How resilient are southwestern ponderosa pine forests after crown fires?

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Abstract: The exclusion of low-severity surface fire from ponderosa pine (*Pinus ponderosa* P. & C. Lawson) forests of the Southwest has changed ecosystem structure and function such that severe crown fires are increasingly causing extensive stand mortality. This altered fire regime has resulted from the intersection of natural drought cycles with human activities that have suppressed natural fires for over a century. What is the trajectory of forest recovery after such fires? This study explores the regeneration response of ponderosa pine and other species to crown fires that occurred in the region from the late 1940s to the mid-1970s. We address two main questions: (1) What is the success of ponderosa regeneration and establishment, and (2) Can these sites, burned in stand-destroying fires, be "captured" by other species on the scale of decades? Two main trajectories of recovery were found: (1) establishment of unnaturally dense ponderosa pine stands vulnerable to further crown fire and (2) establishment of nonforested grass or shrub communities.

Résumé : L'exclusion des feux de surface peu sévères dans les forêts de pin ponderosa (*Pinus ponderosa* P. & C. Lawson) du Sud-Ouest a modifié les fonctions et la structure de l'écosystème de telle sorte que des feux de cime sévères causent de la mortalité de plus en plus importante parmi les peuplements. Cette modification du régime de feu est le résultat combiné des cycles naturels de sécheresse et de l'activité humaine qui a supprimé les feux d'origine naturelle depuis plus d'un siècle. Quelle est la trajectoire de la récupération de la forêt après de tels feux? Cette étude explore la réaction de la régénération de pin ponderosa et des autres espèces aux feux de cime qui sont survenus dans la région entre la fin des années 1940 et le milieu des années 1970. Les auteurs ont examiné deux questions principales : (1) Quel est le taux de succès de la régénération et de l'établissement du pin ponderosa? (2) Est-ce que ces sites, une fois brûlés par des feux qui détruisent le peuplement, peuvent être envahis par d'autres espèces après plusieurs décennies? Ils ont observé deux voies principales de récupération : (1) l'établissement de peuplements artificiellement clairsemés de pin ponderosa vulnérables à d'éventuels feux de cime et (2) l'établissement de communautés non forestières d'herbacées et d'arbustes.

[Traduit par la Rédaction]

Introduction

What happens to forest ecosystems when key natural processes, such as disturbance regimes, are drastically deflected by human impacts? In southwestern ponderosa pine (*Pinus ponderosa* P. & C. Lawson) forests, a century or more of domestic grazing, logging, and fire suppression has altered the fire regime from one of frequent, low-impact surface fires to one of severe crown fires that cause extensive stand mortality. If history matters in the development of natural systems (Ricklefs 1987), how is the alteration of this key process changing the patterns and dynamics of the regional ponderosa pine forest? That is, how resilient is this system to a human-induced fire regime that is markedly outside the range of natural variability?

The concept of range of natural variability (RNV) refers to the spectrum of conditions characterizing dynamic systems over time and space (Morgan et al. 1994; Landres et al. 1999). RNV can provide a benchmark against which human alterations in dynamic systems can be evaluated (Stephenson 1999). In southwestern ponderosa pine forests, RNV prior to fire suppression has been extensively reconstructed using historical records, dendrochronology, stand reconstruction, and relict stands (e.g., Swetnam and Baisan 1996; Fulé et al. 1997; Mast et al. 1999; Covington 2003). For at least 300–500 years prior to the late 19th century, a regime of high-frequency, low-intensity fires prevailed (with return intervals of approx. 2–20 years), while low-frequency, high-intensity crown fires were rare or nonexistent (Swetnam and Baisan 1996). An evolutionary environment of frequent, low-intensity fire promoted adaptive traits such as thick bark, rapid seedling growth, longevity, resinous needles, and flammable litter (Agee 1998). Surface fires thinned seedlings, left the overstory largely intact, and in most areas resulted in relatively open stands of uneven-aged ponderosa pine. While the timing varied somewhat from place to place, the rapid onset of intensive livestock grazing in the late 19th century, followed soon after by active fire suppression efforts, brought an abrupt end to the surface-fire regime throughout the regional forest (Swetnam and Baisan 1996).

The large-scale shift to stand-destroying fires in southwestern ponderosa pine forests over the past century tracks a marked shift toward unprecedented increases in small-tree density, surface fuels, and landscape connectivity caused by

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human activities (e.g., Weaver 1951; Covington and Moore 1994*a*; Swetnam et al. 1999). Fire suppression, grazing, and other activities created heavy ladder fuels that now conduct fires into the canopy and burn hotly enough to cause large areas of near-complete tree mortality. Stand-destroying fires, historically rare in these forests, are now increasing in size (e.g., Swetnam 1990; Covington et al. 1997). Prior to the 1960s, a 20-ha crown fire was considered large (Friederici 2003), whereas in recent years single crown-fire events have burned thousands of hectares (Dahm and Geils 1997; Swetnam and Betancourt 1998).

Climate trends affect the severity, extent, and synchrony of fires in southwestern forests (Swetnam and Betancourt 1992,1998). The phenomena of stand-destroying fires first manifested in the region a half century or so ago (Swetnam 1990; Covington and Moore 1994*b*) when decades of anthropogenic fuel accumulation intersected with the regional drought of the 1950s, which prevailed for varying time periods and severity in different areas. Local climatic conditions also influence recovery from fire, since ponderosa pine regeneration and establishment has been shown to be sensitive to specific precipitation and temperature patterns (Savage et al. 1996).

Relatively short-term effects of recent severe fires have been investigated (e.g., Foxx 1996; Allen 1996; Crawford et al. 2001), but we have little understanding of the longer term effects of such fires on forest demography and structure. Here we study vegetation recovery at 10 sites across the Southwest where crown fires burned from the late 1940s to the 1970s, to investigate ponderosa pine forest resilience to such fires. We use the term "recovery" to refer to the trajectory of the establishment of vegetation after fire and not to the recovery of a forest similar to prefire or RNV structures. In addition, we use Holling's (1973) definition of resilience as "the degree to which a system can absorb disturbance — kind, rate and intensity — before it shifts into a fundamentally different behavior". Specifically, we ask the question, Are stand-destroying crown-fire burn sites recovering to the ponderosa pine forest type on the decadal scale?

