006, 2010, and 2014. The 4-year fire interval is an average of pre-fire-exclusion fire frequencies from the northern Arizona region (Baisan and Swetnam 1990, Fulé et al. 1997). The use of relatively cool fires in autumn differs from pre-1876 patterns but the season and intensity had to be controlled in practical terms as the study area is adjacent to buildings, dense forest, and a highway. The partial treatment had no further intervention after the 1993 tree thinning.

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Tree-ring Data. Condition (living, declining, or several dead categories) and DBH were remeasured in 2004 and again in 2014-2015 for all old trees. In addition, all younger trees in the Full and Partial treatments were remeasured as well as a 6.7% random subsample of younger trees in the Control. In the autumn of 2016 after the growing season had ended, short increment cores intended to capture the past 40-50 years of growth were collected from the measured trees; all cored trees were living in 2016. Full-length cores had been previously collected in 1992 to determine age (Mast et al. 1997). Cores were glued to wooden mounts and surfaced so that cells were clearly visible under magnification. Tree rings were crossdated with ponderosa pine tree-ring chronology AZ521 (Graybill 1987) and our unpublished chronologies. Ring widths were measured and crossdating was checked for possible errors with the COFECHA program (Holmes 1983). Ring widths were converted to annual basal area increment (BAI) by calculating inside-bark diameter (Laughlin et al. 2011) and then subtracting annual growth from the measured tree diameters using the baiout function in R package dplR (Bunn 2008, 2010).

Climate data

Climate data in the form of monthly temperature and precipitation were obtained from the Flagstaff Airport weather station (NOAA ID USW00003103) for the years 1950-2016. The weather station is at 2135 m elevation and is located approximately 23 km SE of the study site (Figure 2).

Analysis

We addressed hypothesis H_1, that survival of old trees would be higher in treated areas than control areas, by checking the condition of the original 146 pre-1876 trees that were alive in

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the three treatments in the initial 1992 measurement at the start of the experiment (Mast et al. 1997). We calculated survival (%) of old trees on each of the N = 15 plots and tested the effect of treatment on survival with one-way ANOVA in R, checking that ANOVA assumptions were met.

We tested H_2, that tree growth would respond positively to thinning, with younger trees growing relatively faster than older trees, by fitting linear mixed effects models to samples from each age category (old and young) using the lmer function in the lme4 package (Bates et al. 2015) in R (The R Foundation for Statistical Computing, v. 4.0.4). We analyzed changes in individual tree BAI, or tree growth, measured using increment cores collected at breast height. Growth was modelled as a function of the following fixed effects: a three-level treatment factor, year, treatment-by-year interaction, and a pre-treatment covariate (i.e., pre-treatment DBH; to account for potential pre-existing differences). Autocorrelation of repeated measurements was accounted for by estimating random intercepts for each tree, while allowing responses for each tree to have varying slopes with respect to time. Quantifying the random variation among trees was undertaken to better understand the nature of responses to restoration treatments (Munson et al. 2015; Laughlin et al. 2017). To this end, we computed the marginal R^2 (hereafter, R_m^2, the proportion of variance explained by the fixed effects) and the conditional R^2 (hereafter, R_c^2, the proportion of variance explained by both fixed and random effects) using the r.squaredGLMM function in the MuMIn package in R (Nakagawa & Schielzeth 2013; Barton 2015).

We tested H_3, that drought would reduce tree growth, but both old and young treated trees would experience less drought impact on growth than control trees, by comparing mean BAI reduction in the three driest years of the post-treatment record: 1996, 2000, and 2002. Numerous authors have developed indices or models of tree-ring drought response based on

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multiple-year data (e.g., Lloret et al. 2011, Sangüesa-Barreda et al. 2015, Peltier and Ogle 2019). Even when modeling takes lagging drought effects into account (Peltier and Ogle 2019), there are limitations to pre/post-drought methods associated with the number of years chosen for comparison (Schwarz et al. 2020, Ovenden et al. 2021). In the present case, a full assessment of drought impact is particularly complicated by the fact that the study has been in drought essentially since the experiment was initiated (treatments 1993-94, drought initiated 1995-96) and two of the three driest years, 2000 and 2002, are within two years of each other. Therefore, we constrained the analysis to comparing BAI from the pre-drought year to the drought year by calculating Drought Reduction (DR) = $(BAI_{dr} – BAI_{dr-1})/BAI_{dr-1}$. We tested for statistically significant differences in DR by treatment and old/young category in each drought year with Analysis of Variance (ANOVA) in R. We checked diagnostic plots of residuals and normal distribution of the data to be sure that ANOVA assumptions were met. Post-hoc testing of differences in DR between treatments and categories was done with Tukey´s Honest Significant Difference test.

Finally, we tested H_4, that fine-scale (monthly) influence of climatic factors would be attenuated for treated trees by correlating monthly climate values with BAI of old and young trees in each of the three treatments. BAI values from 1983-2016, as described above, were converted to dimensionless indices by fitting a horizontal line through the mean and averaging the values using the R package dplR (Bunn 2008). This procedure creates deviations from the overall mean without any detrending. Correlations of the six BAI chronologies with monthly precipitation and temperature data were done with the R package treeclim (V. 2.0.5.1, Zang and Biondi 2020, https://github.com/cszang/treeclim). Statistical significance of the Pearson's

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correlation coefficient was assessed with 1000 bootstrapped samples taken from the original distributions of climate and BAI data.

