Applied Vegetation Science **16** (2013) 457–469

Pre-fire fuel reduction treatments influence plant communities and exotic species 9 years after a large wildfire

Kristen L. Shive, Amanda M. Kuenzi, Carolyn H. Sieg & Peter Z. Fulé

Keywords
Exotic species; High-severity fire; *Pinus ponderosa*; Succession; Wildfire

Nomenclature
USDA-NRCS PLANTS (Database USDA-NRCS 2011)

Received 9 August 2012
Accepted 22 October 2012
Co-ordinating Editor: David Ward

Shive, K.L. (corresponding author, kls448@nau.edu) & **Fulé, P.Z.** (pete.fule@nau.edu): School of Forestry, Northern Arizona University, Flagstaff, AZ, 86001, USA
Kuenzi, A.M. (akuenzi@swca.com): SWCA Environmental Consultants Inc, Durango, CO, 81301, USA
Sieg, C.H. (csieg@fs.fed.us): Rocky Mountain Research Station, Flagstaff, AZ, 86001, USA

Abstract

Questions: How did post-wildfire understorey plant community response, including exotic species response, differ between pre-fire treated areas that were less severely burned, and pre-fire untreated areas that were more severely burned? Were these differences consistent through time?

Location: East-central Arizona, southwestern US.

Methods: We used a multi-year data set from the 2002 Rodeo–Chediski Fire to detect post-fire trends in plant community response in burned ponderosa pine forests. Within the burn perimeter, we examined the effects of pre-fire fuels treatments on post-fire vegetation by comparing paired treated and untreated sites on the Apache-Sitgreaves National Forest. We sampled these paired sites in 2004, 2005 and 2011.

Results: There were significant differences in pre-fire treated and untreated plant communities by species composition and abundance in 2004 and 2005, but these communities were beginning to converge in 2011. Total understorey plant cover was significantly higher in untreated areas for all 3 yr. Plant cover generally increased between 2004 and 2005 and markedly decreased in 2011, with the exception of shrub cover, which steadily increased through time. The sharp decrease in forb and graminoid cover in 2011 is likely related to drought conditions since the fire. Annual/biennial forb and graminoid cover decreased relative to perennial cover through time, consistent with the initial floristics hypothesis. Exotic plant response was highly variable and not limited to the immediate post-fire, annual/biennial community. Despite low overall exotic forb and graminoid cover for all years (<2.5%), several exotic species increased in frequency, and the relative proportion of exotic to native cover increased through time.

Conclusions: Pre-treatment fuel reduction treatments helped maintain foundation overstorey species and associated native plant communities following this large wildfire. The overall low cover of exotic species on these sites supports other findings that the disturbance associated with high-severity fire does not always result in exotic species invasions. The increase in relative cover and frequency though time indicates that some species are proliferating, and continued monitoring is recommended. Patterns of exotic species invasions after severe burning are not easily predicted, and are likely more dependent on site-specific factors such as propagules, weather patterns and management.

Introduction

In several regions of the world, climate change has been linked to increases in fire severity, frequency and extent (Westerling et al. 2006; Pausas & Fernandez-Munoz 2012). Although there is uncertainty as to how fire regimes will be affected by future climate change (Hessl 2011), many areas are likely to experience increases in

Doi: 10.1111/avsc.12015

wildfire activity (Flannigan et al. 2009). Changes to historical disturbance regimes may significantly alter native plant communities, including shifts in species assemblages (Pausas & Lloret 2007), the potential for persistent vegetation type conversions (Savage & Mast 2005; Keeley & Brennan 2012) and increased risk of exotic species invasions (D'Antonio & Vitousek 1992).

Dry ponderosa pine (*Pinus ponderosa*) forests of the southwestern US are experiencing altered fire regimes due to a decade of drought conditions and over a century of fire suppression policies. Large-scale stand replacing fires have become more common, which is a significant departure from an evolutionary history of frequent, low-severity surface fires (Covington & Moore 1994). Given predictions for a warmer and drier climate in this region (Seager et al. 2007), such fires are likely to continue. These areas have the potential to convert to shrublands or grasslands (Savage & Mast 2005), and even if pines do recapture these sites, it could take decades (Haire & McGarigal 2008).

Because these fires are creating novel conditions in these ecosystems, post-fire plant community trajectories are not well understood. The relative lack of long-term research (vs studies focused on the first few years post-fire) in severely burned ponderosa pine forests limits our understanding of post-fire plant community dynamics. Exceptions from this region include Bataineh et al. (2006), who detected persistent differences in the dominant understorey species in burned areas 30 yr post-fire as compared to unburned areas, and Foxx (1996), who reported changes in understorey species dominance of both native species and seeded exotic species through 16 yr post-fire. Given current and projected increases in severe fire, more long-term research studies are needed to better understand post-fire successional trajectories.

The initial floristics hypothesis, originally developed in reference to old-field succession, predicts that post-disturbance plant community succession is determined in large part by life-history characteristics (Egler 1954). Under this hypothesis, early post-disturbance communities are dominated by annual/biennial forbs and graminoids that are well suited to the immediate post-disturbance environment. Early communities are slowly replaced by later successional species such as perennial herbaceous plants and woody shrubs. Observational studies in burned areas generally support this hypothesis, at least in terms of the prevalence of annual/biennial species in the early post-fire environment (Turner et al. 1997; Crawford et al. 2001; Barclay et al. 2004; Bataineh et al. 2006). Similarly, annual/biennial species can also respond positively to lower-severity disturbances such as prescribed fire (Moore et al. 2006; Sabo et al. 2009), although this response is less consistent.

This successional pattern is important in part because some exotic species may fill such opportunistic roles immediately post-fire. Although exotic species exhibit a myriad of plant strategies and tolerances (Martin et al. 2009), many are ruderal annual or biennial species, that are well adapted to colonizing disturbed areas (Grime 1977). In addition, many exotic species are also shade-intolerant, making severely burned sites more suitable habitat than forests with an intact canopy for these species (Weaver et al. 2001; Sutherland 2004).

Exotic species invasions have been repeatedly linked to high-severity fire with exotic species invasions in semi-arid ecosystems (Crawford et al. 2001; Floyd et al. 2006; Dodge et al. 2008), yet some studies have documented a limited exotic response (Fornwalt et al. 2003; Huisinga et al. 2005; Kuenzi et al. 2008; McMaster 2010), making predictions about exotic response to fire difficult. In addition, fuel reduction treatments such as thinning and burning are routinely used in ponderosa pine forests to thin overly dense stands and reduce crown fire risk (Fulé et al. 2012), yet the disturbance associated with these treatments may also facilitate exotic species response (Korb et al. 2005; McGlone et al. 2009; Sabo et al. 2009). How exotic species respond to the interaction of wildfire with pre-fire treatments has only received research attention in the last decade. Hunter et al. (2006) found that fire severity had a much stronger impact than pre-fire treatment, whereas Kuenzi et al. (2008) detected no difference in exotic response relative to pre-fire treatment or fire severity. Increasing our understanding of exotic response to both wildfire and fuel treatments is crucial because exotic species invasions have the potential to displace native species (Rejmánek et al. 2005) and some can alter future fire regimes (Brooks et al. 2004).

