THESIS

IS THIN AND CHIP AN ECOLOGICALLY VIABLE FUELS REDUCTION OPTION?

INITIAL RESULTS IN BLACK HILLS PONDEROSA PINE FORESTS

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ABSTRACT

INITIAL RESULTS FOLLOWING THINNING AND CHIPPING PONDEROSA PINE

Across the dry western forests of the United States, accumulated hazard fuels increase the risk of catastrophic wildfires. Chipping or mastication of mechanically thinned fuels is becoming a common fuels reduction technique that aims to both reduce the risk of catastrophic fire and dispose of non-merchantable thinned material. We conducted an experiment to examine the ecological effects of thinning and chipping in ponderosa pine forests at two National Park Service locations in the Black Hills, South Dakota. By using an unthinned control and a thin-only treatment to compare to thin-chip treatment we were able to separate the effects of thinning from the effects of wood chip application. A greenhouse experiment was used to assess the effects of wood chip depth on seedling emergence and growth of several grass and forb species common to the study sites. Thin-only and thin-chip treatments greatly reduced hazard fuels by lowering pole tree density by 96%. Thinning did not elicit much of an understory response in the first year following treatment, while wood chip application caused slight decreases in understory plant richness and cover. Thin-chip plots had one-third lower graminoid cover than unthinned plots and half the number of annual species richness than thin-only plots. There was no difference in non-native species cover or richness, or in overall plant community composition as a result of treatments. Ponderosa pine germinated equally well in wood chips as in other areas. We observed a small decrease in NO_3^--N in thin-chip plots at one study site, but no effect at the other site. In the greenhouse, increasing wood chip depth created an increasing barrier to seedling emergence and growth in both grass and forbs. Complete suppression of plant emergence in the greenhouse occurred at wood chip depths ≥ 6 cm and plant biomass was undetectable at wood chip depths ≥ 3 cm. Our initial results suggest that thin-chip is a viable fuels treatment option. Although wood chip application slightly reduced some measures of understory cover and richness, the results we detected were subtle. Future examination will determine if delayed thinning effects reverse the slightly suppressive effects of wood chip application on understory vegetation.

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1. Introduction

Across the dry western forests of the United States, accumulated hazard fuels increase the risk of catastrophic wildfires. Wildfire risk is greatest in the wildland urban interface and in forests that have experienced fuel build-up due to fire suppression. Federal fire policy mandates the reduction of hazard fuels in the wildland urban interface (USDA/USDOI, 2009). Federal fire management agencies mechanically treated an annual average of 486,000 ha between 2004-08 (QFR, 2009), but managers can find it difficult to keep up with the ever increasing need for fuels reduction. Pile-burning is a common method of disposing of small diameter, non-merchantable thinned fuels. Pile creation often outpaces pile burning due to weather constraints and personnel needs, thus perpetuating the problem of fuels maintenance. Managers would benefit from alternative methods of hazard fuel disposal. Chipping or mastication of mechanically thinned fuels, collectively referred to as "mulching" (Battaglia *et al.*, 2010), is becoming a common fuels reduction technique utilized by managers in conifer ecosystems of the western U.S. (Miller and Seastedt, 2009; Owen *et al.*, 2009; Wolk and Rocca, 2009; Battaglia *et al.*, 2010).

Federal fire policy also mandates managing to achieve ecosystem sustainability, including managing for ecological components (USDA/USDOI, 2009). Although a handful of studies have examined the ecological effects of chipping and mastication, results defy generalization. Some concerns regarding the effects of thinning and mulching include a decrease in understory plant cover (Miller and Seastedt, 2009), invasion or expansion of non-native species (Perchemlides *et al.*, 2008; Owen *et al.*, 2009; Wolk and Rocca, 2009), exclusion of rare plant species (Miller and Seastedt, 2009), and altering of soil available N (Homyak *et al.*, 2008; Miller and Seastedt, 2009; Owen *et al.*, 2009).

We examined the ecological consequences of thinning and chipping ponderosa pine (*Pinus ponderosa*) in the southern Black Hills of South Dakota. Fire suppression and rapid natural regeneration have created overgrown forests dominated by small-diameter trees in some areas of the Black Hills (Brown *et al.*, 2008). Thinning ponderosa pine reduces wildfire risk and achieves restoration goals, but the problem of disposal of thinned material persists. This study will join a small number that have examined the understory effects of thin and mulch treatments with both unthinned and thin-only controls (Perchemlides *et al.*, 2008; Wolk and Rocca, 2009; Kane *et al.*, 2010), in order to tease apart the effects of thinning from the effects of mulch application. We randomly assigned treatments, thin-only (TH) and thin-chip (TC), plus an unthinned (UT) control at two sites to examine understory plant, soil nitrogen and ponderosa pine regeneration responses to thin and chip. In order to investigate the impact of wood chip depth on plant growth we conducted a greenhouse study to assess short term seedling emergence and growth of several grasses and forbs common to our study sites. Our research approach is described below by our research questions.

Does wood chip application increase or decrease understory plant cover? Are plant life forms (forb, shrub, graminoid) affected differently? When used in fuels reduction activities, mulch application follows forest thinning. Simultaneously opening the forest canopy and applying woody surface amendments may have opposing effects on understory vegetation cover. Mulch residue creates a beneficial microenvironment with increased moisture retention and moderated temperature (Gower *et al.*, 1992; Homyak *et al.*, 2008; Miller and Seastedt, 2009; Owen *et al.*, 2009). It may also create a physical barrier and reduce light to emerging plants similar to the effects of surface amendments (Facelli and Pickett, 1991; Teasdale and Mohler, 2000). Thinning ponderosa pine in the Black Hills increased total understory biomass (Wienk *et al.*, 2004). Several studies reported an increase in understory cover following thinning that was unchanged with the application of mulch material (Perchemlides *et al.*, 2008; Wolk and Rocca, 2009; Kane *et al.*, 2010). Another study in ponderosa pine noted a qualitative increase in understory cover following thinning , but reported a decrease in understory cover following mulch application (Miller and Seastedt, 2009). The majority of studies reported no change in the cover of plant functional groups in mulched compared to thin-only treatment. Two studies in ponderosa pine, however reported a decrease in graminoid cover following thin-chip treatment (Law and Kolb, 2007; Miller and Seastedt, 2009). The effects of thin- mulch on understory cover are unclear. We add to this small body of knowledge with an assessment of understory vegetation cover following thin-chip treatment compared to thin-only treatment and unthinned controls. The use of a thin-only treatment for comparison should allow us to tease apart the effects of thinning from those of mulch application. Resulting vegetation cover was additionally examined by life form (forb, shrub, graminoid). We hypothesized increased understory vegetation cover following thin-only treatment and decreased cover following thin-chip treatment. Thus we expect the largest change to be detected between the two thinning treatments.