It has been suggested that natural communities can exist in alternative states (e.g., May 1977; Van de Koopel 2001). 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. In ecological terms, this phenomenon is consistent with the "inhibition model" proposed by Connell and Slatyer (1977), where a species assemblage captures a site for some period of time without a successional trend. Varying initial conditions and the spatial scale of a disturbance (Gilpin and Case 1976) can result in different trajectories of community development. Petraitis and Latham (1999) describe the mechanism pushing a system into another state (sensu Moir and Mowrer 1995) as a "switch". Here we consider alternative states to include those of structure as well as composition, and we ask whether anomalous crown fires are driving these forests past a critical threshold into new states via the "switch" of a novel disturbance regime.

The study used a natural experiment and thus lacked experimental control. There are numerous uncertainties related to variance in site factors, prefire stand structure, and postfire management history that reduce site comparability and constrain interpretation of results. Moreover, a set of only 10 fires scattered across a broad region constrains our conclusions. Our intention is not to analyze the causes of variation in regeneration pathways at different sites. Instead, we attempt a broad-brush portrait of forest recovery at crown-fire burn sites across the regional landscape.

Materials and methods

Study sites

We sampled woody species recruitment at 10 sites in the Southwest where ponderosa pine forests burned in crown fires that occurred from 1948 to 1977. Sites were selected from the relatively small set of old crown fires provided by the nine national forests in the Southwest and were considered suitable if they (1) were surrounded by mature, near-monotypic ponderosa pine forest, (2) were located centrally in the ponderosa pine range, and (3) had documentation on fire location, size, and behavior. In all cases, burn sites were clearly demarcated from surrounding relict stands by a visible contrast in stand structure. Sites were on gentle to moderate slopes (<8° for most sites; range 2°–14°) (Table 1). The elevation range of the sites was <600 m (Table 1).

Burn sites were located throughout the regional forest, across the Mogollon Rim in Arizona, and in northern and southern New Mexico (Fig. 1). Forests with a dominant ponderosa pine overstory occur from 2150 to 3000 m under a similar climate regime. Mean annual temperature 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). Climate variation is reflected in shifts in associated understory vegetation. Shrubs tend to be widely and irregularly spaced (Howard 2003). In the more xerophytic sites, broadleaf evergreen species predominate in the understory, and at the lowest elevations woody species occur from adjoining pinyon–juniper woodlands (primarily *Pinus edulis* and *Juniperus* spp.). In the more mesophytic zones at higher elevation, the ponderosa pine forest grades into mixed-conifer forest with few understory shrubs and a grassy understory of *Festuca arizonica* and *Muhlenbergia montana*.

The burn sites studied vary by factors such as time since burn, environmental traits, postfire climatic conditions, and postfire manipulations (Table 1) and thus are not comparable. Prefire forest structure and compositional characteristics, which we have been unable to document, may also have influenced both the nature of the fire and the vegetation that established afterward. We assume frequent fires ceased at the study sites around the same time as the synchronous regional decline in the late 19th century (Swetnam and Baisan 1996).

Vegetation sampling

At each burn site, tree and shrub structure, herbaceous cover, and slope were sampled in 2001 or 2002. The sampling design consisted of a series of five 1 km long parallel transects at each burn site, spaced 500 m apart, and located centrally in the burn. At 200-m intervals along each transect, a 10 m × 10 m plot was established, for a total of 30 plots per site. Within each plot, we recorded diameter and species of adult trees (≥1.4 cm in height and diameter at breast height (dbh) ≥6 cm), counted the number of saplings (≥1.4 m

Table 1. Site characteristics and qualitative land-use variables at each site.

Fire site	Fire date	Fire size (ha)	Sampling elevation (m)	Mean slope (min.–max.)	Current dominant vegetation	Planted with trees?	Planted with grass seed?
Fort Valley	1948	837	2580–2630	4° (0°–8°)	Forest	Yes	Yes
A1 Mountain	1950	406	2380–2620	5° (0°–20°)	Meadow	No	Yes
Faught Ridge	1950	1 012	2370–2440	3° (0°–8°)	Shrubfield and forest	No	No
Escudilla	1951	8 000	2920–2960	8° (1°–18°)	Forest	No	Yes
Circle Cross	1953	9 308	2580–2660	11° (4°–27°)	Shrubfield	No	No
Ocate	1956	20 000	2850–2920	4° (1°–7°)	Forest	No	No
Slaughter Mesa	1967	1 192	2960–2990	2° (0°–15°)	Meadow	Minor	Minor
Black River	1971	36 420	2600–2650	14° (0°–32°)	Forest	Minor	No
Bull Flat	1971	890	2610–2700	5° (0°–10°)	Forest	Multiple	Minor
La Mesa	1977	6 180	2510–2600	4° (0°–10°)	Meadow and forest	No	Yes

Fig. 1. Location of 10 sampled crown-fire sites in the southwestern United States, with distribution of *Pinus ponderosa* represented by shaded area.

