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Long-term effects of burning slash on plant communities and arbuscular mycorrhizae in a semi-arid woodland

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Summary

1. Burning of slash (woody debris) piles resulting from the harvest of fuel wood is a common management technique designed to reduce fire risk and increase establishment of understorey vegetation in many semi-arid woodlands. However, the consequences of slash burning on plant communities and their below-ground fungal mutualists are poorly understood.

2. We examined how the burning of slash piles affected understorey plant communities and arbuscular mycorrhizal (AM) fungi in a pinyon–juniper woodland in northern Arizona, USA, 5 years after harvesting. We analysed plant communities and AM inoculum potential along 16 transects in: (i) burned slash pile sites; (ii) interspaces between burned slash piles; (iii) non-burned canopy sites; and (iv) non-burned interspaces. We quantified AM colonization of dominant native and exotic plants in burned and non-burned areas.

3. Burned areas had significantly fewer understorey plant species than non-burned areas, and exotic species were four times more abundant at burned slash sites than at other sites.

4. Exotic plants from burned and non-burned areas exhibited levels of AM colonization that were 50% greater than native plants. Bioassay and field-collected plants exhibited similar levels of AM colonization and there were no significant treatment differences.

5. The total biomass of bioassay plants grown in soil from burned slash sites averaged 19% greater than plant biomass from other sites, and had 27% more phosphorus in their shoot tissue; however, tissue nitrogen contents were similar.

6. *Synthesis and applications*. These results suggest that either fire did not reduce AM inoculum potential, or that AM fungal populations recovered in the 5 years after the slash was burned. Changes in understorey plant communities and increases in exotic species with burning could result from other soil changes (e.g. species of AM fungi present), reduction of native species in the seed bank or greater dispersal ability of exotic plants compared with native plant species. We suggest that burning slash piles as a management tool in pinyon–juniper woodlands can result in plant communities that are persistently dominated by exotic species. Management approaches that utilize fuel wood harvest alone or that incorporate seeding of native plants may achieve the desired results.

Key-words: exotic plant species, fire, forest management, pinyon–juniper woodlands

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Introduction

Fire is used as a management tool in a variety of ecosystems in an effort to increase biodiversity and promote ecosystem sustainability (Frost & Robertson 1985; Covington *et al*. 1997; Korb, Johnson & Covington 2003). Some of the benefits that make burning such a popular management tool include temporary increases in soil nitrogen mineralization (Raison 1979; DeBano, Perry & Overby 1987; Ellingson *et al*. 2000), reduction of surface fuel loads that could cause catastrophic fires (Covington *et al*. 1997) and increased herbaceous productivity (Barney & Frischknecht 1974). However, burning can also have important negative consequences for plant communities that establish after burning. These negative attributes include the destruction of the soil structure and soil microbial communities

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associated with the top few centimetres of soil (Dumontet *et al.* 1996; Neary *et al.* 1999), increased susceptibility to soil erosion (Neary *et al.* 1999), alteration of the soil seed bank (Clark & Wilson 1994), and increased opportunity for the colonization of exotic plant species (Allen 1991).

The effects of fire on soil microbes have received less attention than above-ground processes, but the soil microbial community may have significant impacts on plant community composition. For example, fire has been shown to significantly reduce the levels of bacteria, actinomycetes and mycorrhizal fungal propagules in the top few centimetres of soil (Deka & Mishra 1983; Pattinson *et al.* 1999). Also, because mycorrhizal fungi generally promote plant growth and can be critical to the establishment and survival of many plant species (Berliner, Jacoby & Zamski 1986; Smith & Read 1997), a reduction in mycorrhizal fungal propagules may severely affect the re-establishing plant community by reducing the abundance of mycorrhiza-dependent plant species. Many native grass species, which are desirable as sources of forage for ungulates, are dependent upon arbuscular mycorrhizal (AM) fungi for establishment and growth (Wilson & Hartnett 1998). Furthermore, fire has been shown to alter the AM fungal community present in the soil (Vilariño & Arines 1991), which can in turn affect plant community structure (van der Heijden *et al.* 1998; Hartnett & Wilson 1999; O'Connor, Smith & Smith 2002).

Pinyon–juniper woodlands cover approximately 24 million ha of the western USA (West 1984). Traditionally, they have not been intensively managed because management costs have exceeded the value of the products obtained (Doughty 1987). However, recent increases in the demand for wildlife and livestock forage, fuel wood production (Dalen & Snyder 1987) and the desire to limit the expansion of pinyon–juniper woodlands into grasslands (Miller & Wigand 1994) have led to the implementation of management techniques such as fuel wood cutting and burning of the resulting slash in pinyon–juniper woodlands. Slash consists of small branches and other debris from felled trees. The likely effects of fuel wood harvest and burning in this ecosystem are unclear. The role of fire in pinyon–juniper woodlands is highly variable, with natural fire return frequencies that range from approximately 10 to 400 years (Wright, Neuenschwander & Britton 1979; Floyd, Romme & Hanna 2000). Shorter term experimental studies on the effect of burning in pinyon–juniper woodland field soils and microcosms indicate AM fungal reductions of 90% or more (Klopatek *et al.* 1994), with the greatest effects observed beneath tree canopies rather than in interspaces between trees. In addition, burned slash piles can act as foci for the establishment of exotic plant species (Dickinson & Kirkpatrick 1987) that may in turn affect the success of native plant species (Klironomos 2002).

