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ARTICLE

Double whammy: high-severity fire and drought in ponderosa pine forests of the Southwest

Melissa Savage, Joy Nystrom Mast, and Johannes J. Feddema

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Abstract: We examine regeneration dynamics across landscapes under extreme climate conditions and a human-altered fire regime in ponderosa pine (*Pinus ponderosa* Douglas ex Lawson & C. Lawson) forests of the American Southwest. Our research asks how well these forests recover when unprecedented conditions of a high-severity fire regime combine with historical drought conditions. Tree recruitment is documented at five sites in New Mexico after high-severity fires that burned forests in the drought that prevailed from ~1945 to 1958. We develop a water-balance type model to evaluate how altered microclimate conditions in the years after a fire and during a drought may inhibit ponderosa pine regeneration in comparison with drought conditions alone. We empirically identify two pathways of forest recovery following high-severity fires during drought: recovery to nonforest types, either dense shrubfields or shrubs in grasslands (four sites) or recovery to hyperdense forest (one site). Model simulations predict fewer favorable opportunities for germination, fewer periods favorable for seedling establishment, shortening of favorable establishment periods, and more adverse conditions because of later spring and earlier fall hard freezes. Our research suggests that a specific climate window critical to the capacity of southwestern ponderosa pine trees to regenerate is narrowed by a synchronous occurrence of high-severity fire and drought.

Résumé : Nous avons étudié la dynamique de la régénération dans des paysages soumis à des conditions climatiques extrêmes et à un régime de feux modifié par l'homme dans les forêts de pin ponderosa (*Pinus ponderosa* Douglas ex Lawson & C. Lawson) du sud-ouest des États-Unis. Nous voulions déterminer dans quelle mesure ces forêts récupèrent lorsqu'un régime de feux dont la sévérité est sans précédent est associé à une sécheresse exceptionnelle. Des données sur le recrutement des arbres ont été recueillies dans cinq stations au Nouveau-Mexique à la suite de feux sévères qui ont incendié des forêts durant la sécheresse qui a prévalu de ~1945 à 1958. Nous avons élaboré un modèle analogue à celui du bilan hydrique pour évaluer comment les conditions climatiques extrêmes durant les années qui suivent un feu pendant une période de sécheresse peuvent inhiber la régénération du pin ponderosa comparativement à la sécheresse seule. Nous avons empiriquement identifié deux voies de récupération de la forêt après des feux sévères pendant une période de sécheresse : récupération aboutissant à des types non forestiers, soit des champs dominés par des arbustes denses, soit des arbustes dans des prairies (quatre stations), ou récupération aboutissant à une forêt hyperdense (une station). Les simulations du modèles prédisent qu'il y a moins d'occasions favorables pour la germination, des périodes favorables pour l'établissement des semis moins nombreuses et plus courtes ainsi que des conditions plus défavorables à cause du printemps tardif et des forts gels qui surviennent plus tôt à l'automne. Nos travaux de recherche indiquent qu'une fenêtre climatique spécifique, essentielle pour que les pins ponderosa du sud-ouest puissent se régénérer, est réduite par l'occurrence synchrone d'un feu sévère et d'une sécheresse. [Traduit par la Rédaction]

Introduction

The impacts of drought and warmer temperatures on tree mortality through an increased incidence of high-severity fires and heat-related water stresses are well-documented both in the American West and globally (Westerling et al. 2006; Breshears et al. 2009; van Mantgem et al. 2009; Allen et al. 2010). Less is understood about the impact on tree regeneration of the altered conditions of a post-high-severity burn environment coupled with the drought conditions that foster such fires. In southwestern ponderosa pine (*Pinus ponderosa* Douglas ex Lawson & C. Lawson) forests, our body of ecological knowledge suggests that regeneration will be poor when drought and high-severity fires are coincident, since the species is adapted to regenerate in a low-severity fire regime and fairly precise favorable climate conditions (Savage et al. 1996; Mast et al. 1999). Here, we empirically quantify the regenerational success of ponderosa pine trees in those portions of high-severity fires where near-complete canopy mortality occurs. We then create a model of climate conditions adequate for ponderosa pine regeneration to compare documented regeneration with predicted regeneration: (*i*) under conditions of drought alone and (*ii*) under conditions of drought combined with high-severity fire. Savage and Mast (2005) documented vegetation type conversion on the scale of decades at many postfire ponderosa pine forest sites under a variety of climate conditions. Here, we ask, what characterizes the microclimate envelope that permits or constrains the regeneration of ponderosa pine trees and what are the climate factors that permit or constrain regeneration at the intersection of drought and high-severity fire?

Climate patterns shape southwestern ponderosa pine forest demography. Episodic regeneration and age-cohorts associated with periods of optimal climate typify historical age structure of these forests, with periodic regeneration failures being common during unfavorable climate periods in the past (Fulé et al. 1997; Mast et al. 1999; Brown 2006). Ponderosa pine regeneration and establishment is sensitive to specifically timed precipitation and temperature patterns (Maguire 1956; Savage et al. 1996). A series of relatively wet years, which tend to damp down fires, can present a

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window of opportunity for regeneration (Brown and Wu 2005). Baseline climate parameters, however, are distorted in a high-severity burn environment, as many altered conditions present a harsh environment for regeneration. Bare blackened soils create lower albedo, higher daytime and lower nighttime surface temperatures, and lower soil moisture due to higher daytime surface temperatures and reduced water infiltration. These challenging postfire conditions exacerbate larger scale drought conditions that typically accompany high-severity fire events.

Secular climate trends are strongly correlated to the severity, extent, and synchrony of fires in southwestern ponderosa pine forests (Swetnam and Betancourt 1992; Brown 2006; Westerling et al. 2006). Historically, frequent low-severity fires occurred during dry, warm periods, and patterned ponderosa pine forests by thinning abundant young trees, leaving canopy trees intact and shaping uneven-age, low-density stands (Swetnam and Betancourt 1998; Brown et al. 2001; Brown and Wu 2005). Over the past century or more, human influences, such as fire exclusion and domestic grazing, have altered forest structure such that it now supports high-severity fires, the size and frequency of which are out of the range of natural variability (Covington and Moore 1994; Brown and Seig 1996; Allen et al. 2002; Littell et al. 2009). Large high-severity fires first manifested in the region in the mid-20th century, when decades of anthropogenic fuel accumulation intersected with a regional drought from ~1945 to 1958 (here termed the "1950s drought"). Areas of complete or near-complete tree mortality typically constitute about a quarter to a third of burned areas (Hayes and Robeson 2011).

The depth and timing of droughts in the Southwest are in turn controlled at decadal to century-long scales by low-frequency oscillations in wet–dry cycles, such as El Nino-Southern Oscillation (ENSO), Pacific Decadal Oscillation, and the Atlantic Multidecadal Oscillation (Swetnam and Betancourt 1998; Grissino-Mayer and Swetnam 2000; Milne et al. 2003). The 1950s drought was severe in New Mexico (NM) particularly because both cool and warm seasons experienced drought over an extended period of time, an unusual condition in the climate record (Stahle et al. 2009). Drought was persistent at varying strengths in different locations in this period, with very few years reaching normal conditions, and was accompanied by the first large anthropogenic high-severity fires in the region (Savage and Mast 2005). The 1950s drought was followed by a period of increasing moisture, turning into several decades of relatively wet conditions (Stahle et al. 2009).

In this study, we investigate the role of climatic factors on germination and establishment of ponderosa pine and other woody species in the doubly challenging circumstances of a high-severity burn environment and drought conditions. We estimate establishment dates of ponderosa pine at five sites in NM in the decades after fires, only in those areas of the burn with near-complete tree mortality. We develop a model that identifies climatic variables important to ponderosa pine regeneration to compare actual regeneration data with regeneration predicted in the absence of high-severity fire but with prevailing drought conditions. This allows us to identify the postburn microclimate factors that influence regeneration. The postburn microclimate conditions reflect what Rietveld and Heidmann (1976) consider to be the greatest threats to ponderosa pine seedling survival, namely moisture stress and frost heaving. In general, carbonized and bare soil surfaces lead to increased absorption of solar radiation and higher daytime temperatures, whereas reduced surface roughness, altered wind profiles, and reduced retention of longwave radiation result in lower nighttime temperatures. Radical reduction of vegetation cover and litter, and warmed daytime soil surfaces, in turn increase runoff and reduce soil moisture availability.

High-severity fire and drought can affect reestablishment of ponderosa pine via three pathways: (*i*) biogeophysical changes to climate variables or physical factors such as soil properties (e.g., Zhang and Cregg (2005) and Puhlick et al. (2012)), (*ii*) biogeochemical changes such as changes to nutrient level access (e.g., Gundale et al. (2005) and Lezberg et al. 2008), and (*iii*) ecological changes such as altered seed banks and predation rates (e.g., Elliott and White (1987), Oliver and Ryker (1990), Bailey and Covington (2002), and Keyes and Maguire (2007)). In this study, we do not examine geochemical and ecological impacts that can be altered by high-severity fire, e.g., nutrient pools, soil chemistry, competing vegetation, and seed sources (Puhlick et al. 2012). Nor do we investigate the important spatial dimension of dispersion of trees into burned areas, which has been addressed by others (Bonnet et al. 2005; Haire and McGarigal 2008, 2010). Since soil characteristics are closely linked to microclimate conditions, we also analyze soil characteristics at the sites to identify variability across sites that may influence postburn conditions. This analysis focuses on biogeophysical challenges for regeneration of altered microclimate conditions after high-severity fire coupled with a natural drought.