Results

Ecological restoration treatments caused major changes in forest structure following thinning of young trees in 1993. Thinning removed an average of 2226 trees ha^{-1} and basal area declined nearly by half (Fig. 3). Subsequent measurements showed relatively stable density and gradual basal area increase in the two treatments. By the end of the study period (2014-2015), the Control averaged 2941 trees ha^{-1} and 46.7 m^2 ha^{-1}, the Partial averaged 165 trees ha^{-1} and 19.7 m^2 ha^{-1}, and the Full averaged 175 trees ha^{-1} and 21.9 m^2 ha^{-1}. The control displayed substantial mortality, primarily of young trees, approximately 1000 trees ha^{-1} by 2014-2015, while basal area continued to increase (Fig. 3).

Survival of old trees was not different in treated areas compared to the control (90.5% control, 92.3% full, 82.6% partial; $F = 0.56$, $P = 0.59$), contradicting H_1. Of a total of 146 living old trees (mean age 245 years) at the beginning of the experiment in 1992, a total of 16 (10.9%) had died by 2016 (Table 1). Mortality was numerically approximately equally distributed temporally between the first and second decade following the initial treatments and among the three treatments (6 trees died in the control, 5 in each of the treatments). On a percentage basis, however, mortality was 65% higher in the partial treatment (15.2%) than the control (9.2%), with the full treatment intermediate (10.4%) (Table 1).

Growth of young and old treated trees was significantly higher than that of their counterparts in the control, supporting H_2, despite the region entering into extended drought essentially concurrent with the start of the experiment (Fig. 4). Both old and young tree

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categories of treated trees displayed high and sustained growth in the first two decades following treatment. Sharp declines occurred in the severe drought years but BAI growth remained higher than that of control trees and rapidly returned to the pre-drought trajectory. In the most recent decade (2007-2016) after the most severe drought years had passed, control old tree BAI averaged 12.0 $cm^2\ yr^{-1}$, 36% less than for old trees in the full (18.8 $cm^2\ yr^-1$) and 49% less than the partial (23.6 $cm^2\ yr^{-1}$) treatments. The difference was much greater for young trees: controls averaged 2.6 $cm^2\ yr^{-1}$, 83% less than trees in the full (15.3 $cm^2\ yr^-1$) and 86% less than the partial (18.2 $cm^2\ yr^{-1}$) treatments. Fixed effects (treatment, time, and pre-treatment covariate) explained about a third of the variation in BAI growth, and random tree effects accounted for just over two-thirds the total variation (R_m^2 = 0.30, R_c^2 = 0.67) in old trees while fixed effects and random tree effects accounted for almost 60% and 80% of the variation, respectively, (R_m^2 = 0.59, R_c^2 = 0.78) observed in young trees.

Growth reductions in both old and young trees in the control were significantly greater than those of treated trees in all three of the most severe drought years (Fig 5), supporting H_3. The greatest year-to-year declines in BAI growth were in old trees in the control, dropping by 60%, 42%, and 98% in 1996, 2000, and 2002, respectively. Corresponding values for old trees in the full treatment were 37%, 41%, and 83%, and for old trees in the partial treatment they were 37%, 31%, and 77% (Fig. 5). In 2002, 46 out of the 51 old control trees (90%) had absent rings, meaning zero BAI growth. In comparison, 51% of old trees in the full treatment and 26% of old trees in the partial treatment had absent rings in 2002. Growth declines in younger trees were similar to older ones in their respective treatments except in 1996, when younger treated trees had significantly less decline (Fig 5).

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Fine-scale climatic variables of precipitation and temperature (H_4) were significantly correlated with old and young tree BAI growth in numerous months (Fig. 6). Precipitation was always positively correlated with BAI and temperature was always negatively correlated, except for one case each of the opposite correlation. Growth of control trees was more than three times as often strongly correlated to climate compared to treated trees. From a total of 36 possibly significant correlations between climate and growth for the months of previous October to current July, there were 15 significant correlations for old and young control trees, vs. 4 (plus 1 opposite correlation) for the full treatment and 3 (plus 1 opposite) for the partial treatment. The most notable seasonal grouping of climate effects was the negative effect of temperature on control trees, old and young, in May-July of the current year (Fig. 5). Significant correlations for the treated trees were more common for old than for young trees, but there were only 1-3 months that were linked to climate for old treated trees for precipitation or temperature, in contrast to 4-6 months for old control trees.

Discussion

The unique opportunity to study restoration in the setting of multi-century-old ponderosa trees in the Pearson Natural Area has been of high scientific value (Covington et al. 1997, Kaye et al. 2005, Kolb et al. 2007, Laughlin et al. 2017). This experiment is a case study from within the subcontinental range of ponderosa pine, but numerous other southwestern studies provide useful points of comparison, as described in detail below. Across the broader range of ponderosa pine in North America, findings from the Pearson Natural Area experiment are broadly consistent with studies farther north (e.g., Keeling and Sala 2012, Tepley et al. 2020), albeit with regional differences.