This study examined the responses of understorey plants and AM fungi to slash burning following fuel wood harvest in a pinyon–juniper woodland. Approximately 400 ha of USA Forest Service land in Northern Arizona were opened up to fuel wood harvest in 1995. After the harvest, the slash was raked into piles at the base of stumps and burned. This created a heterogeneous environment consisting of burned patches (slash piles) and adjacent non-burned or lightly burned interspaces in the treated sites. The management goal was to increase forage production, preferably of native perennial bunchgrasses, for wildlife and livestock. Adjacent tracts of woodland were left as non-burned controls. This study investigated two questions. First, how did the burning of slash piles affect the understorey plant communities of pinyon–juniper woodlands? Secondly, did the burning of slash piles affect AM inoculum potential 5 years after the burn? Although several studies have addressed the effects of slash burning on plant communities and AM fungal propagule abundance immediately following a burn, this study differs in that it examined these variables after a longer period of time (5 years) to determine if the management goals were obtained.

SITE DESCRIPTION

This study was conducted in pinyon–juniper woodland in the Coconino National Forest (1585 m a.s.l.). The study was replicated at two sites that were 2 km apart, approximately 80 km south of Flagstaff, Arizona, USA (34°46′N, 111°41′W). This region obtains most of its annual moisture from monsoonal rains that occur in July and August and from winter precipitation. The area is grazed/browsed by native ungulates. The dominant vegetation consists of pinyon pine *Pinus edulis* Engelm. and Utah juniper *Juniperus osteosperma* (Torr.) Little. The study sites are similar in plant community composition, soil characteristics and grazing intensity to many other pinyon–juniper woodlands in the USA. They had 60% overstorey coverage prior to harvest (Overby, Moir & Robertson 2000), whereas after treatment the overstorey coverage was zero. Soils at the sites are classified as typic haplustalfs with a basalt parent material (Overby, Moir & Robertson 2000). In 1995, the sites were opened up to fuel wood harvest by local citizens. The remaining slash was piled up around tree stumps and burned by USA Forest Service personnel. No heavy equipment was used so that possible effects of soil compaction were minimal. The data presented in this study were collected in 2000–01, approximately 5 years after the treatment was implemented.

Methods

We studied the effect of slash burning following fuel wood harvest on understorey plant communities in two ways. First, we compared the overall understorey plant communities of treated sites to adjacent non-burned sites (hereafter referred to as control sites). Secondly, we compared the plant community of burned slash areas and interspace areas in treated sites with canopy areas and interspace areas in control sites. Burned slash areas that were formerly canopy areas were determined by the presence of burned stumps. The control sites were located adjacent to the treated sites and resembled the original habitat prior to treatment. In each of two locations (*c.* 2 km apart), we established four 50-m transects in both burned and control sites, giving a total of 16 transects, eight in treated and eight in control sites. Each transect contained interspace areas and either slash areas or canopy areas depending on whether it was a burned or control site, respectively. Using the line intersect method, we identified plant species that fell beneath the transect line every 0·5 m along the 50-m transect, giving a total of 100 data points per transect. Plants that could not be identified in the field were collected away from the transect line, placed in a plant press and identified using reference specimens from the Deaver Herbarium at Northern Arizona University, Flagstaff, AZ. We calculated species richness, evenness and diversity (Simpson's diversity index) from the 100 data points collected from each transect.

To assess whether differences in the AM fungal communities of burned soils contributed to plant community differences, we conducted an inoculum potential bioassay using intact soil cores collected in the field. This method detects a range of inoculum sources that are active at the time of collection and under greenhouse conditions. The inoculum sources may include spores and fragments of mycorrhizal roots and hyphae, and thus may better represent the inocula of the soil than methods that rely on spores alone (Brundrett *et al.* 1996). However, because different species of AM fungi vary in their reliance on spores as inoculum and in their rates and timing of spore germination, our methods may have missed some fungal species. We collected 10 soil cores per transect, giving a total of 160 soil cores with 40 cores from each of four different categories: burned canopy, burned interspace, control canopy and control interspace. Soil cores were collected to a depth of 10 cm and immediately transferred to pots (16 × 5 cm, 314 cm^3) in the field. An organically grown maize *Zea mays* L. seed was planted in each pot and covered with 2·5 cm of Vermiculite to help maintain soil moisture. Maize was used in the bioassay because it forms mycorrhizal associations with a variety of fungal species and also grows rapidly and uniformly in a range of soils (Johnson, O'Dell & Bledsoe 1999). Prior to planting, maize was surface sterilized in 10% bleach solution for 30 min and then soaked in tap water for 90 min. The maize was grown in a greenhouse for 5 weeks. Greenhouse conditions provided a 16-h photoperiod per day with air temperatures averaging 25 °C and 15 °C, for day and night, respectively. Plants were watered when the soil became dry to the touch.