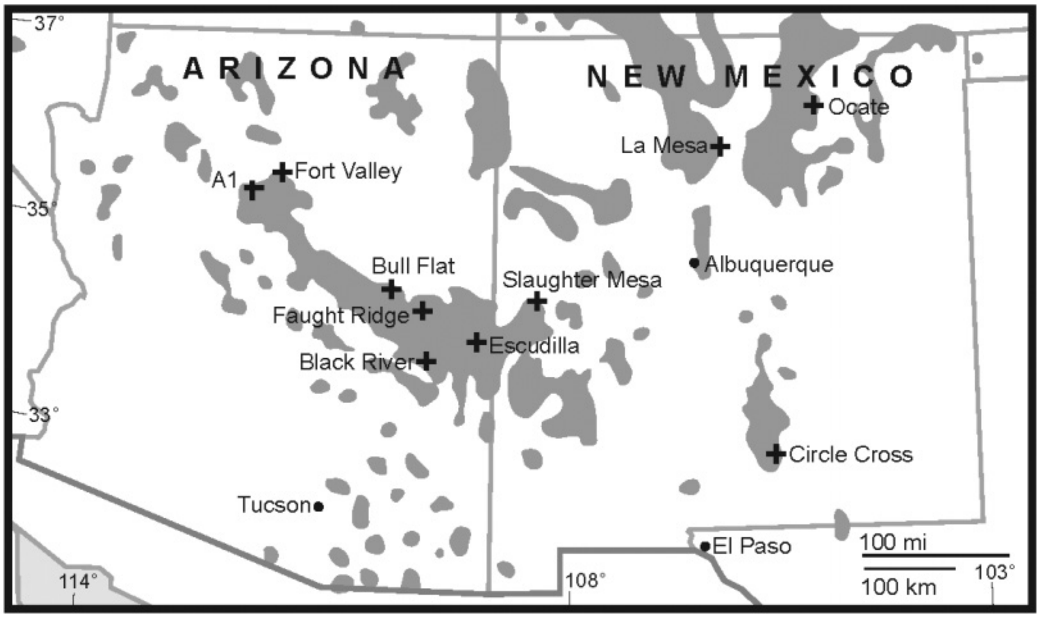


Table 2. *Pinus ponderosa* adult tree density, basal area, diameter at breast height (dbh), and ground cover.

	Density (trees·ha^{-1})		Basal area (m^2·ha^{-1})		dbh (cm)		Percent mean cover		
Fire site	Mean (SEM)	Min.–Max.	Mean (SEM)	Min.–Max.	Mean (SEM)	Min.–Max.	Grass	Forb	Total
Fort Valley	183 (31)	0–600	7.7 (1.4)	0–26.0	22 (1.1)	7–41	30	8	38
A1 Mountain	77 (31)	0–800	5.0 (1.9)	0–43.5	28 (1.4)	9–40	35	10	45
Faught Ridge	417 (04)	0–2300	5.6 (1.2)	0–30.0	12 (0.4)	7–25	2	1	3
Escudilla	616 (88)	0–1800	11.4 (1.5)	0–24.9	14 (0.5)	6–59	15	4	19
Circle Cross	40 (13)	0–300	0.8 (0.4)	0–8.0	16 (2.1)	8–32	3	2	5
Ocate	443 (66)	0–1800	10.8 (1.9)	0–45.1	16 (0.6)	6–42	37	13	50
Slaughter Mesa	20 (7)	0–100	0.9 (0.4)	0–9.1	21 (4.1)	8–34	47	7	54
Black River	600 (89)	0–1800	6.4 (1.3)	0–21.5	11 (0.5)	6–60	7	3	10
Bull Flat	757 (139)	0–3800	11.2 (1.7)	0–32.5	13 (0.4)	6–40	3	2	5
La Mesa	97 (28)	0–600	1.5 (0.8)	0–23.7	11 (1.7)	6–55	29	12	41

Note: SEM, standard error of the mean.

in height but dbh <6 cm), seedlings (<1.4 m in height), and shrub stems, and measured the slope. We estimated percent understory cover separately for herbaceous and graminoid plants in five randomly located 1-m^2 plots within each 10 m × 10 m plot, for a total of 150 plots per site. Nomenclature follows Vines (1960).

We took an increment core at 0.3 m height from every adult tree in the larger plots to broadly estimate establish-

Table 3. Mean density of woody species per hectare in 10 crown fire sites.

	PIPO			PIED			PIST			PSME			POTR		
Fire site	A	Sp	Se	A	Sp	Se	A	Sp	Se	A	Sp	Se	A	Sp	Se
Fort Valley	183	23	27	—	—	—	—	—	—	—	—	—	—	—	—
A1 Mountain	77	7	2	—	—	—	—	—	—	—	—	—	—	—	—
Faught Ridge	417	267	180	10	17	17	—	—	—	—	—	—	—	—	—
Escudilla	616	750	247	—	—	7	—	—	—	—	—	—	300	23	10
Circle Cross	40	10	63	3	20	80	—	—	—	—	—	—	—	—	—
Ocate	443	467	687	—	7	7	3	7	57	—	—	—	223	—	73
Slaughter	20	83	117	—	—	—	—	—	—	—	—	—	—	—	—
Black River	600	1033	687	—	—	—	—	—	—	—	7	23	—	—	—
Bull Flat	836	4212	2864	—	—	—	—	—	—	—	4	12	—	—	—
La Mesa	97	240	140	—	—	—	—	—	—	—	—	—	—	—	—

Note: A, adult; Sp, sapling; Se, seedling; S, shrub stem (<1.4 m). PIPO, *Pinus ponderosa*; PIED, *Pinus edulis*; PIST, *Pinus strobiformis*; PSME, monosperma; QUGA, *Quercus gambelii*; QUGR, *Quercus grisia*; RONE, *Robinia neomexicana*; ARPU, *Arctostaphylos pungens*.

ment dates of trees in the burns. Cores were prepared according to standard procedures (Stokes and Smiley 1968). Tree rings were counted, visually cross-dated, and reported in histograms as an estimate of age at coring height. Where the sample did not intercept the pith, years from innermost ring to the pith were estimated with a pith locator (concentric circles matched to the approximate curvature and density of the remaining inner rings) (Applequist 1958). Because of significant differences in postcrown fire surface conditions for growth as compared to within forest conditions, we do not correct for growth to corning height for age calculation.

Historical records

Information about the land-use history of burn sites was collected from maps and documents in Forest Service records, such as fire incidence reports, and newspaper reports. Records included data on fire location, date, and size (Table 1). In most instances, other documentation about early fires had been discarded, and oral history replaced quantified information on preburn stand structure and postburn treatments such as levels of tree planting, salvage logging, livestock grazing, and seeding with grasses. The lack of quantified information on these important factors compromises an explanation of vegetative recovery after crown fires. Old crown fires with more reliable historical documentation, generally speaking, do not exist. We view this study as a first step in characterizing the trajectory of vegetative change after crown fires in anticipation of an investigation of the successional mechanisms of recovery.

