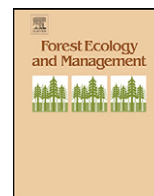




Contents lists available at [ScienceDirect](#)

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



Above- and belowground responses to tree thinning depend on the treatment of tree debris

Suzanne M. Owen^{a,*}, Carolyn Hull Sieg^b, Catherine A. Gehring^a, Matthew A. Bowker^c

^a Department of Biological Sciences, Northern Arizona University, Box 5640, Flagstaff, AZ 86011, USA

^b USDA Forest Service Rocky Mountain Research Station, 2500 S. Pine Knoll Drive, Flagstaff, AZ 86001, USA

^c Área de Biodiversidad y Conservación, Universidad Rey Juan Carlos, c/ Tulipán s/n, Móstoles (Madrid) E-28933, Spain

ARTICLE INFO

Article history:

Received 15 July 2009

Received in revised form 22 September 2009

Accepted 24 September 2009

Keywords:

Arbuscular mycorrhizal fungi (AMF)

Exotic plants

Mechanical mastication

Pinyon–juniper woodlands

Soil nutrients and stability

Slash pile burning

ABSTRACT

Mechanical mastication is increasingly prescribed for wildfire mitigation, yet little is known about the ecological impacts of this fuels treatment. Mastication shreds trees into woodchips as an alternative to tree thinning and burning the resulting slash, which can create soil disturbances that favor exotic plants. Previous research on mastication has not simultaneously considered both the responses of soil organisms and understory plant communities. We compared mastication to slash pile burning (both 6-months and 2.5-years post-treatment) and untreated controls in pinyon–juniper (*Pinus edulis*–*Juniperus osteosperma*) woodland and measured soil properties, arbuscular mycorrhizal fungi (AMF) and understory plant composition. Our results showed that slash pile burns had severely degraded soil properties and low AMF abundance and richness compared to untreated or mastication plots. Pile burns were dominated by exotic plant species and had approximately 6× less understory plant abundance and richness than untreated plots. Only two variables differed between mastication and untreated plots 6-months post-treatment: mastication had lower soil temperature and higher soil moisture. Mastication plots 2.5-years post-treatment had more plant cover and richness than untreated plots or pile burns, although non-native *Bromus tectorum* cover was also greater and AMF spore richness was lower than untreated plots. The structural equation model (SEM) we developed showed that plant cover strongly influenced AMF abundance (0.50) and both plant cover (0.36) and AMF (0.31) positively influenced soil stability. In the short-term, mastication is a preferable method as it creates fewer disturbances than pile burning; however long-term impacts of mastication need further study as this practice could affect native plant communities. Our results suggest that the manner in which woody debris is treated following tree thinning has an important influence on soil stability and native plant biodiversity.

© 2009 Elsevier B.V. All rights reserved.

1. Introduction

Pinyon–juniper woodlands cover >20 million ha in the south-western United States (Miller and Wigand, 1994) and land managers are increasingly thinning these woodlands to prevent wildfires that might endanger archaeological sites or homes in urban–wildland interfaces. High tree densities threaten the sustainability of a number of forest types worldwide, decreasing native biodiversity and ecosystem function (Williams et al., 2002; Verkaik and Espelta, 2006; Wayman and North, 2007). Forests with dense tree stands are more prone to catastrophic wildfires, which can further accelerate the loss of forest resources (Neary et al., 1999; Allen et al., 2002). Even forest types that have not been

affected by past management practices that promoted high tree density could be at risk for increased fire activity because of climatic changes such as prolonged droughts and increasing temperatures (Floyd et al., 2004; Westerling et al., 2006). Tree thinning can help reduce crown-fire potential and increase light and resources for understory vegetation (Neary et al., 1999; Wayman and North, 2007). One common method of removing tree debris (slash) is piling and burning it. Burning slash piles is an economical method for disposing of slash, but can decrease the abundance of mycorrhizal fungi and alter soil attributes (Korb et al., 2003; Haskins and Gehring, 2004). Mechanical mastication is a newer fuel treatment and its impact to soil properties and above- and belowground communities is unknown. Our study was conducted in a pinyon–juniper woodland and is the first to compare plant–soil–microbe responses and interactions following mechanical mastication and slash pile burning.

Although burning slash piles reduces forest fuels and may improve resiliency to wildfires, this practice could alter native communities and contribute to soil loss. The long duration of fire

* Corresponding author. Tel.: +1 928 853 2610/556 2193; fax: +1 928 556 2130.

E-mail addresses: Suzanne.Owen@nau.edu (S.M. Owen), csieg@fs.fed.us (C.H. Sieg), Catherine.Gehring@nau.edu (C.A. Gehring), Matthew.Bowker@urjc.es (M.A. Bowker).

from pile burns can heat soils over 300 °C in the center and 175 °C at the pile edge (Jiménez Esquilina et al., 2007), which is high enough to kill plant roots and seeds and cause partial soil sterilization. Resulting high soil temperatures can increase surface water run-off, hydrophobicity and nutrient loss and decrease soil pore-size and aggregate stability, leading to erosion and structure loss (Neary et al., 1999). Field and laboratory studies demonstrate that burning slash piles decreases abundance of arbuscular mycorrhizal fungi (AMF) (Pattinson et al., 1999; Korb et al., 2003). AMF are beneficial plant symbionts and can promote soil stability (Chaudhary et al., 2009) and native plant diversity (van der Heijden et al., 1998). Although pile burns can decrease AMF abundance, it is unknown if they affect AMF community structure. Loss of AMF due to high severity ground fires could result in increased soil erosion and a less diverse plant community. Methods of tree thinning that have little negative impact on soils and AMF may be most successful in promoting native plant cover and diversity.

Mechanical mastication is a less-studied method for thinning trees and disposing of slash. Mastication employs 'hydro-mow' equipment, similar to a large mulching lawnmower that uses rotating blades to shred live trees into large wood chips that are distributed across the topsoil. The use of large thinning equipment may cause soil compaction (Corns, 1988); while the addition of woodchips could increase soil moisture and decrease soil temperature (Brockway et al., 2002; Blumenthal et al., 2003). In a ponderosa pine (*Pinus ponderosa*) forest, the addition of woodchips reduced understory plant richness, diversity and cover and resulted in more non-native species (Miller and Seastedt, 2009) and altered plant community composition (Wolk and Rocca, 2009) compared to unchipped plots. In contrast, Brockway et al. (2002) found that carbon additions promoted herbaceous plant cover and diversity in a pinyon–juniper woodland. Also, Blumenthal et al. (2003) found carbon additions to soil decreased N availability. However, little is known about the effects of mastication on soil biota. Previous research on mastication has not simultaneously considered both the responses of soil organisms such as AMF and the understory plant community.

We compared soil properties, AMF and understory plant composition in areas of untreated forest to sites that had been treated 6-months and 2.5-years prior, by mastication or slash pile burns in replicated plots of pinyon–juniper woodland. We tested three main hypotheses: (1) pile burning will result in greater soil erodibility and nutrient loss and less native plant and AMF abundance and richness than untreated plots; (2) mastication will enhance the species richness of understory plants and AMF compared to untreated controls and pile burning, yet cause soil compaction and N immobilization and (3) both treatments will affect plant cover, which will in turn influence AMF and soil stability. We constructed an *a priori* structural equation model (SEM) to test our third hypothesis based on the prediction that thinning treatments would affect AMF and soil stability, but have stronger effects on plant cover. Also, we predicted that plant cover would indirectly affect AMF abundance (Eom et al., 2000) and soil stability and that AMF would also directly affect soil stability (Chaudhary et al., 2009).

2. Methods

2.1. Study sites and sampling design

This study was conducted in the San Juan National Forest of southwestern Colorado (37°44'N, 108°52'W), USA in a semi-arid pinyon–juniper (*Pinus edulis* Engelm., *Juniperus osteosperma* (Torr.) Little) woodland. The mean annual precipitation (MAP) is 480 mm and the mean annual temperature is 8.9 °C (years 1948–2004;

WRCC, 2004). Most precipitation occurs as monsoonal rains in late July and August and temperatures drop enough to have snow in the winter. Droughts are common. We sampled in 2 years with above average precipitation: in 2005 (MAP = 520 mm) and in 2006 (vegetation data only) (MAP = 540 mm). Other common native plants in this area include Gambel oak (*Quercus gambelii* Nutt.), mountain mahogany (*Cercocarpus montanus* Raf.), and squirreltail (*Elymus elymoides* [Raf.] Swezey). The study sites have been exposed to cattle grazing and fire suppression since the early 1900s (Ramsey, 2003) and pinyon mortality has recently increased due to drought and pinyon bark beetle (*Ips confusus*) infestation (Harris, 2003).

