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Post-fire wood mulch for reducing erosion potential increases tree seedlings with few impacts on understory plants and soil nitrogen

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ABSTRACT

Following high-severity wildfire, application of mulch on the soil surface is commonly used to stabilize slopes and limit soil erosion potential, protecting ecosystem values at risk. Despite the widespread use of mulch, relatively little is known about its effects on ecosystem recovery and soil processes important for plant re-establishment. Following a high-severity wildfire in a Colorado lodgepole pine forest, we studied the effects of both mulch material and application rate on plant recovery and the relative importance of soil abiotic conditions and microbial substrate availability as drivers of plant community development over the first four years of recovery. Mulches were applied to experimental plots in a randomized complete block design immediately following the High Park Fire in July 2012. Treatments included wheat straw, wood strands, and wood shreds applied at two coverage rates (standard and high). Two controls, non-mulched and a microbially-neutral synthetic mulch, were included in each block to assess the relative importance of mulch effects on abiotic versus biotic dynamics. Plant and soil monitoring occurred at least annually for four-years post fire. Understory plants increased in total cover and shifted in composition over time, but these trends were largely unaffected by mulch type or application rate. Non-native understory plant species were not abundant at the end of this experiment, but their cover was higher in plots treated with wheat straw and high-rate wood strands compared to non-mulched control. Lodgepole pine seedling densities were higher in wood shred and mulched control treatments than in wheat straw and non-mulched control treatments. Because there were few effects of mulch treatments on plant available nitrogen, it is likely that effects of mulch on soil abiotic conditions (moisture and temperature) drove ecosystem responses in this system. Our findings indicate wood mulches can provide soil protection for many years and accelerate lodgepole pine establishment following wildfire with few negative near-term effects on plant recovery. In systems such as this, post-fire application of wood mulch can help managers meet site protection goals with minimal impacts on plant recovery.

1. Introduction

Post-fire treatments to limit the potential for soil erosion are increasingly important given that the extensive area burned in recent decades is predicted to increase (Dennison et al., 2014; Westerling, 2016) while human values at risk grow (Schoennagel et al., 2017), and vegetation management becomes more challenging in the face of climate change. Where wildfires burn at high severity, erosion, runoff, and sedimentation may be triggered by high intensity post-fire rain events (Bento-Gonçalves et al., 2012; Moody and Martin, 2009; Napper, 2006). The Burned Area Emergency Response (BAER) program was established in 1974 as a collaborative effort among agencies within the US Departments of Interior and Agriculture to quickly identify and abate soil erosion potential to protect values at risk following large wildfires (Robichaud et al., 2014). Among land treatments implemented by BAER, mulch application is one of the most common and effective at reducing post-fire erosion and sedimentation (Robichaud et al., 2014), yet the implications for vegetation response and effects on soil nutrients are largely unknown.

To be effective in reducing soil erosion potential and fostering post-fire ecosystem recovery, mulch should adequately protect the soil

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surface while not impeding plant establishment and development (Bautista et al., 2009; Napper, 2006; Robichaud et al., 2013c) or significantly altering soil nutrients. Although experimental data on optimal mulch application rates in post-fire environments are limited, a rate that achieves 60–70% ground cover is typically found to be the most effective in terms of limiting erosion and sedimentation (Bautista et al., 1996; Beyers, 2004; Prosdocimi et al., 2016; Robichaud et al., 2013c). However, similar guidelines have not been established for balancing mulch impacts on post-fire plant establishment, mainly due to lack of research on mulch application and plant recovery processes.

Agricultural straw, typically from wheat or rice, is widely used as mulch due to its effectiveness at reducing erosion and sedimentation and its ease of aerial application. However, it is susceptible to wind movement resulting in highly variable mulch distribution and thus effectiveness (Dodson and Peterson, 2010; Robichaud et al., 2013c, 2017). Agricultural straw mulch can also be a vector for invasive, non-native plants capable of having negative long-term effects on post-fire ecosystem recovery (Bontrager et al., 2019; Kruse et al., 2004; Robichaud et al., 2000; Shive et al., 2017). Certified weed-free straw mulches are available, but even these are prone to contamination by undesirable species (Bautista et al., 2009, 1996; Beyers, 2004; Shive et al., 2017). Non-agricultural alternatives, such as wood mulches, are less likely to introduce non-native plant species (Robichaud et al., 2013c, 2014). They have not been widely tested in the field, though wood mulch is just as effective as agricultural straw mulch in reducing soil erosion and less likely to shift in response to wind (Fernández and Vega, 2014; Foltz and Dooley, 2003; Prosdocimi et al., 2016; Robichaud et al., 2013b, 2013c) or introduce non-native plants (Foltz and Wagenbrenner, 2010; Robichaud et al., 2013c). In addition, wood mulch can limit erosion longer than wheat straw. Robichaud et al. (2013c) found that wood strand mulch decreased sediment yields compared to control through the first four-years post fire while wheat straw did not. While wood mulch may be a desirable alternative to wheat mulch from the standpoint of persistence and invasive species, the question of whether wood mulch impedes or promotes post-fire plant recovery remains largely unanswered.

Mulch application has the potential to impact plant establishment and ecosystem recovery (Beyers, 2004; Fernández et al., 2016; Fernández and Vega, 2014; Kruse et al., 2004) because it can change many aspects of the post-fire environment. Mulch can help increase soil moisture by slowing runoff and increasing infiltration (Bautista et al., 2009, 1996; Fernández and Vega, 2014). By impeding solar radiation reaching the soil surface, mulch can also reduce daytime soil warming and evaporative moisture loss (Santana et al., 2014; Stigter, 1984); such impacts on soil moisture and temperature may influence the ability of some plant species to germinate and establish (Bautista et al., 2009; Fernández et al., 2016; Robichaud et al., 2000). Mulch reduces bare mineral soil that many plants need for seedling establishment. The soil microbial community responsible for nutrient processing can also be influenced by mulch (Tiquia et al., 2002). Growth of microbial biomass can be limited by both available carbon and nitrogen for uptake, which could depend on the carbon to nitrogen ratio (C:N) of soil organic matter (Kaye and Hart, 1997). Because mulch has a relatively high C:N, mulch application could increase N demand by soil microbes. As a result, inorganic N, normally at high levels immediately post fire (Certini, 2005), may be reduced for plant uptake during the initial stages of post-fire recovery. Four years after the 2005 School Fire in Washington, Berryman et al. (2014) observed differences in soil C:N and nitrate (NO_3) uptake by vegetation associated with different post-fire rehabilitation treatments, including wheat straw and wood strand mulch. Causal attribution of these effects, however, was difficult in this observational study. In addition, there is a lack of data linking such soil effects to the resulting post-fire plant community.

As the extent of wildfires has been increasing across western US forests in recent decades (Robichaud et al., 2014), there has also been a concomitant decline in the ability of these forest to recover. In a meta-analysis of nearly 1500 sites that burned from 1988 to 2011, Stevens-Rumann et al. (2018) found that conifers are failing to meet recruitment thresholds following mixed-severity wildfires at a larger proportion of sites now than prior to the year 2000. Lodgepole pine (*Pinus contorta*) stands are one of the most common forest types in the Colorado Front Range (Peet, 1981; Veblen and Donnegan, 2005). Producing both serotinous and non-serotinous cones, infrequent high-severity fires play an important role in regeneration of this shade intolerant species (Lotan et al., 1985; Peet, 1981; Veblen and Donnegan, 2005). Compared to other Front Range forest types, mature lodgepole pine stands tend to have a relatively sparse herbaceous understory (Lotan et al., 1985; Moir, 1969) with low species richness (Peet, 1981). However, release from light limitation following canopy reduction may stimulate establishment and growth of lodgepole as well as understory herbaceous and shrub species. In some cases, increased understory growth following high-severity fire can competitively limit lodgepole establishment (Lotan et al., 1985). Given the increasing size and severity of wildfires throughout the western US and continuing use of mulch for post-fire rehabilitation, there is a critical need to understand how these treatments may impact post-fire ecosystem recovery in these and other forests.

The High Park Fire (HPF; Larimer County, Colorado) was ignited by lightning in early June 2012 (Coen and Schroeder, 2015) and burned primarily in mature lodgepole pine forests (USDA Forest Service, 2012). Nearly half of the ~35,000 ha burned were classified as having experienced moderate- or high-severity fire (USDA Forest Service, 2012) as defined by Parsons et al. (2010). As part of the BAER response, mulch was applied to areas of highest risk to critical values immediately following the fire to limit erosion and sedimentation (Robichaud et al., 2017; USDA Forest Service, 2012).

