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Wildland fire effects on forest structure over an altitudinal gradient, Grand Canyon National Park, USA

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Summary

1. Restoration of wildland fire to forests is a challenge when historical fire regimes have been altered. We studied four fires that burned over approximately 7865 ha on an altitudinal gradient in Grand Canyon National Park, USA, in 2003. The fires met criteria for the current USA policy allowing the restoration of fire's ecological role in forest landscapes: Wildland Fire Use for Resource Benefits.
2. After the fires burned out, we remeasured 82 permanent pre-established monitoring plots burned by the fires plus 43 additional plots on unburned companion sites.
3. The maximum height of charring of tree boles and basal area mortality increased in mean value and variability with altitude. At a low-altitude *Pinus–Quercus* site, tree density declined significantly but basal area was unchanged. At a mid-altitude mixed-conifer site and a high-altitude *Picea*/*Abies*/*Populus* site, both density and basal area declined.
4. The thinning effect of fire was concentrated on smaller, shorter, fire-susceptible trees. Small-diameter trees (< 20 cm diameter) made up 79–95% of all tree mortality. Shade-tolerant conifers, particularly true firs and spruce, experienced disproportionate mortality (31–82% basal area decline), while fire-resistant ponderosa pine and Douglas fir tended to survive (2–8% basal area decline). Delayed mortality between the first and second years following the fires accounted for only 4·2% of trees dying at the low-altitude site but 15·6% and 11·2% at the mid- and high-altitude sites, respectively. Regeneration density was highly variable but forest floor and woody debris declined in burned areas.
5. *Synthesis and applications.* This study shows that, even after an unusually long fire-free period (1880–2003), at the mid- and high-altitude burned sites fire effects were consistent with restoration of historical patterns, moving the ecosystems closer to historical reference conditions. Fires simultaneously reduced the living, dead and ladder fuels that made the forest vulnerable to uncharacteristically severe fire. These effects make the forests more resistant to the expected increases in fire size and severity under future climate conditions. Even at longer-than-historical fire intervals, the wildland fire use policy can benefit Grand Canyon forests.

Key-words: aspen, Douglas fir, fuels, Gambel oak, Kaibab Plateau, Ponderosa pine, spruce, white fir, wildland fire use

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Introduction

Recognition that fire plays an important ecological role in south-western forests of the USA goes back over three-quarters of a century (Leopold 1924) but accomplishing even a limited reintroduction of fire has proved challenging (Parsons 2000; Miller & Parsons 2004). The USA policy of wildland fire use (WFU) for resource benefits gives managers flexibility in responding to naturally ignited wildfires (Miller 2003; Stephens & Ruth 2005). Wildland fires that meet predefined criteria can be used to accomplish goals such as fuel reduction, reintroduction of historical fire patterns

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and restoration of fire-maintained patterns of species composition and forest structure (Dale 2006).

The difference between current and historical fire patterns has been central to assessing the impact of changes associated with fire exclusion and other human-caused disturbances. Examples include the USA-wide programme of coarse-scale fuel mapping for developing the Fire Regime Condition Class assessment (FRCC; Schmidt *et al*. 2002) and a finer-scale method in California called the Fire Regime Interval Departure (FRID; Caprio & Graber 2000). These approaches compare modern fire recurrence with a reference condition of historical fire frequency prior to European settlement. Areas with a high departure, particularly those where fires historically burned mostly with low severity, are considered to be at high risk of 'losing key ecosystem components' (Schmidt *et al*. 2002).

A key problem with assessments based on fire frequency comparisons is that the great majority of USA forests have dim prospects for regaining anything close to historical fire frequency under modern constraints (Brown *et al*. 1994). In a nation-wide review, Parsons (2000) noted that even for the agencies most disposed to fire use (National Park Service, Forest Service), in wilderness settings where fire use may be least constrained and in ecosystems where fire might be most easily managed because of historical low- or mixed-severity fire regimes, the application of WFU or the previous policy of 'prescribed natural fire' was orders of magnitude below a level that would emulate historical fire regimes. Rollins, Swetnam & Morgan (2001) calculated modern fire return intervals of > 100–200 years based on approximately two decades of fire use in wilderness areas in Montana and New Mexico. Miller & Parsons (2004) found that fragmentation of wildlands limited the importation of fires from distant ignitions, reducing even the theoretical possibility of fully restoring natural fire. Parsons (2000) underscored the dilemma between the consequences of continued minimal fire use vs. active intervention to supplement natural ignitions with prescribed fires and/or mechanical treatments. At least in preserves and remote landscapes, active intervention raises many social and ecological concerns.

We suggest another option: the actual effects of specific wildland fires may, in some circumstances, be more important than the frequency of fire recurrence. If fires that differed in spacing, season, intensity or other ways from historical patterns nonetheless conserved or restored ecosystem structures and processes within a natural range of variability, then perhaps long-term management goals might be achieved even under altered modern fire regimes. For example, Stephenson (1999) analysed the relative importance of forest structure vs. fire process for restoration in *Sequoiadendron giganteum*–mixed conifer forests. Miller & Urban (2000) used simulation modelling to suggest that relatively infrequent but severe fires could restore mixed-conifer forests by thinning dense stands of young, fire-susceptible trees. Keeley (2006) noted that longer-than-historical fire intervals might reduce the ability of exotic species to capitalize on frequent disturbances.