Maize seedlings were harvested after 5 weeks. We separated roots from shoots and randomly selected a portion (*c.* 20%) of each root system for measurement of AM fungal colonization. Roots were cleared in 10% potassium hydroxide and stained using 0·5% trypan blue in lactoglycerol, following the methods of Phillips & Hayman (1970) but omitting phenol. We chose 25 samples randomly from each treatment group to quantify percentage root length colonized by arbuscules, vesicles and hyphae, as well as total AM colonization, using the methods of McGonigle *et al.* (1990). Analysing the types of fungal structures that occur within different root systems can provide insight into the functional relationship between plant and fungus (Johnson 1993; Rillig & Allen 1998). The remainder of the maize roots and the shoots were oven dried (60 °C for 24 h) and mass was calculated.

To compare the AM colonization results from our maize bioassay with plants that were growing naturally in the field, we collected three to five specimens of many of the dominant native and exotic plant species found along the transects. Fine roots from all plants were collected, stained and examined for AM colonization using the methods described above.

Total nitrogen and phosphorus concentration of maize shoot tissue was examined using a modified micro-Kjeldahl digestion (Parkinson & Allen 1975) followed by colorimetric analysis on a Lachat Flow-Injection Analyser (Lachat Instruments 1992a,b). Total Kjeldahl nitrogen and phosphorus concentrations were calculated on an ash-free, oven-dry mass basis.

DATA ANALYSIS

Plant community composition data were assessed using a multivariate ordination method, non-metric multidimensional scaling (NMDS). NMDS is a non-parametric analytical technique that is applied to the dissimilarity matrix calculated among species using the Bray–Curtis dissimilarity coefficient (Faith, Minchin & Belbin 1987). Species data were not standardized or transformed prior to analysis. Comparisons between treatment groups were made using an analysis of similarity (ANOSIM) statistical test. This test ranks the elements of the Bray–Curtis dissimilarity matrix computed between all samples, and calculates the statistic:

$$R = (r_B - r_W)/[N(N-1)/4]$$

where N is the total number of replicates across all groups, r_B is the average ranked dissimilarity between every pair of replicates from different groups, and r_W is the average ranked dissimilarity for every pair of replicates within the same group. Both of these statistical analyses were conducted using DECODA software (Minchin 1999).

Differences in percentage plant cover, exotic species, native grasses, pinyon–juniper, maize total biomass and nitrogen and phosphorus concentration were determined using two-way ANOVA, in which fire history

Table 1. Comparisons of percentage cover (total plant, exotics and native grasses) in the four sampled areas and maize bioassay results for total biomass, and shoot nitrogen and phosphorus. Data are means (1 SE)

	Burn canopy	Burn interspace	Control canopy	Control interspace
Plant cover	67·1 (7·4)	61·1 (3·3)	47·4 (10·2)	27·8 (4·7)
Exotics	28·3 (9·2)	6·4 (1·8)	4·0 (3·0)	0·4 (0·2)
Native grass	14·6 (7·5)	10·8 (2·6)	9·4 (2·8)	3·8 (1·4)
Total biomass (g)	0·8 (0·1)	0·7 (0·0)	0·6 (0·0)	0·5 (0·0)
Shoot phosphorus (g kg^{-1} P)	3·8 (0·2)	3·0 (0·5)	2·8 (0·3)	2·5 (0·3)
Shoot nitrogen (g kg^{-1} N)	11·4 (0·8)	10·4 (1·3)	9·3 (0·8)	9·4 (1·0)

Table 2. The dominant native plants and the exotic species found on all four treatment areas with their mean percentage cover (1 SE). Nomenclature follows Kartesz (1994). Abbreviations represent the following: N, native; E, exotic; A, annual; B, biennial; P, perennial; BC, burned canopy; BI, burned interspace; CC, control canopy; CI, control interspace