In an area of the HPF that was not treated by watershed-scale mulching, we established experimental plots in late summer 2012 to (1) examine patterns of understory plant community development and lodgepole pine regeneration associated with different mulch materials and application rates, and (2) assess the relative importance of soil environment (i.e., soil moisture and temperature) and microbial substrate availability as potential drivers of plant responses to mulch treatments during the initial phases of recovery. Three types of mulch material were evaluated: wheat straw, and two common types of wood mulches differing in size and shape, one of which is commercially available (wood strands) and one that can be produced on-site (wood shreds). Each of these mulches was applied at either the BAER standard rate or at 150% of the BAER standard rate. To separate mulch effects on the soil physical environment from effects on microbially-driven C or N availability, we included a biologically-inert, synthetic mulch treatment that could mimic effects on soil moisture and temperature without contributing substrate for soil microbial processes. Therefore, unlike many studies of post-fire mulch effects that are unable to include true controls (Kruse et al., 2004), we were able to deploy two different types of controls (non-mulched and mulched) in our replicated experimental treatments to provide information on both pattern and process in post-fire recovery associated with mulch treatments. We expected that if plant responses were driven by mulch effects due to increased substrate available for microbial processing, then there would be differences between synthetic mulch and plant-based mulch treatments. If responses were due to mulch effects on the abiotic environment, we expected to find differences between non-mulched control and plant-based mulch treatments but no differences between synthetic mulch and plant-based mulch treatments.

2. Methods

2.1. Experiment establishment

2.1.1. Site description

This experiment was installed within the South Fork Cache la Poudre River basin in the High Park Fire burned area at approximately 2500 m elevation in the Arapaho and Roosevelt National Forests

(40.6192°N, 105.5153°W) in July 2012. This area has north-facing, 16–23% slopes and was rated as high burn severity (*i.e.*, > 70% overstory tree mortality, > 90% surface charred or with bare mineral soil) by the Burned Area Emergency Response team following the HPF (USDA Forest Service, 2012). Prior to the fire, the site had a dominant overstory of lodgepole pine (12.7–22.6 cm DBH) with a minor aspen (*Populus tremuloides*) and Douglas-fir (*Pseudotsuga menziesii*) component, and a sparse grass-dominated understory according to a National Forest System stand survey (USDA Forest Service, 2019). Soils are shallow, loamy-skeletal, micaceous Lamellic Haplocryepts (Bullwark-Catamount families), formed on colluvium and residuum from schist, gneiss, and granite (USDA Soil Survey, 2017).

2.1.2. Treatment design

We used a randomized complete block design consisting of six replicate blocks with at least 10 m between proximate blocks. Each block had eight 3- × 7-m plots with a 1-m buffer between plots (8 plots per block × 6 blocks = 48 plots in total) (Supplement A). Treatments consisted of three biological mulch materials (wheat straw, wood strands, and wood shreds) applied at either the BAER standard rate (hereafter, standard rate) or 150% of the BAER standard rate (hereafter, high rate). In addition to the six biological mulch treatments (3 material × 2 rate), each block had two control plots: one mulched with a synthetic material (hereafter, mulched control) and one non-mulched control. Control treatments were designed to facilitate separating mulch effects on microbial substrate availability from effects on the soil physical environment (soil moisture and temperature).

2.1.3. Mulches

Mulches were applied to achieve approximately 70% surface cover in plots receiving the standard application rate. Locally-sourced, certified weed-free wheat straw was applied at 0.14 kg·m^{-2} (standard rate) or 0.21 kg·m^{-2} (high rate). Wheat plots were covered with bird netting after mulch application to limit wind- and water-driven loss of straw from plots. Two types of wood mulch were used, each having different physical characteristics that may affect mulch persistence and decomposition rate. Wood strands (WoodStraw®, Forest Concepts, Auburn, WA[2]) are an engineered wood product with generally uniform particle size and shape, ranging from 6.3- to 16-cm long, with cross-sectional dimensions of about 0.3 cm by 0.5 cm. Wood shreds (Morgan Timber Products, Fort Collins, CO) are a heterogeneous mix of shredded wood containing larger chips and finer particles mixed together. This shredded wood mulch can be produced onsite with truck-mounted equipment (Robichaud et al., 2013a). Both wood mulches were applied at the same two rates: 1.3 kg·m^{-2} (standard rate) or 1.95 kg·m^{-2} (high rate). The synthetic mulch was composed of recycled rubber tires (Front Range Tire Recycle, Sedalia, CO) chopped so particle size was similar to that of wood shreds. It was applied at 0.018 m^3 m^{-2} to achieve approximately 70% surface cover.

2.2. Data collection

2.2.1. Soil physical environment

Prior to mulch application, soil moisture and temperature loggers were installed in three replicates of each treatment (24 plots). Soil moisture probes were buried at 5- and 20-cm depths and connected to a datalogger (EC-5 Soil Moisture Probes connected to Em5b dataloggers, Meter Group, formerly Decagon Devices, Inc., Pullman, WA) programmed to record volumetric soil moisture every 4 h. Soil temperature was also recorded every 4 h using sensors buried at 5-cm soil depth (DS1921G-F5# Thermochron iButtons, Maxim Integrated, San Jose, CA). To prevent failure from moisture exposure, iButtons were tightly wrapped in thin plastic.

[2] Tradenames are provided for the benefit of the reader and do not imply endorsement by Colorado State University or US Department of Agriculture.

2.2.2. Mulch persistence

To monitor changes in mulch persistence, ground cover (mulch, rock, soil, moss, charcoal, or charred wood) was recorded every 10 cm within a 1- × 1-m quadrat (100 points per quadrat) by the point-intercept method (Robichaud and Brown, 2002). Two frames were sampled in the central portion of each plot in July 2014 to 2016.

2.2.3. Inorganic nitrogen dynamics

To determine mulch effects on plant-available nitrogen, inorganic soil nitrogen (N_i), ammonium-N ($NH_4^+{-}N$) and nitrate-N ($NO_3^-{-}N$), were monitored each year using Plant Root Simulator (PRS) resin membrane probes (Western Ag Innovations, Saskatoon, SK, Canada). We placed four pairs of probes (one anion, one cation) randomly throughout each plot during the growing season of each year. Probes were in the field from August to October (late season) in 2012 and 2013, from May to August (early season) 2013, and from May to late September or early October (growing season) of 2014–2016. Shorter incubation periods were chosen for the first two sampling seasons due to the potential for N saturation of PRS probes in high-nitrogen conditions (Harrison and Maynard, 2014) typical of post-burn environments. After retrieving PRS probes from the field, they were rinsed with distilled deionized water to remove soil particles adhering to the probes and then returned to Western Ag Innovations for analysis. The four probe pairs were composited during analysis for one result per plot for each of NO_3-N and NH_4-N.

A leaf nitrogen reductase enzyme assay was used to determine mulch effects on inorganic nitrogen uptake by plants. Assimilation of nitrate by plants was assessed using a field-based Nitrate Reductase Assay (NRA) method (Högberg et al., 1986; Jaworski, 1971). Seeds of a native forb, showy goldeneye (*Heliomeris multiflora*), were planted in a small section of each plot in July 2012 so the NRA assay could be performed on the same species in all plots from 2013 to 2016. Each July, the assay was performed on samples from two showy goldeneye individuals of similar size and phenological state in each plot. For each individual sampled, a 1-cm^2 tissue sample was removed from each of two leaves and incubated in 4 ml of KNO_3-KH_2PO_4-(*n*-propanol) buffer solution under cool, dark conditions. After 1 hr, 0.5 ml of buffer solution was placed in a new vial and mixed with 0.5 ml each of two color reagents [1% w/v sulfanilamide in HCl and 0.02% w/v N-(1-napthyl) ethylene diamine dihydrochloride in distilled deionized water]. Leaf extract samples were stored at 4 °C prior to colorimetric analysis. Colorimetric analysis was performed using the Tecan i-Control application running an Infinite 200 spectrophotometer (Tecan Group Ltd, Switzerland) measuring absorbance at 540 nm wavelength. A dilution series was used to create a standard curve for translating field assay sample absorbance measurements into leaf nitrite concentrations for showy goldeneye in each plot. Assayed leaf tissue samples were oven-dried at 55 °C for 48 h prior to weighing in order to adjust nitrite concentrations to a per unit biomass basis.

2.2.4. Plant responses

Understory plant cover was measured in July of each year to determine mulch effects on plant recovery. Using a direct ocular estimation technique, foliar cover was estimated to the nearest 1% for each plant species in 1-m^2 (0.5- × 2-m) quadrats. Three quadrats, spaced 0.5 m apart, were sampled in the center of each plot. The number of lodgepole pine seedlings was also recorded for each quadrat.

2.3. Statistical analysis

2.3.1. Univariate responses

To meet the normality assumption for statistical tests, response variables were transformed as necessary prior to analyses: soil moisture and temperature variables did not require transformation; mulch and plant cover variables were square-root transformed; showy goldeneye leaf NRA data were natural log + 0.01 transformed, and soil inorganic nitrogen and pine seedling density variables were natural log + 1 transformed. Univariate statistical analyses used an alpha (α) = 0.05 and were conducted in SAS Software v 9.4 (SAS Institute, Cary, NC).