We examined the effects of pre-fire fuel treatments on plant community response over time on the Rodeo–Chediski Fire of east-central Arizona (Fig. 1). This fire burned 189 000 ha in 2002, and at that time was the largest fire on record in the southwestern US by an order of magnitude. We built on an investigation by Strom & Fulé (2007), who examined the effects of pre-fire treatment on fire severity and post-fire forest structure on the Apache-Sitgreaves National Forest. They observed that untreated areas were generally severely burned, with few surviving overstorey trees and near-total loss of canopy cover. To examine understorey plant community response to treatment, we measured understorey characteristics in 2004, 2005 and 2011, using a subset of the plots installed by Strom & Fulé (2007). We addressed the following questions: (1) how did understorey plant community response differ between pre-fire treated areas and pre-fire untreated areas, and were these differences consistent through time; (2) did the ratio of perennial cover to annual/biennial cover

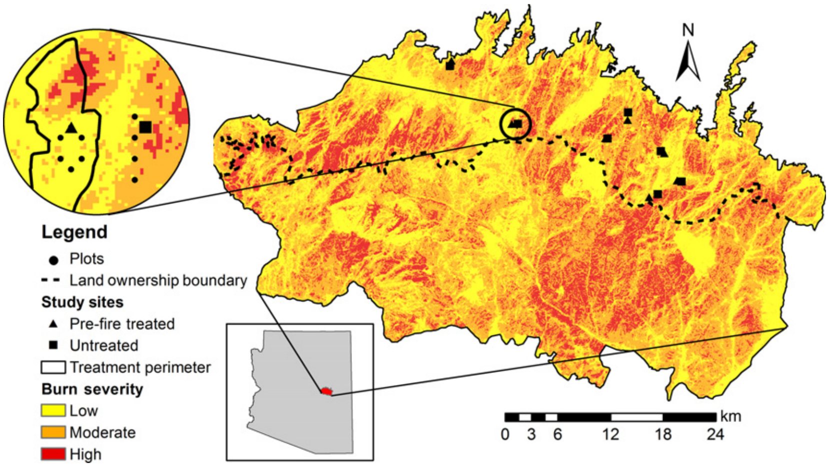

Fig. 1. Location of the 2002 Rodeo–Chediski Fire within Arizona (grey map) and burn severity map of the fire with paired sampling sites. The Apache-Sitgreaves National Forest is to the north of the dashed line bisecting the fire (White Mountain Apache Tribal Land is to the south). Close-up view is an example of one of seven site pairs with treatment boundary and individual sampling plots (site centre also represents a sampling plot).

increase as expected under the initial floristics hypothesis, and did this pattern differ between pre-fire treated and untreated areas; and (3) was exotic species response stronger in the early post-fire community, or was it persistent through time?

Methods

Study area

The study area is in east-central Arizona in the Apache-Sitgreaves National Forest (Fig. 1). The average annual precipitation was 45.5 cm (SD ± 9.61). Total precipitation in each measurement year was 33.5 cm in 2004, 40.7 cm in 2005 and 22.5 cm in 2011, and average or below average for all but one of the 9 yr of post-fire vegetation recovery. The maximum average monthly temperature was 29.2 °C, which occurred in July, and the minimum average monthly temperature was −8.7 °C, which occurred in January. Weather data from 1950 to 2011 recorded at the Heber Ranger Station are available from the Western Regional Climate Center (http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?azhebe).

We measured understorey plant community characteristics using the same 14 sites (seven pre-fire treated sites paired with seven pre-fire untreated sites) where Strom & Fulé (2007) measured overstorey characteristics. Treated sites were originally selected where treatment had occurred within 12 yr prior to the fire. Untreated sites were in adjacent untreated areas of similar topography with no natural firebreak between treated and untreated areas. Treatments were non-commercial thinning, followed by pile burning of the slash (except for one site where slash was lopped and scattered and one where slash was crushed; Strom & Fulé 2007). The entire burn area on the Apache-Sitgreaves National Forest was seeded in both 2002 and 2003 with a mix of native and exotic species. Two exotic grasses were seeded: *Lolium perenne*, a sterile annual (2002), and the perennial *Festuca ovina* (2003; Kuenzi 2006). Post-wildfire disturbances included fuelwood collection and contracted removal of dead trees in some areas (Gayle Richardson, U.S. Forest Service, pers. comm., 15 Mar 2012). There is no spatial information for fuelwood collection, but it likely occurred primarily in the severely burned untreated sites where there were more dead trees. Contract tree removal occurred on two of the seven untreated sites and along some road corridors.

Measurement

We measured overstorey structure in 2004 and 2011, and understorey plant community characteristics in 2004, 2005 and 2011. Understorey characteristics were measured on a subset of the plots established by Strom & Fulé (2007). In 2004, six subsample plots were measured at each of 14 sites, for a total of 42 plots per pre-fire treatment (84 plots total). In subsequent visits, four plots were not re-located, and so two untreated sites had five subsample plots and one site had only four, for a total of 80 plots. We used a variable radius prism plot (basal area factor 2.3 $m^2 \cdot ha^{-1}$) for overstorey trees, on which we recorded the tree species and measured DBH at 1.37 m for each tree in the plot. A hemispherical fisheye lens (Nikon CoolPix E4300, Tokyo, Japan and FC-E8 Fisheye Converter Lens) was used to photograph canopy cover, and these photographs were analysed with the Gap Light Analyzer software (v. 1; Institute of Ecosystem Studies, Simon Fraser

University, Vancouver, BC, Canada) to quantify percentage canopy openness. The plot overview was re-photographed to record a series of plot images through time.

We measured understorey characteristics using two perpendicular 44.8-m transects that comprised the diagonals of a 1000-m^2 plot. Plant canopy cover was measured using Daubenmire (1959) cover classes in ten 20 × 50 cm quadrats along each transect, for a total of 20 quadrats per plot. We recorded cover data by life form and nativity (tree regeneration, shrubs, total forbs, total graminoids, exotic forbs, exotic graminoids) and as well as by species, including trees shorter than 1.37 m, and generated a species occurrence list for the entire plot area. Plant nomenclature and nativity followed the USDA-NRCS PLANTS Database (USDA-NRCS 2011). One exception was *Portulaca oleracea*, which was listed as 'introduced' on the PLANTS database, but along with Kuenzi et al. (2008), we classified it as 'native' based on Byrne & McAndrews (1975). When we were unable to identify plants to species, we classified them to the lowest taxonomic level we could identify with certainty, generally to the genus level.

Statistical methods

Plant community analyses were based on the subset of species that occurred in at least 5% of the plant cover quadrats, and richness analyses on species that occurred on at least 5% of the plots, in order to reduce the influence of uncommon species (McCune & Grace 2002). Multivariate analyses of plant community differences were analysed separately for each year. We conducted a one-way perMANOVA, a non-parametric permutation procedure, on pre-fire treatment (treated, untreated) in PC-ORD (Version 4; MjM Software Design, Gleneden Beach, OR, US) using the Bray–Curtis dissimilarity measure with 9999 permutations at $\alpha = 0.05$ ($n = 14$).