We compared treatments of mastication and slash pile burning to untreated areas within wildland–urban interfaces. The USDA Forest Service and USDI Bureau of Land Management conducted thinning treatments in order to reduce overstory 40–60% near homes and archaeological sites. Managers randomly chose areas to either thin and pile burn or treat with mechanical mastication, leaving mosaics of treated canopy openings averaging 15 m² in size within areas of untreated, intact forest. Trees with dbh >25 cm and all healthy pinyons were left intact. Treated areas varied in size. Slash pile burning resulting in charred areas approximately 3–6 m² and involved cutting trees with hand-held chainsaws, piling slash and burning. Mastication created jagged cut stumps to ground level and randomly scattered mulched material ranging from <2 to 15 cm in size, in areas roughly 10–12 m² in size. Litter depth in the mastication treatments was heterogeneous with some areas having no litter while others had litter with a maximum depth of 7 cm.

Three sites were examined for this study (one in which treatments were conducted in February 2005 and two in which treatments were conducted in February 2003). We sampled in August 2005 and designated our three sites as: Site-A (6-months post-treatment) and Sites B and C (both 2.5-years post-treatment). Site-A included treatments of mastication, slash pile burns and untreated plots within a ~2 km × 1 km area. At this site, all three treatments were in areas with comparable soil and vegetation. Treatments conducted in February 2003 could not be found on the same soil type; therefore they were examined at two different sites, each with its own control. The first of those two sites (Site-B) included pile burns and untreated plots in an area approximately 1 km × 1 km and the last site (Site-C) included mastication and untreated plots in an area roughly 2 km × 1 km. The average elevation is 2149 m; the percent slope ranges from 5 to 20 and the soil parent material is sandstone and shale. The soil at Sites A and B is brown stony sandy loam and classified as loamy-skeletal, mixed, mesic Aridic Haplustalfs and the soil at Site-C is dark brown very bouldery, sandy clay loam and classified as loamy-skeletal, mixed, superactive mesic Ustic Haplargrids (Ramsey, 2003).

We opportunistically sampled existing treatments, yet they were very similar to those currently underway on larger spatial scales. We randomly chose 25 areas of untreated intact-forested and 25 treatments of either mastication and/or slash pile burns treatments at each site (totaling 175 plots). All untreated sites were randomly chosen from each of the three sites and were selected if they had similar elevation, slope, soil and overstory tree canopy cover as the treatments. For further details on treated sampling selection see Neal (2007). Since pile burning and mastication are very different ways to treat fuels, it is hard to capture the entire treatment and measure as many variables as we wanted in a timely manner. We decided to sample only the center of each treatment, acknowledging that they vary in size and that we would not capture areas between the treatments. We measured soil properties, AMF and plant cover within one 1 m × 1 m frame placed in the center of each treatment and or untreated area and defined this as a treated or untreated 'plot.' We maintained at least

a 30-cm buffer zone between the 1 m × 1 m frame and the edge of the treatments. All sampling was done in August 2005 and only plant cover was measured again in August 2006.

2.2. Soil sampling and analyses

Soil moisture, temperature, bulk density and aggregate stability were measured in all plots to determine if treatments altered the physical properties of soil. In August 2005, three mineral soil (0–15 cm) samples were collected and composited from each plot with a soil core (3 cm diameter × 15 cm length) within a 1 m × 1 m frame inside each plot. A portion of this soil was either refrigerated at 4 °C or frozen for analysis. Gravimetric soil moisture was determined after drying in an oven at 105 °C (Carter, 1993). Soil temperature was measured at a depth of 10 cm with a Digisense type K thermocouple field thermometer (Eutech Instruments). Bulk density, a measure of soil compaction, was assessed by taking a core of soil of known volume (14.85 cm³) from each plot and dividing the dry weight (after 3 days at 60 °C) by the known volume of soil. Soil aggregate stability (a measure of erodibility) was determined for surface and 10-cm subsurface soils using a soil stability kit (Synergy Resource Solutions, Inc., Bozeman, MT). Soil aggregates were ranked on an ordinal scale of 0 (least stable) to 6 (most stable) ('slake scores') (Herrick, 2000). Although we only measured soil properties in one season, we tried to sample all plots as close together in time as possible, collecting around the same time of day and finishing within 2 weeks to reduce variability in the data.

Soil pH and soil nutrients were measured to determine if treatments altered soil chemistry. Soil pH was measured following the method of Carter (1993) with an Orion 550A pH meter (Thermo Electron Corporation, Beverly, MA). Concentrations of nitrate, ammonium and phosphate (NO₃⁻, NH₄⁺, PO₄³⁻) were measured on a Lachat AE Flow Injection Autoanalyzer (Lachat Instruments, Inc., Milwaukee, WI, USA), using methods listed in Neal (2007). Total carbon and nitrogen were measured on a C/N analyzer (Thermo Quest EA Flash 1112, Milan, Italy).

2.3. Arbuscular mycorrhizal fungi (AMF)

The abundance, species richness and species composition of AMF were assessed using spore morphology and extramatrical hyphae (EMH). From 10 randomly selected plots from each treatment type, a 25-g homogenized soil sample was used for AMF spore extraction using a sucrose centrifugation method (Johnson et al., 1999). Spores were mounted onto slides, examined with a compound microscope (100–400×) and identified to morphospecies when possible using Schenck and Perez (1990) and INVAM (<http://invam.caf.wvu.edu/>). Species richness and spore abundance were calculated for each sample. EMH in the soil was measured as a second indicator of AMF abundance because of its strong correlation with soil stability (Chaudhary et al., 2009). EMH was measured on a random sub-sample of 15 plots from each treatment using methods modified from Staddon et al. (1999). Soil (~1.5 g) was blended with water and passed through a 0.45-μm filter. The resulting hyphae were mounted onto microscope slides and EMH length assessed using the grid-line intercept method using 50 grids per filter. These data were converted to hyphal lengths (or density) per dry mass of soil.

2.4. Plant communities

Plant canopy cover was measured over 2 years: 6-months post-treatment and 1.5-years post-treatment for the first site (Site-A) and 2.5-years and 3.5-years post-treatment for the second sites (Sites B and C). Total plant, litter, bare ground, life form

(herbaceous plants, graminoids and shrubs) and individual species cover were estimated by seven coverage classes: 0 = <1%, 1 = 1–5%, 2 = 5–25%, 3 = 25–50%, 4 = 50–75%, 5 = 75–95%, and 6 = 95–100% in a 1 m × 1 m frame, a method modified from Daubenmire (1959). One frame was placed in the middle of each plot for a total of 175 frame measurements. Midpoints of the cover classes were used to calculate average coverage estimates for each treatment. Plants were identified to species in the field or collected and identified to species at the Deaver Herbarium at Northern Arizona University, or at the USDA Rocky Mountain Research Station. Scientific nomenclature and nativity follows the PLANTS Database (<http://plants.usda.gov>).

2.5. Statistical analyses

All three treatment sites (Sites A–C) were analyzed separately due to differences in treatments, soil and plant cover. The statistical software program JMP for Windows 5.1.2 (2004) was used to analyze all data (except for community composition) with $\alpha = 0.05$. One-way ANOVAs were used to test for differences in response variables among treatments and the post hoc Tukey–Kramer HSD test was used for subsequent pair-wise comparisons. If variables failed to meet assumptions of normality and homogeneity of variances, transformations were applied or the nonparametric Kruskal–Wallis test was used, followed by Kolmogorov–Smirnov pair-wise tests. The Kruskal–Wallis test was also used for the categorical soil stability data. Principal component analysis (PCA) was used for soil variables (moisture, temperature, bulk density, %C, %N, pH, NO₃⁻, NH₄⁺ and PO₄³⁻) to reduce this data set into smaller composite variables and focus on the strongest covariation (McCune and Grace, 2002). Ordinations of soil variables were constructed and the largest eigenvectors (over ±0.3, representing the combined original variables) and their associated eigenvalues (over 10%, representing variance of the principal component or axis) were shown (McCune and Grace, 2002). Plant cover, bare ground and litter; plant life form and most abundant individual plant species cover were compared with two-way MANOVAs (with treatment and time (bivariate) as independent variables) and if significant then one-way ANOVAs were used to test for individual differences among treatments.