To differentiate effects due to mulch material from those of mulch application rate, responses to biological mulch treatments were analyzed using repeated measures randomized complete block 3-way factorial (mulch material × mulch rate × year) restricted maximum likelihood (REML) analyses in proc glimmix. Control treatments (mulched control, non-mulched control) were excluded from these analyses because they have either no rate (non-mulched control) or only one level of rate (mulched control) which would result in an incomplete factorial design. There were three levels of mulch material (wheat straw, wood strands, and wood shreds) and two levels of the application rate factors (BAER standard rate, 150% of the BAER standard rate). The year factor was included as a repeated measure using a first-order autoregressive error covariance structure. In the model, block was a random effect and the Kenward-Roger denominator degrees of freedom method was used to adjust for unequal replication due to missing values and unequal variances (Kenward and Roger, 2009; Littell et al., 2006; Padilla and Algina, 2007). For significant effects, Tukey's multiple comparison adjustment was used for post hoc pairwise comparisons to control Type I error (Westfall et al., 1999). If an interaction involving year was significant, post-hoc comparisons of the interaction were conducted on the main effect(s) separately for each year using the slice statement. Soil N variables were analyzed as above except as a 2-way factorial (mulch material × mulch rate with year removed from the model) for each year separately due to the unequal length of time that PRS probes were buried each year which can influence analytical results.

To identify mechanisms driving plant responses as those due to environmental effects versus biological effects, the six mulch material × rate treatments were compared to each of the two types of control in separate sets of one-way REML analyses that were conducted for each year individually. Each treatment was compared to the non-mulched control in the first set of analyses and to the mulched control in the second set of analyses. In both sets of analyses, Dunnett's multiple comparison adjustment was used to control Type I error when comparing treatments to controls (Westfall et al., 1999), block was a random effect, and the Kenward-Roger denominator degrees of freedom method was applied. Differences between the two control treatments (non-mulched vs mulched control) were similarly assessed.

Periodic soil moisture and temperature logger failures during the four years of this study resulted in only 1 or 2 replicates of some treatments during many time periods. Therefore, soil temperature and moisture data were only analyzed for treatments and time periods in which all three replicate sensors were concurrently operational. Monthly average moisture and temperature variables were analyzed using one-way REML analyses comparing all 8 treatments (6 biological mulches and 2 controls) with Month included as a repeated measure using a first-order autoregressive error covariance structure. Each time period with one or more consecutive months of data was analyzed separately. In the model, block was a random effect and the Kenward-Roger denominator degrees of freedom method applied. For significant effects, Tukey's multiple comparison adjustment was used for post hoc pairwise comparisons to control Type I error.

2.3.2. Multivariate responses

All multivariate analyses were conducted in R version 3.5.3 (R Core Development Team, 2019). Multivariate analysis of understory plant community responses to mulch treatments was based on non-metric multidimensional scaling (NMDS) of the Bray-Curtis distance from the square-root transformed species matrix with function metaMDS() in package *vegan* (Oksanen et al., 2019). Species with only a single occurrence in a single year were removed from the community matrix because we were primarily interested in broad community characteristics rather than incidental species occurrences (Cao et al., 2006). Two sets of analyses were conducted: one using data from all plots but without soil data included in the set of explanatory environmental variables (n = 192, 48 plots × 4 years), and another using only those plots for which July 5-cm depth soil moisture and temperature data were available (n = 44, 2014 and 2016 only, unequal replication). Relationships between NMDS axes scores and continuous explanatory variables were assessed by maximum correlation using the envfit() function in package *vegan* (Oksanen et al., 2019), with significance determined using a Dunn-Sidak adjusted alpha (α') based on the number of explanatory variables in the analysis to maintain an overall alpha (α) = 0.05 (Gotelli and Ellison, 2004). A blocked 3-way permutation MANOVA (perMANOVA) was used to test community responses to mulch material, mulch rate, and year using Euclidean distances and 9999 permutations with function adonis() in package *vegan* (Oksanen et al., 2019). Pairwise comparisons for significant main or interaction effects identified in the perMANOVA were assessed using 9999 permutations in the function pairwise.perm.manova () in package RVAideMemoire (Hervé, 2019) with Dunn-Sidak adjusted alpha based on the number of pairwise comparisons in the analysis as described above. We used the method of De Cáceres et al. (2012) to identify combinations of indicator species for each mulch treatment in each year with sensitivity (B) ≥ 0.25, indicator value (IV) ≥ 0.50 and positive predictor value (A) ≥ 0.60 on the lower bound of the 95% confidence interval from 1000 bootstrap iterations using function indicators() in package *indicspecies* (De Caceres and Jansen, 2016). Using these parameters, indicator species associations will have been found in at least 25% of replicates for a given treatment and would be expected to accurately identify a given treatment in at least 60% of instances (De Cáceres et al., 2012).

3. Results

3.1. Soil environment

During times of relatively high precipitation, mulched treatments tended to have higher soil moisture than non-mulched controls at both depths (Fig. 1). Soil moisture at 5-cm depth deceased significantly from July to August 2012 in the standard-rate wood shred treatment when statistically comparing all treatments and controls except standard-rate wheat straw (Fig. 1B; Month $F_{1,14} = 25.63$, $p = 0.0002$, Treatment $F_{6,11.53} = 0.79$, $p = 0.59$, Month * Treatment $F_{6,14} = 3.22$, $p = 0.03$). At 20-cm depth, soil moisture in standard-rate wood strand plots was significantly higher than in high-rate wood strand plots during January–February 2015, months for which data sufficient for statistical analysis were available from only these two treatments (Fig. 1C; Month $F_{1,4} = 0.33$, $p = 0.60$, Treatment $F_{1,1.003} = 263.13$, $p = 0.04$, Month * Treatment $F_{1,\ 4} = 1.82$, $p = 0.25$). Mulch treatments had no consistent significant effects on soil temperature or moisture based on months and treatments for which statistical analysis were possible (Supplement B1), but statistical power was generally low which limits our ability to interpret non-significant results. Otherwise, soil moisture (Figs. 1B–C, 2A–B) and temperature (Fig. 2C; Supplements B2, C) did not differ significantly among treatments, and generally reflected seasonal changes.

3.2. Mulch persistence

Mulched plots had higher mulch cover than non-mulched controls throughout the study even though a small amount of mulch was transported from mulched plots onto non-mulched controls by wind and water (Table 1; Supplement B3). Wheat straw treatments had significantly lower mulch cover than mulched control and all wood mulch treatments in 2015 and 2016 (Table 1). Wheat straw mulch cover decreased faster than that of either wood shreds or wood strands from 2012 to 2016 (Table 1; Material $F_{2,29} = 37.65$, $p < 0.0001$, Rate $F_{1,29} = 1.08$, $p = 0.31$, Material * Rate $F_{2,29} = 0.09$, $p = 0.92$).

3.3. Nitrogen dynamics

Inorganic nitrogen (N_i) peaked one-year post fire, but most measurements were below the detection limit by three- and four-years post

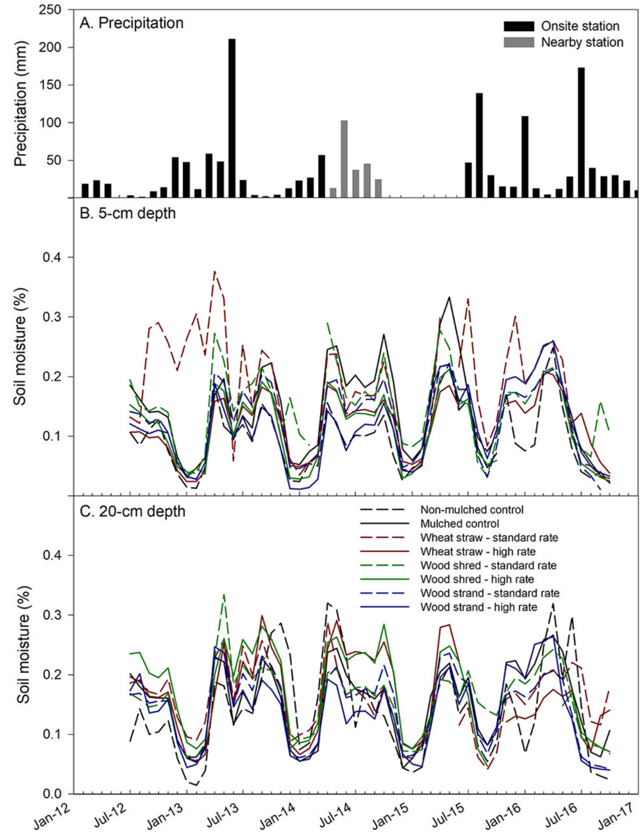

Fig. 1. (A) Total monthly precipitation (mm), and average monthly soil moisture (% volumetric water content) at (B) 5- and (C) 20-cm soil depth in each treatment. Mulch application rate treatments were Burned Area Emergency Response (BAER) standard (dashed) and 150% of BAER standard by weight (high rate, solid). Mulches were applied in July 2012. In panel (A), data for precipitation from mid-2014 through early-2015 from the study site are missing due to logger failure, gray bars indicate data from a similar tipping bucket logger approximately 0.81 km from the study site at ~0.4 km lower elevation (S. Ryan, unpublished data). Data presented and analyzed on the original scale.