In south-western *Pinus ponderosa* and mixed-conifer forests, considered among the most negatively impacted by fire exclusion in North America (Allen *et al*. 2002; Schmidt *et al*. 2002), there are several lines of evidence to support the hypothesis that surface fires can have effects consistent with restoration and conservation even at historically atypical intervals. First, frequent fires by themselves do not necessarily restore historical characteristics. Three decades of controlled experimentation with reintroduction of frequent surface fire have shown remarkably little effect in restoring historical forest structure, composition, productivity and nutrient cycling (Peterson *et al*. 1994; Hart, Classen & Wright 2005), leading people to look for alternatives that include tree thinning and fuel treatments in addition to fire (Covington *et al*. 1997). Secondly, never-harvested 'relict' forests in Arizona and Mexico that continue to experience surface fires, even at much longer intervals than historical fires, have maintained open forests and a productive understorey, in contrast to paired fire-excluded forests (Stephens & Fulé 2005). Thirdly, postfire studies of relict forest sites have shown that native species dominate (Laughlin *et al*. 2004; Huisinga *et al*. 2005; Laughlin, Bakker & Fulé 2005), unlike forests where logging and grazing have left a legacy of invasive exotics (Crawford *et al*. 2001; Korb, Johnson & Covington 2003).

We tested the effects of fire use on a landscape scale over an altitude gradient after extensive WFU fires ignited by lightning in 2003 on the North Rim of Grand Canyon National Park. The park conserves the largest unharvested forest in Arizona, over 48 800 ha (Warren *et al*. 1982), and has been a leader in fire restoration since the 1980s. The 2003 WFU fires burned over 82 permanent plots, representing 1872 ha. We remeasured these plots and companion unburned sites after the fires to ask: (i) how the WFU fires varied in severity over the altitudinal gradient; (ii) whether tree structural (density, basal area, canopy cover, regeneration) and compositional changes were consistent with conservation and restoration of historical reference conditions; (iii) how forest floor fuels changed following the fires; and (iv) what the implications for future management were.

Methods

STUDY AREA

The study area was on the North Rim of Grand Canyon National Park, Arizona, USA. Weather records were taken from the Western Regional Climate Center (www.wrcc.dri.edu; accessed 17 March 2006). Average annual precipitation at the North Rim ranger station (altitude 2542 m) from 1948 to 2005 was 658 mm. Average annual snowfall depth was 371 cm. The decade 1996–2005 averaged 91% of the long-term average

Table 1. Species names and codes used in the text

Species	Common name	Code
Abies lasiocarpa (Hook.) Nutt.	Subalpine fir	ABLA
Abies concolor (Gordon & Glendinning) Hoopes.	White fir	ABCO
Picea engelmannii Parry ex Engelm.	Engelmann spruce	PIEN
Picea pungens Engelm.	Blue spruce	Combined with PIEN
Pinus edulis Engelm.	Rocky Mountain pinyon	PIED
Pinus ponderosa var. *scopulorum* P. & C. Lawson	Ponderosa pine	PIPO
Populus tremuloides Michx.	Quaking aspen	POTR
Pseudotsuga menziesii (Mirb.) Franco var. *glauca* (Beissn.) Franco	Rocky Mountain Douglas fir	PSME
Quercus gambelii Nutt.	Gambel oak	QUGA
Robinia neomexicana Gray	New Mexico locust	RONE

Table 2. Wildland fire-use fires on the North Rim, Grand Canyon National Park, 2003. Scientific names of species are shown in Table 1

Fire name	Date of ignition	Final size (ha)	No. burned plots	No. unburned plots	Altitude of plots (m a.s.l.)	Forest vegetation
Powell	15 Jun 2003	1460	36	25	Low, 2204–2316	PIPO, QUGA, RONE
Big and Rose	24 Aug 2003 (Big), 7 Oct 2003 (Rose)	1592	29	None	Mid, 2433–2560	PIPO, ABCO, POTR, PSME
Poplar complex	4 Sept 2003	4813	18	18	High, 2599–2678	ABLA, PIEN, PSME, PIPO, POTR

precipitation, but six of the 10 years were below average and 2002, 1 year before the WFU fires, was the driest year in the records (excluding years with missing data). Temperatures ranged from an average July maximum of 25 °C to an average January minimum of −8·2 °C. Soils were derived from limestone substrates (Warren *et al*. 1982). Forests varied with altitude; scientific names and codes are in Table 1 and species associations are in Table 2.

Fire regimes were reconstructed from fire-scarred trees on the low- and mid-altitude study sites by Fulé *et al*. (2003a, 2003b) and nearby by Wolf & Mast (1998). Composite fire return intervals through 1879 averaged 3·2–5·5 years (all fires) and 6·4–9·2 years (fire dates in which 25% or more of the sample trees were scarred; Fulé *et al*. 2003b). At the higher altitude study site, Fulé *et al*. (2003a) used a combination of fire scars, tree age and species composition data to show that these forests had a mixed-severity fire regime. Fires ceased after 1879 across much of the North Rim, initially because of livestock introduction then because of fire suppression. The North Rim was fenced to exclude livestock by 1938. No large fires were recorded on fire scars or in park records at the mid- and high-altitude sites after 1879, until the WFU fires in 2003. Both low-altitude sites, in contrast, had at least three large, spreading surface fires after 1879 (Fulé *et al*. 2003b).

FIELD METHODS

From 1997 to 2001, we established permanent plots covering an altitudinal gradient from *c.* 2200 m to *c.* 2700 m. Plot grids were spaced at 300 × 300 m below 2600 m altitude and 600 × 1200 m at higher altitudes, where the landscape was characterized by a coarser-grained fire and stand pattern (Fulé *et al*. 2003a). Sampling plots were 0·1 ha (20 × 50 m) in size. All plot data were corrected for slope. Trees were tagged and measurements included species, condition, diameter at breast height (d.b.h.), height and crown base height. Trees larger than 15 cm d.b.h. were measured on the entire plot; trees between 2·5 and 15 cm d.b.h. were measured on a 0·025-ha subplot. Trees smaller than 2·5 cm d.b.h. (regeneration) were tallied by species and height class on a 50-m^2 subplot. Along the 50-m sidelines of the plot, canopy cover was recorded with a vertical densitometer every 30 cm in prefire measurements and every 3 m in 2001–04. Forest floor and woody debris were measured along four 15·24-m planar intersect transects (Brown 1974). Litter and duff (fermentation + humus layers) depths were measured every 1·52 m along each transect, and woody debris was recorded by time-lag classes of 1 h (0–0·62 cm diameter), 10 h (0·62–2·54 cm), 100 h (2·54–7·62 cm) and 1000 h (> 7·62 cm). Time-lag classes, commonly used in fire behaviour applications, refer to the approximate time required for fuels of these sizes to reach two-thirds equilibrium with atmospheric moisture content (Pyne, Andrews & Laven 1996). Fuel loadings were calculated from the planar transect data (Brown 1974; Sackett 1980).