The program PC-ORD 4.02 (McCune and Meford, 1999) was used to examine community-level differences. Multi-response permutation procedures (MRPP) were used to determine if the plant and AMF spore communities were different among treatments. The "A" statistic is a descriptor of within-group similarity compared to random expectation. An A value greater than 0.1 is a strong indicator of a difference among groups (McCune and Grace, 2002). We visualized differences in communities among treatments using NMS ordinations in PC-ORD. The axes are unitless, but show how similar or dissimilar each community is in environmental space (McCune and Grace, 2002). Indicator species analysis was used to determine if particular species were the main sources of community differences determined by significant MRPP analyses. We considered indicator species to be significant if they had an indicator value (frequency × relative abundance) > 25 and a $P < 0.05$.

To better understand the causal network of relationships among treatments, plants, AMF and soil properties we developed a structural equation model (SEM) using the program AMOS 5 (Arbuckle, 2003). SEM is a unique tool because it allows for the separation of direct and indirect effects that one variable may have upon another and allows testing of a causal configuration of the variables. SEM creates a probability that the hypothesized model is a likely determinant of the correlations observed in the data. Because not all causal hypotheses 'fit' the data, SEM allows a strengthening of the causal inference that can be drawn from

observations (Grace, 2006, McCune and Grace, 2002). Our *a priori* model is described above in our third hypothesis. The model included thinning treatments (exogenous variables) and total percent plant cover, EMH and soil stability scores (endogenous variables). We used EMH as the measure of AMF because of its relationship with soil stability (Chaudhary et al., 2009). We used a maximum likelihood χ^2 goodness of fit test and reported the CMIN (χ^2) test statistic and its *P*-value to determine if the hypothesized SEM was a good fit. A high *P*-value indicates a good fit and suggests that our model accounts for patterns in the data. However, a high *P*-value does not rule out the possibility of better fitting models. Jöreskog's GFI statistic was used as a second indicator of model fit (Grace, 2006). Total, direct and indirect influences of treatments and response variables were calculated in AMOS 5. We added a covariance arrow between treatments to account for site variation.

3. Results

3.1. Soil properties

Pile burns had lower surface soil aggregate stability 6-months post-treatment than both mastication and untreated plots ($\chi^2 = 21.9$, $P < 0.01$) (Fig. 1A). We observed similar patterns 2.5-years post-treatment ($\chi^2 = 16.1$, $P < 0.01$), with no significant differences between mastication and untreated plots (Fig. 1B). There were no differences among treatment groups in soil aggregate stability 10 cm below the surface in either treatment year ($P > 0.05$) (Fig. 1A and B).

The PCA ordination of the remaining soil variables (moisture, temperature, bulk density, %C, %N, pH, NO_3^- , NH_4^+ and PO_4^{3-}) illustrates that pile burning alters the physical and chemical properties of soil, such that the first axis clearly separates soil properties from pile burns from both mastication and untreated plots (Fig. 2A and B-Site-B). Six-months post-treatment, the variables that strongly separated pile burn soils were high soil temperature, NO_3^- , NH_4^+ and PO_4^{3-} with this first axis explaining 40.5% of the variance among treatments (Fig. 2A). The second axis accounts for less variation than the first (14.5%), but it shows some differences between mastication and untreated plots with more of the untreated plots having higher soil temperature and bulk density and lower soil moisture (Fig. 2A).

Pile burns also clearly separate from untreated plots 2.5-years post-treatment, mostly due to low soil moisture and high soil

temperature, NO_3^- and NH_4^+ compared to untreated or mastication plots (explaining 37.2% of the variation). Axis 2 explains some within-treatment variation mostly due to differences in PO_4^{3-} , %N and %C (Fig. 2B-Site-B). Mastication and untreated soils did not clearly differ 2.5-years post-treatment and the ordination suggests within-group variation and between-group variation were similar between these treatments (Fig. 2B-Site-C). The PCA results support the more detailed list of soil results found in Appendix A.1 and A.2 which show that most all of the soil properties of pile burns differ from mastication and untreated soils (some by 4-fold) and mastication soils only vary from untreated soils in having lower temperature and higher moisture.

3.2. AMF response to treatments

Six-months post-treatment, pile burns differed from untreated and mastication plots in AMF propagule abundance and richness. Mean EMH density, AMF spore abundance and morphotype species richness were all lower in pile burns than mastication or untreated plots ($F = 13.3$, 13.1 , 15.3 , respectively; $P < 0.01$) (Fig. 3A, C and E). Burned plots had approximately half the EMH density, five times lower spore abundance and less than half the morphotype species richness found in masticated or untreated plots. We identified a total of 23 AMF morphospecies (Appendix B.1). The most abundant species was *Glomus aggregatum* which was found in 29 of the 30 plots. Six of the fourteen described genera of AMF were represented in the mastication and untreated plots, but only three were found in the pile burns. Also, only smaller species of spores ($< 110 \mu\text{m}$) were found in the pile burns while spores greater than $410 \mu\text{m}$ were found in mastication and untreated plots. Two species were found only in the mastication plots and three were observed only in the untreated plots (Appendix B.1).

Spore morphotype communities 6-months post-treatment were different in pile burns compared to mastication or untreated plots (Fig. 3G) (total MRPP; $A = 0.15$, $P < 0.01$ and multiple comparisons: pile burns and both untreated and mastication; $A = 0.15$, $P < 0.01$; untreated and mastication; $A = 0.0008$, $P = 0.39$). An indicator species for mastication was *Glomus mosseae* ($P < 0.01$) and indicator species for untreated plots were *G. aggregatum* ($P = 0.03$), *Glomus fasciculatum* ($P < 0.04$), *Glomus constrictum* ($P = 0.01$) and *Scutellospora calospora* ($P = 0.03$). There were no indicator species for pile burns.

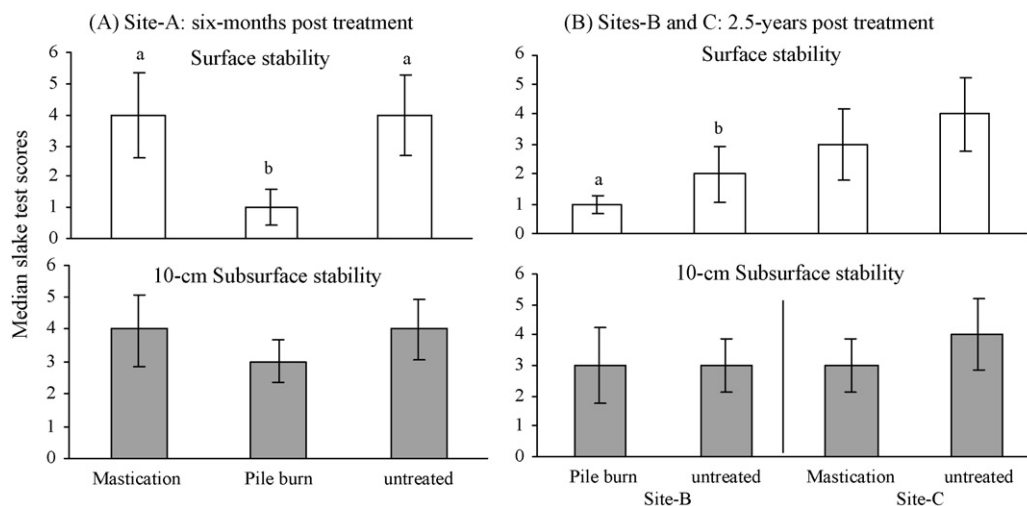


Fig. 1. Median surface aggregate soil stability (white bars) with median absolute deviation as error bars for (A) Site-A: 6-months and (B) Sites B and C: 2.5-years post-treatment was lower in the pile burns, but no differences were found between mastication and untreated soils or in 10 cm subsurface stability (gray bars) between treatments or sites. The y-axes represent Slake-Test scores ranging from high (5) to lower (1) stability.