Results

Ponderosa pine forest reestablished across five of the postburn sites. Of the remaining sites, ponderosa pine trees coexist with large areas of shrubfields on two other sites and with meadow on another site. Meadows dominate the remaining two sites.

Woody-species density and structure

Forest

At five sites, a dense ponderosa pine forest has established or is establishing. Ponderosa pine densities range from moderately dense to very dense (Table 2). This includes sites that were planted with ponderosa pine seedlings and those that were not (Table 1), those with ongoing regeneration, and those with little continued establishment (Table 3). Ponderosa pine densities are high at Escudilla (616 adults·ha^{-1}, 750 saplings·ha^{-1}, 247 seedlings·ha^{-1}), Ocate (443 adults·ha^{-1}, 467 saplings·ha^{-1}, 687 seedlings·ha^{-1}), Black River (600 adults·ha^{-1}, 1033 saplings·ha^{-1}, 687 seedlings·ha^{-1}), and Bull Flat (836 adults·ha^{-1}, 4212 saplings·ha^{-1}, 2864 seedlings·ha^{-1}) (Table 3). The number of saplings and seedlings at these sites often equal or exceed the number of adults. At Fort Valley, a notably lower density forest has established (183 adults·ha^{-1}, 23 saplings·ha^{-1}, 27 seedlings·ha^{-1}).

Mixed forest and shrubfields

At two sites, ponderosa pine stands are interspersed with shrubfields. At Circle Cross, a low level of ponderosa pine regeneration (40 adults·ha^{-1}, 10 saplings·ha^{-1}, 63 seedlings·ha^{-1}) coexists with highly dense *Quercus grisia* (grey oak) and *Quercus gambelii* (Gambel oak) shrub thickets and a low density of other tree species (Table 3). Faught Ridge is characterized by robust ponderosa pine regeneration (417 adults·ha^{-1}, 267 saplings·ha^{-1}, 180 seedlings·ha^{-1}) on ridgetops. However, large swaths of the site are covered exclusively by dense *Arctostaphylos pungens* (manzanita) thickets and completely lack ponderosa pine regeneration (Table 3). Fourteen of 30 plots (47%) at Circle Cross and 8 of 30 plots (27%) at Faught Ridge lacked adult trees.

Mixed forest and meadow

Mean density values of ponderosa pine are much lower at La Mesa (97 adults·ha^{-1}, 240 saplings·ha^{-1}, and 140 seedlings·ha^{-1}), the most recent burn (1977). Dense stands of ponderosa pine trees occur near seed sources at the edges of the burn. Fifteen of 30 plots (50%) are dominated by meadow and lack pine trees.

Meadow

Two sites, A1 Mountain and Slaughter Mesa, are dominated by meadow communities (Table 2). At both sites, a ground cover comprised primarily of grass species is correlated with low levels and very low levels, respectively, of ponderosa pine regeneration (A1 Mountain: 77 adults·ha^{-1},

ABCO			PIEN			JUDE			JUMO			QUGA		QUGR		RONE	ARPU
A	Sp	Se	A	Sp	Se	A	Sp	Se	A	Sp	Se	A	S	A	S	S	S
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	50	53	77	—	—	—	53	586	50	57	—	5383
3	3	30	—	—	3	3	13	—	—	—	—	283	960	—	—	—	—
—	—	—	—	—	23	53	83	133	—	3	—	90	20276	—	35997	1073	—
37	43	297	—	—	—	—	—	57	—	—	—	3	1477	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	7	3	—	—	—	500	2403	—	63	1073	—
—	4	16	—	—	—	—	—	—	—	—	—	36	1020	—	—	—	—
—	—	—	—	—	—	—	—	7	—	—	33	—	1876	—	—	2650	—

Pseudotsuga menziesii; POTR, *Populus tremuloides*; ABCO, *Abies concolor*; PIEN, *Picea engelmanii*; JUDE, *Juniperus deppeana*; JUMO, *Juniperus*

7 saplings·ha^{-1}, 2 seedlings·ha^{-1}; Slaughter Mesa: 20 adults, 83 saplings, 117 seedlings ha^{-1}). Many plots at both sites contain only grasses: 67% (21 of 30) of the A1 Mountain and 80% (24 of 30) of the Slaughter Mesa plots lack trees. The domination by grass species at these sites is reflected in the concentration of regeneration of ponderosa pines near meadow edges, close to seed sources.

Understory cover

Understory cover ranges widely (3%–54%) across the 10 sites (Table 2). Forb cover is <5% at over half the sites and <12% at all sites. Grass cover ranges from 2% to 47%. Grass cover values are predictably highest at sites dominated by meadow, including A1 Mountain (35%) and Slaughter Mesa (47%). Grass cover values are lowest in sites with dense shrub populations, including Circle Cross (3%) and Faught Ridge (2%), and relatively low at sites with dense tree populations, including Bull Flat (5%), Black River (10%), and Escudilla (19%).

Tree size

Ponderosa pine trees at most sites are small, with a mean dbh of 16 cm or less (Table 2). Mean dbh values at Slaughter Mesa (21 cm; range 8–34 cm), Fort Valley (22 cm; range 7–41 cm), and A1 Mountain (28 cm; range 9–40 cm) are larger, yet still relatively small. Mean ponderosa pine basal area values are also low, ranging from 0.8 to 11.4 m^2·ha^{-1} (Table 2). Neither mean dbh nor stand basal area for ponderosa pine trees shows a linear trend associated with time since burn.