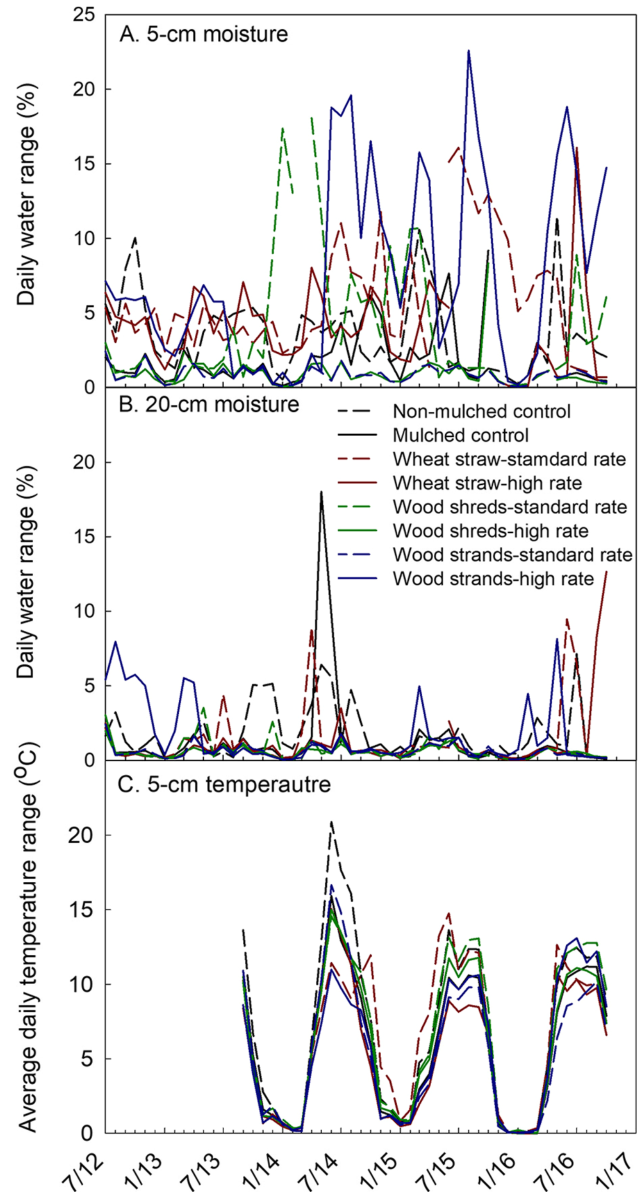

Fig. 2. Monthly average daily water range at (A) 5-cm and (B) 20-cm depth, and (c) daily temperature range at 5-cm depth measured as the difference between daily maximum and minimum percent volumetric water content or soil temperature, respectively. Mulch application rate treatments were Burned Area Emergency Response (BAER) standard (dashed) and 150% of BAER standard by weight (high rate, solid). Mulches were applied in July 2012. Due to periodic logger failure, statistical analysis included only treatments and months with data available from at least three replicate plots (Supplement B). Data presented and analyzed on the original scale.

fire. Nitrate-N made the largest contribution to total N_i through the first 3 years, but NH_4-N was dominant in the fourth post-fire year when NO_3-N was negligible (Fig. 3B, inset). During the first three months following fire, high-rate wheat straw had lower N_i ($t_{30} = -4.22$, $p < 0.01$), NH_4-N ($t_{30} = -2.96$, $p = 0.03$) and NO_3-N ($t_{30} = -4.04$, $p < 0.01$) than both the mulched and non-mulched control; no other mulch treatments differed from controls in any other period sampled. Wheat straw treatments also had lower N_i than wood strand treatments during this time (Fig. 3; $F_{2,25} = 7.68$, $p < 0.01$, Rate $F_{1,25} = 7.75$, $p = 0.01$, Material * Rate $F_{2,25} = 1.38$, $p = 0.27$); a similar pattern was seen in both NH_4-N and NO_3-N (Supplements B4, D). Standard-rate treatments had significantly higher N_i and NO_3-N (Material $F_{2,25} = 6.28$, $p = 0.01$, Rate $F_{1,25} = 10.01$, $p < 0.01$, Material * Rate $F_{2,25} = 2.05$, $p = 0.15$) than high-rate treatments in the 2012 period, although treatments other than high-rate wheat straw did not differ from mulched or non-mulched controls (Supplement B). Only the mulch material main effect was significant for N_i in both early-season (Material $F_{2,25} = 5.64$, $p = 0.01$, Rate $F_{1,25} = 0.10$, $p = 0.75$, Material * Rate $F_{2,25} = 0.28$, $p = 0.76$) and late-season (Material $F_{2,25} = 9.06$, $p < 0.01$, Rate $F_{1,25} = 0.46$, $p = 0.51$, Material * Rate $F_{2,25} = 2.64$, $p = 0.09$) periods in 2013, with wood strands having higher N_i than wheat straw and wood shred treatments (Fig. 3); this pattern was driven by changes in NO_3-N (Supplement D).

Showy goldeneye leaf nitrite concentrations differed in all years analyzed, being highest in 2013 and lowest in 2015 (Fig. 4; Supplement B5). Leaf NRA did not demonstrate significant effects of treatments on inorganic nitrogen uptake by showy goldeneye. Leaf NRA data from 2014 were not analyzed due to quality control concerns.

3.4. Understory plant responses

Total understory plant species richness (Fig. 5A) and foliar cover (Fig. 5B) increased each year of the study on all mulch materials and rates (Table 2A–B). Wood shred plots had lower species richness (9 ± 1 species, mean ± standard error) than wood strand (11 ± 1 species) and wheat straw (11 ± 1 species) plots as a significant mulch material main effect (Fig. 5A; Table 2A). Species richness in non-mulched controls tended to be lower than other treatments, but the

Table 1
Mulch cover (% ± standard error) in each treatment in 2014, 2015, and 2016. Mulches were applied in July 2012. Plus (+) indicates significant difference between non-mulched and mulched controls. In a given year, difference between material × rate treatments and controls are indicated by an asterisk (*) for non-mulched control and a caret (ˆ) for mulched control based on separate 1-way analyses using the Dunnett adjustment. Lowercase letters indicate significant differences based on mulch material × application rate × year 3-way analyses using the Tukey adjustment for pairwise comparisons. Data are presented on the original scale, statistical analyses were conducted on square-root transformed proportion data. Relative change in mulch ground cover (%) based on estimated mulch cover in October 2012 of standard rate = 84% and high rate = 88% cover across mulch materials.

Treatment	2014	2015	2016	2012–2016 relative change (%)
Non-mulched control	0.0 ± 0	0.1 ± 0.1	0.2 ± 0.1	+0.2
Mulched control	40.2 ± 5.9 +	51.6 ± 5.9 +	44.8 ± 4.3 +	−39
Wheat straw-standard rate	26.4 ± 4.2 *b	13.4 ± 5.4 *ˆc	7.5 ± 3.8 *ˆb	−77
Wheat straw-high rate	35.5 ± 4.9 *ab	29.9 ± 5.0 *ˆb	13.3 ± 3.5 *ˆb	−75
Wood shred-standard rate	43.4 ± 5.9 *ab	55.3 ± 4.2 *a	45.2 ± 5.2 *a	−39
Wood shred-high rate	59.8 ± 3.5 *a	65.1 ± 7.3 *a	58.1 ± 6.3 *a	−30
Wood strand-standard rate	53.5 ± 3.1 *a	69.2 ± 4.5 *a	48.2 ± 4.2 *a	−36
Wood strand-high rate	53.8 ± 4.1 *a	69.9 ± 5.8 *a	54.3 ± 1.7 *a	−34