Plant species	Location Plant family	Exotic/ native	Life history	BC	BI	CC	CI
Bromus japonicus Thunb. ex. Murr.	Poaceae	E	A	15·9 (5·6)	3·1 (1·3)	1·7 (1·7)	0·3 (0·2)
Bromus rubens L.	Poaceae	E	A	0·7 (0·5)	0·4 (0·2)	1·8 (1·4)	0·2 (0·2)
Sisymbrium irio L.	Brassicaceae	E	A	8·3 (4·5)	1·1 (0·9)	0·5 (0·5)	0
Lactuca serriola L.	Asteraceae	E	A	1·4 (1·4)	0	0	0
Melilotus officinalis (L.) Lam.	Fabaceae	E	A/B	0	0·5 (0·3)	0	0
Linaria dalmatica (L.) P. Mill.	Scrophulariaceae	E	P	0	0·2 (0·2)	0	0
Taraxacum officinale G.H. Weber ex. Wiggers	Asteraceae	E	P	0·3 (0·3)	0·2 (0·02)	0	0
Ipomopsis aggregata (Pursh) V. Grant	Polemoniaceae	N	B	5·4 (2·9)	2·3 (1·8)	0	0·2 (0·2)
Gutierrezia sarothrae (Pursh) Britt. & Rusby	Asteraceae	N	P	6·7 (3·1)	21·0 (4·0)	8·3 (3·0)	6·9 (1·8)
Elymus elymoides (Raf.) Swezey	Poaceae	N	P	8·0 (3·9)	5·6 (1·9)	6·9 (2·5)	2·2 (1·0)
Heliomeris multiflora Nutt.	Asteraceae	N	P	5·9 (2·4)	8·6 (3·5)	0	0·3 (0·3)
Bouteloua curtipendula (Michx.) Torr.	Poaceae	N	P	0·2 (0·2)	3·3 (1·4)	1·0 (1·0)	1·5 (0·8)
Hymenoxys rusbyi (Gray) Cockerell	Asteraceae	N	B/P	1·0 (0·6)	2·0 (0·6)	0·3 (0·3)	0·3 (0·2)
Penstemon linarioides Gray	Scrophulariaceae	N	P	0·8 (0·7)	1·9 (1·1)	4·8 (2·2)	5·5 (2·0)
Menodora scabra Gray	Oleaceae	N	P	0	1·6 (0·6)	0·5 (0·5)	4·1 (2·0)
Agropyron pascopyrum (Rydb.) Á Löve	Poaceae	N	P	1·6 (1·4)	1·5 (0·7)	1·5 (1·2)	0

(burned vs. control) and canopy presence (canopy vs. interspace) were fixed factors. All ANOVAS were performed using SPSS for windows, v. 10.0.5. Species richness, evenness and Simpson's diversity values were determined using PC Ord (McCune & Mefferd 1999). Arbuscular mycorrhizal colonization by fungal structure (proportion of hyphae, arbuscules and vesicles) and species richness, evenness and diversity were analysed using a multivariate ANOVA, where burning (burned vs. control) and canopy presence (canopy vs. interspace) were fixed factors. A univariate ANOVA was used to analyse total AM colonization for field-collected plants. Origin (native vs. exotic) was the fixed factor. With the exceptions of maize total biomass, nitrogen and phosphorus concentration, and species richness, evenness and diversity, data were all proportional and were arcsine-square root transformed prior to analysis (Zar 1984).

Results

PLANT COMMUNITIES

In support of other studies that have examined the effects of burning on plant cover (Barney & Frischknecht 1974), burned sites had significantly more plant cover than control sites (Table 1; $F_{1,28}$ = 12·58, P = 0·001). However, there was no significant effect of canopy cover (canopy vs. interspace; $F_{1,28}$ = 2·07, P = 0·16). Similarly, there was no significant interaction between burning and canopy cover ($F_{1,28}$ = 0·44, P = 0·51).

We found a total of 50 plant species (for a partial list see Table 2) but only 44% were common to both burned and control sites. The composition of the understorey plant communities in areas that were burned was significantly different than that in control areas

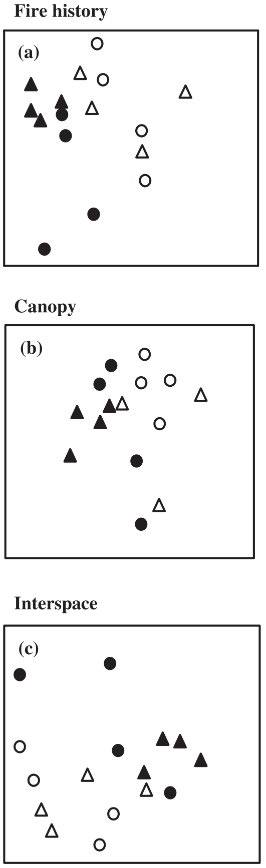

Fig. 1. Understorey plant community composition differed significantly between burned and control areas (a) (n = 8, $R = 0{\cdot}37$, $P < 0{\cdot}01$) and burning significantly altered plant communities in both canopy (b) (n = 8, $R = 0{\cdot}27$, $P = 0{\cdot}02$) and interspace sites (c) (n = 8, $R = 0{\cdot}40$, $P < 0{\cdot}01$) based on ANOSIM analyses. Circles represent site 1 and triangles represent site 2. Solid symbols represent burned areas and open symbols represent controls.