Does thin-chip treatment change understory plant richness or composition? Are certain plant strategies favored or excluded? Thin and mulch studies have detected no change in plant diversity and richness (Perchemlides *et al.*, 2008; Wolk and Rocca, 2009) and a decrease in diversity and richness (Miller and Seastedt, 2009) following mulch treatment. Several studies reported a change in plant community composition following forest thin and mulch (Perchemlides *et al.*, 2008; Owen *et al.*, 2009; Wolk and Rocca, 2009), although one study reported no change in composition following treatment (Kane *et al.*, 2010). Wolk and Rocca (2009) observed an increase in rhizomatous species richness and Miller and Seastedt (2009) provided evidence that locally rare plants were excluded from areas treated with wood chips. We examined the effect of thin-chip and thin-only treatments on understory plant richness and composition. Richness is reported by life form (forb, shrub, graminoid) and plant strategy (annual species). We hypothesized lower understory plant richness in thin-chip plots and greater richness in thin-only plots. We did not expect a change in plant community composition one year following treatment.

Do thin-only or thin-chip treatments increase or decrease non-native plants? Do effects differ between treatments? Treatment effects on non-native plants may be confounded by the effect of thinning versus the effect of wood chip application. Thinning may increase light, precipitation or nutrient availability to the forest floor and create opportunities for non-native plant introduction or expansion. Wood chip application may create a physical barrier to non-native plant introduction or expansion and thus reverse the effect of thinning. Additionally, the use of machinery may facilitate non-native plants either by introducing a seed source or causing additional disturbance. Several thin-mulch studies reported an increase in non-native species compared to unthinned controls (Collins *et al.*, 2007; Perchemlides *et al.*, 2008; Owen *et al.*, 2009; Kane *et al.*, 2010), while several reported a decrease or no change in non-native species compared to thin-only treatment (Perchemlides *et al.*, 2008; Miller and Seastedt, 2009; Wolk and Rocca, 2009; Kane *et al.*, 2010). Such results provide evidence that thinning treatments increased non-native plants, while in some cases, mulch residue suppressed non-native plants. We identified all understory species in sampling plots which allowed us to detect non-native species introductions. Additionally, cover estimates included an estimate of non-native plant cover to detect any relative expansion of non-natives between treatments. Because non-natives, while present, were not prevalent at either study location, we did not anticipate an increase in non-native species one year post-treatment.

Does wood chip depth affect understory plant cover? Is there a threshold above which plant growth is suppressed? Woody debris and litter cover was negatively correlated with forb and shrub cover following mastication in ponderosa pine (Kane *et al.*, 2010). Following thin-chip treatment in ponderosa pine, increasing litter + wood chips was correlated with decreasing understory vegetation cover and total understory suppression at 8.4-11-cm depth (Wolk and

Rocca, 2009). In order to examine wood chip depth on plant growth we conducted a greenhouse study to assess short-term seedling emergence and growth of several grass and forb species common to our study sites. We hypothesized no effect on growth at shallow wood chip depth, with increasingly negative effects as wood chip depth increased. We anticipated complete suppression of plant emergence and growth at the deepest wood chip depths.

Does wood chip application increase or decrease inorganic nitrogen (N) availability? Application of wood chips or masticated residue is essentially an application of a low quality organic residue, i.e. high C:N ratio, high lignin content and high biological recalcitrance. Theoretically, introduction of high C:N material results in net N immobilization. Reported results regarding the effects of mulch residue on nitrogen availability are inconclusive. Many studies detected a decrease in soil available nitrogen with the application of wood chips or masticated residue (Holtz *et al.*, 2004; Homyak *et al.*, 2008), although several reported an increase (Tahboub *et al.*, 2007; Miller and Seastedt, 2009; Owen *et al.*, 2009). Change in inorganic nitrogen occurred either following a heavy application of wood chips or as a latent result, occurring two to three years following treatment. Gower et al (1992) also reported a decrease in inorganic nitrogen in the forest floor, but no change in mineral soil following wood chip application. We examined the effect of thin-chip, thin-only and unthinned treatments on soil nitrogen availability. We did not anticipate detecting change in soil available nitrogen in the first year post-treatment.

Does wood chip application affect ponderosa pine regeneration? Prolific regeneration of ponderosa pine in the Black Hills perpetuates the problem of hazard fuels. Optimal temperature and precipitation conditions for establishment and growth of ponderosa pine trees are often met and seed crops are regularly abundant resulting in seedling densities ≥ 1,000 stems ha^{-1} (Shepperd and Battaglia, 2002). Within 10-20 years following disturbance, seedling and pole trees contribute to ladder fuels and increase fire risk (Battaglia *et al.*, 2008). Very few studies have examined the effects of mulch residue on tree regeneration (Miller and Seastedt, 2009; Wolk and

Rocca, 2009). Because mulch residue has in some cases suppressed growth, we hypothesized that ponderosa pine regeneration might be inhibited by wood chip application.

2. Methods

2.1. Study area

The Black Hills is an isolated mountain range located in southwestern South Dakota and extending into northeastern Wyoming. The roughly 1.5-million-ha area is comprised of four distinct geomorphologic features that collectively rise 305-1219 m above the surrounding northern Great Plains prairie. Elevation ranges from 1006 m in the rolling Red Valley that encircles the Black Hills, to 2164 m in the western Limestone Plateau of the central Black Hills (Shepperd and Battaglia, 2002). The Black Hills region is named for its forest cover and ponderosa pine is the dominant tree species in the region. There is a strong precipitation pattern present in the Black Hills, with a general increase in precipitation at northern latitudes and in higher elevations. Average annual precipitation increases from 41 cm in the south, to 74 cm in the north (Driscoll *et al.*, 2002). Geology, climate, and topography interact to influence forest distribution and growth throughout the Black Hills.