The model builds on the concepts developed in Savage et al. (1996), in turn based on Maguire's (1956) framework of ponderosa pine regeneration, which suggests that specific climate conditions are required during several consecutive years: (*i*) in the year prior to flowering, (*ii*) the flower or conelet year, (*iii*) the mature cone year, and (*iv*) the years following germination (Savage et al. 1996). An expanded water balance model uses daily precipitation and temperature to estimate thermal and moisture variables that define the climate envelopes to predict ponderosa pine regeneration. We model altered microclimate conditions for a 7-year period following a fire at each of the study sites to assess how regeneration might be altered under drought conditions alone and under drought conditions after a high-severity fire (Feddema et al. 2013). Because there is insufficient empirical data to compare site outcomes for a null hypothesis, we simulate alternatives conditions as sensitivity tests in a model and assess the different modeled outcomes.

While relatively short-term effects of high-severity fires have been investigated (e.g., Foxx (1996), Crawford et al. (2001), and Kuenzi et al. (2008)), there is little understanding of the effects of anthropogenically altered fire regime on the long-term recovery of ponderosa pine forests in the Southwest. Is it possible for the combination of novel stressors such as high-severity fire and climate shifts to allow replacement of forest by alternative communities? Alternative states are defined by Sutherland (1974) as the persistence of one of several potential sets of coexisting species with relatively similar abundances for some period of time. Holling (1973) defines resilience as "the degree to which a system can absorb disturbance — kind, rate and severity — before it shifts into a fundamentally different behavior." Our research aims to contribute to the development of an explanatory theory of forest resilience for forests under anthropogenic and natural stresses, and to explore the mechanisms that may lead a shift into alternative communities and disturbance regimes.

Methodology

Study sites

We document woody species regeneration and climate patterns at 5 sites where high-severity fires occurred at different times during the 1950s drought (Table 1 and Supplementary data[1] Fig. 1). Information was obtained from land management agencies about the dates, size, and locations of the fires and postfire treatments

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2012-0404.

Table 1. High-severity fire sites sampled in New Mexico (NM).

Fire date	Fire name	Elevation range (m) and mean slope (range)	Area (ha)	Soil texture	Land manager	Postfire treatment
1945	Cebollita	2529–2560 and 3.2° (1°–8°)	405	Sandy loam	Santa Fe National Forest	Contouring for erosion control
1951	Archuleta Mesa	2131–2180 and 11.8° (0°–23°)	1012	Sandy loam	Jicarilla Apache Reservation	Light salvage logging
1951	Allen Canyon	2134–2200 and 9.8° (2°–23°)	5977	Sandy clay loam	Lincoln National Forest	Light tree planting (3%–5% est. survival); 56% of area seeded
1953	Circle Cross	2580–2660 and 10.3° (5°–27°)	9308	Loamy sand	Lincoln National Forest	None
1956	Ocate	2850–2920 and 3.6° (1°–7°)	20000	Sandy clay loam	NM State Forest Lands	None

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(Table 1). Aerial photographs of sites were examined to identify a cover of relatively monotypic ponderosa pine forest before fire and location of patches of high mortality of canopy trees postfire. The only prefire management was light logging at Archuleta Mesa. Postfire management treatments ranged from none at two sites, light tree planting at one site, light salvage logging of dead trees at another, and some postfire soil contouring at another (Table 1). Study sites were broadly distributed across NM on the topographically simple terrain of plateaus and mesa tops, with an elevation range of <600 m (Table 1). We assume frequent fires ceased at the sites around the same time as the synchronous regional decline in the late 19th century (Swetnam and Baisan 1996).

A monsoonal climate regime prevails at all sites, with a majority of precipitation arriving as snow in winter and convective storms in summer. Mean annual temperature in ponderosa pine forests ranges from 5 to 7 °C, and mean annual precipitation ranges from 520 to 660 mm, depending on latitude and elevation (Moir et al. 1997). The dry late-spring season in May and June fosters the majority of fires in these forests. Ponderosa pine forests are largely monospecific, but species assemblages, especially of understory plants, may vary on climatic and elevational gradients. In the lower and more xerophytic sites, stands adjoin piñon–juniper woodlands, primarily piñon pine (*Pinus edulis* Engelm.) and alligator juniper (*Juniperus deppeana* Steud.). At higher, more mesophytic sites, the ponderosa pine forest grades into mixed-conifer forest, codominating with Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.), and aspen (*Populus tremuloides* Michx.). Understory shrubs, typically at low densities, include Gambel oak (*Quercus gambelii* Nutt.), gray oak (*Quercus grisea* Liebm.), wavyleaf oak (*Quercus* X *undulata* Torr.), New Mexico locust (*Robinia neomexicana* A. Gray), antelope bitterbrush (*Purshia tridentata* (Pursh) DC.), Colorado barberry (*Berberis fendleri* A. Gray), and Woods' rose (*Rosa woodsii* Lindl.).

Field sampling

Tree and shrub density and herbaceous cover were sampled in each burn site. At Cebollita, Allen Canyon, and Archuleta Mesa (sampled in 2008 or 2009), six 200-m long transects were spaced 200 m apart, with 10 m × 10 m plots spaced every 40 m along each transect (n = 30). For the two largest fires, Ocate and Circle Cross (sampled in 2003), transects were 1000 m long and 500 m apart, with 10 m × 10 m plots placed every 200 m (n = 30). In each 10 m × 10 m plot, we recorded the diameter and species of live and dead adult trees (≥1.4 m in height and >6 cm diameter at breast height (DBH)), and counted saplings (≥1.4 m in height but <6 cm DBH), seedlings (<1.4 m in height), and shrub stems. We cored live adult trees in each plot to establish age, angling the borer diagonally at the base of the tree toward the zone of first-year seedling height to capture the maximum number of annual rings. While this approach has been found reliable (Savage et al. 1996), there remains a measure of uncertainty about the specific year of germination in the analysis. Since seedlings and saplings were neither cored nor aged, we end our tree age analysis in the year 1990. We do not account for trees that may have germinated and died owing to natural rates of attrition. We estimated percent cover (cover classes: ≤5%, 5%–25%, 25%–50%, 5%–75%, and ≥95%) for grass and forbs in ten 1 m × 1 m plots located every 20 m along transects (n = 60) at Cebollita, Allen Canyon, and Archuleta Mesa, and in five 1 m × 1 m understory cover plots located randomly in each larger plot (n = 150) at Ocate and Circle Cross. Soil samples were taken to a depth of 15 cm in the corner of 30 large plots per site (n = 150).

Laboratory analysis

To estimate tree age, increment cores were prepared according to standard procedures (Stokes and Smiley 1968). To estimate date of germination, annual rings were counted and visually cross-dated. Where the core did not intercept the pith, years from innermost ring to pith were estimated with a pith locator (Applequist 1958). Core ages were double-checked by cross-dating in an independent dendrochronology lab (P. Brown, Rocky Mountain Tree-Ring Research, Fort Collins, Colorado). The soil parameters examined were texture, % gravel, water-holding capacity, pH, and nutrient analyses (P, N, and K). Samples were air-dried and sieved at 2 mm to separate out gravels, which were weighed to determine % soil vs. gravel. Test tube separation methods were used to determine texture classes. Nutrients and pH were analyzed using LaMotte soil tests.

Model simulations

To test how fire-related microclimate alterations can change regeneration conditions, we developed climate envelopes to simulate a series of events that influence the relative success of seed production, germination and postgermination survival (Supplementary data;[1] Feddema et al. 2013). Savage et al. (1996) demonstrated that climate factors, such as threshold temperatures and relative temperature and moisture conditions, will influence flowering, seed development, germination conditions, and postgermination seedling survival at the Gustav A. Pearson Natural Area near Flagstaff, Arizona, based on ponderosa pine – climate interactions described by Maguire (1956). In this study, we modify this approach to create seven indices to represent the relative success of the following phases of ponderosa pine regeneration: the cone production (1, *flower*, and 2, *cone* stages), the likelihood of germination (3, *germ*), seedling success in the year of germination based on the number of days with optimal conditions following germination (4, *Days*), soil moisture conditions in the fall following germination (5, *Oct(St)*), and potential seedling stress based on actual evapotranspiration minima in the two years following germination (6, $(Yr + 1)AE$; 7, $(Yr + 2)AE$).

Each of these phases is associated with a specific set of climate envelopes as listed in Table 2. To avoid measuring success or failure based on a single value for each climate variable, we developed a range of values for each climate-envelope variable (Table 2). We divide value ranges into six equal intervals. If the

Table 2. Climate conditions (Cond.) associated with specific development stages of ponderosa pine.