Plant community data were graphically displayed at the plot level in ordination space, using non-metric multidimensional scaling (NMDS) conducting 250 runs with real data and 250 runs on randomizations from a random starting point, with an instability criterion of 0.00001. The final number of axes selected had stress levels <20 with P-values <0.05 (McCune & Grace 2002). We used PC-ORD to identify indicator species for each treatment, based on relative frequency and percentage cover for each species. Species with values ≥ 25 and a P-value (based on a Monte Carlo test) <0.05 were considered indicator species for that treatment (Dufrene & Legendre 1997).

Univariate response variables, including cover by life form and life-history strategy, species richness, tree density, canopy openness and basal area, were analysed using a generalized linear model to perform repeated-measures analyses on year and treatment using SAS (v. 9.2; SAS Institute Inc., Cary, NC, US). Distributions for the different response variables were based on characteristics of the responses. For count data, we modelled richness using a Poisson distribution since it assumes the mean equals the variance, whereas a negative binomial distribution was used to model tree density in order to account for over-dispersion in the data set. A log-normal distribution was selected for basal area since the log of the data was normally distributed. For percentage cover responses, we used a beta distribution. Because this distribution cannot model zero values, the data were re-scaled to eliminate zero values, using the transformation method described in Smithson & Verkuilen (2006). We evaluated pair-wise comparisons for year when the main effect was significant. Where an interaction was significant at alpha = 0.05 (or approached significance at alpha ≤ 0.10), *post-hoc* contrasts were generated for treatment within year, and between years for a given treatment.

Results

We documented the presence of 384 species from 199 genera and 51 families, including 39 exotic species from 11 families, mostly from *Poaceae* (14). For multivariate plant community analyses on cover we focused on the 104 species found on at least 5% of the quadrats, and for richness analyses we focused on the 163 species found on at least 5% of the plots, of which 16 were exotic species (Table 1).

Overall plant community response

To assess treatment effects on the overall plant community, we focused on plant composition from species cover data, related overstorey structure variables, cover by life form and species richness. We detected significant differences in plant cover by species between treated and untreated plant communities in 2004 ($P = 0.039$) and 2005 ($P = 0.025$), but not in 2011 ($P = 0.10$). The ordinations for each year reflect the distinction between treated and untreated plant communities of 2004 and 2005 and the slightly less distinct plant communities in 2011 (Fig. 2). Overstorey structure variables overlaid on these ordinations (basal area, canopy openness, tree density) varied in how they changed between the 2004 and 2011 measurements.

Basal area was significantly lower in untreated areas ($P = 0.0004$) but did not differ by year (Fig. 3). Since there were significant treatment-by-year interactions for both tree density ($P = 0.0049$) and canopy openness ($P = 0.0007$), we investigated contrasts for treatment differences within years and within treatment through time. Canopy openness was significantly higher in untreated areas in both 2004 ($P = 0.0017$) and 2011 ($P = 0.0007$);

Doi: 10.1111/avsc.12015 © 2013 International Association for Vegetation Science

Table 1. Frequency of exotic species (percentage of plots out of a total of 80) by year and pooled frequency for all years (percentage of plots out of a total of 240). Species in bold occurred on ≥5% of the pooled total and were used in analyses. Life history notation: A (annual), B (biennial), P (perennial).

Species	Life history	2004	2005	2011	Total
Forbs					
Amaranthus blitoides	A	1.25			0.42
Bassia hyssopifolia	A		1.25		0.42
Bassia scoparia	A	1.25			0.42
Chenopodium album	A	42.50	6.25		16.25
Chenopodium botrys	A	5.00			1.67
Cirsium vulgare	B	23.75	30.00	12.50	22.08
Erodium cicutarium	A	18.75	17.50	16.25	17.50
Lactuca serriola	P	53.75	73.75	45.00	57.50
Malva neglecta	ABP	1.25	2.50	1.25	1.67
Medicago lupulina	P	2.50	3.75	6.25	4.17
Medicago sativa	P	1.25	2.50		1.25
Melilotus officinalis	P	8.75	8.75	13.75	10.42
Polygonum aviculare	AP	5.00	6.25	1.25	4.17
Polygonum convolvulus	A		1.25		0.42
Rorippa sylvestris	P		1.25	1.25	0.83
Rumex acetosella	P	3.75	2.50	1.25	2.50
Rumex crispus	P	2.50	1.25	1.25	1.67
Salsola tragus	A	1.25	1.25		0.83
Sanguisorba minor	P	1.25	2.50		1.25
Sisymbrium altissimum	AB		3.75	3.75	2.50
Sonchus sp.	P		5.00		1.67
Taraxacum officinale	P	26.25	28.75	25.00	26.67
Tragopogon dubius	AB	46.25	56.25	61.25	54.58
Verbascum thapsus	B	58.75	63.75	60.00	60.83
Graminoids					
Agropyron desertorum	P		2.50		0.83
Avena fatua	A		1.25		0.42
Bromus inermis	P	5.00	7.50	23.75	12.08
Bromus japonicus	A	11.25	8.75	6.25	8.75
Bromus racemosus	A		1.25		0.42
Bromus tectorum	A	13.75	28.75	20.00	20.83
Dactylis glomerata	P	2.50	3.75	1.25	2.50
Echinochloa crus-galli	A		1.25		0.42
Eragrostis curvula	P			22.50	7.50
Festuca ovina	P			1.25	0.42
Lolium perenne	AP	30.00	12.50		14.17
Poa compressa	P		13.75	28.75	14.17
Poa pratensis	P	12.50	5.00	3.75	7.08
Schedonorus pratensis	P		3.75		1.25
Triticum aestivum	A	15.00	2.50		5.83

however when looking at treatments through time, canopy openness did not differ between years in untreated areas, but canopy openness decreased from 2004 to 2011 in treated areas ($P = 0.0029$; Fig. 3). Tree density was significantly lower in untreated areas in 2004 ($P = 0.0001$) when compared to treated areas. In 2011, this trend reversed in terms of mean tree density, but the difference was not significant ($P = 0.96$; Fig. 3). The high variability and higher mean response for tree density in untreated areas in 2011 was driven by two of the 80 plots that had exceptionally high density counts of *Juniperus deppeana*, a species that vigorously sprouts when top-killed. Tree density in treated areas did not change significantly between 2004 and 2011 ($P = 1.00$).

We then examined cover by life form, beginning with total understorey plant cover. Total plant cover was significantly higher in untreated than treated areas, and was highest in 2005 and lowest in 2011, and these differences were also significant (Table 2, Fig. 4). Treatment-by-year interaction was significant for tree regeneration cover, and *post-hoc* contrasts revealed significantly higher cover in untreated areas in 2011 over 2004 ($P = 0.0054$) and 2005 ($P = 0.0018$). Mean shrub cover was higher in untreated areas, although this difference only approached significance ($P = 0.058$); however, mean shrub cover increased through time and in 2011 was significantly higher than in 2004 and 2005 (Table 2, Fig. 4). Shrub species dominance shifted from slightly higher cover of *Ceanothus fendleri* over *Arctostaphylos pungens* in 2004, to five times higher cover of *A. pungens* relative to *C. fendleri* in 2011.