Intensive Euro-American settlement began in 1874 in the central and northern Black Hills. Heavy timber harvest began at the time of settlement and continues to present day (Shepperd and Battaglia, 2002; Brown, 2006). Fire suppression, timber harvest, and grazing have resulted in more dense forests and less variability in forest structure (Brown, 2006). Numerous fire scars throughout the central and southern Black Hills, indicate a pre-settlement surface fire regime, but less frequent and more variable than that reported in Southwest ponderosa pine forests (Brown, 2006).

This study was conducted at two National Park Service locations in the Black Hills: Mount Rushmore National Memorial and Wind Cave National Park. Mt. Rushmore is located in the central and heavily forested region of the Black Hills, while Wind Cave is located in the ponderosa pine – mixed grass prairie ecotone in the southern Black Hills. Our study area at Wind Cave was located in the region of the park that is mostly forested with occasional grassy openings. Ponderosa pine dominates at both locations and 99% of sampled trees were ponderosa pine. Bur oak (*Quercus macrocarpa*) and paper birch (*Betula papyrifera*) were the only other tree species recorded in research plots.

Wind Cave had greater seedling density, litter cover and litter depth than Mt. Rushmore ($p = 0.033$, $p = 0.0004$ and $p = 0.002$, respectively, Table 1). Both seedling and pole densities were highly variable at each site (Table 1) and seedlings and poles were often found in clumped patches of dense regeneration.

2.2. Treatments and experimental design

Experimental units and permanent sampling plots were established in 2008, one year prior to treatment. Fire managers identified a 48-ha area at Mt. Rushmore and a 24-ha area at Wind Cave in need of hazard fuels thinning. Operational-scale treatment units [1.7-4.3 (average 2.7) ha] were delineated within these areas. Twelve and nine treatment units were designated at Mt. Rushmore and Wind Cave respectively (Fig. 1). Treatment units at both sites were located on all aspects. Slopes ranged from flat to 50%, but were generally moderate. Areas with rocky outcrops that were impossible for the tracked chipper to access were excluded from treatment units.

The two fuels reduction treatments, thin-only and thin-chip, plus an unthinned control were randomly assigned to experimental units at each of the two sites (Fig. 1). Treatments were replicated at the unit level four times at Mt. Rushmore and three times at Wind Cave. Thin and chip operations were completed in 2009 from April to July. In thin-only and thin-chip experimental units, all trees ≤ 15-cm dbh were hand felled with a chainsaw. In thin-only units, removed biomass was hand-piled for subsequent pile burns when conditions permitted. Because we were interested in studying thin-only treatment effects, all piles were placed at least 2 m outside any research plot. In thin-chip units, thinned biomass was processed through a chipper and resultant wood chips were left on site.

Chipping was conducted with a remotely-operated, tracked chipper produced by Bandit Industries, Inc®. The swivel head and mobility of this particular machine allowed the operator some control of wood chip distribution on the forest floor. In fact, wood chip distribution visually appeared more evenly distributed than we had expected (Fig. 2A). Wood chips were generally small, thin and relatively uniform in size (Fig.2B).

Multiple plots were randomly placed within each treatment unit in order to average sampling data and better represent each unit. With this experimental framework, unit provided the level of replication, and sampling was conducted at the plot level. Sampling plots were placed no less than 20 m from treatment unit boundaries to minimize edge effects. Three plots were placed in each of 12 units at Mt. Rushmore and two plots were placed in each of nine units at Wind Cave. In total 54 plots were placed within 18 treatment units across two sites.

2.3. Sampling methods

Sampling plots were comprised of a 30-m belt transect of variable widths. All overstory trees (trees < 15 cm dbh) were measured and identified to species in a 10-m-wide belt. Pole-size trees (trees ≤ 15-cm dbh and > 1.37-m tall) and seedlings (< 1.37-m tall) were tallied by species and status in 4-m- and 2-m- wide belts, respectively. Ponderosa pine germinants were also tallied within 1-m^2 quadrats, as described below.

Plant species richness, understory cover and ground cover were estimated for each plot. A species search was conducted in a 4 m-wide belt along the 30-m center transect to obtain plot richness for an area 120 m^2 in size. We identified 223 vascular species across both sites. Ten 1-

m^2 quadrats were spaced along the 30-m centerline. Within each $1m^2$, all vascular species were identified and ocular estimates of cover were made for the life form categories shrub, forb and graminoid, and for total non-native species. Total understory cover was estimated by adding shrub, forb and graminoid estimates. Ocular estimates of ground cover (bare ground, rock, litter and wood chips) were also made in each $1\text{-}m^2$ quadrat.

Two measurements of litter and duff depth were made at standardized locations within each $1m^2$. Litter was defined as fresh and partially decomposed organic matter, while duff was defined as the decomposed or partly decomposed organic matter layer located between litter and mineral soil. Wood chip depths were included in total litter depths as it was sometimes difficult to make a clear distinction between wood chip and litter layers. Some mixing occurred during treatment operations and by one year post-treatment, fresh litter had fallen over the wood chips in many places.

2.4. Soil nitrogen availability

We sampled plant available nitrogen using ion-exchange resin bags (Binkley and Matson, 1983). Resin bags were made by filling nylon stocking material with one tablespoon (approximately 10 g) each of cation and anion exchange resin beads (Sybron C-249 Cation and ASB-1P Anion Exchange Resins). Assembled resin bags were stored in a refrigerator and transported in coolers until placed in the field for incubation.

Resin bags were incubated during summer growing seasons (mid-June to mid-August, 53-57 days) in each of three years: the summer prior to treatment (2008), the summer of treatment implementation (2009) and the summer following treatment (2010). In addition, resin bags were incubated for one winter/spring season immediately following treatment, from August 2009 to June 2010 (309 days). Two resin bags were installed in each plot in summer seasons 2008 and 2009 and winter season 2009-10. For the summer season of 2010, an additional two resin bags were placed in each plot in an effort to reduce sampling variation and minimize the impact of any missing bags. Resin bag incubation locations remained the same throughout the study. Resin bags were buried approximately 5 cm in mineral soil by inserting a trowel into mineral soil at a shallow angle, positioning the resin bag at the far end and flattening the resin bag before removing the trowel. Burial depth from the surface varied with depth of the forest floor. Brightly colored nylon string was tied to each resin bag and affixed to a pin flag to ease retrieval of bags at the end of each incubation period. A small number of samples went missing each season, most likely due to curious or hungry animals. At the time of collection, resin bags were placed in separate plastic bags and stored in coolers during transport and in a refrigerator until laboratory analysis.