Other tree species

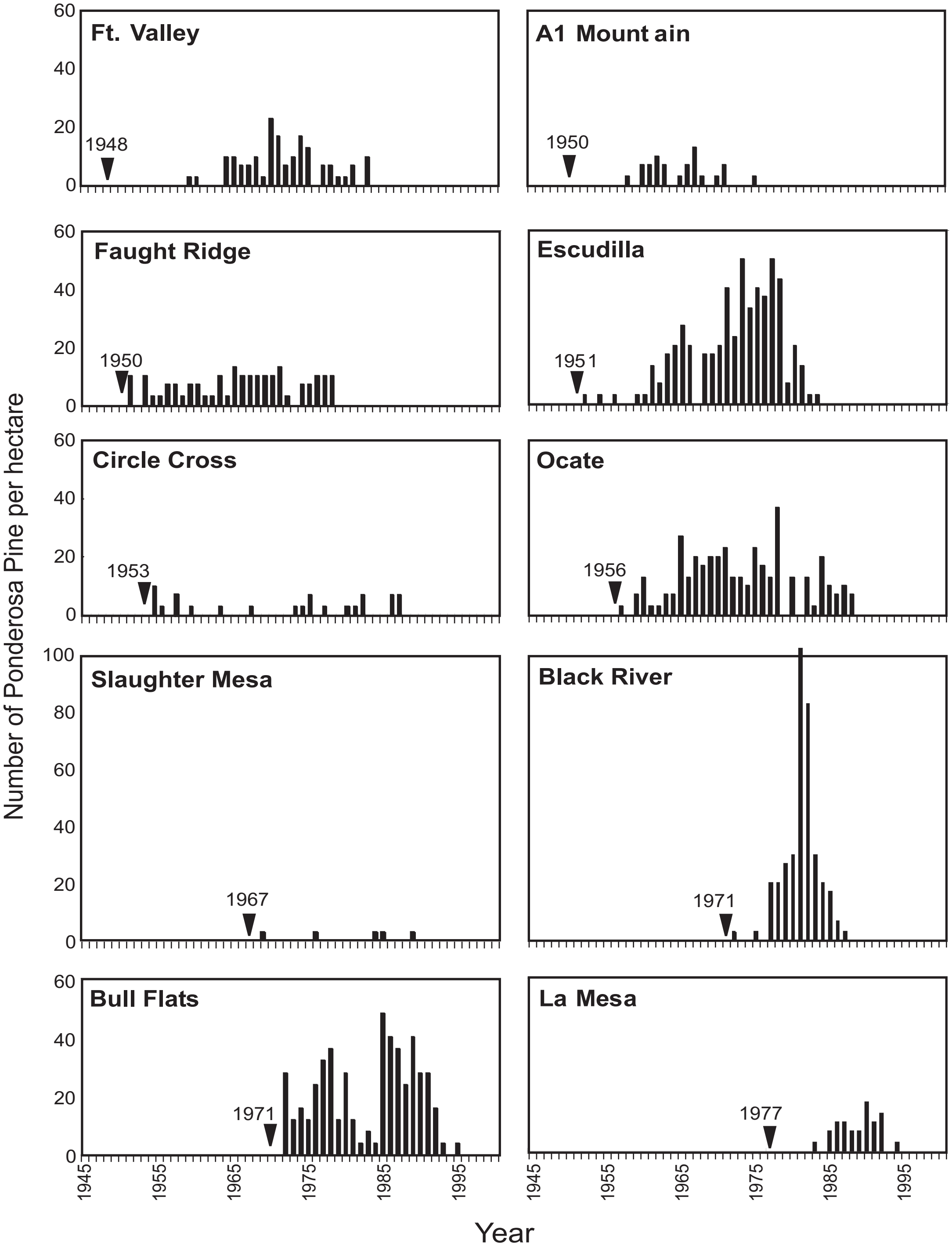
At most sites, ponderosa pine was the most abundant of any tree species. All adult trees at A1 Mountain, Fort Valley, La Mesa, Slaughter Mesa and 96% at Bull Flat are ponderosa pine trees. Lower percentages of adult ponderosa pine trees (72% at Faught Ridge, 63% at Ocate, 55% at Black River, 51% at Escudilla, and only 22% at Circle Cross) reflect the degree of success of other tree species in establishing postburn (Table 3). These species include primarily those that commonly occur in low numbers in ponderosa pine dominated forests, for example, *Populus tremuloides*, *Pinus edulis*, *Quercus* spp., and *Juniperus* spp. A higher proportion of mixed-conifer forest species, specifically *Abies concolor* (white fir) and *Populus tremuloides*, occur at higher elevation (approx. 2900 m) burn sites that regenerated to forest, such as at Escudilla and Ocate. *Pseudotsuga menziesii* (Douglas-fir) occurs at mid-elevation (approx. 2600 m) burn sites that regenerated to forest or shrubfield, such as Black River, Bull Flats, and Circle Cross.

Tree establishment dates

A total of 1119 trees (922 of which were ponderosa pine) were aged to pith at coring height. Because we do not correct for growth to coring height for age, the actual dates of establishment precede the dates reflected in Fig. 2. In northern Arizona, 2–7 years is considered typical for ponderosa pine seedling for growth to our coring height of 0.3 m (Sackett 1984). While there is an inherent uncertainty, we conservatively estimate up to 5–10 years for the number of years of growth to coring height, or less where postfire regeneration conditions were favorable. A shift backward in time of establishment dates on this order is consonant with the time since fire. Recruitment of ponderosa pine trees appears to commence soon after fires, even at those sites with little overall regeneration (Fig. 2). It also appears that at many sites, if establishment dates are shifted back in time up to a decade, there was an abundance of regeneration that began during the years of the 1950s drought and which survived for many decades (Fig. 2).