Forb cover was significantly higher in untreated areas ($P = 0.0046$). This was driven primarily by four annual or annual/biennial species, *Bahia dissecta*, *Chenopodium graveolens*, *Conyza canadensis* and *Polygonum douglasii*, as well as the perennial *Heliomeris multiflora*. *H. multiflora* was an indicator species of untreated areas for all 3 yr. Forb cover was also significantly different for all years, where the mean trend followed that of total cover (highest in 2005, lowest in 2011). Forb species with the highest cover values generally followed this trend, with the exception of annual species *P. douglasii* and *C. graveolens*, which steadily declined over time.

Graminoids also followed this general pattern of mean cover over time (highest in 2005, lowest in 2011), and this difference was significant among all years. Of the individual graminoid species, only the annual *Muhlenbergia minutissima* consistently declined in cover over the years. Of the higher cover graminoid species (>1%), the seeded native *B. carinatus* did increase in 2005 but declined much more markedly in 2011 than other graminoids, to <0.1%. Although mean graminoid cover was slightly higher for untreated areas, this difference was not significant ($P = 0.44$).

Finally, overall species richness was not significantly different by treatment, but was significantly higher in 2005 than 2004 ($P = 0.0011$). Indicator species for each treatment varied through time (Table 3). As noted above, the only consistent indicator species for all 3 yr was the perennial forb *H. multiflora* for untreated areas. The untreated areas had more indicator species than treated areas, including one seeded native species (*B. carinatus*) in 2005, and one exotic species, *Tragopogon dubius*, in 2011. Treated sites had no indicators for 2004, the seeded perennial grass,

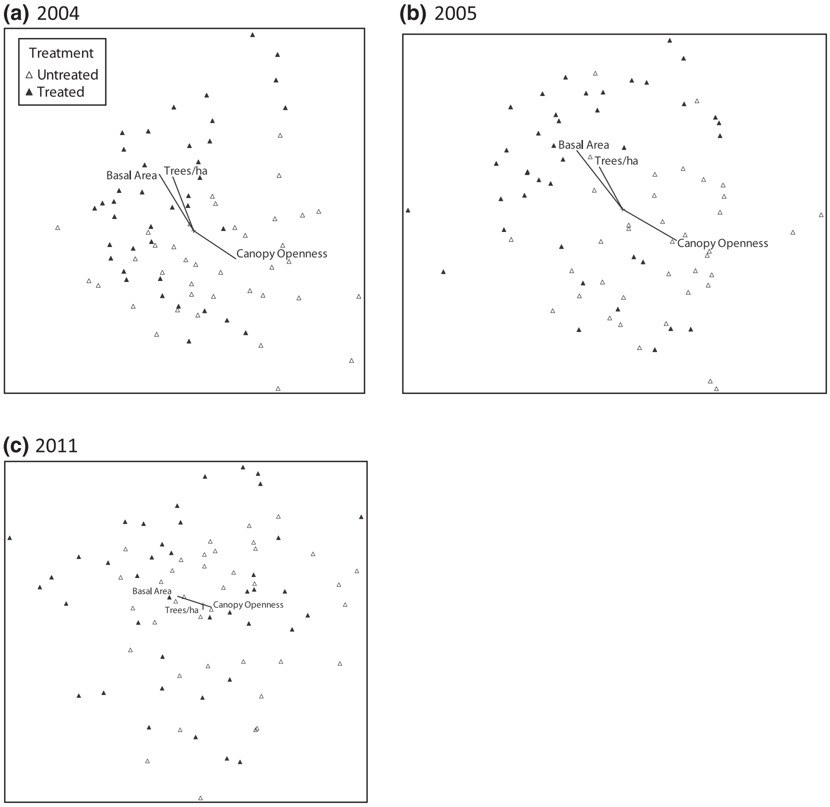

Fig. 2. Non-metric multidimensional scaling (NMDS) ordinations showing plot-level communities for each year with basal area, tree density and canopy openness overlaid as vectors. Vectors in the ordinations for (**a**) 2004 and (**b**) 2005 both use 2004 stand structure data. 2011 ordination (**c**) uses 2011 stand structure data. Stress levels and final dimensionality are: (**a**) 2004: 15.80, four dimensions; (**b**) 2005: 15.93, four dimensions; (**c**) 2011: 15.49, four dimensions.

K. macrantha, for 2005, and the perennial forb, *Packera neomexicana*, for 2011.

Annual/biennial and perennial response

Mean annual/biennial cover (both forbs and graminoids) was significantly lower in 2011 than in previous measurements, and the higher mean response in untreated areas approached significance ($P = 0.073$; Fig. 5, Table 2). Perennial plant cover was significantly higher in untreated than treated areas, and also differed among years. The ratio of perennial to annual/biennial cover changed dramatically over time, from the 2004 ratios 1.6:1.0 and 1.7:1.0 in untreated and treated areas, respectively, to 9.0:1.0 and 10.4:1.0 in 2011 (Fig. 5). The changes in annual/biennial cover relative to perennial cover was not markedly different between treated and untreated areas, but the perennial to annual/biennial ratio was slightly lower in the untreated areas. For all years and both treatments, the majority of annual plant cover was from forb species, but the majority of perennial cover was from graminoid species.

Exotic species response

Exotic forb cover was significantly higher in 2005 than in 2004 or 2011, and the higher mean exotic forb cover in untreated areas approached significance ($P = 0.071$; Fig. 4, Table 2). Mean exotic forb cover values for all years were consistently low, <2.5%. Exotic graminoid cover did not differ significantly by treatment or among years, and mean cover values were all <1%. Exotic species richness was not significantly different among years, but higher mean exotic species richness in untreated areas approached significance ($P = 0.071$; Fig. 4, Table 2). Mean exotic species richness was more similar between treatments in 2004 and 2005, but somewhat higher in untreated areas (4.9 vs 3.0) in 2011.

In addition to cover, we also examined turnover of exotic species in terms of frequency (presence/absence by

Doi: 10.1111/avsc.12015

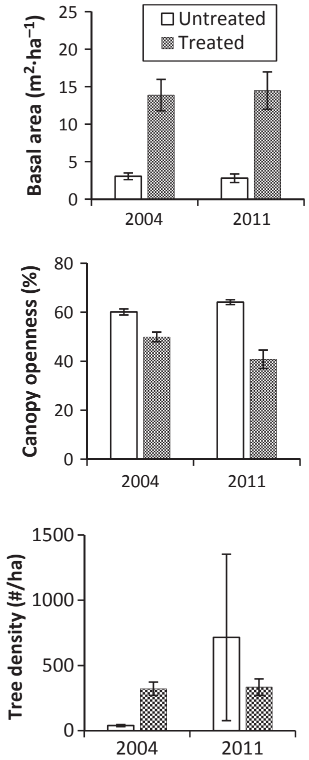

Fig. 3. Basal area, tree density and percentage canopy openness by treatment and year, with SE.

Table 2. *P*-values for year, treatment and interaction for univariate variables, including total cover, cover by life form and richness. Significance at alpha = 0.05 is denoted by *. Only significant *P*-values for pair-wise comparisons for year are included.