Eighty-two plots on the North Rim were burned in 2003 (Table 1). In 2004, we remeasured all forest attributes and added measurement of the height of charring on the tree boles. Also in 2004, we remeasured 25 unburned plots at a low-altitude comparison site and two unburned plots at a high-altitude comparison site. Postfire mortality is often not evident in the first growing season following burning (McHugh & Kolb 2003). Therefore we returned in 2005 to remeasure the condition of all tagged trees on the burned plots. In 2005 we also completed remeasurement of the remaining 16 unburned plots at the high-altitude comparison site.

STATISTICAL METHODS

This research was an observational study taking advantage of wildland fires that burned across pre-existing monitoring plots. The design was a before–after control–impact (BACI) study (Eberhardt & Thomas 1991) for the low- and high-altitude sites where we could measure nearby unburned sites. At the mid-altitude site, only before- and after-fire data could be compared. The scope of inference was limited to these particular sites and fires.

Forest structural variables, including tree density, basal area, canopy cover and regeneration density, were compared between burned and unburned sites at low and high altitudes with Kruskal–Wallis two-sample tests ($\alpha = 0{\cdot}05$). Following a statistically significant result (Mann–Whitney U-statistic) for a total variable, such as total basal area, the basal areas of individual species were compared between burned and unburned sites with pairwise Kruskal–Wallis two-sample tests. Because some species were sparsely distributed at some sites, only species that were present on ≥20% of the plots at a given site were tested for statistical significance of changes. Alpha levels for these tests were adjusted by dividing by the number of pairwise tests (Bonferroni correction).

Changes over time from the prefire to the postfire measurements within sites were tested with Wilcoxon signed-ranks tests to take advantage of the repeated measurements on the permanent plots. We followed the same procedure as with the between-site tests: following a statistically significant result (Wilcoxon Z statistic) for a total variable, we proceeded to Bonferroni-corrected pairwise comparisons by individual species. Test results are reported in the text below rather than the tables to distinguish between-site and within-site differences.

We used non-metric multidimensional scaling (NMS) ordinations to illustrate multivariate changes in basal area of all tree species among plots using PC-ORD software (McCune & Mefford 1999). Basal area was selected because it is likely to be more reliably reconstructed than past tree density (Moore *et al*. 2004). Three time periods were compared at each altitude: (i) reference conditions reconstructed with dendroecological data (Fulé *et al*. 2002, 2003a); (ii) prefire conditions and (iii) postfire conditions. At the low- and high-altitude sites, both the burned and unburned areas were compared together on the same set of axes. We used the Bray–Curtis distance measure (Faith, Minchin & Belbin 1987) with random starting configurations, 40 runs with real data, a maximum of 400 iterations per run and a stability criterion of 0·00001. A Monte Carlo test with 50 randomizations was used to determine how likely the observed stress value of the final solution would be by chance alone.

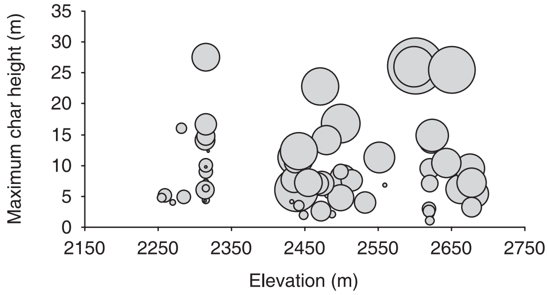


Fig. 1. Distribution of maximum char height (highest char value per plot) as an indicator of fire behaviour over all the burned plots from lowest to highest altitude. Bubbles are proportional to basal area mortality between the pre- and postfire measurements.

Results

TREE MORTALITY

The fires produced higher maximum bole char height per plot and greater basal area killed as altitude increased (Fig. 1). The absolute and relative (%) values of basal area killed were highly correlated ($r = 0{\cdot}93$, $P < 0{\cdot}001$). At low altitude, the maximum mortality on any plot reached 13·7 $m^2\ ha^{-1}$ (58%). This was the only plot with > 10 $m^2\ ha^{-1}$ mortality; the mean mortality was 1·6 $m^2\ ha^{-1}$, with an average of 6% of prefire basal area. In contrast, at the mid-altitude site, 12 of 29 plots had > 10 $m^2\ ha^{-1}$ mortality. Mean mortality was 9·5 $m^2\ ha^{-1}$, with an average of 23%, reaching a maximum of 32·4 $m^2\ ha^{-1}$. The highest single-plot relative mortality was 83%. Severity was greatest at the high-altitude sites, where 10 of 18 plots exceeded 10 $m^2\ ha^{-1}$ mortality. Mean mortality was 14·4 $m^2\ ha^{-1}$, corresponding to an average of 39% and reaching a maximum of 53·4 $m^2\ ha^{-1}$. Two plots had 100% overstorey mortality and a third reached 92% mortality.

Changes were minimal at the low-altitude sites (Table 3). Total density and basal area were not significantly different between the burned and unburned sites in the prefire measurement. After the fire, however, density was significantly lower in the burned site ($U = 310$, $P = 0{\cdot}04$) but neither pines nor oaks separately were significantly different between burned and unburned sites. Basal area remained non-significantly different between sites.