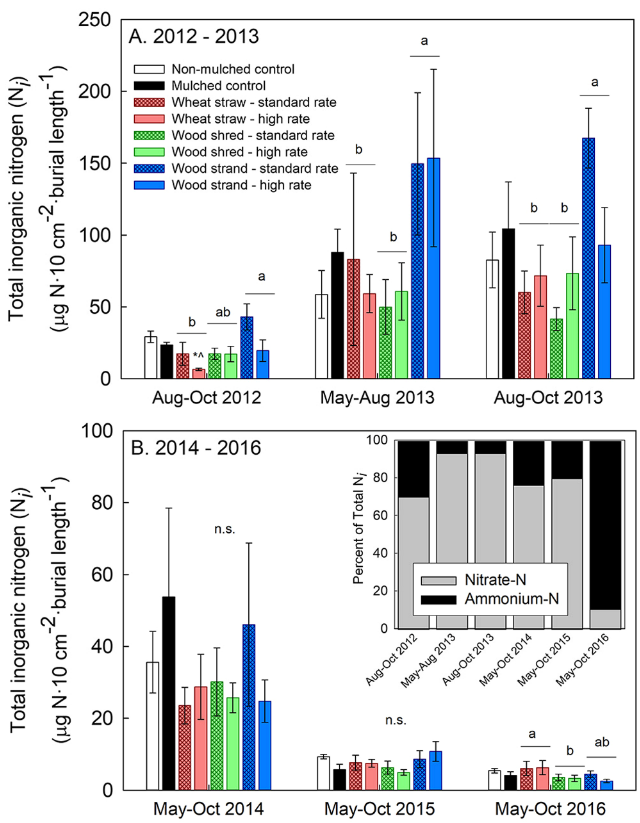

Fig. 3. Plant available soil nitrogen (μg·10 cm^{-2} burial length^{-1} of N). Samples were assayed from controls (white bars: non-mulched, black: mulched control), and mulch material (red: wheat straw, green: wood shred, blue: wood strand)-x-application rate [hatched: Burned Area Emergency Response (BAER) standard, solid: 150% of BAER standard] treatments in 2012, two periods in 2013, and full growing seasons of 2014 through 2016. Mulches were applied in July 2012. Analyses were run for each year individually due to different lengths of probe deployment. Letters over bars indicate significant effects of mulch material after Tukey adjustment was applied to *post hoc* pairwise comparisons; bars with lowercase letters in common do not differ. Plus (+) over a mulched control bar indicates it differed significantly from non-mulched control. Asterisk (*) indicates significant difference between non-mulched control and material × rate treatments in a given year and caret (ˆ) indicates a significant difference from the mulched control as determined by 1-way analyses using the Dunnett multiple comparison adjustment. Data are presented on the original scale, statistical analyses were conducted on natural-log + 1 transformed data. Error bars represent ± 1 standard error. n.s. = no statistical difference among treatments for a given time period. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

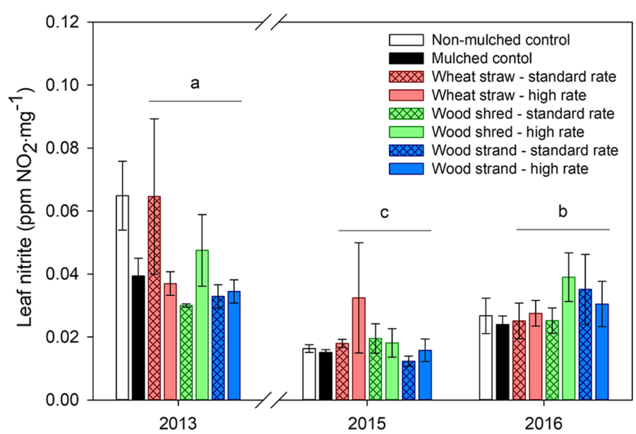

Fig. 4. Average ± standard error showy goldeneye (*Heliomeris multiflora*) nitrite concentration (parts per million per mg of leaf tissue of nitrite, ppm·mg^{-1} of NO_2) as determined by leaf nitrate reductase assay (NRA). Mulch treatments were applied in July 2012. Notation as described for Fig. 3. Data presented on the original scale, statistical analyses were conducted on natural log + 0.01 transformed data. Error bars represent ± 1 standard error.

relationships were not consistently significant over time (Fig. 5A, asterisks; Supplement B6). None of the material × rate treatments differed from non-mulched control in total plant cover, and total plant cover was not affected by mulch material or rate treatments as main effects or as the material × rate interaction (Fig. 5B). Non-native plants, while not abundant by the end of this study (6.7 ± 1.1% experiment-wide cover in 2016), were generally increasing in cover at the site (Fig. 5C; Table 2C). In 2014 and 2015, wheat straw treatments had significantly higher non-native plant cover than wood shred treatments (Fig. 5C). Wheat straw mulch treatments also had higher non-native species cover than non-mulched controls in 2014–2016 (Fig. 5C, asterisks) and mulched control in 2015 (Fig. 5C, carets). The mulched control had significantly higher non-native plant cover than non-mulched control in 2016.

Plant communities changed significantly each of the first 4 years following the HPF (Fig. 6A; Supplement B6). Over these 4 years, communities in non-mulched controls differed significantly from all three plant-based mulches. However, this pattern was largely driven by patterns in 2013 and 2014 when non-mulched controls differed significantly from all other treatments (Fig. 6A, lowercase letters); there were no significant differences among communities in 2015 or 2016. Decreases in cover of mulch (r^2 = 0.55, p = 0.0001), charcoal (r^2 = 0.21, p = 0.0001) and downed wood (r^2 = 0.11, p = 0.0003), as well as decrease in soil NO_3-N (r^2 = 0.36, p = 0.0001) were most strongly associated with annual shifts in plant composition (Fig. 6A).

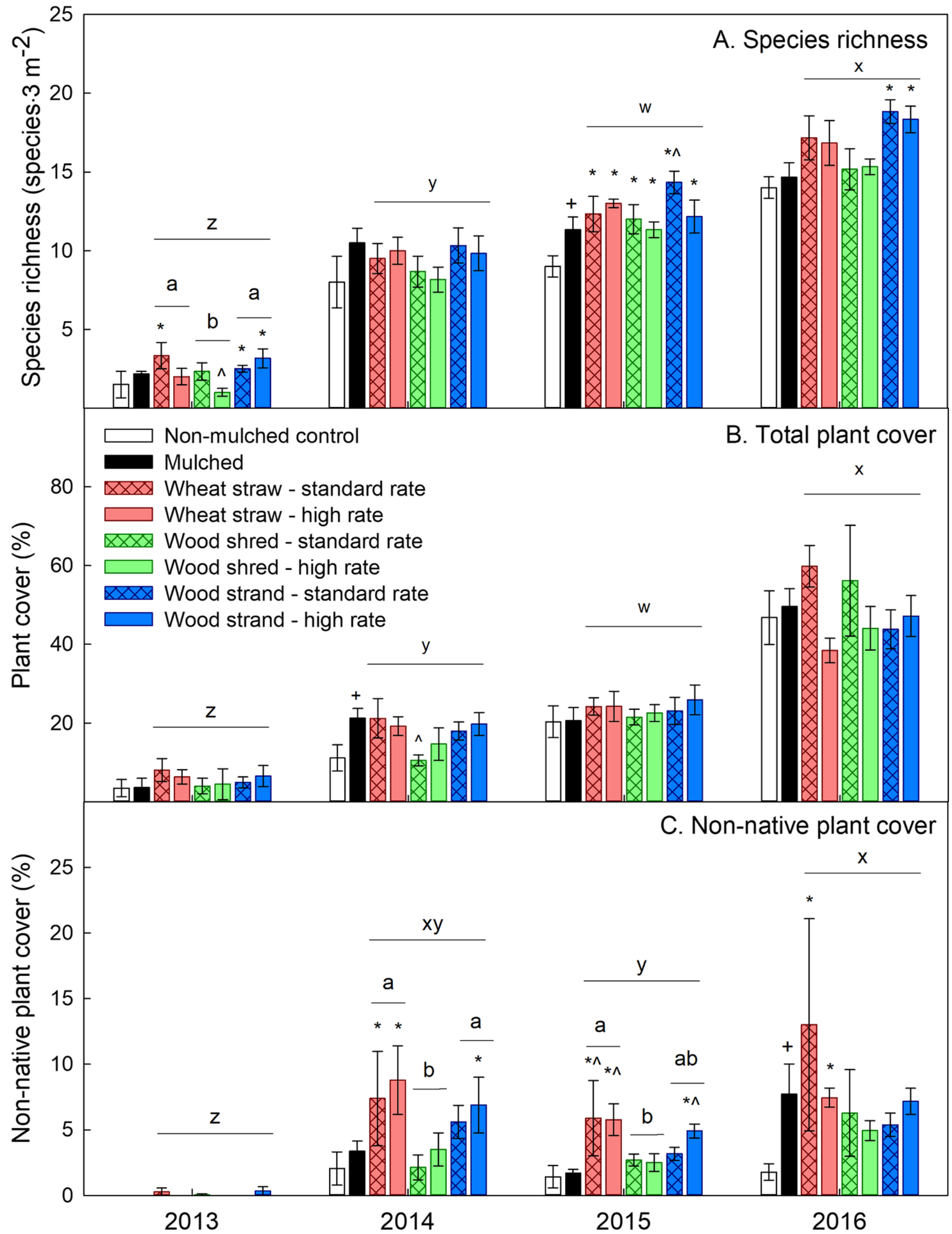

Fig. 5. Average ± standard error (A) plant species richness (number of species per three 2- × 0.5-m^2 frames per plot) and percent cover of (B) all plant species and (C) non-native species from one- to four-years postfire in all treatments. Mulches were applied in July 2012. Notation as described for Fig. 3. Data presented on the original scale, statistical analyses were conducted on natural log + 1 (species richness) or square-root (total and non-native cover) transformed data. Error bars represent ± 1 standard error.