Inorganic nitrogen was extracted from resin beads with 100 ml of 2M potassium chloride (KCl). KCl extracts were filtered and frozen until analysis. Extracts were analyzed for ammonium (NH_4^+-N) and nitrate (NO_3^--N) concentrations with a Lachat QuickChem FIA+ 8000 series.

2.5. Greenhouse experiment

In order to directly examine the effects of wood chip depth on plant growth we conducted a greenhouse study. We assessed short term seedling emergence and growth of several grasses and forbs common to our study sites from under five wood chip depths: 0, 3, 6, 9 and 12 cm. Seeds of four perennial grasses: western wheat (*Pascopyrum smithii*), green needle (*Nassella viridula*), blue gramma (*Bouteloua gracilis*) and little bluestem (*Schizachyrium scoparium*); and two perennial forbs: blacksamson echinacea (*Echinacea angustifolia*) and wild bergamont (*Monarda fistulosa*) were commercially obtained and grown in 0.12-m^2 greenhouse trays. Thirty seeds of each species were hand scattered over a planting media of 1:1, sand: general purpose potting mix (Farfard © 4P mix). A handful of sand was sprinkled over sown seeds and handpressed to keep seeds in place. Five replicates of wood chips depths were randomly assigned to greenhouse trays and placed in each tray over sown seeds. Plants were allowed to grow for 10 weeks. After 10 weeks, plants were identified and clipped at the root-shoot interface. Plants were bundled by species, oven-dried and weighed. For each species, total dry biomass weight was divided by the number of individuals to obtain average biomass per individual plant.

2.6. Data analyses

A mixed model ANOVA was used to test for pre- and post- treatment differences at each site for tree densities (seedlings and poles), overstory BA, litter depth and ground cover (litter, bare ground and wood chip cover). Site and treatment were treated as fixed variables, while unit (nested within site-by-treatment) was treated as a random variable. Statistical tests were executed with Proc Mixed in SAS v9.2 (© 2002-2008, SAS Institute Inc.).

A similar mixed model ANOVA was used to test for treatment differences across both locations for plant species richness, understory cover, ground cover, ponderosa pine regeneration and inorganic nitrogen variables. All comprehensive variables, e.g. total understory cover and richness, were tested for treatment differences prior to treatment and none were found. Vegetation data were examined to detect treatment differences in vegetation response one year post-treatment. Pre-treatment variables found significant in the statistical model ($p < 0.05$), were used as covariates to adjust post-treatment data for differences that existed before treatments were applied. Pre-treatment covariates were used for all vegetation and ground cover analyses. Because they were not significant, pre-treatment covariates were not used in ponderosa pine regeneration or nitrogen analyses. All mixed-model ANOVAs used for analysis had 15 degrees of freedom and we report model-based pooled standard errors. Vegetation cover, 1-m^2 richness and ponderosa pine germinant data were square root transformed to meet the assumptions of standard regression. Where the main treatment effects were significant, Tukey-Kramer adjustments were used for pairwise comparisons between treatments across sites.

We used multi-response permutation procedure (MRPP) to test for treatment differences at the plot scale in plant community composition at each site following treatments. MRPP outputs a measure of effect size, *A*, that describes within-group similarity and a measure of significance (McCune and Grace, 2002). In our analyses group is treatment. Species occurring in less than 10% of plots were deleted from each site before conducting analyses. Treatment differences detected with MRPP were further investigated with nonmetric multidimensional scaling (NMS) ordination. Sorenson distance metric was used for all plant community analyses.

Greenhouse plant response variables (number of plants and average biomass per plant) were tested for differences between wood chip depths within species using ANOVA. Statistical tests were executed with Proc GLM in SAS v9.2 (© 2002-2008, SAS Institute Inc.). Because we were not interested in making all possible comparisons between means, we used an alternative method for multiple comparisons. Student-Neuman-Keuls adjustment for multiple comparisons applies the Tukey-Kramer adjustment sequentially beginning with the greatest difference between groups. Comparisons are stopped once no significant difference is found, slightly reducing the total number of comparisons made.

3. Results

3.1. Treatment effects on trees and ground cover

Seedling tree densities, both pre- and post- treatment were highly variable and differed between sites, but were generally similar between treatments (Tables 1 and 2). Seedling trees were not targeted with thinning prescriptions and average densities exceeded 1000 stems ha^{-1} (Tables 1 and 2). Overstory trees, also not targeted, did not differ between treatments pre- or post- treatment (Tables 1 and 2). Thinning treatments targeted pole-sized trees only. Pole densities in thinned units were 82-100% lower than unthinned units ($p = 0.002$, Table 2). Litter depth (inclusive of wood chips) in thin-chip units was greater than either unthinned or thin-only units ($p = 0.001$, Table 2), and averaged 3.8 cm across both sites. Litter cover comprised the greatest ground cover pre-treatment in all units (Table 1). One year post-treatment, litter cover was buried in places by wood chips in thin-chip units. Litter cover was lower and wood chip cover greater in thin-chip units than unthinned and thin-only units ($p = 0.0001$ and $p < 0.0001$, Table 2). Average bare ground cover was low in all units (< 1%) and no differences were detected between treatments pre- or post- treatment (Tables 1 and 2).

3.2. Vegetation response

No significant site-by-treatment interactions were found in analysis of vegetation characteristics, therefore results are reported averaged across sites. Total understory vegetation cover did not differ between treatments ($p = 0.127$, Table 3, Fig. 3). Graminoid cover in thin-chip treated areas was approximately one-third lower than in unthinned areas, (6.4 vs. 10 %, Tukey-Kramer adjusted $p = 0.017$, Table 3, Fig. 3). No treatment differences in forb or shrub cover were detected (Table 3, Fig. 3).

There was no treatment difference detected in total species richness at the plot scale ($p = 0.222$, Table 4, Fig. 4A). Thin-chip plots supported fewer than half the number of annual species per plot than thin-only plots (Tukey-Kramer adjusted $p = 0.001$, Table 4, Fig. 4A). No treatment differences were detected in total, forb, shrub or graminoid richness at the plot scale (Table 4, Fig. 4A).