Within the low-altitude sites, the burned site tree density dropped significantly in total ($Z = -3{\cdot}98$, $P < 0{\cdot}001$) and for ponderosa pine ($Z = -2{\cdot}65$, $P = 0{\cdot}008$) and

Table 3. Forest structure (trees ≥ 2·5 cm d.b.h.) at low-, mid- and high-altitude study sites before and after wildland fire-use fires. Unburned comparison sites at low and high altitudes are included. Species codes are shown in Table 2. Data values are shown from the measurement carried out before the fires, followed percentage change (positive or negative) as measured after the fires. See text for measurement dates

Site	Total	ABCO	ABLA	PIEN	PIED	PIPO	POTR	PSME	QUGA	RONE
Tree density (trees ha^{-1})										
Low burn prefire	574·7					217·1			276·0	81·5
Percentage change	–36					–15			–42	–100
Low unburned prefire	800·9	6·4			0·4	157·0	7·3		578·3	51·5
Percentage change	–6	464			0	–8	–25		–13	16
Mid-burn prefire	930·4	459·6				156·3	256·0	52·8		5·8
Percentage change	–54	–55				–31	–65	–61		–100
High burn prefire	1061·2	291·0	145·5	215·2		91·9	277·0	29·3		11·5
Percentage change	–57	–60	–68	–53		–22	–65	–19		–100
High unburned prefire	1046·1	100·4	209·9	407·8		61·5	190·6	56·7		
Percentage change	–11	–12	–4	–10		–1	–18	–4		
Basal Area (m^2 ha^{-1})										
Low burn prefire	26·2					24·3			1·6	0·3
Percentage change	–6					–4			–35	–100
Low unburned prefire	26·5	0·1			0·0	21·7	0·007		4·4	0·4
Percentage change	–2	112			8	–2	53		–2	6
Mid-burn prefire	40·9	14·6				19·4	5·4	1·5		
Percentage change	–23	–31				–8	–65	0		–100
High burn prefire	34·7	10·7	2·3	6·5		7·1	6·3	1·9		
Percentage change	–42	–61	–82	–37		–6	–51	2		–100
High unburned prefire	33·3	4·7	4·4	9·4		4·5	6·3	4·0		
Percentage change	–6	–11	–12	–6		2	–9	0		

Gambel oak ($Z = –3·22$, $P = 0·001$). All New Mexico locust trees, averaging 82 stems ha^{-1} before the fire, were killed or topkilled on the burned site. Probably because of drought, the unburned site density decline was also significant in total ($Z = –2·09$, $P = 0·04$) and for ponderosa pine ($Z = –3·17$, $P = 0·002$) and Gambel oak ($Z = –2·48$, $P = 0·01$). Basal area in the burned site declined significantly by 6% ($Z = –2·21$, $P = 0·03$). Ponderosa pine basal area did not change significantly but Gambel oak did ($Z = –3·22$, $P = 0·001$). Basal area did not change significantly at the unburned site (2% decline).

At mid-altitude, because there was no companion unburned site available, results were simply the changes over time from prefire to postfire measurements. Tree density declined by 54% (Table 3), a significant decrease from pre- to postfire ($Z = –4·70$, $P < 0·001$), driven by significant declines in white fir ($Z = –4·37$, $P < 0·001$), ponderosa pine ($Z = –3·59$, $P < 0·001$), and aspen ($Z = –4·18$, $P < 0·001$) but not Douglas fir. The 23% decline in total basal area was also significant ($Z = –4·29$, $P < 0·001$) but in this case only white fir and aspen were significantly lower ($Z = –4·23$ and $–4·08$, respectively, both $P < 0·001$).

The most pronounced declines in tree density and basal area occurred at the high-altitude sites (Table 3). Before the fire, total density and basal area were indistinguishable between the sites ($U = 170$ and 168, $P = 0·80$ and 0·89, respectively). After the fire, both variables were significantly lower in the burned sites ($U = 79$ and 56, $P = 0·009$ and $P < 0·001$, respectively). Tree density differences were driven by significant differences between sites in subalpine fir and spruce ($U = 75$ and 62, $P = 0·004$ and $P = 0·001$, respectively). Basal area differences were also the result of significant differences between sites in subalpine fir and spruce ($U = 68$ and 77, $P = 0·002$ and $P = 0·006$, respectively).

Within high-altitude sites, the burned site tree density dropped 57%, a significant decrease in total ($Z = –3·72$, $P < 0·001$) and white fir, spruce and aspen ($Z = –3·07$, $–2·69$, and $–3·46$, $P = 0·002$, 0·007, and 0·002, respectively). Basal area declined 42% in the burned site, also significant ($Z = –3·72$, $P < 0·001$), driven by declines in white fir and spruce ($Z = –3·01$ and $–3·46$, $P = 0·003$ and 0·002, respectively). In contrast to the findings at low altitude, significant declines also occurred over time in the unburned site. Unburned site tree density decreased significantly by 11% ($Z = –3·72$, $P < 0·001$) but the only individual species with a statistically significant decline was spruce ($Z = –3·12$, $P = 0·002$). Unburned site basal area declined significantly by 6% ($Z = –2·98$, $P = 0·003$) but no individual species had a statistically significant decline.

Tree mortality in both burned and unburned sites occurred predominantly in the smaller size classes, evidenced both by diameter distributions (Fig. 2) and the disproportionately greater reduction in tree density (6–57%) compared with the lesser reduction in basal area (2–42%) (Table 3). On the burned sites, the proportion of dying trees ≤ 20 cm d.b.h. was 95% at the low-altitude site, 83% at the mid-altitude site and 79% at the high-altitude site. On the two unburned sites, 100% of the dying trees at the low-altitude site and 74% of the dying trees at the high-altitude site were