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The effects of forest restoration treatments were positive on tree growth according to the objectives of restoration and did not negatively affect old-tree survival in the first two decades following treatment, despite entering into an extended warm drought with climate-change-type characteristics. Pre-existing differences provide an important context to consider at the outset. The control treatment had higher tree density and lower BAI growth than the two thinning treatments prior to the experiment, although initial BA and age distributions were nearly identical (Fig. 3, 4, Table 1). These differences may be an artifact of the constraint that the treated areas were a contiguous block decommissioned from the southern end of the Natural Area, meaning that random assignment of treatments was only possible for the thinned areas while the control had to be the adjacent forest that remained in Natural Area status.

A separate distinction related to treatment design likely explains the higher BAI growth of young trees in the thinned areas prior to treatment, shown in Fig. 4c. The thinning treatments removed an average of 2,226 trees ha^{-1}, all of which were in the young category (Covington et al. 1997). The retained young trees in the thinned treatments were selected based on spatial proximity to evidence of past tree structures in the forest (Covington et al. 1997). Of the young trees potentially suitable for retention, those of larger size and seemingly good condition for survival and growth based on attributes such as a relatively full crown and vertical stature were selected for retention. These trees likely had better BAI growth on average than the control young trees which included a random assortment of trees growing in the dense forest, including highly suppressed and snow bent individuals.

Survival of old trees was not statistically distinguishable among treatments, contradicting our first hypothesis. Mortality was equally distributed over time and differed by only one tree per treatment (Table 1), so there is not a strong basis for drawing conclusions about differences

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between treatments. It should also be noted that due to the limitations of the initial experimental design - the need to protect the historic Fort Valley Experimental Forest headquarters - our findings regarding mortality may have been consequently hindered (i.e,, non-independence of replicates and small sample sizes, a limitation common in ecological work) and may not represent conditions elsewhere. However, one clear early indicator is that the prescribed burning initiated in 1994 and repeated every 4 years in the full treatment did not lead to a pulse in mortality. Fire can lead to tree death through numerous pathways, including soil, root, and cambial heating (Hood et al. 2018b). High cambial temperatures associated with lengthy smoldering of deep forest floor material likely contributed to high mortality at the Chimney Spring research site, approximately 3 km from our study area with similar forest characteristics (Sackett et al. 1996). Those observations led to recommendations for manual fuel reduction prior to fire re-introduction in our experiment, where raking reduced accumulated duff from an average of 8.4 cm to 1.0 cm before burning (Covington et al. 1997). High mortality associated with forest floor burning has not been detected consistently in studies on other ponderosa pines in Arizona (Fowler et al. 2010, Fulé et al. 2002, 2007) or elsewhere (Hood et al. 2018b), but given the high density of old, large pines at the Pearson Natural Area, the fuel removal was judged worthwhile (Covington et al. 1997). The cumulative mortality data in the first two decades following treatment suggest that neither the initial prescribed burn nor the five subsequent ones in the full treatment led to old tree death.

Overall, old-tree mortality in this experiment was substantially less than at a larger-scale, long-term experimental ponderosa forest restoration experiment carried out at Mt Trumbull in northwestern Arizona (Roccaforte et al. 2010). Mortality of old trees in the current experiment averaged 11% two decades after the initial measurement, with 16 trees dying out of 146 total

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(Table 1). At Mt Trumbull, old-tree mortality averaged 27% by 21 years post-treatment, with 39 old trees dying out of 147 total (Control 22%, Full 31%; unpublished data, J.P. Roccaforte and others). The slightly lower elevation of the Mt Trumbull forest (range 2000–2250 m vs. 2200 m in the current study) and relatively severe fire effects in parts of the initial prescribed burns following thinning (Fulé et al. 2002) may be factors contributing to the higher mortality rate.

Growth data supported our remaining hypotheses of increased growth, less growth decline during severe drought, and attenuated influence of fine-scale climate factors on treated trees. The rapid post-thinning growth responses of old trees averaging close to 250 years old in this experiment was reported shortly after treatment by Feeney et al. (1998) and Stone et al. (1999), who linked growth with higher (less negative) predawn water potential, leaf nitrogen content, and increased stomatal conductance and net photosynthetic rate. Wallin et al. (2004) showed that the treatment-induced ecophysiological changes persisted seven years after treatment. The present study shows that growth differences were strongly sustained into the second post-treatment decade with old trees in the partial treatment averaging nearly double the annual BAI of those in the control (Fig. 4). Young trees also had quick, positive responses to thinning which were consistent with ecophysiological attributes (Skov et al. 2004, 2005). Over the most recent decade, the present study shows that BAI growth differences among young trees were closer to an order of magnitude greater in the treatments vs. the control, with young trees moving closer in absolute growth to old trees: the combined average for young trees in the full and partial treatments for 2007-2016 was a BAI = 16.8 cm^2 yr^{-1} compared with an average BAI = 21.2 cm^2 yr^{-1} for old trees in these treatments. Our experiment did not have a “burn-only” treatment, but a repeated burning experiment was installed nearby at Chimney Spring in the Fort Valley Experimental Forest in 1976 (Sackett et al. 1996). Forest growth was statistically

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indistinguishable between controls vs. plots burned at fire rotations of 1 to 10 years (Peterson et al. 1994). The difference between the burn-only treatment and the treatments in the present experiment are the effects of tree thinning: basal area was substantially reduced by thinning in the present experiment, but the low-intensity surface fires caused no significant reduction of basal area in the Chimney Spring experiment (Peterson et al. 1994).