Variable	Year	Treatment	Interaction
Total cover	0.0001*	0.0011*	0.73
2004–2005	0.047*		
2004–2011	0.0004*		
2005–2011	0.0002*		
Tree regeneration cover	0.0091*	0.27	0.02*
2004–2005	0.0001*		
2004–2011	0.0001*		
2005–2011	0.0001*		
Shrub cover	0.029*	0.058	0.72
2004–2005	0.041*		
2004–2011	0.041*		
Forb cover	0.0001*	0.0046	0.72
2004–2005	0.0059*		
2004–2011	0.0001*		
2005–2011	0.0001*		
Graminoid cover	0.0001*	0.44	0.94
2004–2005	0.0007*		
2004–2011	0.0001*		
2005–2011	0.0001*		
Annual/Biennial cover	0.0001*	0.073	0.51
2005–2011	0.0001*		
Perennial cover	0.0001*	0.0048*	0.17
2004–2005	0.0001*		
2004–2011	0.0001*		
2005–2011	0.0001*		
Richness	0.0037*	0.19	0.21
2004–2005	0.0024*		
Exotic forb cover	0.0039*	0.071	0.97
2004–2005	0.0023*		
2005–2011	0.016*		
Exotic graminoid cover	0.60	0.67	0.51
Exotic richness	0.28	0.071	0.18

plot; Table 1). Several exotic forb species decreased between 2004 and 2011, including *Chenopodium album*, *Cirsium vulgare* and *Lactuca serriola*. *Verbascum thapsus* and *Taraxacum officinale* frequency remained relatively constant, although mean *V. thapsus* cover increased slightly through time in untreated areas. *Tragopogon dubius* had the highest increase in frequency through time, from 46.25% in 2004 to 61.25% in 2011, although overall cover changes were minimal.

Exotic graminoids decreasing in frequency between 2004 and 2011 were the annuals *Bromus arvensis* and *Bromus tectorum*, despite the slight increase in *B. tectorum* frequency in 2005. The perennial grasses *Poa pratensis* decreased whereas *Poa compressa* increased, but we suspect there may have been identification errors between these similar species; when combined, frequency increased from 12.5% to 32.5% of the plots. In addition, two other perennial grass species strongly increased in frequency. The strongly rhizomatous *Bromus inermis* increased from 5.00% to 23.75%, and *Eragrostis curvula* was first detected in 2011 on 22.50% of the plots. Of the two exotic species seeded as part of the post-fire rehabilitation effort the sterile annual *L. perenne* was detected in early years, but was absent from any plots by 2011. In contrast, the seeded perennial *F. ovina* was first detected at very low frequency (1.25%) in 2011.

Discussion

Overall plant community response

Plant community composition was distinct between pre-fire treated and untreated areas in 2004 and 2005 but was beginning to converge in 2011. We suspected that differences in the plant communities were driven by overstorey structure differences, yet these overstorey variables did not change much through time. Another possible explanation for this trend toward convergence may be that the close proximity of pre-fire treated areas to the untreated sites facilitated faster colonization than may have occurred in the interior of larger, high-severity burn patches (Turner et al. 1998). We also suspect

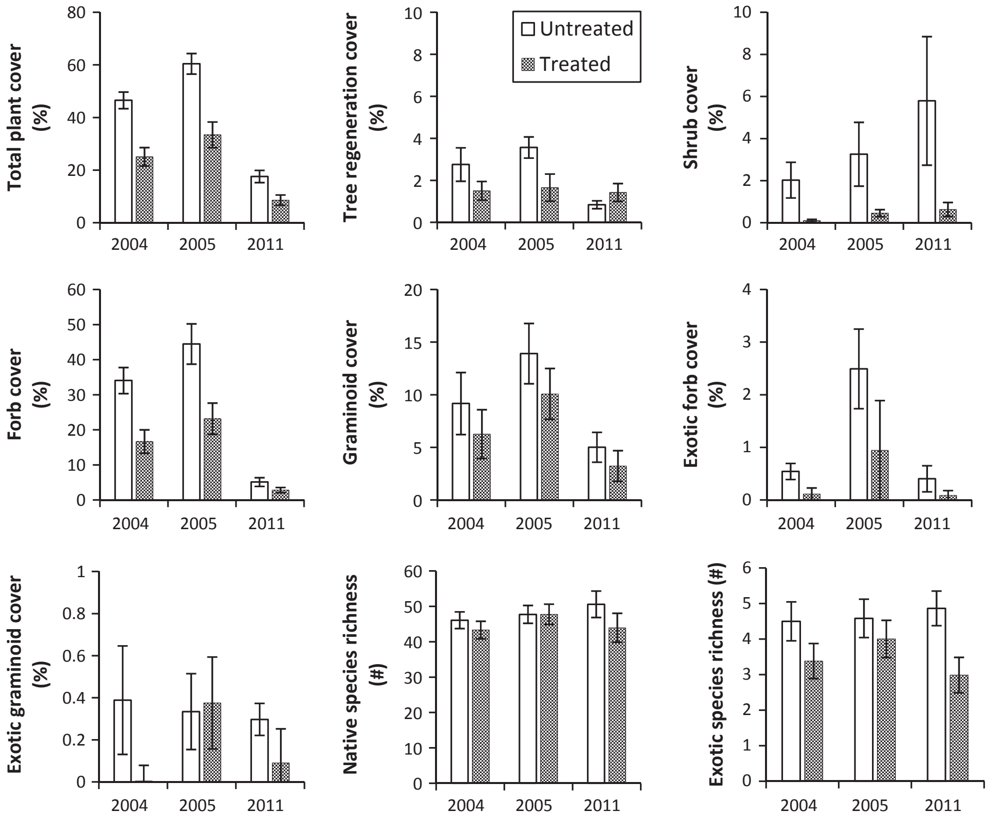

Fig. 4. Total plant cover, species richness and cover by life form, plus exotic forb and graminoid species cover and richness, by treatment and year with SE. Note differences in scale on *y*-axes.

Table 3. Indicator species by pre-fire treatment (treated, untreated) and year.

	2004	2005	2011
Untreated	*Bahia dissecta* *Erigeron divergens* *Eriogonum racemosum* *Heliomeris multiflora* *Packera neomexicana*	*Bromus carinatus*[a] *Erigeron divergens* *Heliomeris multiflora* *Juniperus depeanna*	*Cirsium wheeleri* *Epilobium brachycarpum* *Heliomeris multiflora* *Tragopogon dubius*[b]
Treated	None	*Koeleria macrantha*[a]	*Packera neomexicana*

[a] Species seeded after the Rodeo–Chediski Fire on the Apache-Sitgreaves National Forest in 2002 and 2003.

[b] Exotic species.

that our sampling protocols, which were adequate in 2004 and 2005, may have underestimated the regeneration of sprouting tree species, such as *Quercus gambelii*, *J. deppeana* and *Robinia neomexicana* (Fig. 6), in 2011. Because many individuals were over breast height in 2011, they were not included in our understorey cover estimates. However, because of their shrub-like morphology at this stage of growth, the small diameter leaders were rarely included in the variable radius plots. Thus this component of the vegetation community, which was strong in the untreated areas, was probably under-represented in our results. Despite these caveats, we still find it encouraging that the understorey herbaceous community on severely burned, untreated sites is becoming more similar to that of the less severely burned, treated areas.