Development stage	Time relative to germination	Climate variable	Cond. 1 min value	Cond. 2 min value	Cond. 3 min value	Cond. 4 min value	Cond. 5 min value
Flowering phase	3 years prior	June GDD	375 °C	400 °C	425 °C	450 °C	475 °C
	3 years prior	June Tn	–5 °C	–4 °C	–3 °C	–2 °C	–1 °C
	3 years prior	Sep–Oct GDD	575 °C	600 °C	625 °C	655 °C	675 °C
	2 years prior	Jun–Jul GDD	900 °C	930 °C	960 °C	990 °C	1020 °C
Cone-development phase	2 years prior	Aug–Oct AET/PET	0.65	0.70	0.75	0.80	0.85
	2 years prior	Aug–Oct GDD	1070 °C	1100 °C	1130 °C	1160 °C	1190 °C
	1 year prior	Jul AET/PET	0.55	0.6	0.65	0.7	0.75
	1 year prior	Sep–Nov GDD	640 °C	670 °C	700 °C	730 °C	760 °C
	Germ year	May GDD	225 °C	250 °C	275 °C	300 °C	325 °C
Germination phase	Germ year	5 day Tn	–6 °C	–5 °C	–4 °C	–3 °C	–2 °C
	Germ year	5 day GDD	55 °C	65 °C	75 °C	85 °C	95 °C
	Germ year	5 day Rain+Melt	15 mm	20 mm	25 mm	30 mm	35 mm
	Germ year	Soil Moisture	87.5% WHC	90.0% WHC	92.5% WHC	95.0% WHC	97.5% WHC
Seedling phase	Germ year	Tn	–6.5 °C	–5.25 °C	–4 °C	–2.75 °C	–1.5 °C
	Germ year	Daily AET	0.7 mm	0.85 mm	1.0 mm	1.15 mm	1.3 mm
Postgermination phase	Germ year	October Surplus	40% WHC	55% WHC	70% WHC	85% WHC	100% WHC
	Year following	15 May – 15 Sep min daily AET	0.3 mm	0.4 mm	0.5 mm	0.6 mm	0.7 mm
	2 years following	15 May – 15 Sep min daily AET	0.2 mm	0.3 mm	0.4 mm	0.5 mm	0.6 mm

Note: GDD, growing degree-days (measure of heat accumulation); AET, actual evapotranspiration; PET, potential evapotranspiration; Tn, minimum temperature; WHC, water-holding capacity.

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calculated climate variable falls below the minimum value of the range (the values listed in the column Condition 1), it is scored 0, indicating that climate conditions inhibit successful completion of that development phase. Scores above the maximum value (Condition 5 column) are scored 5 for very high likelihood of success, and values between these extremes are scored 1 through 4, representing, respectively, increasing the likelihood of success based on the thresholds listed under Conditions 2, 3, and 4. By combining these scores across all phases of development, a single numerical score was created representing the relative success of a regeneration event in any given year (*regen*) (Supplementary data).[1]

Using soil and land surface conditions and daily precipitation and temperature as input, our model calculates each of the climate factors described in Table 2 and simulates initiation of ponderosa pine germination events each year. It then calculates a *regen* score for each simulated event. By modifying the input variables it is possible to simulate the impact of altered soil and surface conditions and modified temperature or precipitation conditions associated with post-severe fire conditions on calculated *regen* scores. Thus, we alter model inputs to simulate microclimate conditions that result when a fire denudes and blackens the soil surface and removes the protective cover of vegetation and litter, resulting in higher temperature variability and lower soil moisture.

To represent postfire conditions in the model, the soil and climate inputs of the model are altered as follows over a 7-year period in three stages. Modifications for simulated postfire conditions over 400 days immediately following the fire event (stage 1) include (*i*) elevating daily maximum temperatures by 4 °C, (*ii*) lowering daily minimum temperatures by 2 °C, and (*iii*) changing runoff conditions. The Soil Conservation Services (SCS; 1972) runoff methodology is used to simulate changes in runoff (see the Supplementary data).[1] To represent increased runoff conditions, we change the curve numbers (CN) used by this methodology from 60/78/90 to 86/94/98 for CN1/CN2/CN3 (based on SCS (1972) and Mather (1978)) on August 1st in the year of a fire. For the next 1200 days (stage 2), to simulate the loss of black carbon from the surface over time and, hence, a reduction in modified microclimate conditions, simulated conditions are changed to a maximum temperature increase of 2 °C, a minimum temperature decrease of 1 °C, and CN numbers of 71/86/94. Finally, in a last stage (stage 3), for the next 2400 days maximum temperature is altered to increase by 1.0 °C, a minimum temperatures decrease by 0.5 °C, and CN numbers are set to 64/81/92. Following stage 3, conditions return to normal relative to fire impacts, that is, there are no modifications in temperature or runoff parameters. This simulation approximates the observed conditions for the sites, and we will refer to this simulation as the ***burn*** simulation. To assess the impact of fire, we compared this with a ***control*** simulation where we used unaltered soil, surface, and temperature and precipitation conditions. The ***control*** simulation represents climate conditions that would have prevailed without the incidence of observed fires at each study site.

In this study we examine in detail the effect of a simulated pattern of microclimate conditions on the germination process. We analyze two parameters: (*i*) how many days were there with climate conditions considered sufficient for germination and (*ii*) how many periods were there with favorable climate conditions considered sufficient for establishment following germination. Conditions are defined as favorable for germination when the four climate conditions representing immediate and long-term moisture and thermal conditions are all met (Table 2, germination phase). A period favorable for establishment is defined by at least 45 days of favorable seedling conditions following the germination event.

Results

Tree recruitment

We sampled a total of 501 adult trees (391 live and 110 dead) established in the five burn sites, which included 248 adult ponderosa pine trees (232 live and 16 dead). Dates of establishment were estimated from the ring count for 94% of the live trees. Soils were similar across sites and do not appear to be a factor in differential postfire recovery. No significant differences in soil texture, pH, or nutrient analysis were determined among sites. Sandy loam is the predominant texture at all five sites (Table 1), with corresponding water holding capacities of 0.12–0.30 $cm \cdot m^{-1}$. Nitrogen is limited at all study sites, with low to medium levels of phosphorus, medium to high levels of potassium, and a moderately acidic to neutral pH (5.7–7.4). Overall, there is little variability in soil characteristics among sites. Yet recovery trajectories of vegetation types varied widely across the sites (Table 3). Recovery

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Table 3. Mean density of woody species per hectare, live (and dead) at five high-severity fire sites (year of fire).

		Density of woody species per hectare				
		Fire site				
Species	Size class	Cebollita (1945)	Archuleta Mesa (1951)	Allen Canyon (1951)	Circle Cross (1953)	Ocate (1956)
PIPO	A	107	120 (7)	63 (40)	40 (3)	443 (3)
	Sa	37	47	13 (7)	10	467
	Se	50	33	27 (3)	63	687
POTR	A	27 (23)	—	—	—	223 (287)
	Sa	— (3)	—	—	—	—
	Se	40	—	—	23	72
JUDE	A	—	—	77	53	—
	Sa	—	—	37 (7)	83	—
	Se	—	—	50	133	57
JUMO	A	—	—	7	—	—
	Sa	—	—	10	3	—
	Se	—	—	17	—	—
JUOS	Sa	—	—	7	—	—
	Se	—	—	3	—	—
JUSC	Sa	—	13 (3)	—	—	—
	Se	—	10 (3)	—	—	—
PIED	A	—	—	—	3	—
	Sa	—	—	3	20	7
	Se	—	—	17	80	7
ABCO	A	—	—	—	—	37
	Sa	—	—	—	—	43
	Se	—	—	—	—	297
PIFL	A	—	—	—	—	3
	Sa	—	—	—	—	7
	Se	—	—	—	—	57
JUCO	Se	7	—	—	—	—
PSME	Se	—	—	—	43	—
PIEN	Se	—	—	3	23	—
QUGA	A	—	2088 (1808)	—	90	3
	S	1988	10656 (4013)	350	20276	1477
QUGR	S	—	—	—	35997	—
QUUN	S	—	—	41925 (1086)	—	—
QUOS	S	—	—	153	—	—
BEFE	S	266	—	—	—	—
CEMO	S	—	869 (463)	393 (17)	—	—
PUTR	S	—	3333 (157)	—	—	—
RHTR	S	—	—	2087 (736)	—	—
ROWO	S	1938	—	137	—	—
RONE	S	10	—	2864 (163)	1073	—

Note: A, adult; Sp, sapling; Se, seedling; S, shrub stem (<1.4 m). PIPO, *Pinus ponderosa*; POTR, *Populus tremuloides*; JUDE, *Juniperus deppeana*; JUMO, *Juniperus monosperma*; PIED, *Pinus edulis*; JUOS, *Jupiperus osteosperma*; JUSC, *Juniperus scopulorum*; ABCO, *Abies concolor*; PIST, *Pinus strobiformis*; JUCO, *Juniperus coahuilensis*; PSME, *Pseudotsuga menziesii*; PIEN, *Picea engelmannii;* QUGA, *Quercus gambelii*; QUGR, *Quercus grisea*; QUUN, *Quercus undulata*; QUOS, *Quercus oblongifolia*; BEFE, *Berberis fendleri*; CEMO, *Cercocarpus montanus*; PUTR, *Purshia tridentate*; RHTR, *Rhus trilobata*; ROWO, *Rosa woodsii*; RONE, *Robina neomexicana*.

over the decades since the fires has resulted in one site codominated by shrubs, grasses and forbs, three sites dominated by shrubs, and one site recovered to hyperdense forest. At most study sites, ponderosa pine tree recruitment appears to have been hindered by the effects of high-severity fire for some period of time. The term "dominated" refers to density, or number of stems, although, in many cases, scattered young adult ponderosa pine and other trees are present in shrubfields in moderate numbers. Density of ponderosa pine seedlings and saplings also ranges from modest to abundant, and suggests that ponderosa pine is slowly recruiting into shrub and grass-dominated sites.