Despite entering into "climate-change-type" drought—that is, severe drought accompanied by unusually warm temperatures (Breshears et al. 2005, Williams et al. 2021)—both old and young trees in the treatments had significantly less growth reduction in the three driest years than their counterparts in the control. Trees in thinned treatments frequently display improved drought response, consistent with reduced competition for belowground resources and improved water relations and photosynthetic capability compared with dense stands (Feeney et at. 1998, McDowell et al. 2007). The current study lengthens the timeframe of growth responses, showing that trees approaching 500 years of age are capable of extended growth increases following thinning treatments, even after documented declines due to inter-cohort competition with younger trees (Biondi 1996). The young trees in this study, most of them originating in 1914 or 1919 (Savage et al. 1996), have rapidly developed a sustained pattern of high growth nearly an order of magnitude greater than their control counterparts.

High growth and attenuated drought impact support the utility of restoration treatments from a carbon (C) dynamics perspective. James et al. (2018) found that the majority of forest restoration treatments across western North America reported reduced C storage following thinning and prescribed burning, adding that most information was from short-term studies (< 25 years). In these treatments, C reduction is the intended result given the excess of C accumulated through fire regime disruption, compared to reference conditions (Hurteau and Brooks 2011). In

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a ponderosa forest near the present study site, Hurteau et al. (2010) estimated that untreated forests had 2.3 times as much live tree carbon compared to the same sites prior to fire exclusion. The improved growth (C sequestration) and increased size (C storage) per tree after treatment is at less risk of catastrophic loss because of improved tree defenses (Wallin et al. 2004) and greater resilience to severe fire (Fulé et al. 2012) and climate warming (this study). Associated ecosystem benefits include understory community recovery (Laughlin et al. 2017), and, at broader scales, wildlife habitat and watershed properties (O´Donnell et al. 2018). The present study also reports findings < 25 years after treatment but the stable trajectories of growth after 21 years (Fig. 4) suggest that the trends will continue.

The dependence of growth on climate (temperature and precipitation) was strikingly weaker for treated trees of both old and young categories (Fig. 6). Typically, such relationships are relatively stable for centuries over broad spatial scales (e.g., Touchan et al. 2017). We are not aware of a comparable finding in which the positive and negative links between climate variables and tree growth were rapidly altered by forest treatments. The decoupling of temperature and precipitation from tree growth suggests that trees in the treated areas will be less negatively affected by warming temperatures and drier conditions predicted in the coming decades (Anderegg et al. 2019). Reductions of forest density close to historic, pre-fire-exclusion densities have been suggested to enhance resilience not only in terms of reducing vulnerability to wildfire but also favoring robust growth of individual trees (North et al. 2022).

Indicators of difference between full and partial treatments are suggested in the trend toward higher growth of old and young trees in the partial treatment (Fig. 4) and less growth reduction during drought in this treatment as well (Fig. 5). There was no difference between these treatments in terms of the selection of residual trees (Covington et al. 1997) and little

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structural difference between them over time (Fig. 3). The growth differences were generally relatively small and not statistically significant but the trends were consistent. We speculate that while fire treatments have not led to increased mortality, they may contribute to modest growth reductions through various mechanisms of injury (Hood et al. 2018). Burning may impose other financial and social costs such as fire crew expenses, smoke, and risk of escaped fire. However, burning may also bring about benefits such as higher plant diversity (Laughlin et al. 2017), higher nutrient cycling (Covington and Sacket 1992), and maintaining open forest structure in the future by controlling tree regeneration (Hurteau et al. 2014).

The tree responses after the first two decades following treatment are broadly consistent with the objectives of restoration and suggest that these treatments at the Pearson Natural Area have led to substantial, sustained improvement in the growth of old and young ponderosa pines. Treated trees are relatively less impacted by severe drought and less linked to climate controls, implying better performance under continuing warming trends as compared to untreated forests. These results are consistent with findings across a broad southwestern network (Stoddard et al. 2021) and with simulated performance of similar forests under future climate scenarios (Bagdon et al. 2016, O´Donnell et al. 2018). The fact that fire treatments appear not to have increased mortality is also beneficial given extensive calls for re-introduction of surface fire regimes (e.g., Stephens et al. 2019). Warning signs for the future appear in the data, however. Individual mortality of old trees is consequential at about 11% over 21 years, and treatments have not shown a protective effect against it, although the risk of mass mortality from wildfire is substantially lower in treated stands (Fulé et al. 2012) and bark beetle mortality risk is also much lower (Fettig et al. 2007). On the other hand, the rapid growth of young treated trees indicates the development of a new cohort of large trees to replace dying ancient trees. The trend toward

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higher growth performance (albeit lower survival) in the partial vs. the full treatment may imply some negative effects of burning on average growth. Finally, despite strong confirmation that restoration treatments are far superior to no-action in terms of improving future forest adaptation to warming climate, bioclimatic niche estimates (Rehfeldt et al. 2020), simulation studies (Yazzie et al. 2019), and trait-based modeling (Laughlin et al. 2012) indicate that warming may result in severe declines in ponderosa pine in the region during this century.