At many sites, fires were severe enough to cause virtually complete mortality, although there may have been some unauthorized removal of live trees by salvage logging. Fort Valley, A1 Mountain, and La Mesa had no living remnant trees in the burn. Numbers of living remnant ponderosa pine trees are low at half the sites: Slaughter Mesa (3 trees·ha^{-1}), with a median date of establishment (mde) of 1954; Black River (10 trees·ha^{-1}; mde = 1885), Escudilla (53 trees·ha^{-1}; mde = 1939), Circle Cross (40 trees·ha^{-1}; mde = 1940), and Ocate (33 trees·ha^{-1}; mde = 1949). At the remaining sites, 200 ponderosa pine trees·ha^{-1} survived the fire at Faught Ridge (mde = 1940) and 273 trees·ha^{-1} at Bull Flat (mde = 1962). Patches of trees often survive intense fires because of the mosaic of intensities characteristic of most wildfires (Turner et al. 1989; Fulé et al. 2002). Virtually all of these ponderosa

Fig. 2. Histograms of abundances of postfire adult *Pinus ponderosa* trees by date of pith at coring height. Arrow indicates crown fire date.



pine trees germinated in the 20th century, providing postburn seed sources.

The vast majority of tree species other than ponderosa pine appear to have regenerated after the fires: one third of the *Populus tremuloides* at Ocate (67 trees·ha^{-1}, mean pith date = 1956, SEM = 2), all the *Abies concolor* at Ocate (37 trees·ha^{-1}, mean pith date = 1976, SEM = 1), all *Populus tremuloides* at Escudilla (300 trees·ha^{-1}, fire date = 1951, mean pith date = 1956, SEM = 0.5), and all *Quercus gambelii* at Circle Cross (43 trees·ha^{-1}, fire date = 1954, mean pitch date = 1957, SEM = 3). Both *Populus* and *Quercus* resprout, which accounts for the short postburn establishment dates.

Discussion

Two general trajectories of recovery emerged in the decades after stand-destroying crown fire at these sites: (1) a robust recovery to ponderosa pine forest, with densities in excess of ranges of natural variability, or (2) a deflection of forest recovery toward another vegetation state.

Multiple lines of evidence have been used to construct a general consensus on RNV for prefire-suppression southwestern ponderosa pine forest structures, including early historical accounts (e.g., Beale 1858; Lang and Stewart 1910), historical photographs (e.g., Fulé et al. 2002), early forest inventories (Lang and Stewart 1910; Woolsey 1911), and dendrochronological reconstructions (e.g., White 1985; Fulé et al. 1997; Mast et al. 1999). These studies and accounts tend to converge on a characterization of typical prefire suppression forest structure that was open and park-like with relatively low tree densities. For example, Woolsey (1911) conducted a census of ponderosa pine at nine sites in the region and found a mean of 88 trees·ha^{-1} with a dbh > 10.2 cm (ranging from 57 to 141 trees·ha^{-1}). In specific survey sites in New Mexico, ponderosa pine densities with dbh > 10.2 cm averaged 36 trees·ha^{-1} in north central New Mexico; 23 trees·ha^{-1} in western New Mexico; 47 trees ha^{-1} in southeastern New Mexico; 57 and 38 trees·ha^{-1} in northeastern New Mexico, and 116 and 131 trees·ha^{-1} in west central New Mexico (Woolsey 1911). Similar surveys by Lang and Stewart (1910) on the Kaibab Plateau reported a mean stand density of 128 trees·ha^{-1} for ponderosa pine trees with dbh > 15.2 cm in northern Arizona on the Kaibab Plateau.

Stand structure reconstructions of prefire-suppression ponderosa pine forests found comparable densities in northern Arizona ponderosa pine forests, for example, 37 trees·ha^{-1} (White 1985), 86 and 111 trees·ha^{-1} (Cooper 1960), 43 trees·ha^{-1} and 61 trees·ha^{-1} (Covington and Moore 1994*a*), 23 and 56 trees·ha^{-1} (Covington and Moore 1994*b*), 65 trees·ha^{-1} (Fulé et al. 1997), and 60 trees·ha^{-1} (Mast et al. 1999). The relevance of structural values reconstructed from historical forests should be tempered by the knowledge that contemporary climate conditions may provide a significantly different context for regeneration (Fulé et al. 2002).

This study reports far higher mean densities on many sites that reforested after crown fires than these RNV values. For most sites, minimum density values exceed the mean historical density values found in reconstructions. We recalculated mean densities of ponderosa pine trees at our forested sites using a criterion of dbh >10.2 cm to directly compare our data with Woolsey's data: Faught Ridge (mean 280 trees·ha^{-1}; standard error of the mean, SEM = 69), Black River (233 trees·ha^{-1}; SEM = 55), Ocate (320 trees·ha^{-1}; SEM = 57), Bull Flat (470 trees·ha^{-1}; SEM = 79), and Escudilla (450 trees·ha^{-1}; SEM = 62). These density values are three to five times greater than the Woolsey mean density value for a set of sites with 88 trees·ha^{-1}.

Extreme densities of adults and saplings at the reforested sites make these stands vulnerable to crown fire (Covington et al. 1997). Clearly the densest stands, such as at Bull Flat, with over 5000 adults and saplings·ha^{-1}, and Black River, with over 1600 adults and saplings·ha^{-1} (Table 3), are unlikely to escape a crown fire in the near future. Other sites vulnerable to crown fire include Escudilla (1366 adults and saplings·ha^{-1}) and Ocate (910 adults and saplings·ha^{-1}), as well as stands where ponderosa pine populations are spatially crowded, for example, Faught Ridge (684 adults and saplings·ha^{-1}) and La Mesa (337 adults and saplings·ha^{-1}). Of the sites which recovered to ponderosa pine forest, only Fort Valley may not currently be vulnerable to crown fire because of its notably lower density, especially of saplings (183 adults·ha^{-1} and 23 saplings·ha^{-1}). The density values of these reforested postcrown fire sites are comparable to contemporary stands where fire has been excluded since the end of the 19th century (e.g., Cooper 1960; White 1985; Covington and Moore 1994*a*; Fulé et al. 1997). In these forests, which have not burned since fire suppression, density can exceed presuppression values by an order of magnitude, for example, 3097 trees·ha^{-1} (Covington et al. 1997) and 2103 trees·ha^{-1} (Covington and Moore 1994*b*).