(Fig. 1a; $n = 8$, $R = 0{\cdot}37$, $P < 0{\cdot}01$). Furthermore, there were significant treatment differences in both canopy areas (Fig. 1b; $n = 8$, $R = 0{\cdot}27$, $P < 0{\cdot}03$) and interspace areas (Fig. 1c; $n = 8$, $R = 0{\cdot}4$, $P < 0{\cdot}01$), suggesting that burning had effects beyond the slash pile areas.

These patterns were due, in part, to a fourfold higher abundance of exotic species in the burned canopy areas than the other sites (Table 1). Analysis of the percentage of exotic species revealed that there were significant burn ($F_{1,28} = 17{\cdot}03$, $P < 0{\cdot}001$) and canopy ($F_{1,28} = 4{\cdot}96$, $P < 0{\cdot}04$) effects, but the interaction was not significant ($F_{1,28} = 1{\cdot}89$, $P < 0{\cdot}19$). Furthermore, there were no differences in regard to burning, canopy presence and interactions for the percentage of native grasses (Table 1; $F_{1,28} = 3{\cdot}74$, $P = 0{\cdot}06$; $F_{1,28} = 1{\cdot}76$, $P = 0{\cdot}20$; $F_{1,28} = 0{\cdot}57$, $P = 0{\cdot}46$, respectively). There were very few pinyon or juniper seedlings present in any of the treatment areas. The highest mean percentage of seedlings was 2% (SE = 1·4) and was found in the control canopy treatment. Thus, when we examined the percentage of pinyon or juniper seedlings present we found no burn, canopy or interaction effect ($F_{1,28} = 0{\cdot}02$, $P = 0{\cdot}90$; $F_{1,28} = 1{\cdot}96$, $P = 0{\cdot}17$; $F_{1,28} = 0{\cdot}05$, $P = 0{\cdot}82$, respectively).

There were no significant differences in species richness, evenness or Simpson's diversity with respect to either burning (multivariate ANOVA: $F_{3,26} = 1{\cdot}50$, $P = 0{\cdot}24$) or canopy presence (multivariate ANOVA: $F_{3,26} = 1{\cdot}76$, $P = 0{\cdot}18$), and there was no significant interaction (multivariate ANOVA: $F_{3,26} = 1{\cdot}26$, $P = 0{\cdot}31$).

AM COLONIZATION AND INOCULUM POTENTIAL

Exotic plants had 50% greater percentage root length colonized by AM fungi (univariate ANOVA: $F_{1,12} = 6{\cdot}46$, $P = 0{\cdot}03$) than native plants (Fig. 2a, mean colonization for natives 11%; Fig. 2b, mean colonization for exotics 22%). Both native and exotic plant species exhibited similar patterns in distribution of vesicles, arbuscules and internal hyphae, with the exception of the exotic grass *Bromus japonicus* Thunb. ex. Murr., which had higher levels of arbuscules than the other species.

We found no significant differences in AM colonization of the bioassay maize plants with respect to fire history, canopy cover or their interactions (Fig. 3; multivariate ANOVA: $F_{4,93} = 0{\cdot}74$, $P = 0{\cdot}57$; $F_{4,93} = 1{\cdot}27$, $P = 0{\cdot}29$; $F_{4,93} = 1{\cdot}85$, $P = 0{\cdot}12$, respectively). Furthermore, there were no significant differences in the proportions of fungal structures among the groups (Fig. 3). Overall AM colonization in the maize bioassay averaged 16·3% across all four treatment groups, which is consistent with levels observed in field-collected plants and other bioassays conducted in pinyon–juniper woodlands (Klopatek, DeBano & Klopatek 1988; Klopatek *et al.* 1994).

MAIZE PLANT BIOMASS AND NITROGEN AND PHOSPHORUS CONTENT OF CORN SHOOT TISSUE

Despite similar levels of AM colonization, the total dry biomass of maize plants was significantly greater in soil from the burned sites than the control sites (Table 1; two-way ANOVA: $F_{1,151} = 17{\cdot}94$, $P < 0{\cdot}001$). There was no significant effect of either canopy cover ($F_{1,151} = 2{\cdot}33$, $P = 0{\cdot}13$) or an interaction ($F_{1,151} = 1{\cdot}38$, $P = 0{\cdot}24$) on total dry biomass of maize plants. There were no significant differences in root : shoot ratio with respect to burning or canopy cover, nor was there a significant interaction between the two treatments (data not shown; two-way ANOVA: $F_{1,151} = 0{\cdot}02$, $P = 0{\cdot}90$; $F_{1,151} = 0{\cdot}00$, $P = 1{\cdot}00$; $F_{1,151} = 3{\cdot}16$, $P = 0{\cdot}08$, respectively).