At the 1-m^2 scale, thin-chip treatment resulted in fewer understory species compared to thin-only treatment (Tukey-Kramer adjusted $p = 0.041$, Table 4, Fig. 4B). Thin-chip plots supported 17% fewer total species and 18% fewer graminoid species m^{-2} than thin-only plots (Tukey-Kramer adjusted $p = 0.041$and $p = 0.038$, Table 4, Fig. 4B).

One year after treatment no differences in plant community composition were detected between treatments. Although at Wind Cave treatment differences were detected (MRPP, A = 0.036, p = 0.043), those differences were present pre-treatment (MRPP, A = 0.038, p = 0.036) and were unlikely attributable to treatments. Further investigation of Wind Cave plant community composition with NMS ordination did not stabilize, perhaps indicating that species distributions were not responding to strong underlying gradients caused by treatments or by environmental heterogeneity. No treatment differences were detected at Mt. Rushmore (A = 0.007, p = 0.233). There was no treatment effect detected on non-native species richness or cover at the plot scale or the 1-m^2 scale (Tables 3 and 4, Fig. 4).

3.3. Greenhouse study

Average number of grass and forb plants emerging and growing to 10 weeks in the greenhouse decreased with increasing wood chip depth for all species (main depth effect $\alpha < 0.05$, Figs. 4a, c). No plant species emerged from trays covered with 12 cm of wood chips. Very few grass plants grew in 9-cm depths and although some grass species grew in 6 cm of wood chips, the mean number was always statistically indistinguishable from zero. No forbs grew in 9-cm wood chip depth and at 6-cm depth the number of forbs emerging was statistically undetectable. In most species, fewer plants emerged from 3-cm than from 0-cm wood chip depth. Averaged across species, the number of plants emerging under wood chips was undetectable at depths ≥ 6 cm for grass plants and at depths ≥ 3 cm for forb plants (p = 0.001 and p = 0.001)

Increasing wood chip depth suppressed biomass production for all species except western wheat grass and blacksamson echinacea (Figs. 5B and D). For all wood chip depths ≥ 3 cm, plant biomass was effectively zero.

3.4. Soil available inorganic nitrogen

In general, no treatment differences were detected in plant available soil inorganic nitrogen as measured with *in situ* resin bags (Table 5, Fig. 6). NH_4^+-N measured in thin-chip plots was lower than that measured in unthinned plots in both year-of- and post- treatment growing seasons, but data were too variable to indicate a treatment effect (p = 0.338 and p = 0.110, Table 5, Fig. 6A). NO_3^--N measured one year following thin-chip treatment was less than unthinned plots (main treatment p = 0.022, Table 5), but the analysis indicated a site-by-treatment effect (p = 0.041). Therefore, NO_3^--N treatment responses for pre-treatment and year one are presented by site (Table 5, Fig. 6B) and treatment comparisons are adjusted for all site-by-treatment combinations. No differences between treatments were detected at Mt. Rushmore one year following treatment (Tukey-Kramer adjusted p's = 0.999-1.0, Table 5, Fig. 6B). At Wind Cave, however NO_3^--N measured in thin-chip plots trended lower than that measured in unthinned plots (Tukey-Kramer adjusted p = 0.059, Fig. 6B) and thin-only plots (Tukey-Kramer adjusted p = 0.110, Fig. 6B).

3.5. Ponderosa pine germination

There was no significant treatment effect on ponderosa pine germination. Although the density of ponderosa pine germinants in thin-chip plots was more than double the density in unthinned plots, the increase was not significant due to high variability [back-transformed mean (SE) 7.0 (2.0-2.3) vs. 3.0 (1.2-1.5) germinants m^{-2}, p = 0.224].

4. Discussion

4.1. Vegetation response

Thinning treatments reduced hazard fuels by substantially reducing pole-tree densities. Thinning opened the forest canopy in areas formerly populated by dense pole trees. Pole density between plots was highly variable, therefore the magnitude of thinning intensity was quite variable. Although we did not directly measure these variables, it is likely in some areas that thinning only slightly opened the forest canopy to increase light and precipitation to the forest floor. Overstory trees at these sites are the largest contributor to basal area and canopy cover, but only trees ≤ 15-cm dbh were targeted with fuels reduction treatments.

Thinning did not elicit much of an understory response in the first year following treatment. We hypothesized an increase in total understory cover and richness following thin-only treatment. One year post-treatment we did not detect any thinning effect on understory cover. It is possible that thinning was not intensive enough to cause a change in understory cover. It is also possible that thinning effects had not yet manifested one year post-treatment. In another study from the Black Hills, an increase in understory biomass following thinning ponderosa pine was not detected until the second growing season post-treatment (Wienk *et al.*, 2004). In our study thin-only treatments resulted in slight increases in understory plant richness, but a notable increase in annual species richness. These small responses may be early indications of thinning effects that will magnify with time. As expected, no differences were detected in non-native species response. However, we personally noted a small expansion of non-native species in isolated locations not sampled by plots.

Wood chip application caused decreases in understory plant richness and cover. Although we did not detect any thin-chip effects on total understory cover, we did see a decrease in graminoid cover in thin-chip relative to unthinned plots. Graminoid plants constitute the majority of understory cover in the ponderosa pine ecosystem we studied. As the most common species (in terms of cover) graminoid plants are most likely to display treatment effects on cover. Graminoid plants may not be able to push as many tillers or culms through wood chips. Others have also reported a decrease in grass productivity following wood chip or thin-chip treatments. Eschen *et al.* (2007) found decreased grass biomass in the first two years following wood chip application. After thin-chip treatment in a ponderosa pine – grassland ecotone, Law and Kolb (2007) observed a decrease in grass cover and culm density.

Thin-chip plots contained fewer annual species than thin-only plots. Annual species likely responded favorably to conditions created by thinning, but were limited by light and by the physical barrier imposed by wood chips. Annual species, with small seeds and low initial energy reserves, would be more affected by a wood chip barrier than other species. One study on thin-masticate treatment also found an increase in annual species (Perchemlides *et al.*, 2008). Because the increase was relative only to untreated plots, it can be attributed to the thinning portion of the treatment. Because there was no difference between thin-only and thin-masticate treatments, mastication did not provide a barrier to annual species. Wood chip cover likely creates a more continuous barrier to plant emergence than masticated pieces of woody debris and thus would be more likely to inhibit annual species emergence than masticated material. We observed disturbance-associated species in thin-only treatment areas such as *Conyza canadensis* and *Agrostis scabra* that had not been detected prior to thinning. These species were not present in thin-chip areas post-treatment. These findings further indicate opposing effects between thinning and wood chip application.