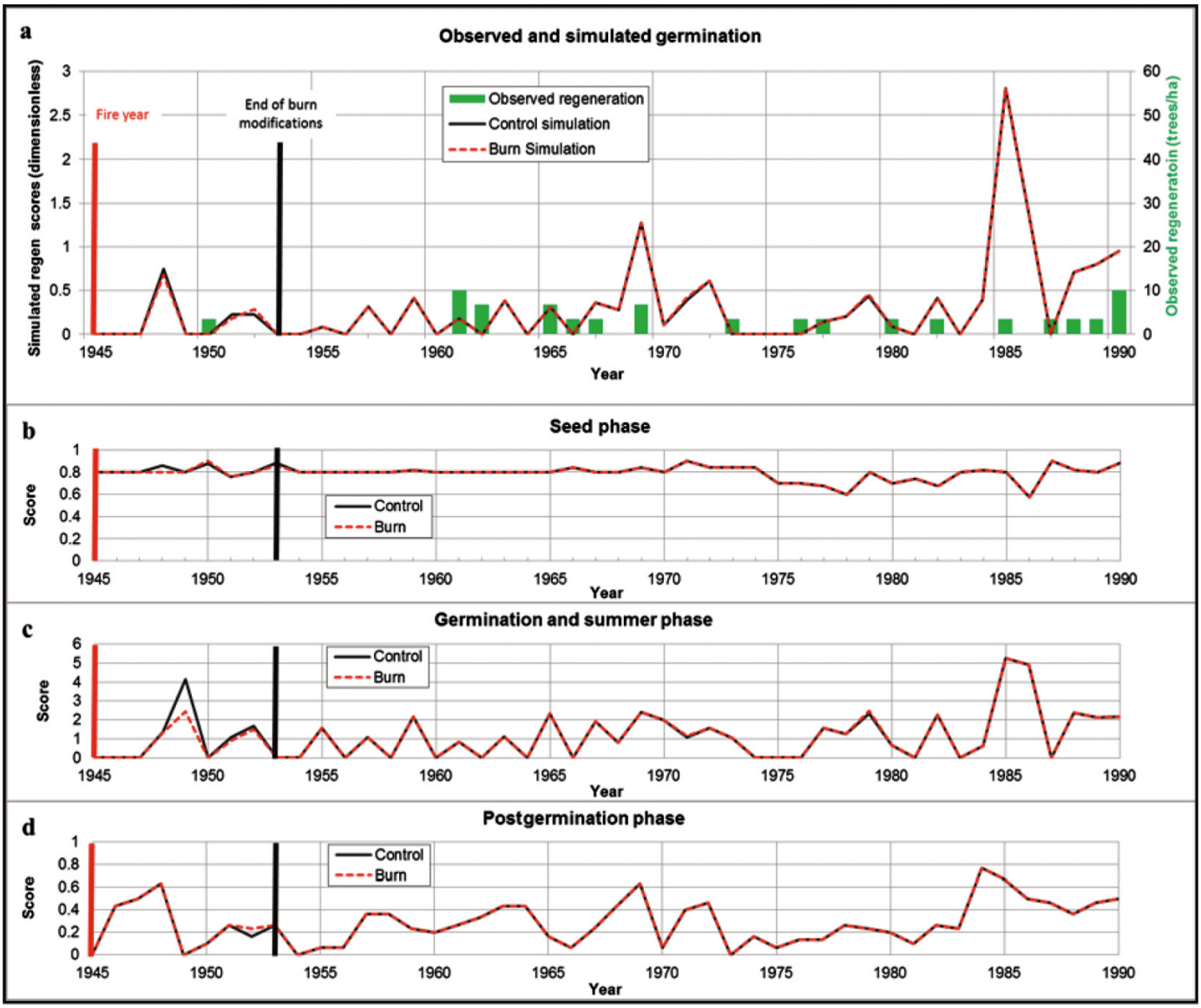
Recovery to mixed shrub – grasses

The site of the Cebollita Fire (1945), the earliest fire within the drought, is dominated by shrubs, grasses, and forbs decades after the fire. Shrubs are abundant, including Gambel oak (live: 1988 stems·ha^{-1}), Woods' rose (live: 1938 stems·ha^{-1}), and Colorado barberry (live: 266 stems·ha^{-1}). Understory cover values are moderately high, at 31% grass and 33% forbs, for a total of 64% cover. In the decades since the end of the drought, ponderosa pine trees have slowly encroached into the meadows, at a current density of 107 live adults·ha^{-1} (plus live: 37 saplings·ha^{-1}; 50 seedlings·ha^{-1}) (Table 3). The relative size of ponderosa pine trees is small on average (22 cm DBH; 53% in the 5–19.9 cm size classes), reflecting continual slow establishment and growth from the 1960s to the early 1990s (Fig. 1). Aspen are present at a density of 27 live adults·ha^{-1} (dead: 23 adults·ha^{-1}; live: 40 seedlings·ha^{-1}).

Recovery to shrubfields

Three sites are currently dominated by dense shrubfields. At the Archuleta Mesa Fire (1951) site Gambel oak forms highly dense thickets (live: 2088 adults·ha^{-1}; 10 656 stems·ha^{-1} <1.4 m tall; dead:

Fig. 1. Cebollita. (*a*) Estimated year of germination for observed ponderosa pine trees and maximum simulated germination (*regen*) scores for the ***burn*** and ***control*** simulations from the fire date through 1990. Detailed regeneration analyses are performed for the period from the burn through the seven years during which climate data are modified as part of the ***burn*** simulation. (*b*) Seed-phase score comparison of the ***burn*** and ***control*** simulations. (*c*) Germination- and summer-phase score comparison of the ***burn*** and ***control*** simulations. (*d*) Post germination-phase score comparison of the ***burn*** and ***control*** simulations.



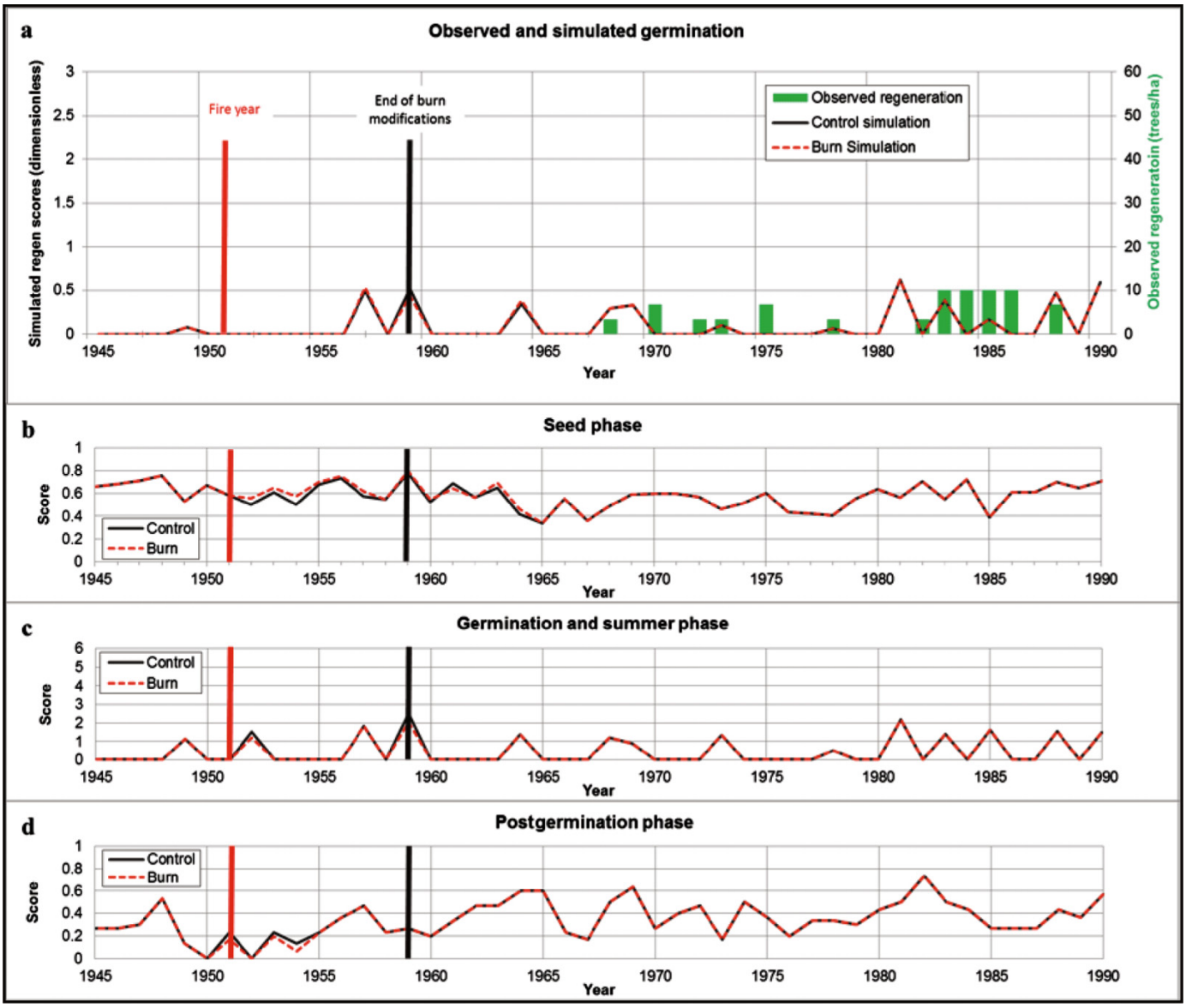
1808 adults·ha^{-1}; 4013 stems·ha^{-1} <1.4 m tall) (Table 3). The abundance of dead shrub stems reflects the impact of a post-2000 drought at the site. Other shrub species include antelope bitterbrush (live: 3333 stems·ha^{-1}; dead: 157 stems·ha^{-1}) and mountain mahogany (*Cercocarpus* Kunth; 869 live stems·ha^{-1}; 463 dead stems·ha^{-1}). But ponderosa pine trees are establishing as well in the shrubfields (live: 120 adults·ha^{-1} with mean DBH 15 cm, 47 saplings·ha^{-1}; 33 seedlings·ha^{-1}; dead: 7 adults·ha^{-1}), with 75% in the 5–19.9 cm DBH class. Most trees established during the 1980s (Fig. 2). Herbaceous ground cover is modest at 14% grass and 11% forbs, for a total of 25% cover.