Indicator species analysis did not find species or species groups associated with any particular mulch treatment in any year, except willowherb (*Epilobium* spp.) being indicative of wood strand treatments in 2013 (Table 3A). Prickly lettuce (*Lactuca serriola*) was characteristic of plant communities in 2014, and the co-occurrence of tall annual willowherb (*Epilobium brachycarpum*) and goldenrod (*Solidago* spp.) was characteristic of plant communities in 2016 (Table 3A).

Using only plots for which July soil moisture and temperature at 5-cm depth were available (partial 2014 and 2016 datasets), year had the only significant effect on plant community dynamics (Fig. 6B; Supplement B6). Higher soil NO_3-N (r^2 = 0.62, p = 0.0001) and soil moisture (r^2 = 0.51, p = 0.0001) were associated with communities in 2014, while increased minimum soil temperature (r^2 = 0.67, p = 0.0001) was correlated with the shift in composition by 2016. The co-occurrence of wheat (*Triticum* spp.) and Canadian horseweed (*Conyza canadensis*) was a strong indicator of wheat straw plots, while the co-occurrence of common yarrow (*Achillea millefolium*), western pearly everlasting (*Anaphalis margaritacea*), and streamside fleabane (*Erigeron glabellus*) was associated with mulched controls (Table 3B) in 2014. By 2016, mulched controls were characterized by the co-occurrence of yarrow, cheatgrass (*Bromus tectorum*), and thistle (*Cirsium* spp.). Non-mulched controls at this time were associated with yarrow when co-occurring with tall annual willowherb, sulphur-flower buckwheat (*Eriogonum umbellatum*), and prickly lettuce (Table 3B). Across all treatments, prickly lettuce was characteristic of plant communities in 2014, while the co-occurrence of showy goldeneye and goldenrod were characteristic of 2016 (Table 3B).

3.5. Lodgepole pine seedling density

Lodgepole pine seedling density was 20–42 times higher in mulched control than in non-mulched control each year (Fig. 7, plus signs; Supplement B7). Density was also higher in both wood shred (34–66

Table 2
Statistical results for 3-way factorial analysis of (A) plant species richness, (B) percent cover of all plant species, (C) percent cover of non-native species, and (D) pine seedling density over the first four years of post-fire recovery in all mulch material × rate treatments (excluding mulched and non-mulched controls). Data were natural log + 1 (species richness and seedling density) or square-root (total and non-native plant cover) transformed to meet assumptions of normality and the Kenward-Roger denominator degrees of freedom (DDF) method was used to adjust for heterogenous variance which can result in fractional denominator degrees of freedom. NDF = numerator degrees of freedom.

Response	Effect	NDF	DDF	F-value	p-value
(A) Species richness	Year	3	76.97	403.26	< 0.0001
	Mulch	2	32.21	10.54	0.0003
	Year * Mulch	6	81.79	1.17	0.33
	Rate	1	32.21	3.37	0.08
	Year * Rate	3	76.97	2.04	0.11
	Mulch * Rate	2	32.21	0.7	0.50
	Year * Mulch * Rate	6	81.79	2.01	0.07
(B) Total plant cover	Year	3	79.18	145.6	< 0.0001
	Mulch	2	24.04	2.32	0.12
	Year * Mulch	6	82.18	1.09	0.38
	Rate	1	24.04	0.33	0.57
	Year * Rate	3	79.18	1.67	0.18
	Mulch * Rate	2	24.04	0.88	0.43
	Year * Mulch * Rate	6	82.18	0.61	0.72
(C) Non-native plant cover	Year	3	84.39	102.14	< 0.0001
	Mulch	2	30.07	6.12	0.01
	Year * Mulch	6	87.53	1.83	0.10
	Rate	1	30.07	0.8	0.38
	Year * Rate	3	84.39	0.63	0.60
	Mulch * Rate	2	30.07	0.42	0.66
	Year * Mulch * Rate	6	87.53	0.37	0.90
(D) Pine seedling density	Year	3	88.87	15.19	< 0.0001
	Mulch	2	29.39	23.57	< 0.0001
	Year * Mulch	6	90.16	1.09	0.38
	Rate	1	29.39	6.39	0.02
	Year * Rate	3	88.87	0.8	0.50
	Mulch * Rate	2	29.39	0.76	0.48
	Year * Mulch * Rate	6	90.16	0.56	0.76

times) and wood strand (16–52 times) mulch treatments than in non-mulched control (Fig. 7 asterisks; Table 2D). In both 2014 and 2016, wheat straw treatments had significantly lower pine seedling density than the mulched control (Fig. 7, carets). High-rate mulch treatments had nearly double the pine density compared to standard rate treatments over the first four years following the fire (Fig. 7).

4. Discussion

Plant diversity and cover varied much more with time since fire than with differences in post-fire mulch material or rate, but our results suggest that mulch treatments could influence longer-term ecosystem recovery if patterns in non-native understory plant cover and tree seedling density persist over time. The aim of our study was not only to identify how mulch application affects post-fire plant community development, but to also examine potential soil processes driving responses. By including a mulched control composed of a synthetic substance (coarsely-ground rubber) to alter the soil physical environment similarly to plant-based mulches without adding substrate to fuel microbially-mediated nitrogen transformations, this study provides a unique opportunity to evaluate the relative roles of soil physical and substrate-induced changes as mechanisms driving ecosystem recovery (Gómez-Rey and González-Prieto, 2014).

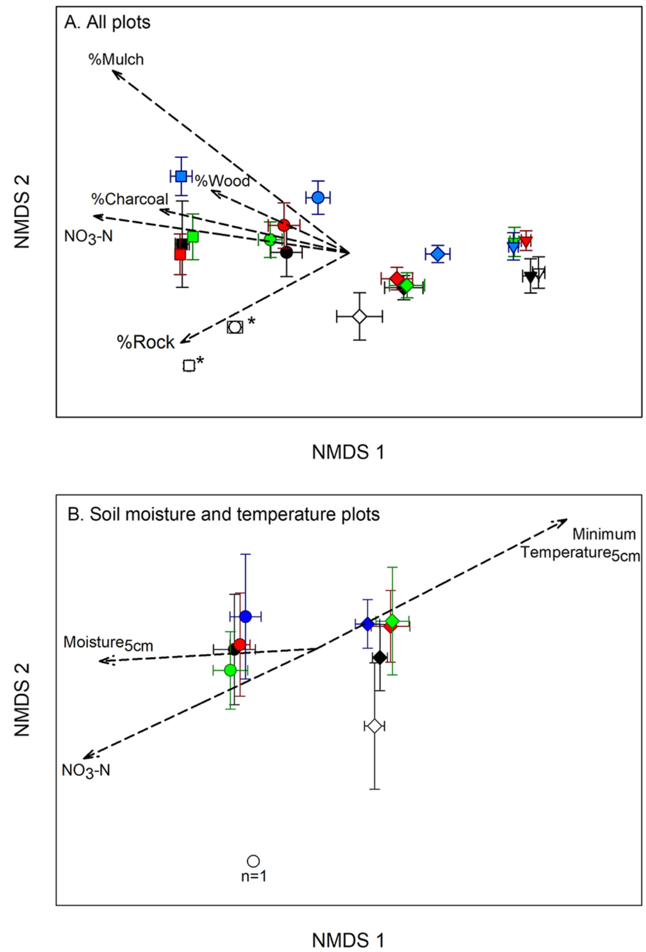

Fig. 6. Average (± SE) non-metric multidimensional scaling axes scores for understory plant communities associated with mulch material in each year for (A) all plots and (B) only plots for which July 5-cm depth soil moisture ($Moisture_{5cm}$) and maximum and minimum (Minimum $Temperature_{5cm}$) temperature were available. Colors indicate treatment: white = non-mulched control, black = mulched control, red = wheat straw, green = wood shred, and blue = wood strand. Symbols indicate year: square = 2013, circle = 2014, triangle = 2015, diamond = 2016. Vectors represent significant continuous environmental variables at α = 0.05; length of the line represents the strength and direction of correlation. Control plot SE bars were smaller than the marker in 2013 (panel A), and absent for 2014 in panel B due soil data available for only 1 control plot. NO_3-N = soil nitrogen available as nitrate. In panel A, asterisks indicate significant difference between control plots and all other treatments sampled in a given year. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

4.1. Understory plant communities

Change over time was the prevailing pattern in understory plant community development as has been shown following wildfire in other pure or mixed conifer forests (Lentile et al., 2007; Robichaud et al., 2013c). We found annual increases in both species richness and understory plant cover such that total plant cover across all treatments and controls was 48 ± 0% by 2016. This is similar to understory cover reported for the fourth year of recovery following the 1988 wildfires in lodgepole pine forests of Yellowstone National Park (Turner et al., 1999). Showy goldeneye was the only species seeded in this experiment, being seeded in a small corner of each plot in order to test plant N_i uptake. This species did well over time regardless of treatment and was a key component of plant communities in 2016 based on the indicator species analysis that included soil abiotic conditions (Table 2B).