There seems to be little evidence of self-thinning in historical southwestern ponderosa pine forests (Biondi et al. 1994), nor would it have been adaptive under a low-intensity fire regime. Self-thinning has not occurred to any extent in the regional 1919 cohort, which survives as thickets of suppressed individuals and provides large amounts of ladder fuel (Covington and Moore 1994*b*; Savage et al. 1996). In some cases, prescribed fires have been used to thin stands, but their use is limited because of the challenges of burning in high-density stands (Sackett et al. 1996; Mast 2003; Fulé et al. 2004).

At the remaining study sites, recovery after crown fire was deflected entirely or partially to another vegetation type. At these sites, density values of ponderosa pine trees with ≥6 cm dbh are relatively low: densities were 77 trees·ha^{-1} at A1 Mountain, 33 trees·ha^{-1} at Circle Cross, and 17 trees·ha^{-1} at Slaughter Mesa. Species other than ponderosa pine are successful in occupying large parts of the site or even largely excluding ponderosa pine trees. At the sites dominated by grasses, one (A1 Mountain) has yet to yield to tree regeneration, while the second (Slaughter Mesa) shows a very slow trend toward ponderosa pine regeneration. Circle Cross is dominated by a shrub community, with a slow trend toward ponderosa pine regeneration. Both shrubs and grasses effectively compete or present allelopathic problems for ponderosa pine seedlings (Harrington 1981). A reburn may favor resprouting grass and shrub species and set back ponderosa pine seedling and sapling establishment. Barton (2002) documents such a conversion of a different species of pine forests to oak woodlands caused by intense fires in southern Arizona.

The herbaceous understory at the study sites is sparse. Even at the two sites dominated by meadow, A1 Mountain and Slaughter Mesa, understory plant cover is still low relative to the >60% cover that Moir and Dieterich (1988) suggest as a generality for full-meadow sites in the region. Studies have found that high-intensity fires in the ponderosa pine system can be implicated in the decline of native grasses, perhaps through negative impacts on duff layer and soil seedbed (Griffis et al. 2001; Crawford et al. 2001) and suggest that understory cover can remain sparse for decades after severe fire. Without data on prefire understory cover or soil type, however, we cannot assess the degree of recovery in understory vegetation at these sites.

A tendency for succession to vulnerable states is illustrated by a model of hypothetical transitions for ponderosa pine forest (Fig. 3). Stands that recover from stand-destroying fires into dense, or what may be considered hyper-dense, ponderosa pine forests may then follow a pathway of repeated crown fire, with similar outcomes, cycling on this pathway indefinitely or until the seed source is exhausted. Stands dominated by *Quercus* or *Arctostaphylos*

Fig. 3. Proposed model of *Pinus ponderosa* forest dynamics in the southwestern United States. PIPO, *Pinus ponderosa*; ARPU, *Arctostaphylos pungens*.

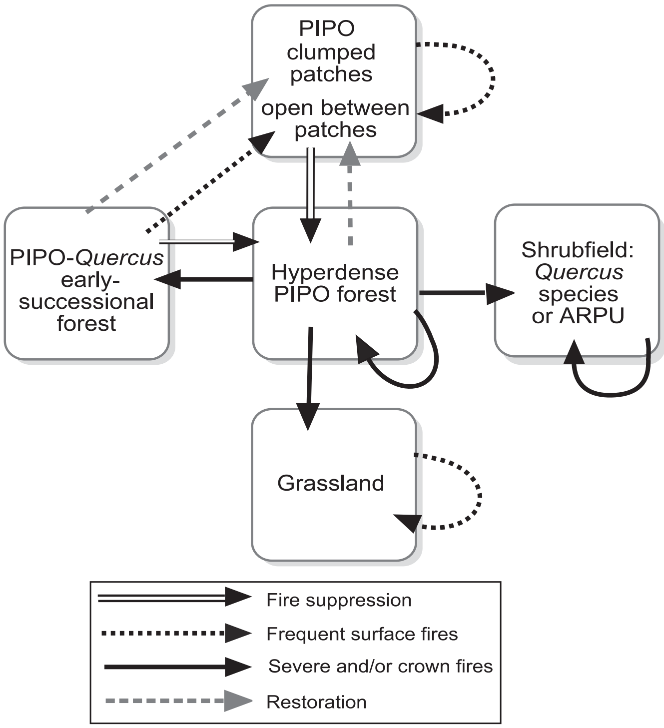
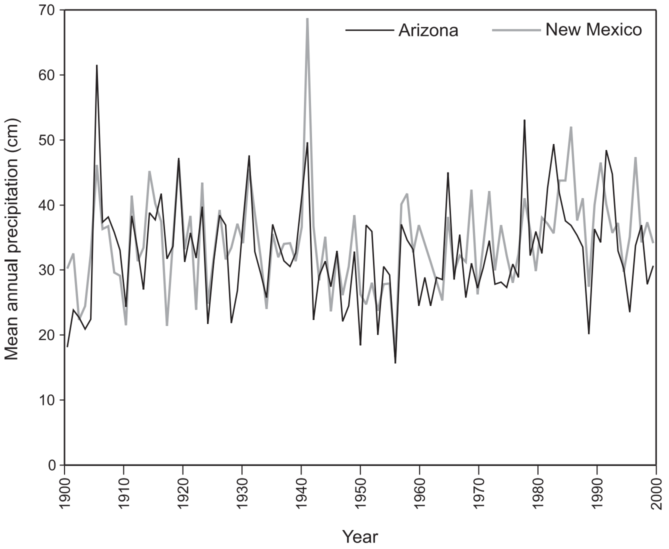


Fig. 4. Mean annual precipitation for the states of New Mexico and Arizona from 1900 to 2000. Available from http://www.ncdc.noaa.gov/oa/ncdc.html.



shrubfields, such as Circle Cross and parts of Faught Ridge, may also experience fires whose intensity would tend to reinforce this pathway. Similarly, grass-dominated sites, such as A1 and Slaughter Mesa, could be self-perpetuating if they continue to exclude ponderosa pine regeneration. Such successional pathways have not been reconstructed in presuppression ponderosa pine forests. Preburn vegetation composition and structure clearly play a significant role in the specifics of rate and kind of recovery, and the lack of such information for our study sites hampers an analysis of the fate of these stands. In the absence of another stand-destroying fire, it is unclear how further successional dynamics will play out in these unnatural stands.