We detected consistently higher total understorey plant cover in the more severely burned untreated areas, where the removal of most overstorey trees reduced competition for light and other resources. This pattern is similar to that observed by Bataineh et al. (2006). Over time, mean total plant cover and cover by life form increased between 2004 and 2005, when higher plant cover in untreated areas was mostly forb species. The dra-

Doi: 10.1111/avsc.12015

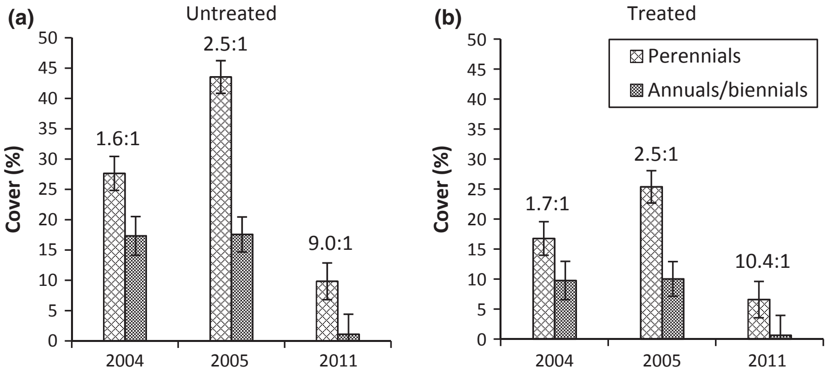

Fig. 5. Cover of perennials and annuals/biennials by year with SE for pre-fire (**a**) untreated and (**b**) treated areas. Perennial to annual/biennial ratios are above bars.

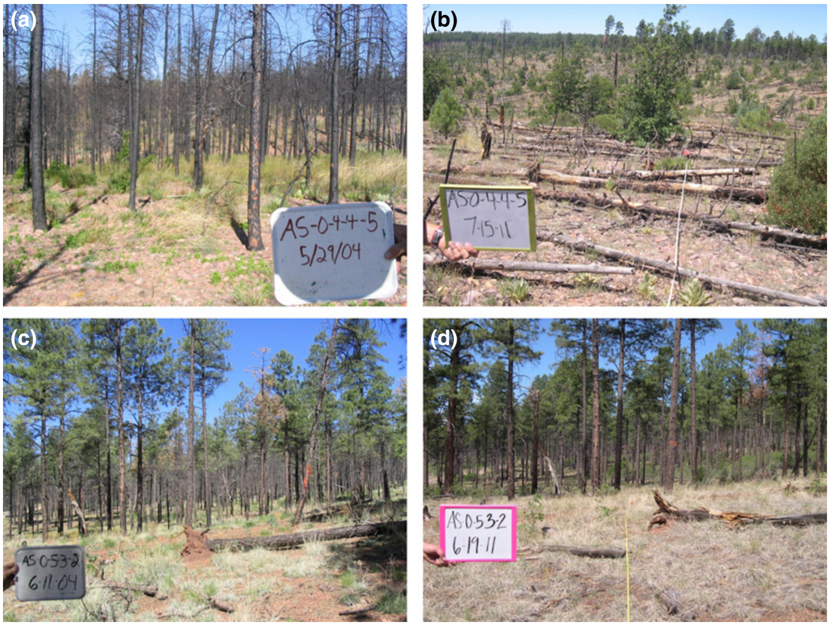

Fig. 6. Photograph series of two sampling sites. From top, untreated plot in 2004 (2 yr post-fire; **a**), and 2011 (9 yr post-fire; **b**); below, pre-fire treated plot in 2004 (**c**) and 2011 (**d**).

matic decrease in total plant, forb and graminoid cover in 2011 may be related to competitive effects from increasing shrub cover on the untreated sites. The continual increase in shrub cover may be due to the slower-growing strategy of many shrub species that are likely to become stronger competitors later in time. Whereas *A. pungens* dominated the 2011 shrub community, *C. fendleri* was more strongly established in the first years post-fire, which may be related to heat-stimulated germination (Huffman & Moore 2004). In addition to competition with shrubby species, drought conditions in the years post-fire likely further suppressed herbaceous response over time. Many studies in the southwest US have detected decreases in cover, which have been linked with persistent drought (Bataineh et al. 2006; Moore et al. 2006).

Annual/perennial response

The first interesting trend in annual/biennial forb and graminoid cover was higher mean annual/biennial cover in the untreated areas (that tended to burn more severely). Although this difference only approached significance, it is not surprising to find a higher mean ruderal response in more severely burned areas. We speculate that post-wildfire disturbances may have also contributed to this response (as well as other variables analysed in this study, e.g. exotic species), but it is not possible to distinguish these effects. Second, annual/biennial cover decreased relative to perennial species over time. In untreated areas, this offers general support for Egler's (1954) initial floristics hypothesis, and emphasizes the importance of life history in trends of secondary succession. In treated areas that were not as severely disturbed, the post-fire response was similar to that observed in other ponderosa pine forests with more open stand structures that burned less severely. Moore et al. (2006) observed an increase in the standing crop of annual/biennial forbs in thinned ponderosa pine stands that had forest floor manipulation and burning, followed by a subsequent decline. In addition, two studies from the Grand Canyon found increases in annual/biennial forb richness (Laughlin et al. 2004) and in annual/biennial forb and grass cover (Laughlin & Fulé 2008) in the first few years post-fire.

Exotic species response

Exotic species response was not limited to a ruderal, immediate post-fire role. In general, the exotic response was quite low ($\leq 2.5\%$ for all years), which may be due in part to the drought conditions in the post-fire years. The response was also highly variable, making the comparison of trends by life-history strategy interesting, but not definitive. One noteworthy trend, despite these limitations, was the higher proportion of mean exotic annual/biennial cover relative to native annual/biennial cover in 2011, particularly in untreated areas. This may suggest that exotic annual/biennial species are more persistent than native annual/biennial species through time. When considering exotic cover by life form, exotic forb cover was significantly higher in 2005 than either of the other 2 yr. These species may have been responding negatively to drought in the later years, just as native forbs were. This is consistent with studies that demonstrate that exotic species generally respond to the same environmental conditions as native species (Meiners 2007), although exotic graminoids did not show any consistent trend.

The low overall exotic response on our sites is consistent with some other studies on high-severity fires in the region (Foxx 1996; Huisinga et al. 2005; Kuenzi et al. 2008; McMaster 2010). With the exception of Kuenzi et al. (2008), many of these areas were not as heavily managed as our study sites, which have been subjected to grazing, recreation, logging and road-building (Kuenzi 2006). When this is coupled with the wildfire disturbance, our results are somewhat surprising, as a number of studies have documented exotic species invasions in severely burned ponderosa pine forests (Crawford et al. 2001; Griffis et al. 2001; Barclay et al. 2004; Dodge et al. 2008). However, it is problematic to compare the exotic response in our study to some of the studies in this region, because of differences in species classification. Some studies do not provide lists of observed exotic species (Griffis et al. 2001), and still others classified species such as *Conyza canadensis* as exotic (Crawford et al. 2001; Barclay et al. 2004), which we consider native based on the USDA Plants database (USDA-NRCS 2011) and local floras (Kearney et al. 1961).