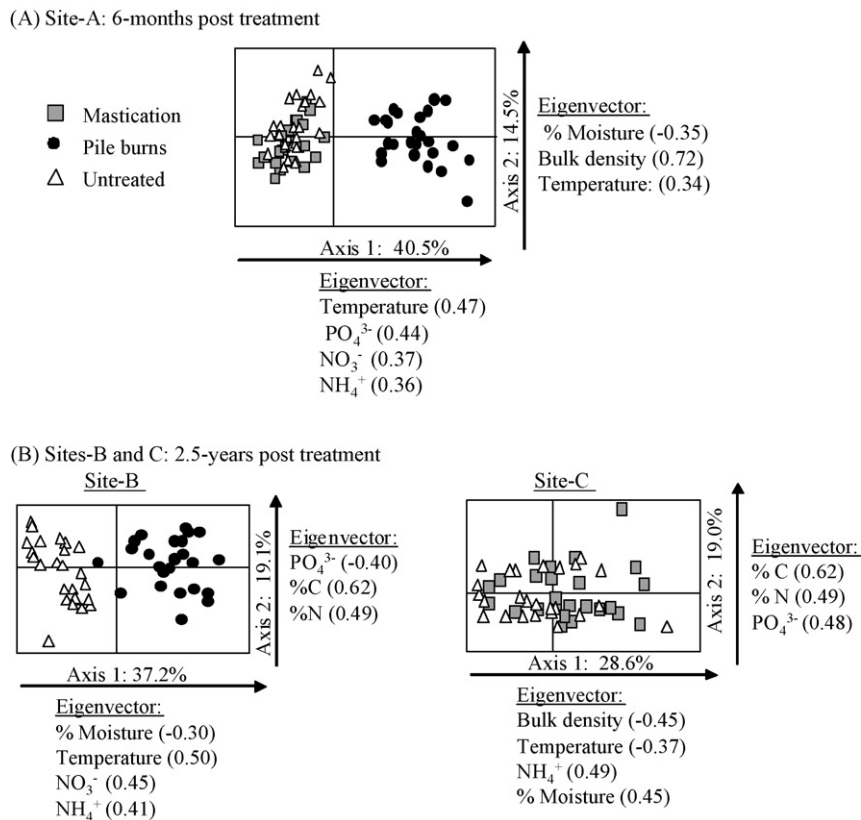


Fig. 2. Ordinations of PCA on soil variables for (A) Site-A: 6-months and (B) Sites B and C: 2.5-years post-treatment. Axes are shown with eigenvalues (next to axes) and strongest eigenvectors. Pile burns (shown by black circles) separated out from other treatments in both 6-months and 2.5-years post-treatment.

Similar patterns in AMF community structure were found 2.5-years post-treatment, although mastication plots had less AMF morphotype species richness than untreated plots ($F = 4.6$; $P = 0.046$) (Fig. 3F). EMH density and AMF species richness were lower in pile burns ($F = 5.0$, $P = 0.04$; $F = 16.6$, $P < 0.01$, respectively) (Fig. 3B and F). Spore abundance tended to be lower in the pile burns than untreated plots ($F = 3.9$; $P = 0.06$) (Fig. 3D). Also, there were no differences between mastication and untreated plots for EMH density and AMF spore abundance ($F = 1.8$, $P = 0.19$; $F = 2.1$, $P = 0.18$; $F = 0.64$) (Fig. 3B and D). Pile burns had seven fewer species than the untreated plots (Appendix B.2). Again, the most abundant species was *G. aggregatum* which was found in all plots. Community composition differed between pile burns and untreated plots ($A = 0.13$, $P < 0.01$) (Fig. 3H). Indicator species for the untreated plots were: *G. fasciculatum* ($P = 0.01$), *Glomus ambisporum* ($P < 0.01$) and *Glomus geosporum* ($P = 0.01$); an indicator species for pile burns was *G. mosseae* ($P < 0.01$). Mastication and untreated plots did not differ from one another in community composition ($A = 0.06$, $P = 0.09$).

3.3. Plant canopy and ground cover

Plant cover was measured twice in consecutive growing seasons for both treatment years: 6-months and 1.5-years post-treatment for treatments implemented in 2005 (Site-A) and 2.5-years and 3.5-years post-treatment for treatments initiated in 2003 (Sites B and C). MANOVAs were significant for both plant cover ($F = 36.03$; $P < 0.001$) and life forms ($F = 8.1$; $P < 0.001$), therefore one-way ANOVAs were applied. No differences were found between the 2 years of sampling (Table 1A and B) and treatment by year interactions were non-significant ($P > 0.05$). For Site-A, pile burns had lower total plant cover and plant cover within all life forms than mastication and untreated plots and

mastication plots had the highest litter cover (Table 1A). An exotic grass, *Bromus tectorum* (cheatgrass), and native grasses, *E. elymoides* and *B. gracilis* dominated the graminoid cover. *Ericameria nauseosa* ssp. *nauseosa* var. *nauseosa* (native rabbitbrush) was the dominant shrub and *Alyssum simplex* var. *micranthum* (exotic mustard) was the most abundant forb (Table 2A).

For 2.5-years and 3.5-years post-treatment (Sites B and C), pile burns still drastically differed from untreated plots and mastication plots had more total plant cover, higher graminoid and litter cover and less bare ground than untreated plots (Table 1B). Pile burns had little plant cover and almost 80% bare ground (Table 1B). In Site-B, two native species were most common in the untreated plots: *P. linarioides* spp. *coloradoensis* (penstemon sp.) and *C. montanus* and pile burns just had trace amounts of plant cover. In Site-C, two exotic species: *B. tectorum* and *A. simplex* var. *micranthum* dominated the plots and in the second year *B. tectorum* cover was higher in the mastication plots and it significantly increased over time (Table 2B-Site-C).

3.4. Plant richness and community composition

Pile burns had lower total ($F = 94.0$; $P < 0.01$), native ($F = 151.21$; $P < 0.01$) and exotic ($F = 23.81$; $P < 0.01$) plant species richness than mastication and untreated plots in Site-A both 6-months (Fig. 4A) and 1.5-years following treatment (not shown). Pile burns had approximately eight times lower plant richness and the greatest percentage of exotic species 80–89% for both years (Fig. 4A). The number of exotic plant species increased from 6-months to 1.5-years post-treatment ($F = 6.43$; $P = 0.01$), but overall plant richness ($F = 1.89$; $P = 0.17$) and native plant richness ($F = 0.01$; $P = 0.93$) did not change with time. Community analysis was not used for this treatment year because only five out of 25 pile burns had any plant cover.

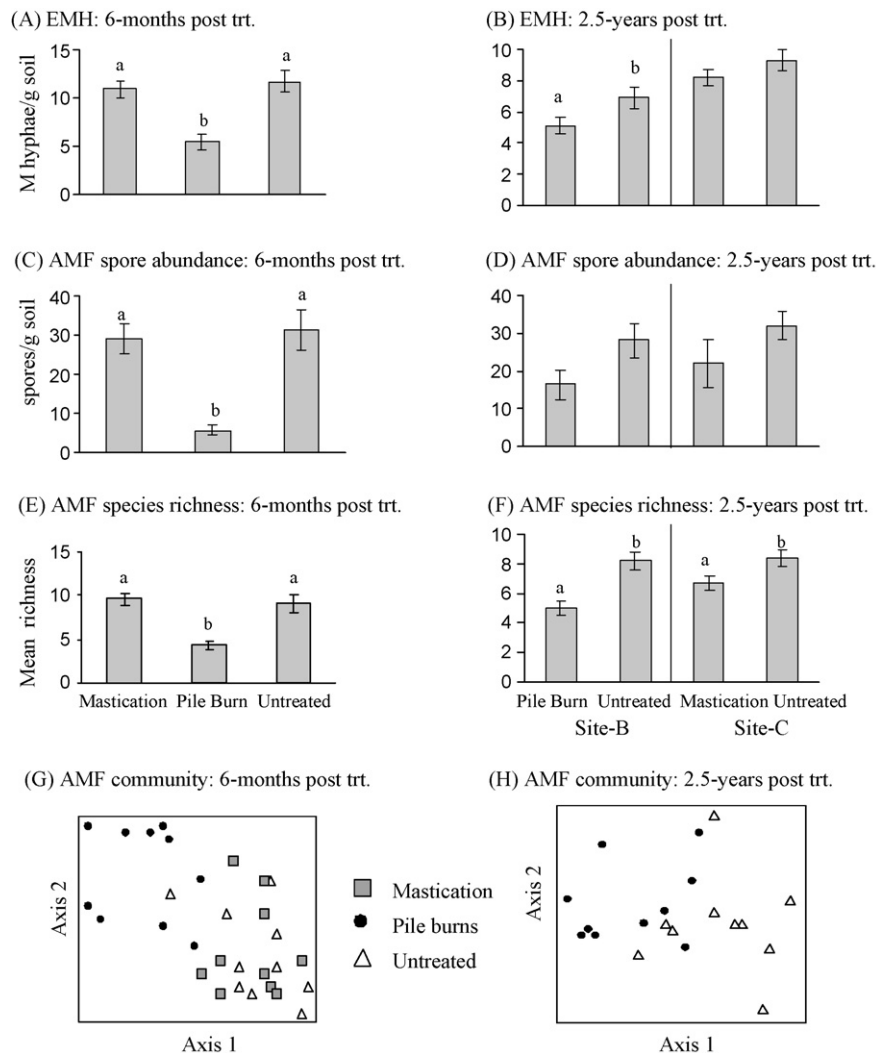


Fig. 3. Mean (A) EMH density, (C) AMF spore abundance and (E) AMF spore morphotype species richness were all lower in the pile burns 6-months post-treatment (Site-A). Mean (B) EMH density and (F) AMF spore morphotype species richness were lower in the pile burns 2.5-years post-treatment (Site-B) compared to untreated plots. Mastication treatments had lower (F) AMF spore morphotype species richness 2.5-years post-treatment (Site-C) compared to untreated plots. There were no significant differences between treatments in (D) AMF spore abundance 2.5-years post-treatment. Different letters indicate significant differences between means (Tukey–Kramer HSD $P < 0.05$). An NMS ordination showing AMF spore morphotype community composition of pile burns was different from (G) untreated sites and mastication plots 6-months post-treatment and (H) AMF community composition of pile burns was different from untreated plots 2.5-years post-treatment (the axes have no units and represent position of communities relative to each other).