The highly dense shrubfield at the site of the Allen Canyon Fire (1951) is dominated by wavyleaf oak (41 925 live stems·ha^{-1} and 1086 dead stems·ha^{-1}), NM locust (2864 live stems·ha^{1} and 163 dead stems·ha^{-1}) and skunkbush sumac (2078 live stems·ha^{-1} and 736 dead stems·ha^{-1}) (Table 3). The most abundant tree is alligator juniper (live: 77 adults·ha^{-1}, 37 saplings·ha^{-1}, and 50 seedlings·ha^{-1}), with moderate numbers of young ponderosa pine trees (live: 63 adults·ha^{-1} and dead: 40 adults·ha^{-1}; live: 13 saplings·ha^{-1} and 27 seedlings·ha^{-1}). Some of these ponderosa pines may have survived from a modest planting effort by the USDA Forest Service in the 1960s, estimated at 3%–5% survival. Ponderosa pine trees are small, averaging 16 cm DBH (89% in the 5–19.9 cm DBH class). The majority of ponderosa pine established from 1973 to 1982 (Fig. 3). Understory cover values were moderate at 4% grasses and 25% forbs, for a total of 29% cover.

The site of the Circle Cross Fire (1953) is dominated by shrubs and has the lowest density of ponderosa pine trees. Extreme densities of gray oak (live: 236 adults·ha^{-1} and 35 934 stems·ha^{-1} <1.4 m tall), Gambel oak (live multistemmed shrub form: 20 276 stems·ha^{-1} with 2950 stems·ha^{-1} ≥1.4 m tall and 17 306 stems·ha^{-1} <1.4 m tall), and NM locust (live: 1076 stems·ha^{-1}) (Table 3) cover the site. Ponderosa pine are slowly establishing (live: 40 adults·ha^{-1}, with a mean DBH of 16 cm) (live: 10 saplings·ha^{-1} and 63 seedlings·ha^{-1}),

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Fig. 2. Archuleta Mesa. (*a*) Estimated year of germination for observed ponderosa pine trees and maximum simulated germination (*regen*) scores for the ***burn*** and ***control*** simulations from the fire date through 1990. Detailed regeneration analyses are performed for the period from the burn through the 7 years during which climate data are modified as part of the ***burn*** simulation. (*b*) Seed-phase score comparison of the ***burn*** and ***control*** simulations. (*c*) Germination- and summer-phase score comparison of the ***burn*** and ***control*** simulations. (*d*) Postgermination-phase score comparison of the ***burn*** and ***control*** simulations.



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with 91% of the adults in the 5–19.9 cm DBH class. Other tree species have also established, some more successfully: Gambel oak (tree form) (90 adults·ha^{-1}), alligator juniper (53 adults·ha^{-1}, 97 saplings·ha^{-1}, and 130 seedlings·ha^{-1}), and piñon pine (20 saplings·ha^{-1} and 80 seedlings·ha^{-1}). Fourteen of 30 plots (47%) at Circle Cross lack trees completely. Establishment of ponderosa pine trees dates primarily from 1973 to 1989 (Fig. 4). Understory cover values are very low at 3% grass and 2% forbs, for a total of 5% cover.

Recovery to forest

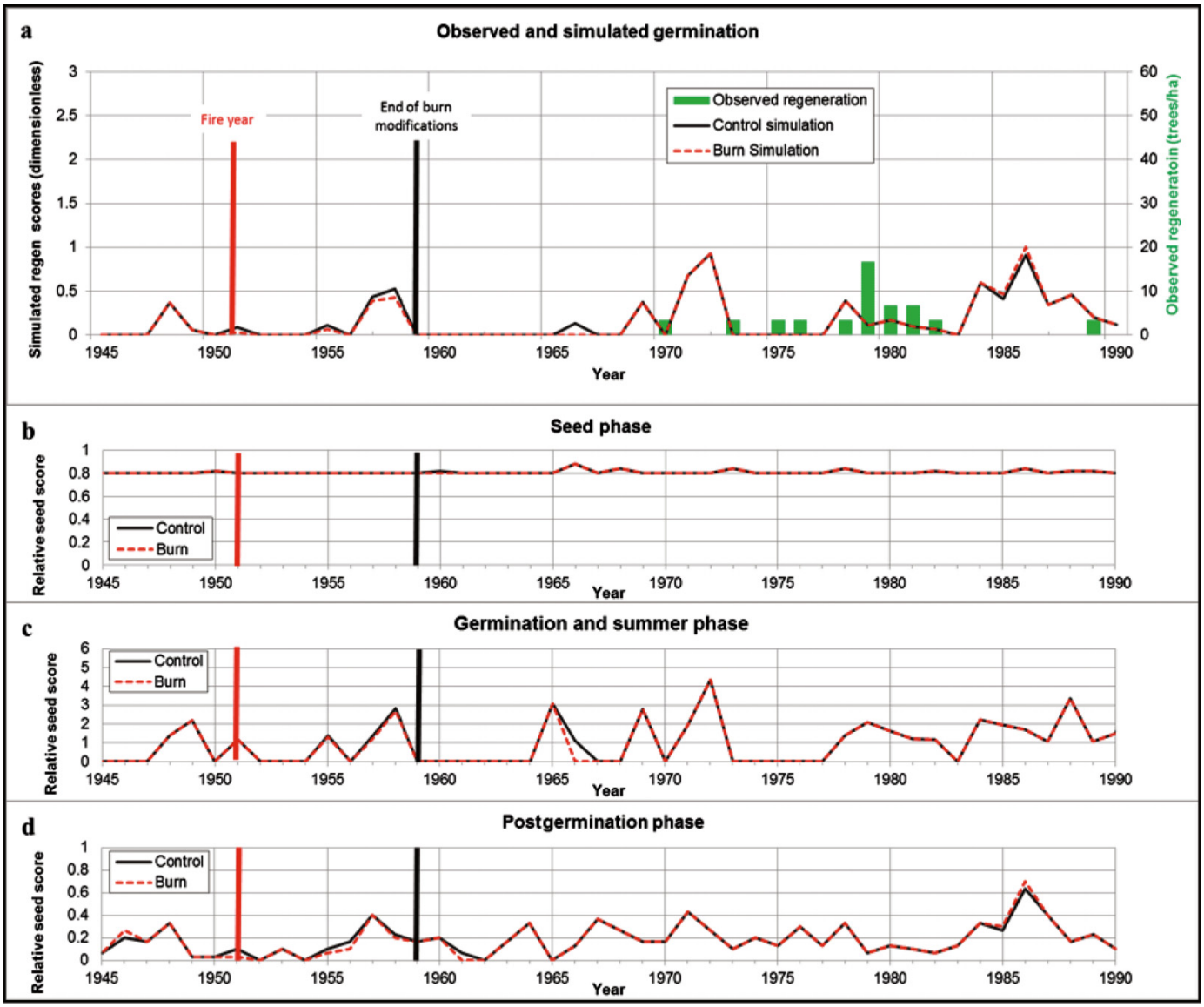
The site of the Ocate Fire (1956), which burned near the end of the drought, is characterized by hyperdense ponderosa pine establishment (live: 443 adults·ha^{-1}; dead: 3 adults·ha^{-1}) and aspen (live: 233 adults·ha^{-1}; dead: 290 adults·ha^{-1}) (Table 3). Most of the adult ponderosa pine regeneration occurred in a pulse of establishment beginning soon after 1960 and peaking in the late 1960s and throughout the 1970s (Fig. 5). Ponderosa pine trees average 16 cm DBH (70% in the 5–19.9 cm DBH class), and dominate recent recruitment as well (live: 467 saplings·ha^{-1} and 687 seedlings·ha^{-1}), together with white fir (live: 43 saplings·ha^{-1} and 300 seedlings·ha^{-1}) and aspen (live: 70 seedlings·ha^{-1}). Herbaceous cover is 37% grass and 13% forbs, for a total of 50% cover.