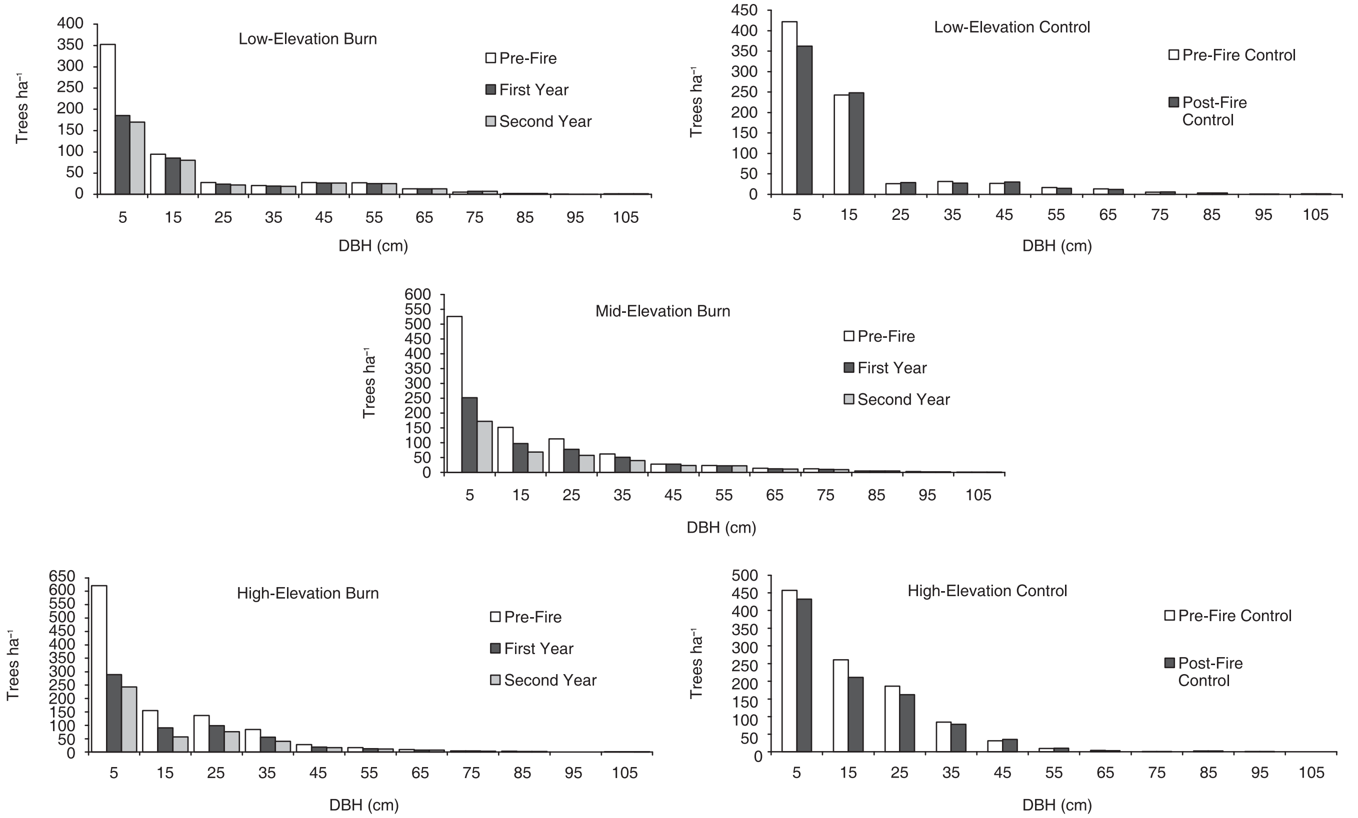


Fig. 2. Changes in diameter distribution at sites burned in wildland fire-use fires over an altitudinal gradient. Diameter class midpoints are shown on the *x*-axes; minimum diameter is 2·5 cm. Tree survival is shown in both the first year after fire (2004) and the second year (2005). Unburned comparison sites were measured once, either in 2004 or 2005.

≤ 20 cm d.b.h. Delayed mortality (trees on the burned sites that died between 2004, the first growing season following the fires, and 2005) accounted for only 4·2% of trees dying at the low-altitude site but 15·6% and 11·2% at the mid- and high-altitude sites, respectively (Fig. 2). As a proportion of basal area, delayed mortality accounted for < 2%, 9·9% and 12·2% at the low-, mid- and high-altitude sites, respectively.

Across all fires, surviving overstorey trees (≥ 15 cm d.b.h.) tended to be larger and have lower maximum bole char heights than trees that died (Fig. 3 and Table 4). These differences were statistically significant for all combinations of species and fires, except for aspen diameter at the high-altitude site and subalpine fir and spruce bole char (Table 4). Species varied in the proportion of large trees dying, with 'large' defined as d.b.h. ≥ 37·5 cm (White 1985). Large trees made up 15% of tree mortality for white fir, 29% for subalpine fir, 16% for spruce, 7% for ponderosa pine, 14% for aspen and none for Douglas fir.

Shifts in the distribution of basal area by species maintained variability in forest structure but moved in the direction of historical reference conditions, as illustrated in ordination diagrams (Fig. 4). At all sites, the distribution of reference plots tended to be somewhat more aggregated than the pre- and postfire distributions. Arrows in Fig. 4 show the change in the geometric centroid from reference to prefire to postfire. At the

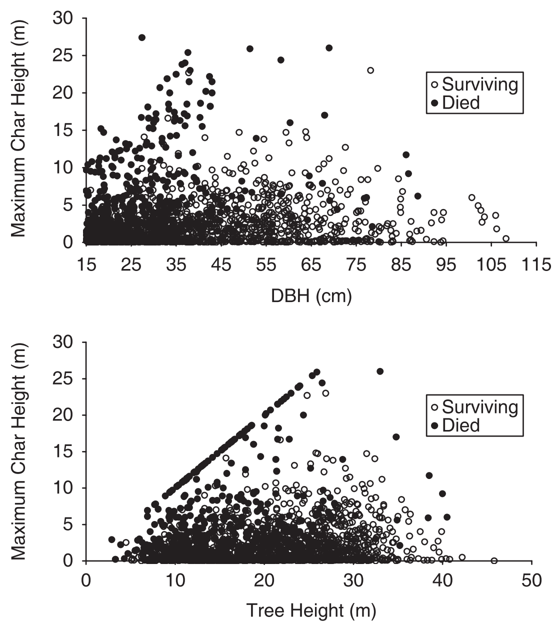


Fig. 3. Maximum char height, as a measure of heat affecting the tree, compared with d.b.h. and tree height. Smaller and shorter trees, particularly those with high char, were most likely to die.