Land-use factors

The current state of the vegetation at these sites reflects postburn management history, such as tree planting, salvage logging, seeding, and livestock grazing (Table 1), which preclude an explanation of recovery after burns. A program of tree planting was instituted at four sites: Slaughter Mesa, where planting failed entirely; Black River and Bull Flat, where survivors became part of a large, natural cohort; and Fort Valley, where visible rows of adults indicate that planting succeeded where natural regeneration did not. Establishment dates from cored trees are not precise enough to allow discrimination between natural regeneration and successful planting of ponderosa pine trees for Black River and Bull Flats. In addition, seeding with grasses was implemented at six sites, but with major uncertainties in the timing and amount of seeding.

Livestock grazing and salvage logging occurred at all burn sites except La Mesa. Records of intensity and continuity of grazing were poor and were generally described qualitatively as "intermittent" or "seasonal". Browsing impacts include impacts on vegetation, soil damage, and increased erosion rates (Beschta et al. 2004). Salvage logging of the dead overstory causes soil compaction and accelerated rates of soil erosion and removes structural components important for ecosystem recovery (Beschta et al. 2004). Control sites and quantitative documentation would be needed on a site-by-site basis to explore the influence of these activities on postfire recovery.

Climate factors

Recovery of vegetation is influenced by postfire climatic conditions. Some crown-fire burns studied here occurred during the most extreme drought in the southern United States in the past 300 years (Stahle and Cleaveland 1988; Meko et al. 1993) (Fig. 4). Tree-ring climate reconstructions in central western New Mexico indicate a severe event from 1945 to 1958 (Grissino-Mayer 1996). This reconstruction reflected a significant correlation with 25 other archaeological tree-ring chronologies in the Southwest, indicating a regional drought. The 1950s drought, however, varied in intensity and length from place to place in the Southwest. For example, little climatic fluctuation was recorded in tree rings during this period in northern Arizona (Biondi 1998; Salzer 2000).

The 1950s drought might have been expected to constrain ponderosa pine regeneration in those parts of the region where it was severe. Six of the crown fires sites studied occurred during this drought: in 1948 (Fort Valley), 1950 (A1 and Faught Ridge), 1951 (Escudilla), 1953 (Circle Cross), and 1956 (Ocate). Two of the sites, Fort Valley and A1, occurred near Flagstaff in northern Arizona, where the drought was not significant. Three of the sites (Faught Ridge, Escudilla, and Ocate) have moderate to high levels of ponderosa pine recruitment during this period, despite potentially unfavorably postfire climate conditions. There appears to have been no significant time lag in the timing of regeneration after the fire at these sites (Fig. 2), although this finding is tentative because of uncertainty in establishment dates.

Natural rates of regeneration in historical ponderosa pine stands have been found by some researchers to be low but relatively continuous (e.g., White 1985), even during the 1950s at sites in northern Arizona (Fulé et al. 1997; Fulé et al. 2002). Other reconstructions of past stand structure in northern Arizona stands indicate regeneration of approximately 1–4 trees·ha^{-1} per decade in the centuries prior to Euro-American influences, but showing broad peaks of tree establishment (Mast et al. 1999). These reconstructions are supported by studies suggesting that ponderosa pine regeneration is generally episodic and depends on favorable local climate conditions (Schubert 1974; Moir et al. 1997). Episodic pulses are visible in reconstructions of establishment over past centuries throughout the regional forest (Schubert 1974; Swetnam and Betancourt 1990).

Vegetation recovery following crown fires at some of the study sites resemble a natural regeneration pulse, characterized by a fairly broad time frame on the order of decades, as suggested by Mast et al. (1999). If establishment dates at these sites are reasonably reliable, we may want to reconsider the suggestion of some studies (e.g., Savage et al. 1996) that such pulses depend on specific, favorable climate conditions.

Conclusion

This study suggests that alternative recovery trajectories can result from anomalous crown fires in southwestern ponderosa pine systems on a decadal scale. Crown fires at the 10 study sites appear to fit Petraitis and Latham's (1999) notion of an abrupt "switch" that can lead ecosystems into states that differ significantly from historical structures. Uncertainties temper the generality of the study, but the community structures at many of the high-density postburn sites appear to represent anthropogenically induced states outside a natural range of variability. Other postburn sites have developed into nonforest communities that Allen et al. (2002) term "landscape scars".

The question that we cannot answer here is, How long will current states persist? Will these burn sites manifest as historical accidents, frozen on the landscape for long periods of time or merely successional stages, albeit changing slowly in some cases? One phenomenon that will promote alternative states is a fire regime that tends to reprise the current structure. If *Quercus* or *Arctostaphylos* shrubfields or hyperdense ponderosa pine foster more crown fires, the pattern will recursively create a self-perpetuating community structure. Ponderosa pine forests with structures within a natural range of variation may then not return to such sites for the foreseeable future. This will be more likely if continued drought conditions or rising temperatures (Gray et al. 2003; Mann et al. 1998) foster more high-intensity crown fires.

The long-term undesirable consequences that appear to result from crown fire at many of these sites make a case for continued attention to an increasingly urgent question: What intervention can enhance the resiliency of southwestern ponderosa pine forests? Mitigation of the effects of intense fires may begin by avoiding actions that increase stress on these ecosystems, such as salvage logging or grazing, and instead taking action to assist natural recovery processes. High-density postcrown fire stands may be just as vulnerable to future crown fires as southwestern ponderosa pine forests already considered at high risk. Restoration treatments recommended for fire-suppressed ponderosa pine forests — thinning of dense, young stands and reestablishing a surface-fire regime at appropriate scales — are also urgently needed to increase resiliency in high-density postcrown fire stands.

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