Table 3
Indicator species or groups as identified by Indicator Species Analysis for each year or year-x-mulch material combination using data from (A) all plots, and (B) only plots for which July 5-cm soil depth temperature and moisture data were available. Significance was identified when the lower 95% bootstrap confidence limits (LCL_A) for the positive predictor score (A_P) ≥ 0.60, sensitivity (B) ≥ 0.25, and Indicator Value (IV) ≥ 0.50. Indicator species groups were limited to ≤ 4 species. Species ordered alphabetically within groupings. In A, mulch material × year grouping significant only for 2013 wood strands. n.s. = not significant.

Year	Mulch material	Indicator	A	LCL_A	B	IV
(A) All plots						
2013	Non-mulched control	n.s.	n.s.	n.s.	n.s.	n.s.
	Wood strand	Willowherb	0.95	0.79	0.67	0.63
	Wood shred	n.s.	n.s.	n.s.	n.s.	n.s.
	Wheat straw	n.s.	n.s.	n.s.	n.s.	n.s.
	Mulched control	n.s.	n.s.	n.s.	n.s.	n.s.
2013	–	n.s.	n.s.	n.s.	n.s.	n.s.
2014	–	Prickly lettuce	0.98	0.94	0.88	0.78
2015	–	n.s.	n.s.	n.s.	n.s.	n.s.
2016	–	Tall annual willowherb + goldenrod	1	1	0.85	0.75
(B) Plots with soil moisture and temperature recorded						
2014	Non-mulched control[a]	n/a	n/a	n/a	n/a	n/a
	Wood strand	n.s.	n.s.	n.s.	n.s.	n.s.
	Wood shred	n.s.	n.s.	n.s.	n.s.	n.s.
	Wheat straw	Wheat + Canadian horseweed	1	1	1	1
	Mulched control	Common yarrow + streamside fleabane + western pearly everlasting	1	1	0.67	0.67
2016	Non-mulched control	Common yarrow + streamside fleabane + sulphur-flower buckwheat + prickly lettuce	1	1	0.67	0.67
	Wood strand	n.s.	n.s.	n.s.	n.s.	n.s.
	Wood shred	n.s.	n.s.	n.s.	n.s.	n.s.
	Wheat straw	Fringed sage + tall annual willowherb + silverleaf phacelia	1	1	0.50	0.50
	Mulched control	Common yarrow + cheatgrass + thistle	1	1	0.67	0.67
2014	–	Prickly lettuce	0.96	0.86	1	0.96
2016	–	Showy goldeneye + goldenrod	1	1	1	1

[a] Not analyzed (n/a): n = 1 control plot with soil moisture and temperature data in 2014.

We saw shifts in plant community composition that were generally associated with decreases in mulch and charcoal cover, and NO_3-N availability over the first four years of recovery (Fig. 6A). That both nitrate and charcoal cover were significant explanatory variables in our ordination is interesting given the finding of DeLuca et al. (2006) that charcoal residue left after wildfire can stimulate net nitrification. Though we were unable to test such a relationship since all of our plots were affected by the wildfire more or less uniformly, it may be possible that any short-term increases in immobilization due to mulch application could have been overridden by increased N_i cycling associated with charcoal deposition during the wildfire.

Plant responses were generally similar among mulched treatments. Total plant cover did not differ between non-mulched controls and mulched treatments, similar to the findings of Robichaud et al. (2013b) studying seven years of post-fire recovery in other western U.S. forests. Plant communities in non-mulched controls differed from all mulched treatments only in the first two years post fire (Fig. 6A). However, species richness tended to be lower in the non-mulched controls than some or all mulched treatments in most years. With few differences in plant responses to plant-based mulches versus mulched control, impacts of mulch application on plant recovery in this dry system are most likely due to altered soil moisture conditions.

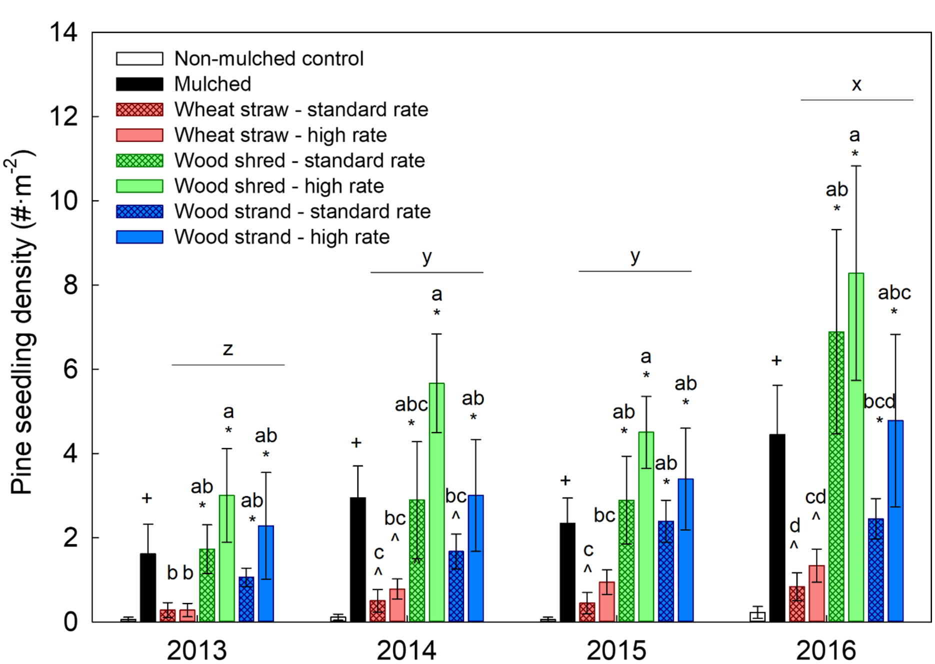

Fig. 7. Lodgepole pine (*Pinus contorta*) density (individuals·m^{-2}) from one- to four-years postfire in controls (white bars: non-mulched, black: mulched control), and mulch material (red: wheat straw, green: wood shred, blue: wood strand)-x-application rate [hatched: Burned Area Emergency Response (BAER) standard, solid: 150% of BAER standard] treatments. Mulches were applied in July 2012. Within a year, bars with lowercase letters a-d in common do not differ; lowercase letters x-z indicate statistical relationships among years. Otherwise, notation as described for Fig. 3. Data presented on the original scale, statistical analyses were conducted on natural log + 1 transformed data. Error bars represent ± 1 standard error. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

The most notable plant response to mulching treatments was higher non-native species cover in wheat straw mulched compared to non-mulched control in most years, consistent with other studies (Dodson and Peterson, 2010; Robichaud et al., 2000). Wood mulches were not expected to act as vectors for non-native species (Foltz and Wagenbrenner, 2010; Robichaud et al., 2014). However, non-native species were present in the high-rate wood strand during the first growing season after fire and non-native cover being higher in this treatment than non-mulched control in the second and third post-fire years. Rather than being brought to the site by contaminated mulch, it is possible that some non-native plant species were present on the site prior to the HPF and conditions conducive to their establishment were provided by some mulch treatments. Prickly lettuce, a non-native annual species, was first recorded in 2014 when it was present in nearly all plots and particularly abundant in blocks 2 and 6 regardless of treatment. That these two blocks were far from each other suggests that patches of this species may have been present in these blocks prior to the fire. It is also possible that activities associated with establishing and monitoring the plots may have brought invasive propagules to the site. However, two annual non-native species on the Colorado noxious weeds list (Colorado Department of Agriculture, 2017), cheatgrass and common mullein (*Verbascum thapsus*), were first found in wheat straw plots. Cheatgrass was present exclusively in wheat straw plots for the first two years post fire, while mullein was not recorded until the third year. Both species were recorded in other treatments in subsequent years. It is interesting that indicator species analysis of the reduced dataset identified a species group including cheatgrass as indicative of mulched controls in 2016 even though cheatgrass was only recorded in a single mulched control plot in 2015 and in no mulched control plot before then. This suggests the synthetic mulch may be an effective trap for seeds, provide an ideal soil environment for cheatgrass germination and establishment once seeds arrive, or both. Whether or not these trends in non-native species will persist over time is unknown. In monitoring areas treated with mulch, Dodson and Peterson (2010) found non-native species in the first two years after the Tripod Fire in Washington. However, Bontrager et al. (2019) reported a very low incidence of non-native species when sampling similarly treated areas within the Tripod Fire nine years post fire. However, on a plot-by-plot basis, non-native species tended to increase in abundance each year once established on our plots, particularly cheatgrass for which we observed up to 30% increases from one year to the next.