We found significantly higher phosphorus concentration in the maize plant shoots from the burned sites than the control sites, and no effect of canopy cover or an interaction (Table 1; two-way ANOVA: $F_{1,36} = 5{\cdot}03$, $P = 0{\cdot}03$; $F_{1,36} = 2{\cdot}56$, $P = 0{\cdot}12$; $F_{1,36} = 0{\cdot}40$, $P = 0{\cdot}53$, respectively). There were no significant differences with respect to burning, canopy cover or an interaction in total nitrogen concentration of maize shoot tissue (Table 1; two-way ANOVA: $F_{1,36} = 2{\cdot}79$, $P = 0{\cdot}10$; $F_{1,36} = 0{\cdot}18$, $P = 0{\cdot}67$; $F_{1,36} = 0{\cdot}17$, $P = 0{\cdot}68$, respectively).

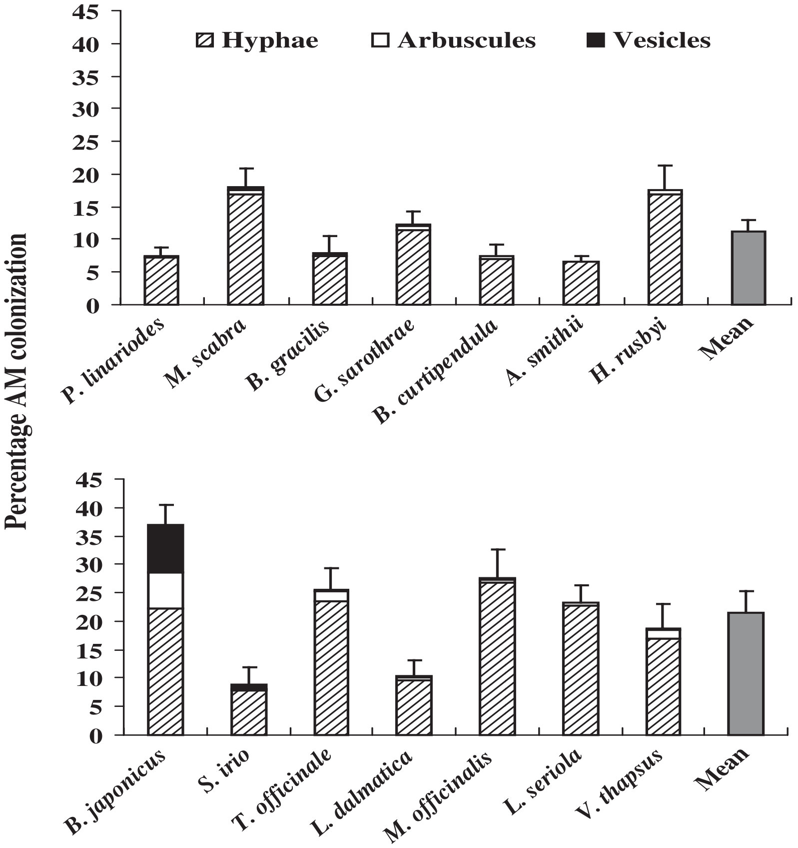

Fig. 2. The mean percentage AM colonization was significantly lower in native (a) than in exotic (b) plants ($F_{1,12} = 6{\cdot}46$, $P = 0{\cdot}026$). Vertical lines denote 1 SEM. Within each bar is the mean percentage of vesicles, arbuscules or internal hyphae for that species. Solid grey bars represent the overall mean for natives (a) and exotics (b).

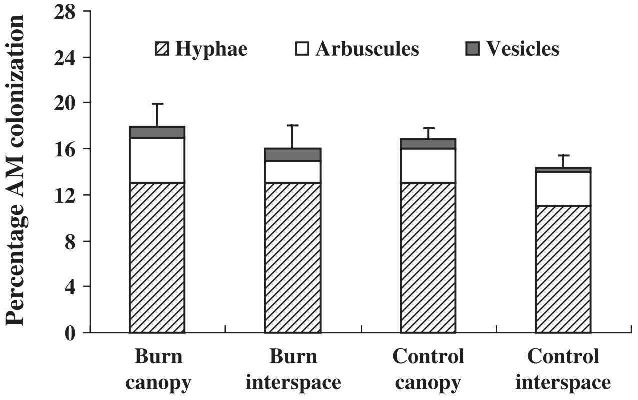

Fig. 3. There were no significant effects of burning on mean total percentage AM colonization ($F_{4,93} = 0{\cdot}74$, $P = 0{\cdot}57$) nor were there differences in the mean percentage of fungal structures of maize plants ($n = 25$). Vertical lines denote 1 SEM. Within each bar is the mean percentage of vesicles, arbuscules or internal hyphae for that treatment group.