Results were comparable for 2.5-years and 3.5-years following treatment (Sites B and C). Pile burns had lower total and native ($F = 131.3, 299.48; P < 0.01$) plant species richness, but no difference in exotic richness ($F = 1.6; P = 0.21$) relative to untreated plots (Fig. 4B). Pile burns had five times less mean species richness than untreated plots for both years and 93% of species richness in pile burns consisted of exotic plant species (Fig. 4B). In Site-B, no differences were found between sampling years for total, exotic or native plant richness ($F = 1.83, 1.4, 0.08; P = 0.18, 0.12, 0.77$, respectively). Mastication plots had greater total, native and exotic plant richness ($F = 22.1, 17.57, 12.2$, respectively; $P < 0.01$) relative to untreated plots 2.5-years following treatment (Fig. 4B). Total richness did not change with time at Site-C ($P > 0.05$), but the number of exotic species increased over time in the mastication plots (F -year = 4.31, $P = 0.04$).

Plant community composition differed among treatments. Pile burns had a different plant community than untreated plots both 2.5-years ($A = 0.14, P < 0.01$) and 3.5-years ($A = 0.16, P < 0.01$) post-treatment (Fig. 5A and B). Indicator species for pile burns were the same for both years and both were exotic species (*Sisymbrium altissimum* L. (tall tumbled mustard, $P = 0.04$) and

Carduus nutans L. (Musk thistle, $P < 0.01$)). Indicator species for untreated plots 2.5-years post-treatment were *P. linarioides* spp. *coloradoensis* ($P = 0.01$) and *A. simplex* var. *micranthum* ($P = 0.01$). Along with these species, five additional indicator species were found for the untreated plots 3.5-years post-treatment; all were native species: *C. montanus* ($P < 0.01$), *E. elymoides* ($P = 0.02$), *Physaria acutifolia* var. *acutifolia* (sharpleaf twinpod, $P = 0.02$), *Ipomopsis aggregata* ssp. *aggregata* (scarlet gilia, $P < 0.01$) and *Machaeranthera gracilis* (slender goldenweed, $P < 0.01$). At Site-C, plant community composition differed between mastication and untreated plots both 2.5-years and 3.5-years post-treatment ($A = 0.07, P = 0.01$ for both years) (Fig. 5C). There were no indicator species ($P > 0.05$); although mastication plots had four to six more exotic species than untreated plots (Appendix C.3). Most exotic species across all sites and treatment years were annuals and most native plants were perennials (Appendix C.1–3).

3.5. Plant–soil–AMF interrelationships: SEM

Our hypothesized structural equation model fit our data well ($\chi^2 = 1.369, P = 0.242, GFI: 0.954$), thus no post hoc alterations

Table 1

Two-year mean (± 1 SE) percent plant and litter cover and cover by plant life forms (averaged between 2 years of sampling due to no differences between sampling years and non-significant treatment by year interactions $P > 0.05$) for (A) Site-A: average of 6-months and 1.5-years post-treatment and (B) Sites B and C: average of 2.5 and 3.5-years post-treatment. Different letters indicate significant differences between treatments within a year.

Response	Treatments			F-Treat.	P-Treat.	F-Year	P-Year
	Mastication	Pile burn	Untreated				
(A) Site-A: 6-months and 1.5-years post-treatment							
Plant	45.9 (4.8)a	1.1 (0.4)b	50.7 (5.0)a	46.82	<0.01	0.09	0.77
Litter	76.2 (4.2)a	3.1 (1.0)b	21.9 (5.5)c	89.56	<0.01	0.09	0.76
Bare ground	0.7 (0.6)a	66.7 (4.8)b	12.3 (3.8)a	97.75	<0.01	0.01	0.85
Graminoid	22.3 (3.2)a	0.1 (0.1)b	27.7 (5.3)a	16.75	<0.01	0.02	0.88
Forb	13.5 (2.5)a	0.9 (0.4)b	15.2 (3.1)a	12.8	<0.01	0.53	0.47
Shrub	7.8 (1.5)a	0.2 (0.1)b	6.5 (1.9)a	8.55	<0.01	0.08	0.78
Response	Treatments		F-Treat.	P-Treat.	F-Year	P-Year	
	Pile burn	Untreated					
(B) Site-B (pile burns): 2.5-years and 3.5-years post-treatment							
Plant	3.7 (1.0)a	26.1 (3.8)b	31.78	0.01	0.76	0.39	
Litter	0.8 (0.6)a	23.9 (5.5)b	17.21	0.01	0.09	0.76	
Bare ground	79.6 (4.4)a	28.8 (5.2)b	56	<0.01	0.5	0.48	
Graminoid	0.0 (0.0)a	1.9 (0.5)b	12.93	<0.01	1.46	0.23	
Forb	3.5 (1.1)a	13.6 (1.8)b	24.59	<0.01	3.4	0.07	
Shrub	0.2 (0.2)a	6.8 (1.8)b	13.57	<0.01	0.15	0.7	
Response	Treatments		F-Treat.	P-Treat.	F-Year	P-Year	
	Mastication	Untreated					
(B) Site-C (mastication): 2.5-years and 3.5-years post-treatment							
Plant	45.6 (3.8)a	28.9 (3.6)b	10.4	<0.01	0.26	0.61	
Litter	68.2 (3.7)a	28.3 (5.8)b	33.4	0.01	0.0	1.0	
Bare ground	1.5 (0.4)a	41.5 (6.1)b	42.13	<0.01	0.85	0.36	
Graminoid	9.4 (1.9)a	2.4 (0.5)b	12.91	<0.01	0.63	0.43	
Forb	24.3 (3.0)	21.9 (3.2)	0.3	0.58	0.01	0.94	
Shrub	4.0 (1.5)	2.8 (1.1)	0.41	0.53	0.26	0.61	

were applied (Fig. 6). The P -value in the χ^2 test estimates the probability that a model fits the data, so traditionally P -values higher than 0.05 and GFI values near one are preferred. This model helped to explain 39% of the variation in EMH and more than half of the variation in both plant cover and soil stability ($R^2 = 0.51$ for both). This model illustrates that pile burning had a strong and direct negative effect upon plant cover, and impacted EMH and soil stability via various direct and indirect pathways which sum to a strong negative total effect. In contrast, mastication had a positive direct effect on total % plant cover, very little total effect on EMH and several indirect effects upon soil stability which sum to a positive total effect. The novel information that this model provides about our study is that impacts upon EMH and soil stability are largely moderated via impacts upon plant cover (Fig. 6). Also, plant cover is strongly, directly positively correlated with both EMH and soil stability and EMH is strongly, directly correlated with soil stability.