Acknowledgements

We thank the Ecological Restoration Institute at Northern Arizona University (NAU), especially S. Curran and J. Crouse for database management. Thanks to the USDA Forest Service Coconino National Forest, especially for assistance with prescribed burns. We thank W.K. Moser and C. Edminster with the Rocky Mountain Research Station (RMRS), Fort Valley Experimental Forest, for continued collaboration and use of this experimental site. Funding was provided by a National Science Foundation grant (DEB-9322706), NAU Ecological Restoration Institute and USDA McIntire-Stennis appropriations to the NAU School of Forestry. Funding for remeasurement and analysis in 2004 was provided by the USDA Forest Service (#03-22 DG-11031600-088), and in 2015 was provided by the DOA/DOI Joint Fire Science Program to M. Moore and others (as RMRS Joint Venture agreements #15-JV-11221633-176 and 15-JV-11221633-179). Funding for analysis and writing was provided to P. Fulé in part by a Fulbright Scholar grant through the Moroccan-American Commission for Educational & Cultural Exchange (MACECE) in 2021.

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Table 1. Old tree survival from the initiation of the experiment in 1992 to 2016 (25 years) in the Fort Valley Experimental Forest, northern Arizona. Ages are age at coring height (≈ 45 cm) in 2016. No old trees died between 2014-2015 and 2016.

Treatment	# Living trees in 1992	# Dead by 2004	# Dead by 2014-2015	Mortality (%)	Age (mean, range) (years)	Age dead trees (mean)
Control	65	3	3	9.2%	232.9 (145-462)	367.5
Full	48	2	3	10.4%	250.4 (139-437)	253.8
Partial	33	3	2	15.2%	264.4 (144-447)	313.4
Total/Average	146	8	8	10.9%	245.2 (139-462)	307.6

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Figure Captions

Figure 1: Study area in the Fort Valley Experimental Forest, northern Arizona. Maps (a & b) and repeat photographs (c-f) depicting forest conditions prior (a & c; 1992), during (d & e), and for contemporary dates (b & f; 2014-2015) for the ecological restoration experimental treatments. Note the two old trees present in each photo of the repeat photography series. Photograph credits: c) 1992: J.P. Roccaforte; d) 1994: J.P. Roccaforte; e) 2004: Ecological Restoration Institute; f) 2015: Ecological Restoration Institute.

Figure 2. Mean annual temperature (top) and precipitation (bottom) from the Flagstaff, Arizona Airport weather station, 1950-2016.

Figure 3. Changes in forest structure (all trees > 0.1 cm DBH) over time in the ecological restoration experimental treatments in the Fort Valley Experimental Forest, northern Arizona. Tree thinning was carried out in 1992-93. Error bars are standard error of the mean.

Figure 4. (a) Precipitation anomalies (overall mean 540 mm; represented by deviation from baseline of 0 mm) from 1980-2016 show dominance of drought during the experimental period, post-1992. (b) Annual mean basal area increment (cm^2 yr^{-1}) by treatment of old trees present prior to fire exclusion *circa* 1876. (c) Annual mean basal area increment (cm^2 yr^{-1}) by treatment of young trees. Error bars are standard error of the mean.

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Figure 5. Drought reduction of growth (calculated as basal area increment change in dry year as a fraction of pre-drought year for the three driest years during the study period—see text for details) for old and young trees in the three treatments, Control, Full, and Partial restoration. Error bars are standard errors of the means. Lower-case letters indicate statistically significant differences among treatments within dry years. Asterisks indicate statistically significant differences between age categories within dry years.

Figure 6. Statistically significant Pearson´s correlation coefficients of monthly precipitation and temperature values with six BAI chronologies for old and young trees in the three treatments, Control, Full, and Partial restoration. Months noted in capital letters (e.g., JUN) are from the year prior to the BAI value, while months noted in mixed letters (e.g., Jun) are from the current year of the BAI value. Positive correlations are indicated by solid blue color, negative by brown color.