Simulation results

Conditions favorable for regeneration predicted by ***burn*** correspond to 64% of observed regeneration (Figs. 1–5) (for more details on model validation see Feddema et al. 2013). The ***burn*** simulation overestimates observed regeneration in sites with the lowest observed regeneration (Allen Canyon and Circle Cross) (Figs. 3 and 4) and underestimates observed regeneration at the site with the greatest observed regeneration (Ocate) (Fig. 5).

The ***burn*** simulation, in comparison with ***control***, predicts, for the 7 years immediately following a high-severity fire, (*i*) a

Fig. 3. Allen Canyon. (*a*) Estimated year of germination for observed ponderosa pine trees and maximum simulated germination (*regen*) scores for the ***burn*** and ***control*** simulations from the fire date through 1990. Detailed regeneration analyses are performed for the period from the burn through the 7 years during which climate data are modified as part of the ***burn*** simulation. (*b*) Seed-phase score comparison of the ***burn*** and ***control*** simulations. (*c*) Germination- and summer-phase score comparison of the ***burn*** and ***control*** simulations. (*d*) Postgermination-phase score comparison of the ***burn*** and ***control*** simulations.

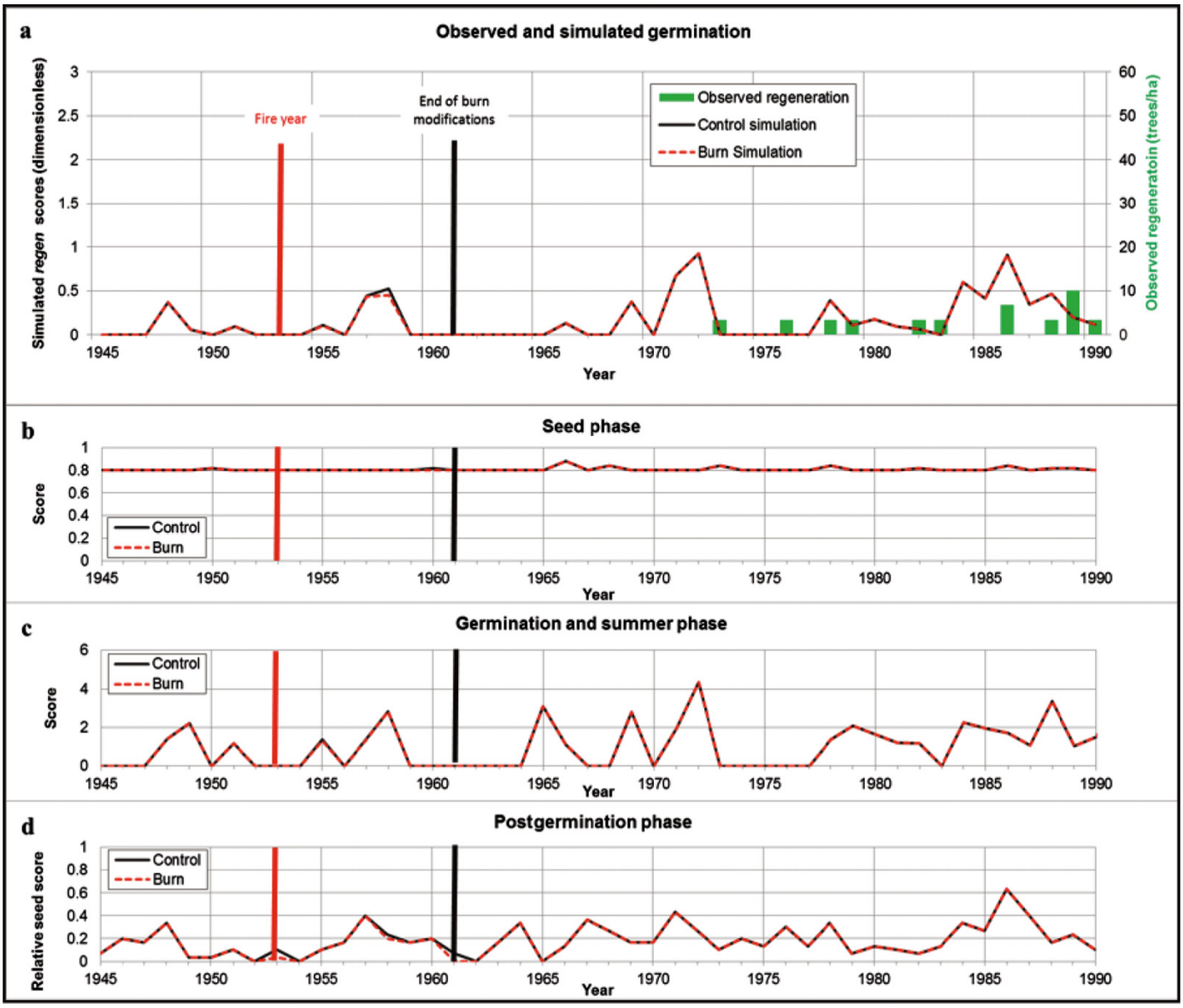


decrease in the number of days favorable for seedling germination and (*ii*) a decrease in the number of favorable 45-day periods considered sufficient for seedling establishment after germination. While not directly apparent from the phase scores (Figs. 1–5), higher evapotranspiration rates associated with the ***burn*** simulation led to consistently poorer environmental conditions (drier) for survival and regeneration success in all postgermination phases. In most instances, altered conditions are slight, however, since ponderosa pine regeneration is sensitive to climate factors, even slight impacts predict reduced regeneration success in many years (longer term sensitivity tests presented in Feddema et al. 2013 confirm this finding and provide additional details).

The development-phase analysis suggests that germination and postgermination phases are most affected by the ***burn*** simulation. Pregermination-, germination-, and postgermination-phase scores are plotted on the same time axis as simulated *regen* scores and observed regeneration events (Figs. 1–5). At Cebollita, the negative effect on germination was pronounced in 1949, even though this did not affect the *regen* score, which was zero in both experiments because of poor postgermination conditions in both experiments (Fig. 1). The ***burn*** simulation can reduce the germination-phase score to zero even when there is a simulated event in ***control***, as illustrated at Archuleta Mesa in 1966 (Fig. 2), although, in this case, the reason is not directly related to the ***burn*** simulation but rather a change in potential evapotranspiration (PET) associated with altered temperature averages because of the inclusion of the ***burn*** altered temperature period. At Archuleta Mesa (Fig. 2*d*), Allen Canyon (Fig. 3*d*), and Circle Cross (Fig. 4*d*), there are small reductions in postgermination-phase scores, whereas in Cebollita there is a slight improvement in one of the postgermination year scores (Fig. 2*d*). At Ocate (Figs. 5*b*–5*d*) and simulated flower and seed development scores slightly increase, but germination scores are slightly reduced and postgermination scores are unaltered. In general, while there are small changes at various sites in all phases of the regeneration, the primary impact of ***burn*** is to favor seed production slightly (although seed trees may be distant at the

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Fig. 4. Circle Cross. (*a*) Estimated year of germination for observed ponderosa pine trees and maximum simulated germination (*regen*) scores for the ***burn*** and ***control*** simulations from the fire date through 1990. Detailed regeneration analyses are performed for the period from the burn through the 7 years during which climate data are modified as part of the ***burn*** simulation. (*b*) Seed-phase score comparison of the ***burn*** and ***control*** simulations. (*c*) Germination- and summer-phase score comparison of the ***burn*** and ***control*** simulations. (*d*) Postgermination-phase score comparison of the ***burn*** and ***control*** simulations.



edges of burns) because of increased average temperatures. In most instances ***burn*** reduces germination and establishment success, as reflected in the reduction in the number of predicted favorable germination days and establishment periods.