At the1-m^2 scale, the pattern of response also indicated that thinning treatment may open opportunities for new species, while wood chips may act as a physical barrier and exclude certain species. There was slightly greater graminoid and total understory species richness following thinning and significantly lower richness in response to wood chip application.

Grass and forb plants grown in the greenhouse displayed the negative effects of increasing wood chip depth (Fig. 4). Increasing wood chip depth created an increasing barrier to seedling emergence and growth of both grass and forb plants and was completely suppressed at 6-cm wood chip depth. Two field studies did not find a negative impact on understory cover at broad scales with average mulch depths greater than 6 cm (Wolk and Rocca, 2009; Kane *et al.*, 2010), but a closer look at multiple studies reveals a more complex story. Although the authors of one study in ponderosa pine concluded that an average wood chip depth of 10 cm did not suppress grass emergence, they reported a decrease in grass cover and culm density (Law and Kolb, 2007). Wood chips applied to an average depth of 7.5 cm at 1.5-m^2 scale, did not completely suppress growth, but substantially reduced total and graminoid cover (Miller and Seastedt, 2009). Similarly, at the 1-m^2 scale, subplots mostly covered with an average depth of 7.5 cm wood chips compared with those mostly free of wood chips, reduced total understory cover by half (Wolk and Rocca, 2009). We observed a negative impact on plant cover in the field at the 1-m^2 scale with an average wood chip depth of 3.8 cm. Graminoid cover was reduced relative to unthinned, but not compared with thin-only. Wood chips can have a negative effect on understory cover, but the extent may be determined by depth and continuity of coverage. Wood chip distribution can suppress plant growth at small scales, but with patchy distribution the effects may be evened out at larger scales. Wood chips in our study were probably more evenly distributed due to the mobility of the machinery used and direct operator control.

We cannot directly compare our greenhouse study with field studies for many reasons. Perennial species in the field grew from dormant root reserves, while greenhouse plants grew from seed. Greenhouse studies were conducted under optimal conditions for growth. Greenhouse trays were covered with a continuous wood chip depth, while field sites generally have patchy mulch cover that varies in depth. It is likely that a continuous cover of wood chips would suppress more vegetation than a patchy cover of wood chips. Further studies would help shed light on the question of “how deep is too deep?” following thinning and mulching. A field-based mulch manipulation study would best detect threshold effects on the suppression of plant growth.

Where treatment differences were detected, thin-chip treatment elicited a decrease in plant cover and abundance indicating a faster response to wood chip application than to thinning.

We hypothesized potentially contradictory effects between thin-only and thin-chip treatments. We anticipated an increase in understory productivity and richness in response to thin-only and a decrease in response to thin-chip. It is likely that we would detect a decrease in vegetation cover and richness sooner than an increase. Wood chip application can create a physical barrier to vegetative growth and reduce cover or richness. Increasing litter depth following thin and mulch treatments in ponderosa pine forests has been associated with decreasing vegetation cover (Wolk and Rocca, 2009; Kane *et al.*, 2010). A physical barrier creates an instant obstacle for plants, while an increase in resources (light, precipitation, nutrients) may take time to affect understory plants. The two studies that observed decreased vegetation cover following thin-chip treatment also described short-term effects, i.e. 1-3 years (Law and Kolb, 2007; Miller and Seastedt, 2009). Studies that measured increased vegetation cover following thin-mulch (compared to untreated plots) detected effects 3-7 years following treatment (Perchemlides *et al.*, 2008; Wolk and Rocca, 2009; Kane *et al.*, 2010). Undoubtedly, the rate and magnitude of potentially opposing effects is determined by the continuity and intensity of treatment, i.e. opening of the forest canopy compared with depth of wood chip application.

4.2. Ponderosa pine regeneration

Season-long precipitation during the summer of 2010 provided favorable growing conditions for ponderosa pine regeneration (personal observation). We hypothesized that wood chip application may inhibit germination, but germinants established equally well in wood chips as in other areas. Relative germination success in the Black Hills has been associated with moderated soil moisture loss due to the presence of litter (Bonnet *et al.*, 2005). Thus, increased moisture retention by wood chips (Gower *et al.*, 1992; Miller and Seastedt, 2009) may even favor germinant establishment. Our results, although too variable to draw conclusions, suggest a potential increase in germinant densities in wood chips.

Seedling growth and survivorship over the next several years will better answer the question of how wood chip application affects ponderosa pine regeneration. Failure of roots to establish in soil due to excessive litter depths has been shown as a major reason for ponderosa pine seedling mortality in Arizona (Stein and Kimberling, 2003). It is unclear whether wood chips would act as a barrier to root establishment in the soil, although Miller and Seastedt (2009) found no difference in ponderosa pine germinant and seedling densities between plots with and without wood chips. Deep and continuous wood chip cover could cause a barrier to root establishment in the soil. Wood chip decomposition rates and nutrient availability have not been reported and may affect seedling survivorship in wood chips.

Hazard fuels treatments aim to reduce small diameter tree densities and ladder fuels, thus thin-chip effects on ponderosa pine regeneration has important implications. Further studies that specifically examine the role of wood chips in ponderosa pine establishment and survivorship would provide important information for managers.

4.3. Soil available inorganic nitrogen

Inorganic nitrogen sampled with *in situ* ion exchange resin was generally too variable to detect treatment effects. Doubling the number of sampling bags one year post-treatment reduced the variability in results for inorganic nitrogen and allowed us to observe a slight treatment effect. We observed a small decrease in NO_3^--N in thin-chip plots at one study site, but no effect at the other site. Wind Cave, the site showing decreased NO_3^--N, is the more productive of the two sites with greater understory cover and more soil available inorganic N. There is likely greater competition between microbes and plants for inorganic N and thus more opportunity for N immobilization following wood chip application at this site relative to the other. Nitrate immobilization by wood chips throughout the first year following harvest has been demonstrated in eastern hardwood forests (Homyak *et al.*, 2008). The two studies that examined soil inorganic

N response to thin-mulch treatments in conifer forests found no change in soil inorganic N in the first year, but greater total inorganic N (Miller and Seastedt, 2009) and greater NH_4^+-N (Owen *et al.*, 2009) 3 and 2.5 years following treatments.