Discussion

CHANGES IN PLANT COMMUNITY COMPOSITION IN RESPONSE TO BURNING

Although fuel wood harvest and burning of the resulting slash increased total plant cover by 68% after 5 years, this treatment did not result in the desired perennial bunchgrass community. Instead, exotic plant species were four times more abundant on burned canopy sites than other sites. It appeared that exotic species were the most successful colonists of the intensely burned slash sites. Five of the seven exotic species found on the burned sites were annuals or biennials and of poor forage quality. For example, due to its sparse foliage, early maturity, stiff awns and sharp pointed florets, *Bromus rubens* L. is rarely grazed by livestock or wildlife (Crampton 1974). Additionally, *Verbascum thapsus*

L. is not grazed due to its woolly textured leaves (Hoshovsky 1988) and *Linaria dalmatica* (L.) P. Mill. is considered unpalatable and potentially poisonous to livestock (Morishita 1991). Thus, the exotic species that colonize the burned slash pile areas are unlikely to serve as useful forage for native grazers or cattle. The exotic species found in our study are common to disturbed sites and roadsides (Hoshovsky 1988; Morishita 1991) and may have dispersed from forest access roads and an interstate highway in the area.

AM INOCULUM POTENTIAL

Alteration of the soil environment through the reduction or elimination of important soil microbes, such as AM fungi, can affect revegetation patterns following disturbances such as fire (Reeves *et al*. 1979). In addition, because some exotic weedy species are non-mycorrhizal, reductions in AM inoculum potential following prescribed burning may favour the colonization of sites by exotic plant species (Allen 1991). However, using standard bioassay methods for detecting soil inoculum potential, we found no differences in AM inoculum potential between burned and control sites. This suggests that either burning had no effect on inoculum potential, or that it recovered during the 5 years since the burn. Because we did not monitor AM inoculum potential immediately following the burn, we cannot determine whether or not there was an initial reduction in AM inoculum potential.

A review of the fire literature (Deka & Mishra 1983; Klopatek, DeBano & Klopatek 1988; Pattinson *et al*. 1999; Korb, Johnson & Covington 2003) suggests that the intensity of the fire and the length of time since the fire occurred could both be important in determining the effects of fire on soil fungal inoculum potential. Klopatek, DeBano & Klopatek (1988) showed that when soil temperatures exceeded 60 °C, the AM inoculum potential in microcosms containing pinyon–juniper woodland soils was reduced by more than 50%. In a field experiment that involved slash burning in a secondary successional forest dominated by bamboo *Dendrocalamus hamiltonii* Nees., Deka & Mishra (1983) found that AM inoculum potential was also drastically reduced in the top 2 cm of soil, but that it recovered to original levels within 1 month. Contrary to these findings, other studies have found that fire has little effect on AM inoculum potential. Brundrett, Ashwath & Jasper (1996) showed no influence of fire on AM inoculum potential, using a bioassay approach with field-collected soil cores from sclerophyllous shrubland in Australia. Additionally, Bellgard, Whelan & Muston (1994) found that a moderate intensity wildfire in Australian sclerophyllous shrubland had no effect on AM spore counts or AM colonization of roots. Thus, fire has variable effects on AM inoculum potential that are likely to depend at least in part on burn severity and the length of time since the burn.

Recent work has shown that many weedy, exotic species found on disturbed sites are mycorrhizal (Pendleton & Smith 1983) and that mycorrhizae might actually enhance the competitive ability of exotic species. For example, Marler, Zabinski & Callaway (1999) found that when *Centaurea maculosa* Lam., an exotic weed, was grown in association with a native bunchgrass, *Festuca idahoensis* Elmer., the presence of AM fungi increased the competitive ability of the exotic, possibly enhancing the ability of *C. maculosa* to invade grasslands. All of the exotic species examined in this study were mycorrhizal to some degree, and combined the exotics had significantly higher AM colonization than the native species. Thus, it is possible that mycorrhizae aid the success of exotic species and help them to persist years after the burn.

OTHER POTENTIAL MECHANISMS

There are several other potential explanations for the changes in plant community structure following burning. First, burning removes existing understorey vegetation, which simultaneously eliminates competition and opens up habitat for invasion by other species. Many weedy, exotic species are able to capitalize on disturbed environments (Miller & Jastrow 1992) because they produce an abundance of seed that may be highly persistent in the seed bank, or they are able to disperse great distances or have minimal germination requirements. For example, one of the exotic species observed in this study, *Verbascum thapsus*, produces on average 100 000–180 000 seeds per plant and these seeds can remain viable for up to 100 years (Hoshovsky 1988). Similarly, another exotic species present at the site, *Linaria dalmatica*, can produce up to 500 000 seeds annually, which can remain dormant for up to 10 years (Carpenter & Murray 1998). Once established on burned sites, the high reproductive output of these exotic species may allow them to compete effectively for new establishment sites and persist for many years.