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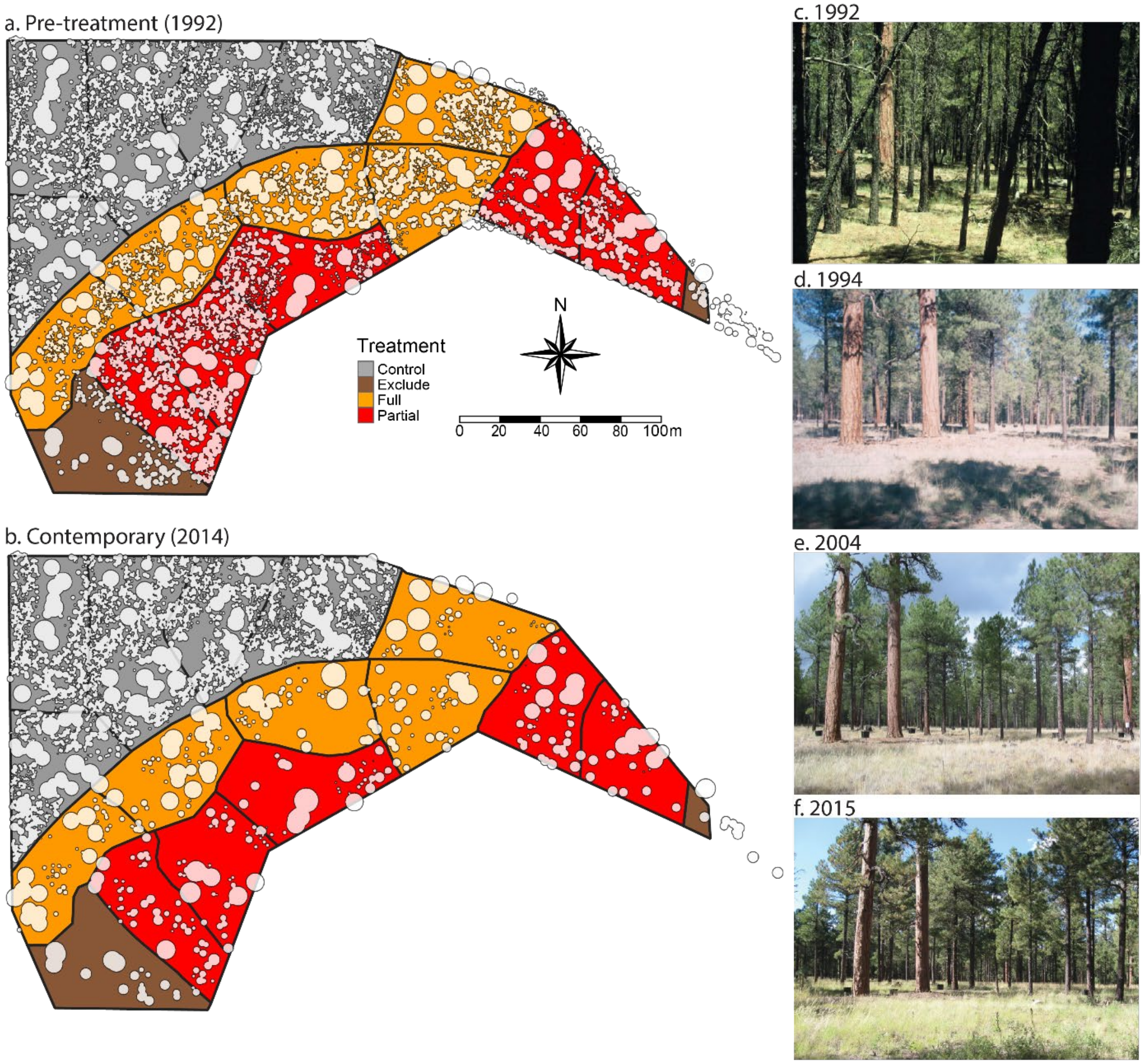

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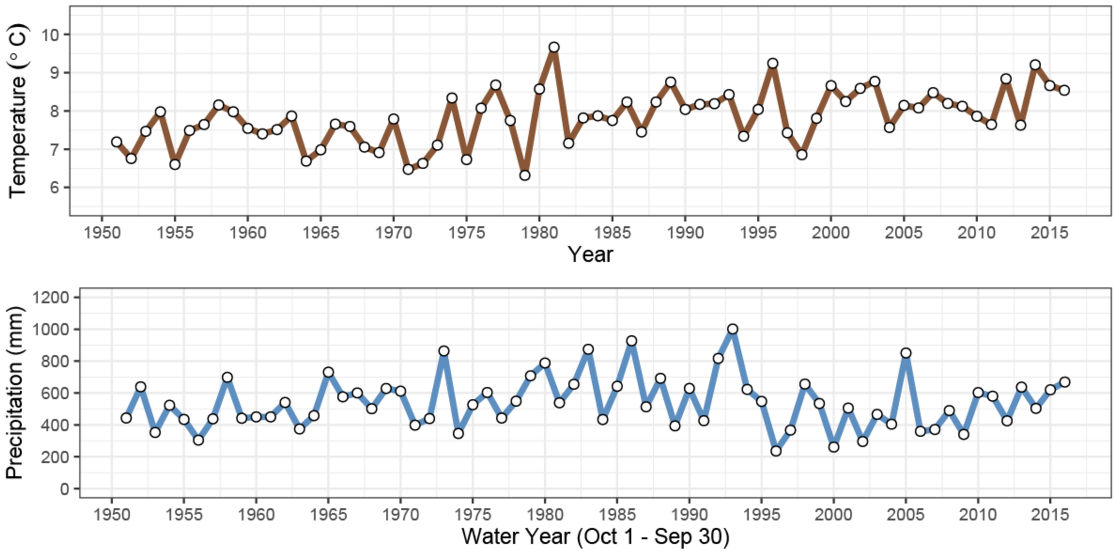

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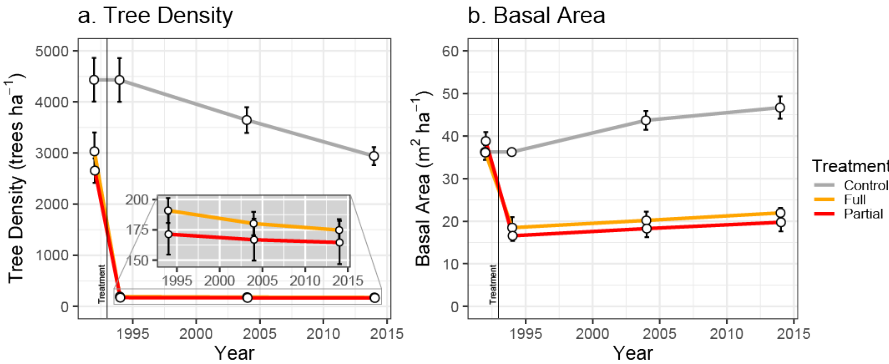