low-altitude site, the change was too small to be graphed, consistent with the minimal changes in total basal area (2–6%). The mid-altitude site showed a distinct shift associated with the burn, moving in the direction of the

Table 4. Mean diameter and maximum bole char of surviving vs. killed overstorey trees (d.b.h. ≥ 15 cm) at low-, mid- and high-altitude burned sites after wildland fire-use fires. Data are only presented for categories with ≥ 12 individuals. Significant differences (Mann–Whitney *U*, $P < 0.05/3$) between surviving and killed trees in each altitude category are indicated with *

Site	ABCO	ABLA	PIEN	PIPO	POTR	PSME
D.b.h. (cm)						
Low burn, surviving				42·4*		
Low burn, killed				27·7*		
Middle burn, surviving	40·1*			41·1*	40·8*	45·1
Middle burn, killed	29·0*			31·3*	27·2*	
High burn, surviving	37·1*	42·4*	37·5*	39·1*	36·7	
High burn, killed	25·6*	30·0*	25·7*	30·3*	31·3	
Bole char, maximum (m)						
Low burn, surviving				3·1*		
Low burn, killed				5·6*		
Mid-burn, surviving	1·7*			2·4*	1·0*	1·9
Mid-burn, killed	5·0*			9·2*	3·3*	
High burn, surviving	1·5*	1·9	1·7	2·4*	0·3*	
High burn, killed	2·6*	2·6	3·3	3·7*	4·2*	

reference pattern. At high altitude, the centroid of the prefire plot distribution moved sharply back within the cloud of reference plots. However, the centroid of the unburned plot distribution also moved a relatively large distance, about 40% as much as the burned plots.

CANOPY COVER

Canopy cover (Table 5) at low-altitude sites did not differ significantly between burned and unburned sites before or after the fire, but declined significantly within both sites over time (burned $Z = -2·49$, $P = 0·01$; unburned $Z = -2·11$, $P = 0·03$). At mid-altitude, canopy cover (Table 4) declined significantly over time ($Z = -2·63$, $P = 0·009$). At high altitude, canopy cover (Table 5) did not differ significantly between burned and unburned sites before the fire. Postfire canopy cover between sites and changes over time in the unburned site could not be assessed because of missing canopy data, but cover declined significantly in the burned site ($Z = -2·94$, $P = 0·003$).

Table 5. Canopy cover (percentage) at low-, mid- and high-altitude study sites before and after wildland fire use fires. Unburned comparison sites at low and high altitudes are included. Canopy data were not measured on the high unburned post-fire plots

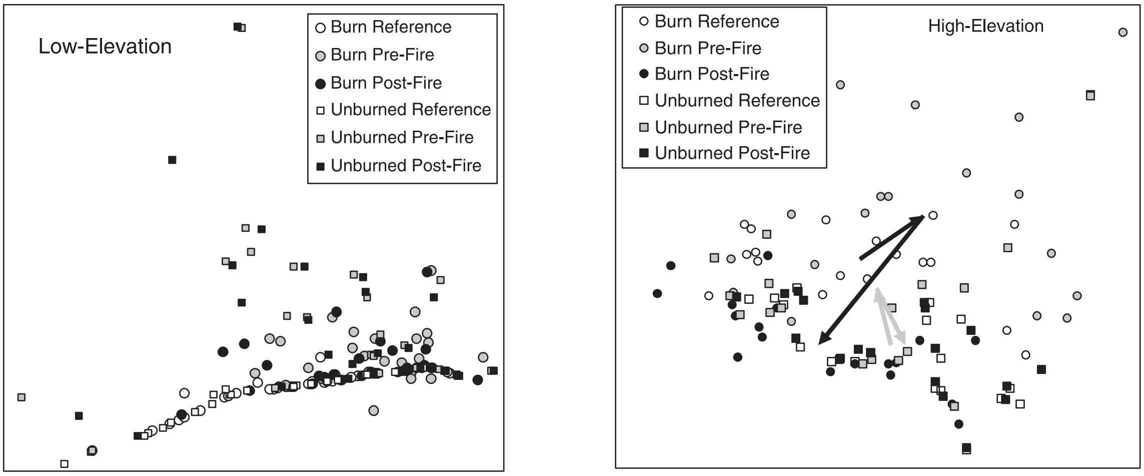
Site	Mean	Minimum	Maximum	SE
Low altitude				
Burn prefire	49·7	15·4	79·2	2·1
Burn postfire	44·7	12·5	75·0	2·6
Unburned prefire	48·3	0·3	85·5	4·3
Unburned postfire	44·0	0	78·1	3·5
Mid-altitude				
Burn prefire	63·2	31·6	84·9	2·3
Burn postfire	54·7	28·1	84·4	3·0
High altitude				
Burn prefire	52·5	31·6	84·6	3·0
Burn postfire	40·3	21·9	75·0	3·6
Unburned prefire	54·3	22·9	80·4	3·4

REGENERATION

Tree regeneration, all trees < 2·5 cm d.b.h. (Table 6), displayed much more variability than the larger trees. Total regeneration was not significantly different between burned and unburned sites at low and high altitudes, either before or after the fires. Within sites, however, only the mid-altitude site failed to show significant differences from before to after the fire. Total regeneration increased significantly at the low-altitude burned site ($Z = 2·29$, $P = 0·02$), driven by a significant increase in New Mexico locust ($Z = 2·74$, $P = 0·006$), which doubled in density. The low-altitude unburned site also increased significantly ($Z = 2·29$, $P = 0·02$) but no individual species had a significant change. At the high-altitude site, both the burned and unburned sites declined significantly in regeneration density over time ($Z = -3·42$ and $-2·67$, $P < 0·001$ and $P = 0·007$, respectively) but the only individual species with a statistically significant decrease was aspen, in the unburned site ($Z = -2·79$, $P = 0·005$). Total regeneration density was not associated with fire severity but was positively correlated with maximum per-plot char height ($r = 0·25$, $P = 0·023$).