Long-term effects of wood chip application on soil available N may be confounded by thinning effects. Thinning ponderosa pine has resulted in increased (Kaye and Hart, 1998), decreased (Grady and Hart, 2006), and no effect (DeLuca and Zouhar, 2000; Hart *et al.*, 2006) on net N mineralization, although all studies report some effect on nitrogen cycling. Grady and Hart (2006), in a review on the long-term effects of ponderosa pine restoration, concluded that microbial activity is closely tied to C inputs and substrate quality in southwest ponderosa pine ecosystems. Because wood chip application directly affects the C input to the forest floor, it will likely have further effects on N cycling and availability.

5. Management Implications

Initial results imply that thin-chip is a viable treatment option and my provide an alternative to the standard practice of thin and pile burn. A single-entry treatment such as thin-chip is logistically simpler to implement than a two-phase treatment such as thin and subsequent pile burn. Vegetation and nitrogen responses to thin-chip treatment were subtle and no obvious negative impacts were detected. Although wood chip application slightly reduced some measures of understory cover and richness, the results we detected were generally not different from untreated areas. Future examination will determine if delayed thinning effects reverse understory decreases in cover and richness following wood chip application. We did not detect any problematic post-disturbance responses such as non-native species expansion or introduction, although continued monitoring is needed to confirm the longevity of those findings.

Our study provides important initial information to fire and resource managers in the Black Hills. It also sheds light on the general impacts of thin-chip treatments. Nonetheless, long-term research is still needed to better inform managers. The goal of further research should be to make generalizations on the impacts of thin-mulch treatments across ecosystems or to distinguish factors that make generalization impractical. Wood chip depth and distribution appear to be important factors, but thresholds for depth or continuous cover and their potential negative impacts could be better understood. The relatively uniform cover of wood chips at our study sites did not allow for further examination of this question in the field. A wood chip manipulation experiment in the field that tests both depth and distribution effects would greatly illuminate potential negative threshold effects on understory plants.

Further understanding of wood chip effects on ponderosa pine regeneration will impact the timing required for maintenance of thinning treatments. Although thinning greatly reduced small-diameter trees and reduced the risk of catastrophic fire, future treatments will be required. The high seedling densities on our plots will contribute to ladder fuels in10-20 years and again increase risk of high-severity fire (Battaglia *et al.*, 2008). Repeated thinning treatments will be needed to further achieve and maintain restoration and fire resiliency goals. Thin-chip treatments may decrease hazard fuels to a point where prescribed fire can be reintroduced, but very few studies have examined how wood chip or masticated woody material effect fire behavior. This study provides insight into mechanisms of understory response by separating thin effects from the effects of wood chip application. The use of a randomized experimental design allows us to make inferences beyond those of observational studies. As managers continue to implement thin-chip and thin-masticate fuels reduction, monitoring for both initial and long-term effects will be crucial.

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Table 1

Mean (SE) pre-treatment forest structure and ground cover by site. P-values refer to ANOVA treatment effect averaged across sites.

	Mt. Rushmore			Wind Cave			
Variable (units)	Unthinned	Thin-chip	Thin-only	Unthinned	Thin-chip	Thin-only	p-value
Trees							
seedlings (stems ha^{-1})	3990 (4070)	1960 (4070)	330 (4070)	11300 (4940)	16700 (4940)	5000 (4940)	0.374
poles (stems ha^{-1})	1070 (680)	2540 (680)	1330 (680)	3540 (890)	3580 (890)	1560 (890)	0.161
overstory BA (m^{2} ha^{-1})	32.8 (3.1)	31.3 (3.1)	32.5 (3.1)	27.4 (4.3)	30.5 (2.5)	20.4 (4.3)	0.474
Ground cover							
litter depth (cm)	2.9 (0.3)	3.1 (0.3)	3.0 (0.3)	3.3 (0.4)	4.3 (0.4)	4.4 (0.4)	0.160
litter cover (%)	91.3 (1.3)	89.4 (1.3)	89.4 (1.3)	92.1 (1.6)	95.9 (1.6)	89.7 (1.6)	0.129
bare ground cover (%)	0.34 (0.13)	0.28 (0.13)	0.13 (0.13)	0.22 (0.18)	0.7 (0.18)	0.55 (0.18)	0.565

Table 2

Mean (SE) one year post-treatment effects on trees and ground cover. Litter depth is inclusive of wood chips. P-values refer to ANOVA main treatment effect averaged across sites. Letters designate a difference between treatments, within each site based on Tukey-Kramer adjustment for multiple comparisons, $\alpha = 0.05$.

	Mt. Rushmore			Wind Cave			
Variable (units)	Unthinned	Thin-chip	Thin-only	Unthinned	Thin-chip	Thin-only	p-value
Trees							
seedlings (stems ha^{-1})	4130 (2570)	1650 (2570)	890 (2570)	9670 (3140)	6890 (3140)	3690 (3140)	0.303
poles (stems ha^{-1})	920 (480)	140 (380)	170 (380)	3350 (600) a	0 b	40 (600) b	0.002
overstory BA (m^2 ha^{-1})	34.0 (3.0)	30.0 (3.0)	31.5 (3.10)	27.0 (4.0)	31.1 (4.0)	17.3 (4.30)	0.175
Ground cover							
litter depth (cm)	2.7 (0.3) a	3.9 (0.3) b	2.4 (0.3) a	2.7 (0.4)	3.7 (0.4)	2.8 (0.4)	0.001
litter cover (%)	89.0 (3.8) a	26.0 (3.8) b	93.0 (13.8) a	93.0 (4.6) a	64.0 (4.6) b	91.0 (4.6) a	0.0001
wood chip cover (%)	0 a	68.0 (3.9) b	0 a	0 a	33.6 (4.6) b	0 a	< 0.0001
bare ground cover (%)	0.05 (0.16)	0.03 (0.16)	0.02 (0.16)	0.67 (0.22)	0	0.25 (0.22)	0.223

Table 3

Mean (SE) understory vegetation cover by life form. P-values refer to ANOVA main treatment effect. Letters designate a difference between treatments based on Tukey-Kramer adjustment for multiple comparisons, $\alpha = 0.05$.