4. Discussion

4.1. Ecosystem responses to slash pile burning

In support of our first hypothesis, pile burns had degraded soil properties and a different AMF composition compared to untreated or mastication plots. The dark color and high sun exposure of the soils likely contributed to the higher soil temperatures and lower soil moisture in burned sites while the addition of ash influenced nutrient concentration and soil pH. High soil temperatures caused by pile burning can lead to reduced AMF abundance in the soil and on plant roots (Pattinson et al., 1999) and increased soil hydrophobicity (Neary et al., 1999). An increase in more 'mobile' forms of nitrogen and phosphorus following burning could also lead to nutrient loss through leaching (Neary et al., 1999). Low soil

stability has been shown to increase the probability of soil erosion (Herrick, 2000) and was negatively correlated with plant cover in arid ecosystems (Beever et al., 2006). Soil erosion and exposed mineral soil may benefit some opportunistic exotic plant species to a greater extent than native species (Vitousek, 1990; Dodge et al., 2008). Also, our SEM showed that pile burning had a direct and indirect (through plant cover) negative effect on EMH (Fig. 6). Soils from pile burns were missing genera of larger spores like *Scutellospora* and *Gigaspora* that decrease in high N soils and may fail to sporulate with nitrogen enrichment, yet the indicator species for pile burns 2.5-years post-treatment was *G. mosseae*, which is known to be a more N-tolerant species (Egerton-Warburton and Allen, 2000; Yoshida and Allen, 2001). The decline in AMF species richness and absence of some genera of AMF in burned plots could have detrimental effects on the plant community as AMF diversity can contribute to plant diversity (van der Heijden et al., 1998).

Pile burned plots had dramatically lower plant cover in all life forms than untreated or mastication plots, regardless of the length of time post-treatment. Pile burns had the highest percentage (80–89%) of exotic plant species and may be providing sources of seeds for exotic plant expansion (Haskins and Gehring, 2004), further reducing functionality. Although understory abundance was low on pile burns, the plant species that were able to establish were almost 90% exotic species. We also observed dense rings of exotic species circling the burn scars. Our SEM showed a strong influence of plant cover upon EMH and soil stability, suggesting that a change in plant cover could affect soil stability and AMF abundance (Fig. 6). Low plant cover and EMH density may contribute to soil erosion (Beever et al., 2006). These results conflict with management goals to increase forest resilience because pile burns do not return to a desired state even 2.5-years post-treatment.

Table 2
Mean (± 1 SE) percent plant canopy cover of most abundant species and over time.

Species	Treatments			χ^2 -Treat.	P-Treat	χ^2 -Year	P-Year
	Mastication	Pile burn	Untreated				
(A) Site-A: 6-months and 1.5-years post-treatment (averaged between 2 years due to no differences between sampling years and non-significant treatment by year interactions $P > 0.05$)							
<i>Bromus tectorum</i> ^a	14.1 (3.7)a	0.3 (0.1)b	17.2 (5.5)a	23.75	<0.01	5.7	0.06
<i>Elymus elymoides</i>	3.6 (1.1)a	0.0 (0.0)b	2.2 (0.8)a	17.8	<0.01	1	0.62
<i>Bouteloua gracilis</i>	1.8 (0.7)a	0.0 (0.0)a	8.0 (2.2)b	29.95	<0.01	0.5	0.8
<i>Ericaria nauseosa</i> ssp. <i>nauseosa</i> var. <i>nauseosa</i>	3.7 (1.8)a	0.0 (0.0)b	3.0 (1.2)a	7.5	0.02	4.1	0.13
<i>Alyssum simplex</i> var. <i>micranthum</i> ^a	0.8 (0.3)a	0.0 (0.0)a	6.5 (1.8)b	25.77	<0.01	2	0.37
Species	Treatments		χ^2 -Treat	P-Treat	χ^2 -Year	P-Year	
	Pile burn	Untreated					
(B) Site-B: 2.5-years and 3.5-years post-treatment							
2.5-years post-treatment							
<i>Cercocarpus montanus</i>	0.2 (0.2)a	4.3 (1.2)b	15.13	<0.01			
<i>Penstemon linarioides</i> ssp. <i>coloradoensis</i>	0.0 (0.0)a	4.6 (1.3)b	16.83	<0.01			
3.5-years post-treatment							
<i>Cercocarpus montanus</i>	0.2 (0.2)a	5.5 (1.3)b	19.11	<0.01	4.25	0.04	
<i>Penstemon linarioides</i> ssp. <i>coloradoensis</i>	0.0 (0.0)a	5.7 (1.7)b	20.35	<0.01	1.06	0.3	
Species	Treatments		χ^2 -Treat	P-Treat	χ^2 -Year	P-Year	
	Mastication	Untreated					
(B) Site-C: 2.5-years and 3.5-years post-treatment							
2.5-years post-treatment							
<i>A. simplex</i> var. <i>micranthum</i> ^a	10.8 (2.1)	10.8 (1.7)	0.02	0.89			
<i>B. tectorum</i> ^a	3.6 (1.7)	0.7 (0.3)	0.96	0.16			
3.5-years post-treatment							
<i>A. simplex</i> var. <i>micranthum</i> ^a	11.3 (2.1)	10.8 (1.7)	0.01	0.95	1	0.32	
<i>B. tectorum</i> ^a	4.5 (1.8)a	0.7 (0.3)b	5.35	0.02	4.25	0.04	

Different letters indicate significant differences between treatments.
^a Exotic plant species.

4.2. Ecosystem responses to mechanical mastication

As we predicted, mastication had a smaller effect on understory communities and soil properties than slash pile burning, although

responses from mastication only partially supported our second hypothesis. The lower soil temperatures and higher soil moisture associated with mastication are likely the result of reduced radiant heat gain and evaporation due the presence of woody debris (Brockway et al., 2002). The higher soil NH_4^+ 2.5-years following mastication (Appendix A.2) was unexpected, as we predicted a decrease in available N due to microbial immobilization in response to extra carbon addition (Blumenthal et al., 2003). Our results are similar to Miller and Seastedt (2009) who found an increase of available N with woodchip addition after 3 years. We predicted that the use of hydro-mow equipment would cause soil compaction and/or erosion (Corns, 1988), but the lack of difference could be from reduced soil erosion resulting from the presence of wood chips. Also, treatments were conducted in the winter when snow-covered, frozen soils may have been more resistant to compaction. Mastication had minor effects on AMF communities relative to pile burning, most likely due to fewer disturbances to soil properties. Although more study is needed to understand the impacts of mastication on soil properties, our results indicate mastication may somewhat improve soil structure and result in less soil disturbance than the burning of slash piles. Also, our final SEM showed that pile burning had a strong direct negative and an indirect negative effect on soil stability, where mastication had a weak indirectly positive (0.1) effect on soil stability (Fig. 6).

Over time plant cover was greater in the mastication plots and *B. tectorum* (cheatgrass) cover increased over time, apparently in response to a mulching effect of the wood chips and resulting higher soil moisture. Simulations and field studies have related expansion of cheatgrass populations with water availability (Bradford and Lauenroth, 2006; Chambers et al., 2007). Cheatgrass is an especially problematic exotic annual that can reduce function by establishing early in the growing season and becoming a persistent member of the plant community, providing continuous fine fuel that can increase fire frequencies (Brooks et al., 2004). It has been shown that many

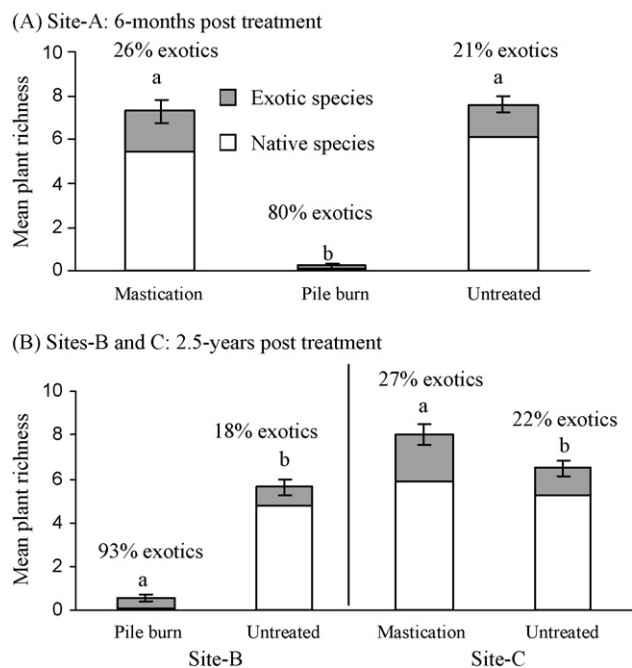


Fig. 4. Mean plant richness was lower in the pile burns 6-months post-treatment (A) and lower in the pile burns in Site-B and higher in the mastication plots in Site-C, 2.5-years post-treatment (B). Error bars and letters are for total mean plant richness; dark color represents mean exotic species richness and white represents mean native species richness.