Days of conditions favorable for germination

At all five sites, many of the postfire years had few or no days predicted to be favorable for germination in the ***control*** or ***burn*** simulations (Table 4). Although all five sites had at least 1 year in which there were a number of days predicted to be favorable for germination, the total number of favorable germination days varied considerably through the 7 years at different sites. For example, both the ***control*** and ***burn*** simulations predict zero favorable germination days at Cebollita in postfire year 5; at Allen Canyon in years 2, 3, and 5; at Archuleta Mesa in years 2, 3, 5, and 7; at Circle Cross in years 1, 2, 3, and 5; and at Ocate in year 6 (Table 4). Generally, the mean number of days favorable for germination was reduced in most years. However, there are exceptions, particularly for postfire year 1, where the number of favorable germination days was increased by 1 at Archuleta Mesa and 3 at Ocate (Table 4). The ***burn*** simulation predicts an overall 8.8% reduction in the number of days favorable for germination averaged over all five sites over the 7-year postburn period compared with ***control*** (Table 4). In only one case, Cebollita, does ***burn*** simulate a reduction from the few favorable germination days in ***control*** to zero (Table 4). At individual sites, ***burn*** either made no overall difference or reduced the number of favorable germination days (Table 4).

Periods of conditions favorable for establishment

There are two general effects of the ***burn*** simulation on the period of climate conditions favorable for establishment (defined for this study as a favorable day for germination followed by at least 45 days of conditions considered favorable for seedling es-

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Fig. 5. Ocate. (*a*) Estimated year of germination for observed ponderosa pine trees and maximum simulated germination (*regen*) scores for the ***burn*** and ***control*** simulations from the fire date through 1990. Detailed regeneration analyses are performed for the period from the burn through the 7 years during which climate data are modified as part of the ***burn*** simulation. (*b*) Seed-phase score comparison of the ***burn*** and ***control*** simulations. (*c*) Germination-and summer-phase score comparison of the ***burn*** and ***control*** simulations. (*d*) Postgermination-phase score comparison of the ***burn*** and ***control*** simulations.



Table 4. Number of days of climate conditions favorable for germination predicted by ***control*** vs. ***burn*** simulations for five sites for each of the first 7 years after high-severity fire (year of fire).

	Predicted no. of days of favourable climate conditions for germination											
	Fire site											
	Cebollita (1945)		Archuleta Mesa (1951)		Allen Canyon (1951)		Circle Cross (1953)		Ocate (1956)		Mean days	
Year after fire	***Control***	***Burn***	***Control***	***Burn***	***Control***	***Burn***	***Control***	***Burn***	***Control***	***Burn***	***Control***	***Burn***
1st	2	0	4	5	0	0	0	0	5	8	2.2	2.6
2nd	5	5	0	0	0	0	6	6	23	23	6.8	6.8
3rd	18	14	0	0	0	0	0	0	16	14	6.8	5.6
4th	29	27	6	6	6	6	14	13	13	5	13.2	10.8
5th	0	0	0	0	0	0	10	9	19	18	5.8	5.4
6th	1	1	27	26	14	13	0	0	0	0	8.4	8.0
7th	4	3	0	0	10	9	3	5	8	8	4.2	4.4
Mean	8.4	7.1	5.3	5.3	4.3	4.0	4.7	4.7	12	10.7	6.8	6.2

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Table 5. Mean no. of favorable versus unfavorable climate periods per year for seedling establishment predicted by ***control*** vs. ***burn*** for five sites aggregated for all 7 years after high-severity fires (the numbers in the columns may not add up exactly because of rounding).

	Predicted periods per year for seedling establishment											
	Fire site											
	Cebollita		Archuleta Mesa		Allen Canyon		Circle Cross		Ocate		Mean	
Climate period	***Control***	***Burn***	***Control***	***Burn***	***Control***	***Burn***	***Control***	***Burn***	***Control***	***Burn***	***Control***	***Burn***
Mean days climate favorable for germination	8.4	7.1	5.3	5.3	4.3	4.0	4.7	4.7	12.0	10.7	6.9	6.4
Favorable periods	5.9	2.7	2.3	2.6	3.1	3.0	3.1	3.0	9.3	8.1	4.7	3.9
Truncated periods	2.6	4.4	3.0	2.7	1.1	1.0	1.6	1.7	2.7	2.6	2.2	2.5
Reason												
Drought	1.4	1.9	2.1	1.9	0	0	0	0	2.7	2.6	1.2	1.3
Spring freeze	0	0.4	0.9	0.9	0	0	0	0	0	0	0.2	0.3
Fall freeze	1.2	2.1	0	0	1.1	1.0	1.6	1.7	0	0	0.8	1.0

Note: favorable period, defined as a day with climate conditions favorable for germination followed by 45 days of climate conditions considered favorable for survival; truncated period, defined as a day with climate conditions favorable for germination followed by fewer than 45 days of climate conditions considered favorable for survival owing to drought or a hard freeze.

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tablishment): (*i*) the truncation of a period by a lack of adequate soil moisture and (*ii*) the truncation of a period by a hard freeze (<6 °C). As expected, because there is a higher standard to meet, there were fewer favorable 45-day establishment periods than favorable germinations days. ***Burn*** simulations predict a decrease in the mean number per year of such favorable periods from 4.7 for ***control*** to 3.9 in ***burn*** in the 7 years after fires across all sites, a decrease of 17% (Table 5). Similarly, ***burn*** simulations predict a decrease in the number of periods, 45 days or longer, of favorable establishment conditions following a favorable germination day, from 68% in ***control*** to 61% in ***burn***. The ***burn*** simulation makes it less likely that conditions favorable for germination would be followed by a favorable establishment period.

In both ***control*** and ***burn*** simulations, adverse conditions can shorten the number of days in a favorable establishment period to fewer than 45 following a favorable germination day, thereby eliminating a chance for seedling establishment. In ***control***, 32% of favorable germination days are followed by fewer than the minimum 45 days defined as necessary for favorable establishment, compared with 39% in ***burn***. For those periods truncated in ***control***, 55% were due to inadequate soil moisture and 45% were due to hard freezes (20% in the spring and 80% in the fall; Table 5). ***Burn*** predicts hard freezes both later in the spring and earlier in the fall of the germination season. A greater proportion of favorable periods in ***burn*** were truncated by hard freezes, 52% (23% in the spring and 77% in the fall), with 48% because of inadequate soil moisture (Table 5). ***Burn*** predicts varying impacts at individual sites on the number of favorable establishment periods. ***Burn*** has the most impact on the establishment periods at Cebollita, where it reduces the number of predicted favorable periods from a mean of 5.9 to 2.6, primarily because of fall freezes (2.1 in ***burn*** vs. 1.2 in ***control***; Table 5). At Ocate, ***burn*** reduces the number of favorable periods from a mean of 9.3 to 8.1 and from 3.1 to 3.0 at both Allen Canyon and Circle Cross, but has a slightly positive influence on the number of favorable establishment periods at Archuleta Mesa (Table 5).

In some cases, a period favorable for seedling establishment extended beyond 45 days (Table 6, values in boldface type). In the ***control*** simulation, there were 20 such extended runs of favorable days, lasting, on average, an additional 27 days beyond the minimum threshold period defined as necessary for seedling establishment (Table 6), providing, presumably, a positive growth opportunity. In the ***burn*** simulation, there were 10% fewer such periods (18) and they were 2.4% shorter, lasting an average of 25 days beyond the minimum favorable period for establishment. For ***burn*** simulations at individual sites, Cebollita had both the greatest reduction of the number of extended periods, 40% compared with ***control***, and the greatest shortening in the length of extended periods, 6% compared with ***control*** (Table 6).

End of the drought

Conditions for regeneration became more favorable at the study sites as the drought ended and moisture increased, vegetation cover grew, and the effects of the fires faded. Longer control simulations (presented in Feddema et al. 2013) indicate that the midcentury period of drought had much reduced regeneration rates when compared with both the earlier and later periods in the 20th century, in agreement with the expectation that the 1950s drought suppressed regeneration. The sites that had low rates of regeneration during the drought years display slowly increasing rates in the years after the drought ended. At Cebollita (Fig. 1), both model predictions and observations suggest a gradual increase in regeneration in the decades after the drought. Observed regeneration was most abundant at Archuleta Mesa during the mid-1980s (Fig. 2). At Allen Canyon (Fig. 3) and Circle Cross (Fig. 4), observed regeneration increased only very slightly in the late 1970s and late 1980s, matching the predicted favorable conditions. In contrast, at Ocate (Fig. 5), where the fire occurred near the end of the drought, observed regeneration is abundant in most years after the fire, declining only when the site became hyperdense.

Discussion

Our research predicts that a specific climate window critical to the capacity of southwestern ponderosa pine trees to regenerate is narrowed by a synchronous occurrence of high-severity fire and drought. At five high-severity fire sites that occurred during the 1950s drought in NM, we empirically identified several pathways of recovery following high-severity fires during drought. Four out of five sites are still dominated by shrubs and grass, with slow trends toward the re-establishment of ponderosa pine trees; one site recovered to dense forest.