SURFACE FUELS

Forest floor depth (litter plus duff) declined in the burned areas but relationships between burned and unburned sites were variable (Table 7). Forest floor depth was significantly lower at the unburned low-altitude site before the fire ($U = 711$, $P < 0·001$) but depths did not differ afterwards. The opposite occurred at the high-altitude site, where forest floor depth was indistinguishable before burning but was significantly lower in the burned site afterward ($U = 43$,



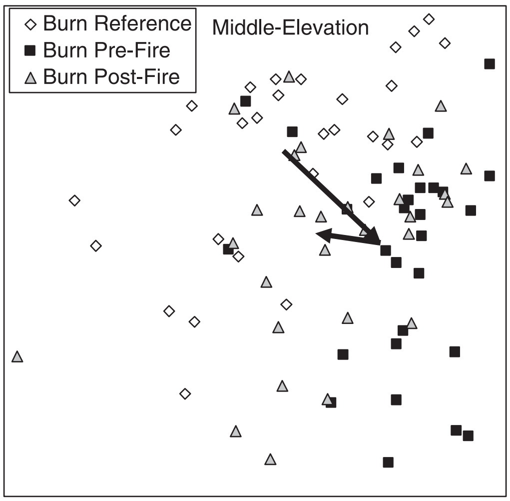


Fig. 4. Non-metric multidimensional scaling ordinations of basal area of all species reconstructed at the onset of fire exclusion (reference condition 1880), before the 2003 fires and after the fires. Changes in the centroid of each distribution from before to after the WFU dates are shown with black arrows (burned sites) or grey arrows (unburned sites). Changes at the low-altitude site were too minor to be graphed. At the low-altitude site, the final solution had two dimensions, stress = 9·7, P = 0·04; mid-altitude, two dimensions, stress = 14·0, P = 0·02; high-altitude, three dimensions, stress = 14·8, P = 0·02.

Table 6. Tree regeneration (seedlings and sprouts < 2·5 cm d.b.h.) (tree density; trees ha^{-1}) at low-, mid- and high-altitude study sites before and after wildland fire-use fires. Unburned comparison sites at low and high altitudes are included. Species codes are shown in Table 2

Site	Total	ABCO	ABLA	PIEN	PIPO	POTR	PSME	QUGA	RONE
Low burn prefire	5817·2				106·3			4050·0	1660·9
Percentage change	42				–79			21	100
Low unburned prefire	6995·7				223·3	18·3		3479·5	3274·6
Percentage change	46				111	–50		87	–3
Mid-burn prefire	9112·2	4223·8			91·0	3726·0	48·8		1022·7
Percentage change	–3	44			–77	–42	–42		–68
High burn prefire	10061·1	1673·2	1962·1	970·9	247·1	4716·2	33·4		458·1
Percentage change	–50	–39	–79	–42	–100	–37	0		–95
High unburned prefire	8153·3	1308·5	2291·7	1301·1	22·6	2973·3	256·2		
Percentage change	–25	77	–50	–42	0	–42	–38		

P < 0·001). Within sites, declines in forest floor depth were highly significant at the low-, mid- and high-altitude sites (Z = –5·03, –4·68, and –3·64, respectively; all P < 0·001). Forest floor depth also declined significantly at the high-altitude unburned site (Z = –2·02, P = 0·04) but did not change significantly at the low-altitude unburned site.

Woody debris biomass was indistinguishable between burned and unburned sites before burning at both low and high altitudes, but both fine and coarse woody debris were significantly lower at the low-altitude site after the fire (U = 235 and 310, P = 0·002 and 0·04, respectively). Coarse woody debris was also significantly lower at the high-altitude burned site after the fire (U = 81, P < 0·01). Within sites, fine woody debris declined significantly at the low-, mid- and high-altitude burned sites (Z = –2·44, –4·08, and –2·46, P = 0·01, < 0·001 and 0·01, respectively). Fine woody debris increased significantly at the low-altitude unburned site (Z = 2·81, P = 0·005). Coarse woody debris declined significantly at the mid- and high-altitude burned sites (Z = –4·70 and –2·72, P = 0·002 and 0·006, respectively). There were

Table 7. Changes in forest floor and woody debris at low-, mid- and high-altitude study sites before and after wildland fire-use fires. Unburned comparison sites at low and high altitudes are included. Fine woody debris is material with diameter < 7·62 cm; coarse woody debris is larger material

Site	No. plots	Forest floor depth (cm)	SE	Fine woody debris (mg ha^{-1})	SE	Coarse woody debris (mg ha^{-1})	SE
Low burn prefire	36	3·28	0·17	3·90	0·51	14·82	3·50
Percentage change		–43·2		–35·1		–39·9	
Low unburned prefire	25	2·30	0·21	3·30	0·45	14·92	5·54
Percentage change		–1·5		61·8		35·3	
Mid-burn prefire	29	3·95	0·29	13·20	1·26	53·89	6·40
Percentage change		–69·0		–50·8		–38·3	
High burn prefire	18	3·75	0·33	12·02	1·14	56·42	14·34
Percentage change		–64·1		–39·9		–59·5	
High unburned prefire	18	3·26	0·25	12·34	1·42	36·96	5·27
Percentage change		–16·7		–20·2		24·8	

no significant changes in coarse woody debris biomass from before to after the fires at the unburned sites.