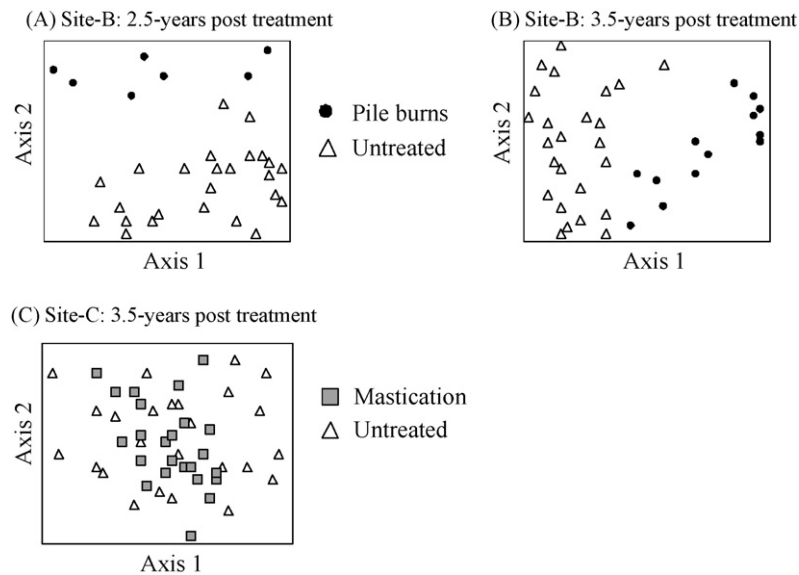


Fig. 5. NMS ordination showing plant species composition was different between pile burns and untreated plots for (A) 2.5-years post-treatment and (B) 3.5-years post-treatment. Fewer symbols are represented for the pile burns because some burns had no plant cover. Plant species composition was different between mastication and untreated plots 3.5-years post-treatment (C), although this ordination shows no observable differences.

forms of disturbance can promote invasions by non-native plant species (Hobbs and Huenneke, 1992; Korb et al., 2004; Fowler et al., 2008). Over 50% of the exotic species we observed were designated as ‘noxious weeds’ in both treatment types, with the potential to negatively impact native plant communities (Sieg et al., 2003) (see spp. with an (*) in Appendix 3). When species have different responses to disturbance it can allow competing species to temporarily coexist, although if some species are exotic this coexistence may not last over time (Hobbs and Huenneke, 1992). The weak difference in plant community composition between mastication and untreated plots 2.5-years post-treatment ($A > 0.1$ being strong (McCune and Grace, 2002)) may be due to an increase in exotic species (Fig. 5C).

4.3. Management and ecological implications

In the face of changing climates and mounting consequences of long-term fire suppression, land managers will be confronted with the challenge of maintaining both ecosystem function and resiliency. In 2003, federal agencies in the United States were

authorized to spend 750 million dollars to conduct tree thinning and fuel reduction treatments (United States Senate, 2004). Pile burning is an effective method for slash removal following thinning, but the disturbed habitat created by pile burns may cause nutrient loss and erosion and provide habitat for exotic species. We acknowledge that the burn scars are only a small portion of the total treated area (approximately 20%) and that our results are only specific to the direct area of the burn, not the entire treated landscape. However, we believe that the burn scars could have negative, long-lasting impacts on the surrounding area because of the loss of AMF and probable loss of nutrients and soil as well as the potential of these areas to act as sources of exotic plant seed dispersal. We suggest using alternative methods than pile burning to improve ecosystem resiliency. Alternatively, burn scars could be covered with nearby topsoil to help prevent erosion and encourage AMF and native seed banks (Korb et al., 2004). Plots treated with mastication deviated less from untreated controls in soil properties, AMF communities and plant composition than pile burning. Although, it is still unclear if mastication will affect ecosystem function over time because of the significantly higher exotic plant cover (especially *B. tectorum*), the wood chip decomposition and the loss of AMF species that could support native plants. Our results show, at least in the short-term, that mastication is a preferred method over slash pile burning. Our final SEM suggested a strong relationship between plants, AMF and soil stability, illustrating the need for simultaneous research on multiple components of the ecosystem when comparing management treatments.

Our results suggest that these tree thinning treatments should be undertaken conservatively and only when it can be reasonably argued that ecosystems are at risk of severe perturbation associated with stand-replacing fire. The variability in structural types of pinyon-juniper ecosystems due to different soils, elevation and climate have caused debate about past fire regimes and both the need for thinning and the potential role that fire should play in that management (Romme et al., 2009). Despite these uncertainties, managers are increasingly thinning trees and treating slash to reduce wildfire risk. As this large-scale manipulation of forest structure is undertaken, it will be valuable to understand treatment effects on multi-ecosystem responses on a landscape scale and over a longer time period. If mastication is used, we recommend confining treatments to high priority areas,

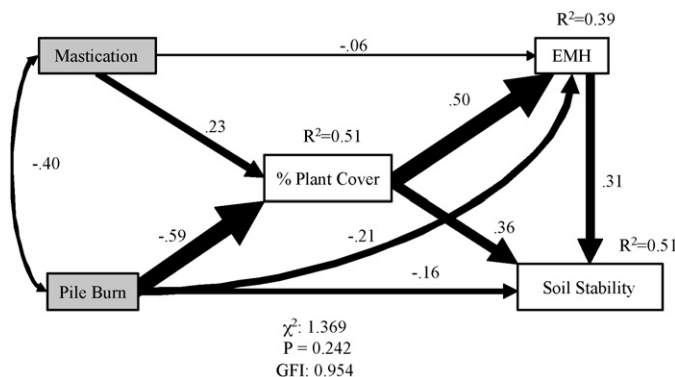


Fig. 6. Final structural equation model for pile burn and mastication treatments (exogenous variables in gray boxes) and percent plant cover, EMH and soil stability (endogenous variables in white boxes). The amount of variance explained for each endogenous variable is shown by the R^2 values. Numbers associated with arrows are path coefficients and together with the widths of arrows indicate the strength of the relationship. The double-headed arrow indicates covariance between the treatments.

monitoring for exotic plants, limiting the amount of disturbance by treating when there is snow on the ground, restoring areas of erosion and promoting native plant diversity. While many management practices cause some level of ecosystem disturbance and can increase the abundance of exotic species, they often create fewer disturbances than a severe wildfire (Covington et al., 1997).

Acknowledgements

We thank Nancy Johnson, Steve Overby, Andrew Owen, Noah Barstatis, Rudy King, Cara MacMillan, Jim Fowler, Lauren Hertz, Dan Guido, John Hockersmith, Anita Antoninka, Bala Chaudhary, Bradford Blake, Ron Hartman and members of the Dolores Forest Service Station, CO and the Gehring and Johnson lab groups at NAU. This project was funded by the USDA Forest Service: Rocky Mountain Research Station: (Cost share agreement: 05CS-11221615-152).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2009.09.044.