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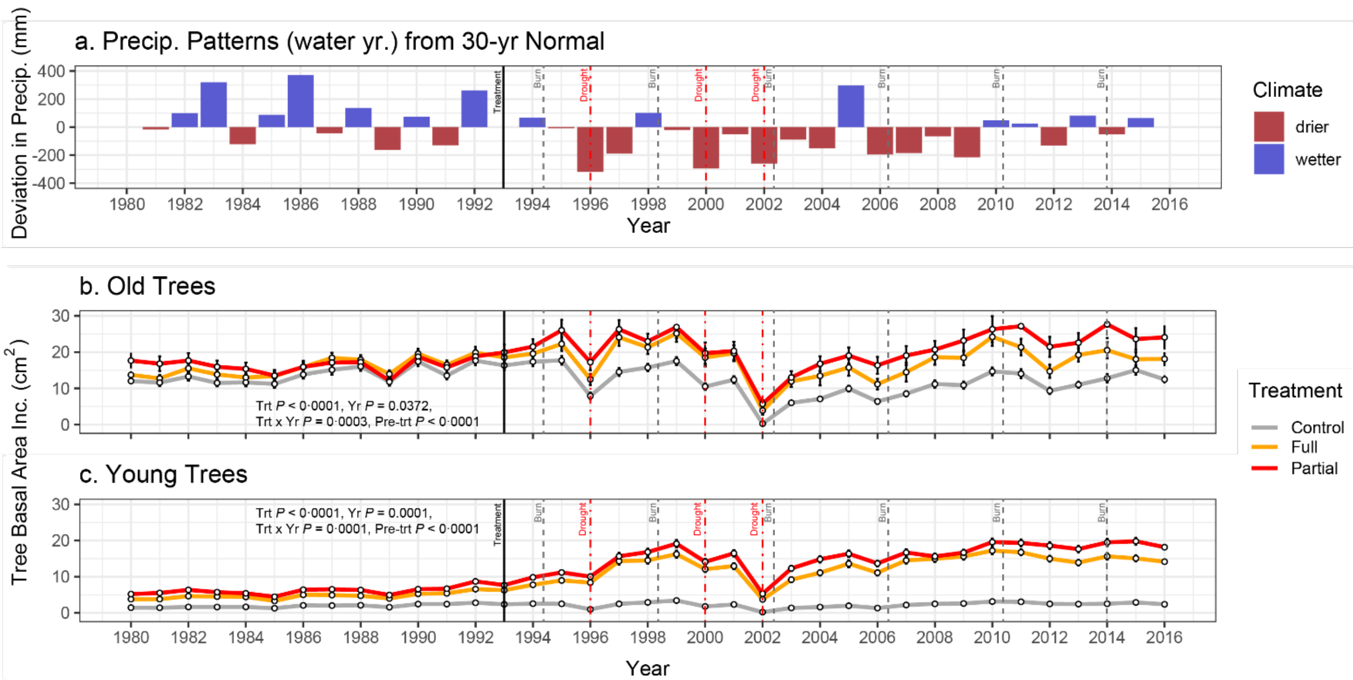

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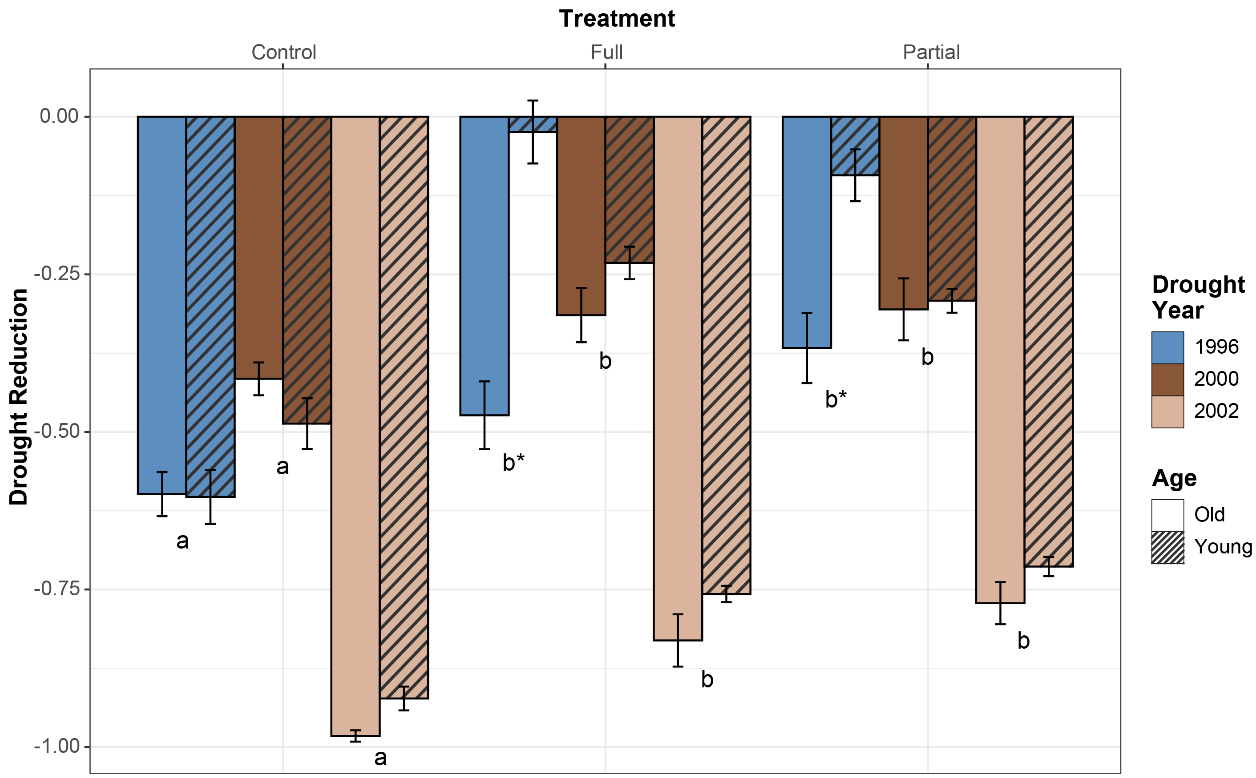