Secondly, the quantity and species composition of seeds in the seed bank may have been altered by fire. Burning slash at low intensity in a Douglas fir *Pseudotsuga menziesii* (Mirbel) Franco forest significantly reduced the density of the seed bank from 88·6 seeds m^{-2} to 18·4 seeds m^{-2} (Clark & Wilson 1994). Furthermore, Koniak & Everett (1982) found that the majority of seeds in the seed bank in pinyon–juniper woodland soils occurred in the top 3 cm of soil, and that these seed banks consisted primarily of annual species (89%) rather than perennial species. Korb (2001) showed that 68% of the seeds found 3 m away from a burned slash pile were exotic, indicating that burning of slash can have far-reaching effects. The burning of slash in this study may have significantly reduced both the density of native seeds and the proportion of perennial seeds in the seed bank, which could further reduce the ability of native plant species to recolonize following burning.

Thirdly, burning slash may alter soil structure (Neary *et al*. 1999) in a way that benefits exotic species. The removal by fire of organic matter at the soil surface and in the top few centimetres of mineral soil can cause changes in soil structure. These changes may include decreases in soil pore size, which could lead to increased surface water runoff and erosion, and reduced water retention within the mineral soil (Neary *et al.* 1999). Reduced water availability can have important impacts on the competitive outcomes of neighbouring plants. For example, Hamilton, Holzapfel & Mahall (1999) found that competition for water was the most likely mechanism explaining the decrease in above-ground growth and seed production of a native perennial bunchgrass *Nassella pulchra* (A. Hitchc.) when grown with non-native annual grasses.

BURNING EFFECTS ON PLANT BIOMASS AND SHOOT NUTRIENT CONTENT

The significantly greater total dry weight biomass of the maize bioassay plants in the burned sites did not appear to be due to the amount of mycorrhizae colonizing plant roots. Furthermore, the shoot : root biomass ratios were not significantly different between burned and control sites, suggesting that the plants allocated similar amounts of energy into shoot and root tissue production. These results suggest that there are differences in the soil properties of burned sites relative to the control sites that affected maize biomass independently of levels of mycorrhizal colonization. We hypothesized that the differences in biomass may be due to differences in soil nutrient availability.

Analyses of nitrogen and phosphorus concentration in maize shoot tissue of plants grown in the burned canopy soils 5 years after treatment indicated that the differences in soil phosphorus, but not nitrogen, may have persisted. Overby, Moir & Robertson (2000) conducted soil analyses at the same study sites, approximately 2 years after the fuel wood was harvested and the slash burned. They found significantly higher concentrations of soil ammonia and nitrate in the burned canopy areas, while available phosphorus appeared greater but this was not statistically significant (Overby, Moir & Robertson 2000). DeBano, Perry & Overby (1987) found that fire acted as a rapid mineralizing agent and that removal of the tree canopy further stimulated the mineralization of both nitrogen and phosphorous in a pinyon–juniper woodland. An increase in the availability of nutrients after burning is often a short-term phenomenon (Lewis 1974; Uhl & Jordan 1984). The elevated phosphorus availability on the sites that experienced exposure to intense burning, as indicated by higher levels of phosphorus in the maize shoot tissue, and had persisted 5 years after burning is unusual and needs further exploration.

CONCLUSIONS

The demand for increased forage production will probably result in the continued removal of pinyon and juniper trees in semi-arid grasslands and pinyon–juniper woodlands. In our study, slash burning preceded by fuel wood harvest resulted in a plant community dominated by exotic species rather than the desired native forage species. Our analysis of data taken 5 years after treatment allowed us to determine three things. (i) Increased abundance of native perennial bunchgrasses did not occur within a 5-year period, but this was not due to persistently reduced AM inoculum potentials. (ii) The increase in exotic plant species following tree harvest and slash burning may be highly persistent. (iii) Elevated levels of available soil phosphorus persisted for at least 5 years, as indicated by the bioassay maize shoot tissue. We suggest that slash burning can be detrimental and should be applied cautiously as a management tool in pinyon–juniper woodlands. The probability that exotic plants will establish following fuel wood reduction in these woodlands may be reduced if burning is eliminated or followed by seeding of native plant species. Furthermore, because water is limiting in semi-arid environments, post-fire soil and plant community recovery may be very slow (DeBano, Neary & Ffolliott 1998). Monitoring the results of management methods for significant periods after management activity is not a common practice (but see Covington *et al.* 1997), yet the knowledge gained from examining the long-term effects of treatment can determine whether a management strategy has been successful.

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