References

- Allen, C.D., Savage, M., Falk, D.A., Suckling, K.F., Swetnam, T.W., Schulke, T., Stacey, P.B., Morgan, P., Hoffman, M., Klingel, J.T., 2002. Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. *Ecological Applications* 12, 1418–1433.
- Arbuckle, J.L., 2003. Amos 5.0 Update to the Amos User's Guide (Computer Software and Manual) Smallwaters, Chicago.
- Beever, E.A., Huso, M., Pyke, D.A., 2006. Multiscale responses of soil stability on invasive plants to removal of non-native grazers from an arid conservation reserve. *Diversity and Distributions* 12, 258–268.
- Blumenthal, D.M., Jordan, N.R., Russelle, M.P., 2003. Soil carbon addition controls weeds and facilitates prairie restoration. *Ecological Applications* 13, 605–615.
- Bradford, J.B., Lauenroth, W.K., 2006. Controls over invasion of *Bromus tectorum*: the importance of climate, soil, disturbance and seed availability. *Journal of Vegetation Science* 17, 693–704.
- Brockway, D.G., Gatewood, R.G., Paris, R.B., 2002. Restoring grassland savannas from degraded pinyon–juniper woodlands: effects of mechanical overstory reduction and slash treatment alternatives. *Journal of Environmental Management* 64, 179–197.
- Brooks, M., D'Antonio, L.C.M., Richardson, D.M., Grace, J., Keeley, J.J., DiTomaso, J.M., Hobbs, R.J., Pellant, M., Pyke, D., 2004. Effects of invasive alien plants on fire regimes. *Bioscience* 54, 677–688.
- Carter, M.R., 1993. *Soil Sampling and Methods of Analysis*. CRC Press, Boca Raton, FL.
- Chambers, J.C., Roundy, B.A., Blank, R.R., Meyer, S.E., Whittaker, A., 2007. What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? *Ecological Monographs* 77, 117–145.
- Chaudhary, V.B., Bowker, M.A., O'Dell, T.E., Grace, J.B., Redman, A.E., Rillig, M.C., Johnson, N.C., 2009. Untangling the biological contributions to soil stability in semiarid shrublands. *Ecological Applications* 1, 110–122.
- Corns, I.G.W., 1988. Compaction by forestry equipment and effects on coniferous seedling growth on 4 soils in the Alberta Foothills. *Canadian Journal of Forest Research* 18, 75–84.
- Covington, W.W., Fulé, P.Z., Moore, M.M., Hart, S.C., Kolb, T.E., Mast, J.N., Sackett, S.S., Wagner, M.R., 1997. Restoring ecosystem health in ponderosa pine forests of the Southwest. *Journal of Forestry* 95, 23–29.
- Daubenmire, R., 1959. A canopy–coverage method of vegetation analysis. *Northwest Scientist* 33, 43–64.
- Dodge, R.A., Fulé, P.Z., Sieg, C.H., 2008. Dalmatian toadflax (*Linaria dalmatica*) response to wildfire in a southwestern USA forest. *Ecoscience* 15, 213–222.
- Egerton-Warburton, L.M., Allen, E.B., 2000. Shifts in an arbuscular mycorrhizal communities along an anthropogenic nitrogen deposition gradient. *Ecological Applications* 10, 484–496.
- Eom, A.H., Hartnett, D.C., Wilson, G.W.T., 2000. Host plant species effects on arbuscular mycorrhizal communities in tall grass prairies. *Oecologia* 122, 435–444.
- Fowler, J.F., Sieg, C.H., Dickson, B.G., Saab, V., 2008. Exotic plant species diversity: influence of roads and prescribed fire in Arizona ponderosa pine forests. *Rangeland Ecology and Management* 61, 284–293.
- Floyd, L.M., Hanna, D., Romme, W.H., 2004. Historical and recent fires in pinyon–juniper woodlands on Mesa Verde, Colorado, USA. *Forest Ecology and Management* 198, 269–289.
- Grace, J.B., 2006. *Structural Equation Modeling and Natural Systems*. Cambridge University Press, New York.
- Harris, J.L., 2003. 2002 Rocky Mountain Region Aerial Survey. USDA Forest Service, Rocky Mountain Region, Forest Health Monitoring, Lakewood, CO.
- Haskins, K.E., Gehring, C.A., 2004. Long-term effects of burning slash on plant communities and arbuscular mycorrhizae in a semi-arid woodland. *Journal of Applied Ecology* 41, 379–388.
- Herrick, J.E., 2000. Soil quality: an indicator of sustainable land management? *Applied Soil Ecology* 15, 75–83.
- Hobbs, R.J., Hueneke, L.F., 1992. Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology* 6, 324–337.
- Jiménez Esquilina, A.E., Stromberger, M.E., Massman, W.J., Frank, J.M., Shepperd, W.D., 2007. Microbial community structure and activity in a Colorado Rocky Mountain forest soil scarred by slash pile burning. *Soil Biology and Biochemistry* 39, 1111–1120.
- Johnson, N.C., O'Dell, T.E., Bledsoe, C.S., 1999. Methods for ecological studies of mycorrhizae. In: Robertson, G.P., Coleman, D.C., Bledsoe, C.S., Sollin, P. (Eds.), *Standard Soil Methods for Long-Term Ecological Research*. Oxford University Press, New York, pp. 378–412.
- Korb, J.E., Johnson, N.C., Covington, W.W., 2003. Arbuscular mycorrhizal densities respond rapidly to ponderosa pine restoration treatments. *Journal of Applied Ecology* 40, 101–110.
- Korb, J.E., Johnson, N.C., Covington, W.W., 2004. Slash pile burning effects on soil biotic and chemical properties and plant establishment: recommendations for amelioration. *Restoration Ecology* 12, 52–62.
- McCune, B., Grace, J.B., 2002. *Analysis of Ecological Communities*. MjM Software Design Gleneden Beach, OR, USA.
- McCune, B., Meford, M.J., 1999. *Multivariate Analysis of Ecological Data*, Version 4.02. MjM Software Design Gleneden Beach, OR, USA.
- Miller, E.M., Seastedt, T.R., 2009. Impacts of woodchip amendments and soil nutrient availability on understory vegetation establishment following thinning of a ponderosa pine forest. *Forest Ecology and Management* 258, 263–272.
- Miller, R.F., Wigand, P.E., 1994. Holocene changes in semiarid pinyon juniper woodlands. *Bioscience* 44, 465–474.
- Neal, S.M., 2007. Tree thinning treatments alter soil properties, arbuscular mycorrhizal fungi and plant communities. M.S. Thesis, Northern Arizona University.
- Neary, D.G., Klopatek, C.C., DeBano, L.F., Ffolliott, P.F., 1999. Fire effects on below-ground sustainability: a review and synthesis. *Forest Ecology and Management* 122, 51–71.
- Pattinson, G.S., Hammill, K.A., Sutton, B.G., Mcgee, P.A., 1999. Simulated fire reduces the density of arbuscular mycorrhizal fungi at the soil surface. *Mycological Research* 103, 491–496.
- Ramsey, D.K., 2003. *Soil Survey of Cortez Area, Colorado, Parts of Dolores and Montezuma Counties*. U.S. Department of Agriculture, National Resources Conservation Service, 628 pp.
- Romme, W.H., Allen, C.D., Bailey, J.D., Baker, W.L., Bestelmeyer, B.T., Brown, P.M., Eisenhart, K.S., Floyd, M.L., Huffman, D.W., Jacobs, B.F., Miller, R.F., Muldavin, E.H., Swetnam, T.W., Tausch, R.J., Weisberg, P.J., 2009. Historical and modern disturbance regimes. Stand structures, and landscape dynamics in Pinon–Juniper vegetation of the Western United States. *Rangeland Ecology and Management* 62, 203–222.
- Schenck, N.C., Perez, Y., 1990. *Manual for the Identification of VA Mycorrhizal Fungi*, 3rd ed. Synergistic Publications, Gainesville, FL, USA.
- Sieg, C.H., Phillips, B.G., Moser, L.P., 2003. Exotic invasive plants. In: Friederici, P. (Ed.), *Ecological Restoration of Southwestern Ponderosa Pine Forests*. Island Press, Washington, DC, pp. 251–267.
- Staddon, P.L., Fitter, A.H., Graves, J.D., 1999. Effect of elevated atmospheric CO₂ on mycorrhizal colonisation, external hyphal production and phosphorus inflow, in: *Plantago lanceolata* and *Trifolium repens* in association with the arbuscular mycorrhizal fungus *Glomus mosseae*. *Global Change Biology* 5, 347–358.
- United States Senate, 2004. Review of implementation of the Healthy Forests Restoration Act of 2003. In: Subcommittee on Forestry, Conservation, and Rural Revitalization of the Committee on Agriculture, Nutrition, and Forestry, One Hundred Eighth Congress, Second Session, Washington DC, USA.
- van der Heijden, M.G.A., Klironomos, J.N., Ursic, M., Moutoglis, P., Streitwolf-Engle, R., Boller, T., Wiemken, A., Sanders, I.R., 1998. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* 395, 69–72.
- Verkaik, I., Espelta, J.M., 2006. Post-fire regeneration thinning, cone production, serotiny and regeneration age in *Pinus halepensis*. *Forest Ecology and Management* 231, 155–163.
- Vitousek, P.M., 1990. Biological invasions and ecosystem processes: toward an integration of population biology and ecosystem studies. *Oikos* 57, 7–13.
- Wayman, R., North, M., 2007. Initial response of a mixed-conifer understory plant community to burning and thinning restoration treatments. *Forest Ecology and Management* 239, 32–44.
- Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and earlier spring increase western U.S. forest wildfire activity. *Science* 313, 940–943.
- Williams, R.J., Cook, G.D., Gill, A.M., Moore, H.R., 2002. Fire regime, fire intensity and tree survival in a tropical savanna in northern Australia. *Australian Journal of Ecology* 24, 50–59.
- Wolk, B., Rocca, M.E., 2009. Thinning and chipping small-diameter ponderosa pine changes understory plant communities on the Colorado Front Range. *Forest Ecology and Management* 257, 85–95.
- WRCC, 2004. Western Regional Climate Center. WRCC <http://www.wrcc.dri.edu/CLIMATEDATA.html> [visited 30 April 2006]
- Yoshida, L.C., Allen, E.B., 2001. Response to ammonium and nitrate by a mycorrhizal annual invasive grass and native shrub in southern California. *American Journal of Botany* 88, 1430–1436.