4.2. Lodgepole pine seedling density

Wood mulch treatments and mulched control supported similar lodgepole seedling densities, which were higher than in non-mulched control. Seedlings were also more abundant in the high-rate wood shred treatment than straw mulch treatments (both rates) in all years. Annual rates of lodgepole pine seedling establishment typically peak in the first 10 years after fire, with recruitment patterns in the first few years indicative of longer term trends (Harvey et al., 2016; Stevens-Rumann et al., 2018; Turner et al., 1999). In our study, these patterns began to emerge after one year becoming most pronounced in the fourth year after the fire (final year of this study). Mulched control and wood shred treatments had 2–3 times higher average seedling densities than reported by Turner et al. (1999) for areas affected by crown fire or severe surface fire during the first four years of recovery after the 1988 Yellowstone Fires. Although Wright and Rocca (2017) reported average two-year post-fire lodgepole seedling densities (~100 seedlings·m^2) in portions of the HPF with the most favorable environmental conditions vastly higher than the best performing treatment in our experiment at that time, they also reported that sites affected by high-severity fire and largely void of a seed source, similar to the post-fire conditions of our experimental site, had average lodgepole seedling densities of only 1.9 seedlings·m^2. In our experiment, seedling densities in non-mulched control and wheat-mulched plots were 60–90% lower than Wright and Rocca (2017) reported for similar sites, while seedling densities in mulched control and most wood-mulched plots were 47–200% higher in 2014.

Wheat straw had lower lodgepole pine seedling densities than most wood mulch treatments and the mulched control throughout our experiment. Wheat straw also consistently had the lowest mulch cover remaining of all the treatments, near or below 25% by 2015, while wood mulches remained around 50% ground cover through 2016, similar to patterns shown in other studies (Robichaud et al., 2013c; Valenzuela-Solano and Crohn, 2006; Wagenbrenner et al., 2006). Elsewhere in the area affected by the HPF, lodgepole pine seedling density increased where some tree canopies remained to serve as a seed source and wheat straw mulch cover was > 40% (Wright and Rocca, 2017). Similarly, Dodson and Peterson (2010) found a higher probability of lodgepole seedling establishment in north-central Washington State when mulch cover was > 25%. Thus, reduced seedling density with wheat straw mulch may be a product of its lower persistence and protection over time.

Effects on abiotic conditions, rather than microbially-mediated N dynamics, were likely driving lodgepole regeneration at this site, given that seedling densities in wood mulches differed from non-mulched control but not mulched control. Romme et al. (2009) found that post-fire regeneration was not N limited in a northern Wyoming lodgepole stand, likely because this tree species is adapted to low N soils. Soil temperature was similar across all treatments and controls throughout the study being within or just below the range considered optimal for lodgepole pine regeneration (Petrie et al., 2016). Mulch also did not influence daily temperature range in our study; although others have reported temperature dampening effects of mulch, application rates in those studies were higher than used here (Cirelli et al., 2016; Santana et al., 2014). Lodgepole establishment is known to be sensitive to soil moisture (Lotan et al., 1985; Petrie et al., 2016). Monthly soil moisture trends were highly variable and our ability to detect change was poor (power < 0.20 in many cases), but we observed non-significant trends toward higher soil moisture and lower daily fluctuations in moisture at 5-cm soil depth under mulched control and wood mulch treatments, particularly over the first year of recovery (Fig. 1B, C). Likewise, Cirelli et al. (2016) also reported increased soil moisture associated with mulch application. This suggests that increased soil moisture may have been key to supporting lodgepole seedling regeneration in wood mulch treatments.

We cannot separate all the possible influences on seedling regeneration from each other. Canopy seed source was found to be a critical driver of lodgepole pine seedling densities in the HPF (Wright and Rocca, 2017). Due to the small size of our study site and near complete consumption of tree crowns, canopy seed source was assumed to be uniform throughout all blocks and treatments. However, retention of fallen seed on the soil surface may have been increased by the wood mulch treatments. Aerial mulching in other parts of the HPF were shown to reduce sediment loss and erosion (Schmeer et al., 2018). Two significant rain events in 2012 and 2013 (Fig. 1A) led to noticeable soil erosion at our site, especially in non-mulched controls, so it is possible that the lack of lodgepole regeneration in non-mulched controls was due to seed loss via erosion. However, erosion of seed would not explain the lower seedling counts in wheat straw, which had high initial mulch cover and lack of noticeable erosion (E. Berryman, personal observation). Future studies on tree seedling and plant regeneration, that consider both small-scale soil processes and hillslope- or watershed-scale impacts on ecosystem recovery, are needed.

4.3. Soil nitrogen

Our results do not support concerns that post-fire mulch application leads to strong initial soil N_i limitation, at least not at this site. Similarly, Cirelli et al. (2016) found chipped lodgepole slash mulch did not significantly alter total N_i when applied as part of a lodgepole reestablishment project on barren 1- to 2-year-old natural gas well-pads in Canada. Among plant-based mulches tested, we expected wheat straw would be the most likely to exhibit short-term N immobilization. Because wheat straw has lower concentrations of recalcitrant carbon compounds than wood, it can be decomposed faster and thus more quickly increase microbial demand for N (Bollen and Lu, 2010; Melillo et al., 1983; Reinertsen et al., 1984). In the first two months after the fire, soil N_i, driven by NO_3, was significantly lower in the high-rate wheat straw treatment than either of the controls which suggests there was some degree of N immobilization. This response in soil N_i was transient and not observed in subsequent years. Rather, in both early and late growing season periods in 2013, wood strand mulch seems to have stimulated N mineralization compared to wheat straw and wood shred mulches, although there were no differences between wood strand treatments versus controls. As with the wheat straw effects on soil N, this was a short-term response that was not detected after the first growing season after fire. Although measures were taken to avoid incubating the probes for too long when soil N cycling was expected to be most rapid, there is a possibility that N probes may have saturated during this time period. Thus, any other differences among treatments during the first 1–2 years post fire could have been obscured by N saturation. As has been widely shown by others (Fernández-Fernández et al., 2016; Giardina and Rhoades, 2001; Gómez-Rey and Gonzalez-Prieto, 2013), N_i was driven by changes in NO_3-N, which was highest during the first full growing season after fire (2013) and then decreased rapidly. We saw a similar trend in which average nitrogen uptake by showy goldeneye on a per tissue weight basis peaked in 2013, but was unaffected by mulch treatments. Because the nitrogen probes were incubated in the ground for months at a time, our estimates represent net inorganic soil nitrogen left after plant uptake at the end of the incubation rather than gross N_i produced (Huang and Schoenau, 2011). Therefore, the marked decrease over time may reflect increasing plant uptake of N_i as plant abundance increased over time, with potential mulch effects on microbially-driven nitrogen transformations being masked.

Although we showed that consequences of treatments are small, we need to understand whether these observations could be different over longer time spans or within different forest and soil types. Our experiment was conducted in a serotinous lodgepole population on the drier end of its range in North America. Sites having plants with different fire adaptations and regeneration strategies, deeper soil, increased/reduced precipitation or higher/lower decomposition rates may exhibit different soil responses to mulching. Given the increasing area of high-severity fires and potential for future increase in expense of post-fire rehabilitation efforts in coming decades, additional experiments should be conducted in other fire-prone forests to more widely inform managers about the potential for adverse effects of post-fire mulching on soil nitrogen.

5. Conclusions

In areas severely burned by large wildfire, managers are tasked with multiple, potentially competing, rehabilitation objectives, such as hillslope stabilization and forest restoration. Using our replicated, controlled field experiment in Colorado's High Park Fire, we found that mulches commonly applied for hillslope stabilization had few detrimental effects on vegetation recovery in a lodgepole pine forest after four years. Further, we found evidence of positive impacts of wood mulch on pine seedling density. With the strategic use of two types of controls, we showed that mulch did not consistently immobilize nitrogen in this system but tended to increase soil moisture. In addition to often having lower lodgepole tree seedling density than wood mulches, wheat straw mulch was less persistent and may have introduced non-native species to our study site, though non-native cover remained low. Application rate was less important than choice of mulch material, even at 150% of rates commonly applied for the purpose of reducing soil erosion potential. Results from this study indicate that, in addition to longer-term persistence, wood-based mulches (especially wood shreds) can enhance lodgepole pine seedling density while having few impacts on understory plant communities over the first four years of post-fire recovery.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.117567.

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