Our simulations of fire effects predict few opportunities for regeneration in most years following a fire during drought at Cebollita, Allen Canyon, Archuleta Mesa, and Circle Cross. Cebollita, with the earliest fire date in the drought, appears to have suffered the most. Ocate, which burned at the tail end of the drought, recovered far faster than the other sites. This site consistently had higher numbers of days with climate conditions favorable for germination and, particularly, the number of days of favorable climate conditions for establishment and growth of seedlings following germination, since the 7 postfire years overlapped with the trend toward a wetter period. Because there is very limited data in these experiments, statistical validation of

Table 6. Maximum no. of days of favorable climatic conditions for seedling establishment following the first day of favorable climate conditions for germination predicted by ***control*** vs. ***burn*** simulations for the first 7 years after high-severity fires (years with multiple runs are separated by unfavorable climatic conditions).

	Maximum no. of days of favorable climatic conditions for seedling establishment											
	Fire site											
	Cebollita (1945)		Archuleta Mesa (1951)		Allen Canyon (1951)		Circle Cross (1953)		Ocate (1956)		Mean days (*n* events)	
Year after fire	***Control***	***Burn***	***Control***	***Burn***	***Control***	***Burn***	***Control***	***Burn***	***Control***	***Burn***	***Control***	***Burn***
1st	26	0	**77**	**76**	0	0	0	0	**58** 25	**58**	**46.5 (4)**	**67.0 (2)**
2nd	38	38	0	0	0	0	**52**	**52**	**124**	**124**	**71.3 (3)**	**71.3 (3)**
3rd	**52** **46** 20	**51** 41 8	0	0	0	0	0	0	**84**	**84**	**50.5 (4)**	**46.0 (4)**
4th	**158**	35 **93**	6	6	**52**	**52**	**55** 33	**54** 30	**59**	**51**	**60.5 (6)**	**45.9 (7)**
5th	0	0	0	0	0	0	**107**	**107**	**68**	**62**	**87.5 (2)**	**84.5 (2)**
6th	**49**	43	**59** **70**	**59** **70**	**55** 33	**54** 30	0	0	0	0	**53.2 (5)**	**51.2 (5)**
7th	**64**	**64**	0	0	**107**	**107**	38	33	**47**	**50**	**64.0 (4)**	**63.5 (4)**
Mean days (*n* events)	**56.6 (8)**	**46.6 (8)**	**53.0 (4)**	**52.8 (4)**	**61.8 (4)**	**60.8 (4)**	**57.0 (5)**	**55.2 (5)**	**66.4 (7)**	**71.0 (6)**	**61.9.0 (4)**	**61.3 (3.9)**

Note: Numbers in boldface type meet the 45-day favorable climate conditions threshold for seedling establishment.

these effects are difficult, and this is further complicated by the fact that the fire simulations do not apply constant changes over the 7-year period; however, such an assessment, using longer simulations periods, is presented in Feddema et al. (2013). Feddema at al. (2013) also suggest that the 1950s drought alone severely reduced ponderosa pine regeneration rates. We predict that the impacts of high-severity fire impair regeneration beyond the effects of drought.

Our model suggests that in a post-high-severity fire environment during drought, fewer favorable opportunities for germination occur, there are fewer periods in which germinated seedlings can establish, there is a shortening of growth periods after establishment, and more adverse conditions occur owing to increased moisture stress and to later spring and earlier fall hard freezes. We assume that germination occurs whenever favorable threshold conditions of moisture and temperature are met during the year (Table 4). While early spring germinations are desirable, because more time is available for seedling establishment, these seedlings are also at risk from lethal spring freezes. Fire-induced conditions can lower spring temperatures, allowing freeze events to suppress germination until after the spring snowmelt has passed. In postburn environments, higher evapotranspiration rates and higher runoff rates lower soil moisture in the summer, which in turn inhibits germination. Drought in the spring and summer is also a major cause of seedling mortality (Rietveld and Heidmann 1976). In the fall, sparse vegetation cover and lower soil moisture lead to earlier freezes, truncating any ongoing favorable establishment period. These effects all occur during the season of germination, the critical season within the series of years favorable for ponderosa pine regeneration.

The timing of the historical fire during the drought appears to have had an effect on the capacity of trees to regenerate. At the four sites that recovered primarily to shrubfields or grasses, the high-severity fires burned from the very start of the drought to about midway through it. For these sites, climate conditions either remained dry or actually worsened for some years after the fire. Cebollita, which burned in the first year of the drought, recovered very slowly, despite the very small size of the burn and the proximity of unburned seed trees. Ocate, on the other hand, burning just at the end of the drought, recovered to hyperdense forest, despite the large size of the burn area.

High-severity fire clearly has other large-scale impacts in addition to microclimate conditions and ecological competition that determine the potential for ponderosa pine recovery. For an integrated understanding of the potential for forest resilience, models of vegetation recovery in the novel conditions that follow high-severity fire should incorporate such factors. An integrated model would include altered surface-energy budgets — including albedo, turbulence, and latent and sensible heat (Peñuelas et al. 2009), together with altered hydrologic systems including rates of snow sublimation and hydrophobic soil traits, which may accumulate at larger landscape and longer temporal scales. Our study did not address the important influence of competition from other species on ponderosa pine recruitment, particularly the establishment of dense shrubfields. Shrub species typically are present beneath mature ponderosa pine canopy and are able to quickly recover after fire. Although the robust response of shrubs at these sites suggest that the resprouting mechanism of many shrub species confers an advantage in postfire conditions, it is also clear from our results that the re-establishment of modest numbers of ponderosa pine trees within the shrubfields is possible. The role of ecological competition in the recovery of ponderosa pine forest after high-severity fire needs explicit study.

Our model suggests that high-severity fires can affect regeneration and establishment by altering microclimatic conditions. Even slight changes, taken together, and for a species sensitive to climate conditions like ponderosa pine, can make a difference in the years after a fire. Where this alteration affects conditions on the margin, they can lead to altered regeneration outcomes. A regeneration delay may allow alternative vegetation to dominate the site for some period of time and alter community flammability.

Conclusion

High-severity fires have increased dramatically in the US Southwest in the current ongoing period of drought. Novel post-high-severity-fire environments are becoming common in the Southwest. Microclimate conditions critical for ponderosa pine regeneration are altered by the unique conditions presented by postfire conditions — higher temperatures and higher water stress — in ways that enhance and exacerbate drought conditions. High-severity fires will unquestionably continue to accom-

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pany drought in southwestern ponderosa pine forests. The unprecedented conditions presented by anthropogenic high-severity fires during drought appear to delay, but not ultimately inhibit, the recovery of ponderosa pine forests.

There are, however, several worrying future scenarios. First, there is a strong interaction between fire regime and vegetation type. Shrubfields function in many different ways from forests in nutrient and hydrologic cycling, but also in disturbance regimes. Often a highly flammable community, shrubfields support fires with different characteristics. We suggest that changes in fuel structure and composition consequent to these recoveries — even if only during the drought years — can initiate a repeat high-severity fire regime, further reducing the potential for recovery by eliminating remnant seed source trees and damaging soils. In fact, large proportions of many 1950s high-severity fire sites in the Southwest have recently reburned in a second high-severity fire in the drought that has prevailed in NM since ~2000. For example, a fire reburned about half of the Allen Canyon site in 2004 (6080 ha) in the dense oak thickets that regenerated after the 1951 fire. Virtually the entire dense young ponderosa pine forest that reestablished on the site of the 1951 Capitan Fire reburned in a second stand-destroying fire in 2002 (18 000 ha). Hyperdense young ponderosa pine forests, such as that covering the Ocate site, but equally, the hyperdense shrub stands on the Archuleta Mesa, Circle Cross, and Allen Canyon study sites, are highly susceptible to a second high-severity fire. A slow trend toward ponderosa pine establishment within shrub or grass communities can be abruptly ended by a reburn. Ponderosa pine is poorly adapted to regenerating under such a fire regime. We suggest that there is currently a high potential for southwestern ponderosa pine forests to be entrained in a new fire regime — one of recurrent high-severity fires, replacing the historic regime of recurrent cool fires.

A second worrying possibility for southwestern forests is the potential for the replacement of periodic drought by more constant warmer and drier conditions under a climate change scenario. Our results point toward the kinds of mechanisms by which future drought and global change type drought may become a constraining factor in the regeneration of trees and the recovery of forests after high-severity fires that accompany such conditions. An analysis of longer term scenarios of combined fire and climate change presented in Feddema et al. (2013) suggest just such results — a future scenario of warming climate and high severity-fire all but eliminates ponderosa pine regeneration.

Remediation of sites both immediately after such a burn and after alternative vegetation becomes established may prove difficult at landscape scales. Managers should be aware that new post-fire assemblages may support repeat high-severity burns, but they may have few tools to treat novel postfire communities. Our study suggests that the case for forest treatments to reduce the risk of high-severity fires through thinning and the use of prescribed fire is compelling. Allen et al. (2010) point out that forest mortality generally happens rapidly, in fires or insect infestations. In contrast, regeneration and establishment of long-lived tree species after disturbance has been seen to occur over a broad period of time. But novel disturbance regimes may lead to landscape-scale ecosystem disruption. The ponderosa pine forests of the Southwest may be facing an abrupt loss of resilience under an anthropogenic high-severity fire regime and natural or global-warming type drought conditions.

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