Despite the overall low cover values we observed, there may be some cause for concern about exotic species on these sites. First, we detected an increase in exotic cover relative to overall cover by life form in untreated areas. The portion of exotic forb cover that comprises the overall forb cover increased from 1.6% in 2004 to 7.9% in 2011; relative exotic graminoid cover increases were slightly smaller, from 4.2% in 2004 to 5.9% in 2011. Although these numbers are not exceptionally large, these increases may allow exotic species to build up enough propagules to facilitate a stronger invasion following future disturbances or in years of high precipitation (McGlone et al. 2009).

The increase in frequency of certain exotic species through time also raises concerns. An experimental study in semi-arid sagebrush ecosystems found that *T. dubius*, a deeply tap-rooted perennial forb, could out-compete native grasses after disturbance due to its ability to access deep water resources that were available after the loss of a foundation species (Prevey et al. 2010). This species was an indicator species in 2011 and had the highest increase in frequency on our untreated sites; since drought conditions are expected to continue in the southwest US (Seager et al. 2007), this species may further proliferate in the future. Finally, the appearance of two exotic perennial bunchgrasses in 2011 may also be of concern. *Eragrostis curvula* was seeded on a nearby fire in 1993, and remained dominant (93% cover) 15 yr post-fire, suggesting it can persist on the landscape (Leonard 2007). In addition, it responds well to burning (McFarland & Mitchell 2000), and since it is now established in the area, future fires may greatly increase the cover of this species on the landscape. *Festuca ovina* was seeded in 2003 and first detected in 2011. In contrast, the seeded exotic grass *L. perenne*, a sterile annual, was absent by 2011; if seeding is required, sterile annuals are recommended over perennial exotic species that are more likely to persist.

Study implications

There is a substantial body of research on exotic species invasions following disturbances such as wildfires. It appears that such invasions are not always strongly related to the severity of the disturbance or pre-fire management practices. Given the lack of a consistent pattern in exotic species composition and abundance across wildfires, local site-specific factors are likely stronger drivers of exotic response. Although high-severity fires can open up growing space for exotic species, the more important drivers may be on-site propagules, post-fire management practices and weather patterns. Few studies have examined longer-term exotic species trajectories following severe wildfires. Our data suggest that exotic species can increase in frequency over time, thus, longer-term monitoring following severe disturbances may be warranted.

Strom & Fulé (2007) detected significant reductions in fire severity in areas treated before the Rodeo–Chediski Fire, and our data show that those treatments also had a persistent effect on vegetation response 9 yr post-fire. Since the plant communities in pre-fire treated and untreated sampling sites were beginning to converge 9 yr post-fire, the close proximity of severely burned areas to less severely burned areas may facilitate native plant community recovery. Collectively, this suggests that pre-fire treatments can help maintain native plant communities associated with an intact ponderosa pine forest.

Acknowledgements

We thank our funders for this project: the Joint Fire Science Program (JFSP 11-1-27), the Ecological Restoration Institute (ERI) and National Fire Plan (FEW-3) through Challenge Cost Share Agreement 09-CS-190 with the Rocky Mountain Research Station (RMRS). We particularly thank RMRS statistician Scott Baggett for statistical advice and Don Normandin of ERI for logistical support. We also thank Apache-Sitgreaves National Forest personnel and Barb Strom for consulting on this project. Finally, we thank field crew members Brooke Benson, Lindsay Wallis, Allison Skrehart, Nick Fransioli and Adam Polinko.

References

Barclay, A.D., Betancourt, J.L. & Allen, C.D. 2004. Effects of seeding ryegrass (*Lolium multiflorum*) on vegetation recovery following fire in a ponderosa pine (*Pinus ponderosa*) forest. *International Journal of Wildland Fire* 13: 183–194.

Bataineh, A.L., Oswald, B.P., Bataineh, M.M., Williams, H.M. & Coble, D.W. 2006. Changes in understory vegetation of a ponderosa pine forest in northern Arizona 30 years after a wildfire. *Forest Ecology and Management* 235: 283–294.

Brooks, M.L., D'Antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.E., DiTomaso, J.M., Hobbs, R.J., Pellant, M. & Pyke, D. 2004. Effects of invasive alien plants on fire regimes. *BioScience* 54: 677–688.

Byrne, R. & McAndrews, J.H. 1975. Pre-Columbian purslane (*Portulaca oleracea* L) in the New World. *Nature* 253: 726–727.

Covington, W.W. & Moore, M.M. 1994. Southwestern ponderosa forest structure – changes since Euro-American settlement. *Journal of Forestry* 92: 39–47.

Crawford, J.S., Wahren, C.H.A., Kyle, S. & Moir, W.H. 2001. Responses of exotic plant species to fires in *Pinus ponderosa* forests in northern Arizona. *Journal of Vegetation Science* 12: 261–268.

D'Antonio, C.M. & Vitousek, P.M. 1992. Biological invasions by exotic grasses, the grass fire cycle, and global change. *Annual Review of Ecology and Systematics* 23: 63–87.

Daubenmire, R.F. 1959. A canopy-coverage method. *Northwest Science* 33: 43–64.

Dodge, R.S., Fulé, P.Z. & Sieg, C.H. 2008. Dalmatian toadflax (*Linaria dalmatica*) response to wildfire in a southwestern USA forest. *Ecoscience* 15: 213–222.

Dufrene, M. & Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67: 345–366.

Egler, R.E. 1954. Vegetation science concepts: I. Initial floristic composition: a factor in old-field vegetation development. *Vegetatio* 4: 412–417.

Flannigan, M.D., Krawchuk, M.A., de Groot, W.J., Wotton, B.M. & Gowman, L.M. 2009. Implications of changing climate for global wildland fire. *International Journal of Wildland Fire* 18: 483–507.

Floyd, M.L., Hanna, D., Romme, W.H. & Crews, T.E. 2006. Predicting and mitigating weed invasions to restore natural post-fire succession in Mesa Verde National Park, Colorado, USA. *International Journal of Wildland Fire* 15: 247–259.

Fornwalt, P.J., Kaufmann, M.R., Huckaby, L.S., Stoker, J.A. & Stohlgren, T.J. 2003. Non-native plant invasions in managed and protected ponderosa pine–Douglas-fir forests of the Colorado Front Range. *Forest Ecology and Management* 177: 515–527.

Foxx, T.S. 1996. Vegetation succession after the La Mesa fire at Bandelier National Monument. In: Allen, C.D. (ed.) *Fire effects in Southwestern forests: Proceedings of the Second La Mesa Fire Symposium, 29–31 March 1994*, pp. 47–69. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, US.

Fulé, P.Z., Crouse, J.E., Roccaforte, J.P. & Kalies, E.L. 2012. Do thinning and/or burning treatments in western USA ponderosa- or Jeffrey pine-dominated forests help restore natural fire behavior? *Forest Ecology and Management* 269: 68–81.

Griffis, K.L., Crawford, J.A., Wagner, M.R. & Moir, W.H. 2001. Understory response to management treatments in northern Arizona ponderosa pine forests. *Forest Ecology and Management* 146: 239–245.

Grime, J.P. 1977. Evidence for existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist* 111: 1169–1194.

Haire, S.L. & McGarigal, K. 2008. Inhabitants of landscape scars: succession of woody plants after large, severe forest fires in Arizona and New Mexico. *Southwestern Naturalist* 53: 146–161.