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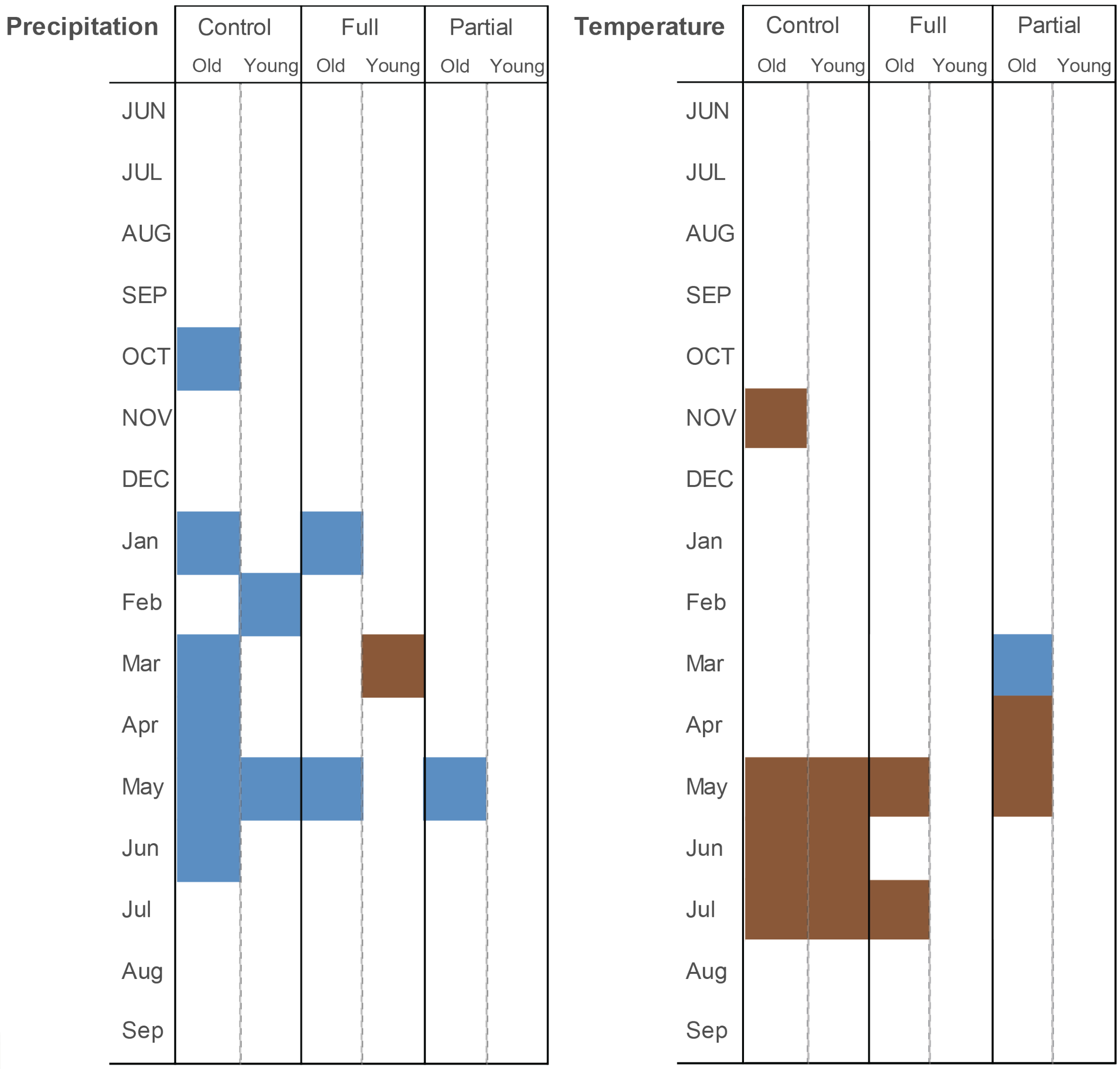

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