Discussion

Fire variability in 2003 was correlated with altitude, forest type and historical fire regime characteristics. Prior to anthropogenic disruption of fire regimes, *c.* 1880, moister conditions at higher altitudes supported productive forests that burned less frequently but with greater severity than the xeric, lower altitude forests (Dutton 1882; Lang & Stewart 1910; Rasmussen 1941; White & Vankat 1993; Wolf & Mast 1998; Fulé *et al.* 2003a). The 2003 WFU fires had patterns of severity that were generally consistent with the historical patterns. The fortuitous combination of prefire plot locations and fire patterns made it possible to compare burned and unburned sites to separate fire effects from background variability. We had a sufficiently high sample size (n = 18–36) and were able to take advantage of the power of repeated measurements for a statistically reliable evaluation. Mortality on the unburned sites reflected the severe drought during the measurement period (Breshears *et al.* 2005) but burned sites had higher mortality and burned–unburned companion sites that were statistically indistinguishable prior to fire became significantly different in tree density and basal area afterwards.

The thinning effect of fire was concentrated on smaller, shorter and fire-susceptible trees (79–95% of all tree mortality), reducing the potential for fuel ladders. Large trees (> 37·5 cm d.b.h) also died, however, at rates from 0% and 7% (Douglas fir and ponderosa pine, respectively) to 29% (subalpine fir). For comparison, in two recent forest restoration experiments near the park during nearly overlapping periods (*c.* 1998–2005), large ponderosa pine trees died by 5 years post-treatment at rates from 9% to 34% following tree thinning and prescribed fire (Fulé, Laughlin & Covington 2005; P.Z. Fulé, unpublished data). Thus the mortality of large trees of fire-resistant species in the free-burning WFU fires was less than mortality in mechanical + fire restoration treatments.

Death of fire-susceptible species shifted species composition towards fire-resistant trees. Shade-tolerant coniferous species favouring mesic conditions, particularly true firs and spruce, experienced disproportionate mortality (31–82% basal area decline), while fire-resistant ponderosa pine and Douglas fir tended to survive (2–8% basal area decline). At the high-altitude site, the latter two species made up 26% of total basal area before the fire but 42% afterwards, compared with an unnoticeable shift in the companion unburned site (26% to 28%). Regeneration favoured fire-susceptible species, including sprouting deciduous species, spruce and true firs. Regeneration density was lowest for ponderosa pine and Douglas fir, the most fire-resistant overstorey species, making up < 1% of all stems. The demographic imbalance does not necessarily forecast future forest structure, however. Many small sprouts fail to reach the stature of established plants, especially if burned again (Gottfried 1980; Harrington 1985).

The effects of the 2003 WFU fires should not be overgeneralized. Perhaps more than other management actions, such as prescribed burning, WFU is inherently highly variable. In moist high-altitude forests, fire spread will not be feasible unless the fuels and weather are fairly dry. This means that managers must be willing to accept a relatively high risk of intense fire behaviour. Also, our conclusions about the 2003 WFU fires are necessarily limited to the portions of those fires where pre-existing plots had been located. In the case of the Poplar fire, specifically, the plots were located at the northern part of the fire, while areas of relatively more severe burning occurred to the south (according to fire severity maps on file at Grand Canyon National Park).

Given these caveats, however, the 2003 WFU fires can be considered broadly successful in ecological terms. Even though an unusually long fire-free period (1880–2003) had occurred at the mid- and high-altitude burned sites, fire effects were consistent with historical patterns of reduced severity at lower altitude and vice versa. The WFU fire had the least impact at the low-altitude site, where, despite the fact that the fire regime had shifted after 1879 from approximately 11 widespread fires per century to fewer than three, forest structure had not changed a great deal from prefire exclusion conditions (Fulé *et al*. 2002; Fig. 4). Forest structural changes were generally consistent with restoration of the historical range of variability, although at high altitude the effects were mild: only three out of 18 plots had > 90% mortality, whereas a reconstruction of the mixed-severity fire regime on this site suggested that as much as one-third of the area might have been in early successional stages following patchy stand-replacing burning before 1880 (Fulé *et al*. 2003a).

The 2003 WFU fires improved logistical conditions for future fires. Now that a large contiguous area of the north-western North Rim has burned, it may be easier for managers to allow future natural ignitions to burn. Unlike the sites studied by Miller & Parsons (2004), both rims of Grand Canyon receive large numbers of natural ignitions (Fulé *et al*. 2002), so the future fire regime should not necessarily be limited by artificial barriers to importing fire. It may also be possible to expand the permissible range of fire intensity to match more closely long-term historical patterns, particularly at high altitude. The evidence suggests that even at longer-than-historical fire intervals, the WFU policy can benefit Grand Canyon forests, suggesting that concerns about the difficulty of emulating historical fire regimes (Parsons 2000) may be alleviated. Instead of judging ecological condition largely by fire regime departures (Schmidt *et al*. 2002), we suggest that Grand Canyon managers should focus on fire-effect monitoring to assess ecosystem status.

Ecological restoration, whether focused on 'restoration of natural fire to wilderness' (Parsons 2000) or in broader assessments of ecosystem structure, composition and function compared with historical reference conditions (Allen *et al*. 2002), can be criticized because future climate conditions will not be like those of the past (Millar & Wolfenden 1999). However, the issue is not whether future climates will be unchanging, they will not, but rather whether native forest ecosystems can persist under future conditions. Climate change, whether through gradual changes or greater extremes that affect disturbance severity, may create novel thresholds beyond which a species or ecosystem type cannot survive (Malcolm *et al*. 2002). But unless or until such a point is reached, the most relevant question for assessing restoration is sustainability (Clewell 2000). If the goal were to restore species or ecosystems characterized by cool, moist environments, then historical reference conditions could well be in conflict with future climate. This may be the case for relict populations of Chihuahua spruce, for example (Ledig *et al*. 2000). In contrast, in the specific case of the 2003 WFU fires at Grand Canyon, fire effects caused the ecosystems to move closer towards historical reference conditions while simultaneously reducing the living, dead and ladder fuels that made the forest vulnerable to uncharacteristically severe fire. These changes help make the forests more resistant to the expected increases in fire size and severity (McKenzie *et al*. 2004).

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