Hessl, A.E. 2011. Pathways for climate change effects on fire: models, data, and uncertainties. *Progress in Physical Geography* 35: 393–407.

Huffman, D.W. & Moore, M.M. 2004. Responses of Fendler ceanothus to overstory thinning, prescribed fire, and drought in an Arizona ponderosa pine forest. *Forest Ecology and Management* 198: 105–115.

Huisinga, K.D., Laughlin, D.C., Fulé, P.Z., Springer, J.D. & McGlone, C.M. 2005. Effects of an intense prescribed fire on understory vegetation in a mixed conifer forest. *The Journal of the Torrey Botanical Society* 132: 590–601.

Hunter, M.E., Omi, P.N., Martinson, E.J. & Chong, G.W. 2006. Establishment of non-native plant species after wildfires: effects of fuel treatments, abiotic and biotic factors, and post-fire grass seeding treatments. *International Journal of Wildland Fire* 15: 271–281.

Kearney, T.H., Peebles, R.H., Howell, H.T. & McClintok, E. 1961. *Arizona flora*, 2nd ed. University of California Press, Berkeley, CA, US.

Keeley, J.E. & Brennan, T.J. 2012. Fire-driven alien invasion in a fire-adapted ecosystem. *Oecologia* 169: 1043–1052.

Korb, J.E., Springer, J.D., Powers, S.R. & Moore, M.M. 2005. Soil seed banks in *Pinus ponderosa* forests in Arizona: clues to site history and restoration potential. *Applied Vegetation Science* 8: 103–112.

Kuenzi, A.M. 2006. *Pre-fire treatment effects and understory plan community response on the Rodeo–Chediski fire*. MS Thesis, School of Forestry, Northern Arizona University, Flagstaff, AZ, US.

Kuenzi, A.M., Fulé, P.Z. & Sieg, C.H. 2008. Effects of fire severity and pre-fire stand treatment on plant community recovery after a large wildfire. *Forest Ecology and Management* 255: 855–865.

Laughlin, D.C. & Fulé, P.Z. 2008. Wildland fire effects on understory plant communities in two fire-prone forests. *Canadian Journal of Forest Research* 38: 133–142.

Laughlin, D.C., Bakker, J.D., Stoddard, M.T., Daniels, M.L., Springer, J.D., Gildar, C.N., Green, A.M. & Covington, W.W. 2004. Toward reference conditions: wildfire effects on flora in an old-growth ponderosa pine forest. *Forest Ecology and Management* 199: 137–152.

Leonard, J.M. 2007. *The influence of parent material on vegetation response 15 years after the Dude Fire*. MS Thesis, School of Forestry, Northern Arizona University, Flagstaff, AZ, US.

Martin, P.H., Canham, C.D. & Marks, P.L. 2009. Why forests appear resistant to exotic plant invasions: intentional introductions, stand dynamics, and the role of shade tolerance. *Frontiers in Ecology and the Environment* 7: 142–149.

McCune, B. & Grace, J.B. 2002. *Analysis of ecological communities*. MjM Software Design, Gleneden Beach, OR, US.

McFarland, J.B. & Mitchell, R. 2000. Fire effects on weeping lovegrass tiller density and demographics. *Agronomy Journal* 92: 42–47.

McGlone, C.M., Springer, J.D. & Laughlin, D.C. 2009. Can pine forest restoration promote a diverse and abundant understory and simultaneously resist nonnative invasion? *Forest Ecology and Management* 258: 2638–2646.

McMaster, M.A. 2010. *Effects of fire and post-fire seeding on plant communities in a ponderosa pine forest*. MS Thesis, School of Forestry, Northern Arizona University, Flagstaff, AZ, US.

Meiners, S.J. 2007. Native and exotic plant species exhibit similar population dynamics during succession. *Ecology* 88: 1098–1104.

Moore, M.M., Casey, C.A., Bakker, J.D., Springer, J.D., Fulé, P.Z., Covington, W.W. & Laughlin, D.C. 2006. Herbaceous vegetation responses (1992–2004) to restoration treatments in a ponderosa pine forest. *Rangeland Ecology & Management* 59: 135–144.

Pausas, J.G. & Fernandez-Munoz, S. 2012. Fire regime changes in the western Mediterranean Basin: from fuel-limited to drought-driven fire regime. *Climatic Change* 110: 215–226.

Pausas, J.G. & Lloret, F. 2007. Spatial and temporal patterns of plant functional types under simulated fire regimes. *International Journal of Wildland Fire* 16: 484–492.

Prevey, J.S., Germino, M.J. & Huntly, N.J. 2010. Loss of foundation species increases population growth of exotic forbs in sagebrush steppe. *Ecological Applications* 20: 1890–1902.

Rejmánek, M., Richardson, D.M., Higgins, S.I., Pitcairn, M.J. & Grotkopp, E. 2005. Ecology of invasive plants: state of the art. In: Mooney, H.A., Mack, R.N., McNeely, J.A., Neville, L.E., Schei, P.J. & Waage, J.K. (eds.) *Invasive alien species: a new synthesis*, pp. 104–161. Island Press, Washington DC, US.

Sabo, K.E., Sieg, C.H., Hart, S.C. & Bailey, J.D. 2009. The role of disturbance severity and canopy closure on standing crop of understory plant species in ponderosa pine stands in northern Arizona, USA. *Forest Ecology and Management* 257: 1656–1662.

Savage, M. & Mast, J.N. 2005. How resilient are southwestern ponderosa pine forests after crown fires? *Canadian Journal of Forest Research* 35: 967–977.

Seager, R., Ting, M.F., Held, I., Kushnir, Y., Lu, J., Vecchi, G., Huang, H.P., Harnik, N., Leetmaa, A., Lau, N.C., Li, C.H., Velez, J. & Naik, N. 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. *Science* 316: 1181–1184.

Smithson, M. & Verkuilen, J. 2006. A better lemon squeezer? Maximum-likelihood regression with beta-distributed dependent variables. *Psychological Methods* 11: 54–71.

Strom, B.A. & Fulé, P.Z. 2007. Pre-wildfire fuel treatments affect long-term ponderosa pine forest dynamics. *International Journal of Wildland Fire* 16: 128–138.

Sutherland, S. 2004. What makes a weed a weed: life history traits of native and exotic plants in the USA. *Oecologia* 141: 24–39.

Turner, M.G., Romme, W.H., Gardner, R.H. & Hargrove, W.W. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. *Ecological Monographs* 67: 411–433.

Turner, M.G., Baker, W.L., Peterson, C.J. & Peet, R.K. 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. *Ecosystems* 1: 511–523.

USDA-NRCS 2011. *The PLANTS database*. National Plant Data Center, Baton Rouge, LA, US. Available at http://plants.usda.gov (accessed 15 November 2011).

Weaver, T., Gusafson, D. & Lichthardt, J. 2001. Exotic plants in early and late seral vegetation of fifteen northern Rocky Mountain environments (HTs). *Western North American Naturalist* 61: 417–427.

Westerling, A.L., Hidalgo, H.G., Cayan, D.R. & Swetnam, T.W. 2006. Warming and earlier spring increase western US forest wildfire activity. *Science* 313: 940–943.