Variable (units)	Unthinned	Thin-chip	Thin-only	p-value
Cover (% m^{-2})[a]				
total	13.8 (1.2-1.3)	10.4 (1.1)	11.3(1.2)	0.127
non-native	0.2 (0.1)	0.2 (0.1)	0.2 (0.1)	0.984
forb	1.6 (0.2)	1.5 (0.2)	1.2 (0.2)	0.318
shrub	0.3 (0.1)	0.5 (0.1)	0.4 (0.1)	0.303
graminoid	10.0 (0.9) a	6.4 (0.7) b	7.9 (0.8) ab	0.021

[a] Analysis was performed on square root transformed data. Back-transformed means (± SE) are presented. See methods for details.

Table 4

Mean (SE) understory vegetation richness at the plot at 1m^2 scales. P-values refer to ANOVA main treatment effect. Letters designate a difference between treatments based on Tukey-Kramer adjustment for multiple comparisons, α = 0.05.

Variable (units)	Unthinned	Thin-chip	Thin-only	p-value
Plot Richness (# species 120m^{-2})				
total	31.1 (1.2)	32.7 (1.1)	34.1 (1.2)	0.222
non-native	3.0 (0.3)	3.1 (0.31)	3.0 (0.3)	0.986
forb	17.9 (0.9)	17.7 (0.9)	19.7 (0.9)	0.259
shrub	3.4 (0.3)	3.8 (0.3)	3.5 (0.3)	0.585
graminoid	9.2 (0.7)	9.6 (0.6)	9.8 (0.6)	0.787
annual	1.5 (0.2) a	1.0 (0.2) a	2.5 (0.2) b	0.002
1m^2 Richness (# species m^{-2})[a]				
total	4.0 (0.2) ab	3.7 (0.2) a	4.4 (0.2) b	0.051
non-native	0.1 (0.03-0.04)	0.1 (0.03)	0.1 (0.02)	0.186
forb	1.4 (0.1)	1.2 (0.1)	1.4 (0.1)	0.382
shrub	0.13 (0.03)	0.17 (0.03)	0.17 (0.03)	0.56
graminoid	1.6 (0.08) ab	1.5 (0.07-0.08) a	1.9 (0.08) b	0.040

[a] Analysis on 1m^2 richness was performed on square root transformed data. Back-transformed means (± SE) are presented. See methods for details.

Table 5

Mean (SE) understory inorganic nitrogen. P-values refer to ANOVA main treatment effect. NO_3^--N site specific responses are presented for pre-treatment and one year post-treatment. Letters designate a difference between treatments based on Tukey-Kramer adjustment for multiple comparisons, α = 0.05. MORU = Mt. Rushmore, WICA = Wind Cave

Variable (units)	Unthinned	Thin-chip	Thin-only	p-value
NH_4^+-N (μ N bag^{-1} day^{-1})				
summer pre-treatment	1.3 (0.3)	1.4 (0.3)	0.9 (0.3)	0.521
summer year of treatment	5.6 (1.0)	4.0 (1.0)	3.7 (0.9)	0.338
summer 1-year post-treatment	5.7 (0.6)	4.9 (0.5)	3.9 (0.6)	0.110
winter year of treatment	1.5 (0.2)	1.0 (0.2)	1.4 (0.2)	0.241
NO_3^--N (μ N bag^{-1} day^{-1})				
summer pre-treatment	1.3 (0.4)	1.8 (0.4)	1.6 (0.4)	0.527
MORU[a]	1.2 (0.7)	1.5 (0.7)	2.2 (0.7)	
WICA[a]	3.6 (1.1)	5.4 (1.0)	4.0 (1.1)	
summer year of treatment	2.7 (0.5)	1.8 (0.4)	2.7 (0.4)	0.440
summer 1-year post-treatment	4.4 (0.4) a	2.8 (0.4) b	4.2 (0.4) ab	0.022[b]
MORU[a]	1.5 (0.4)	1.3 (0.4)	1.5 (0.4)	
WICA[a]	7.2 (0.7)	4.2 (0.6)	6.9 (0.7)	
winter year of treatment	1.6 (0.4)	1.4 (0.4)	1.3 (0.4)	0.887

[a] Main treatment effects are not presented for site specific responses because sites were not analyzed separately. See methods for details.

[b] Summer 1-year post-treatment analysis indicated a site-by-treatment effect (p = 0.041).

Figure Legends

Fig. 1. Unit and plot locations at each study area. Study areas included Wind Cave National Park and Mt. Rushmore National Memorial, both of which are located in southeastern South Dakota, USA.

Fig.2. A) Wood chip distribution at Mt. Rushmore following treatment implementation in 2009. B) Wood chip sizes. Meter tape, in tenths of meters, is stretched across the center of the photo.

Fig.3. Mean ± SE one-year post-treatment responses in understory vegetation cover by life form. Letters designate a significant difference between treatments based on Tukey-Kramer multiple comparison test, $\alpha = 0.05$.

Fig.4. Mean ± SE one-year post-treatment responses in understory vegetation by life form for A) plot richness, B) 1m^2 richness. Letters designate a significant difference between treatments based on Tukey-Kramer multiple comparison test, $\alpha = 0.05$.

Fig.5. Emergence and growth attributes for 10-week-old plants grown from seed in the greenhouse. Mean ± SE by species and wood chip depth for A) number of grass plants, B) oven-dried weight per individual grass plant, C) number of forb plants, and D) oven-dried weight per individual forb plant. Letters designate a significant difference between depths and within species based on Student-Newman-Keuls multiple comparison test, $\alpha = 0.05$. PASM = *Pascopyrum smithii* , NAVI = *Nassella viridula*, BOGR = *Bouteloua gracilis*, SCSC = *Schizachyrium scoparium*, ECAN = *Echinacea angustifolia*, and MOFI = *Monarda fistulosa*.

Fig.6. Mean ± SE treatment responses for inorganic nitrogen sampled with resin bags over summer growing seasons: A) NH_4^+-N by year, averaged over site, and B) NO_3^--N by year and by site. NO_3^--N is separated by site, because of a significant site-by-treatment interaction in one year post-treatment analysis ($p = 0.041$,Table 3). MORU = Mt. Rushmore and WICA = Wind Cave.

Figure 1

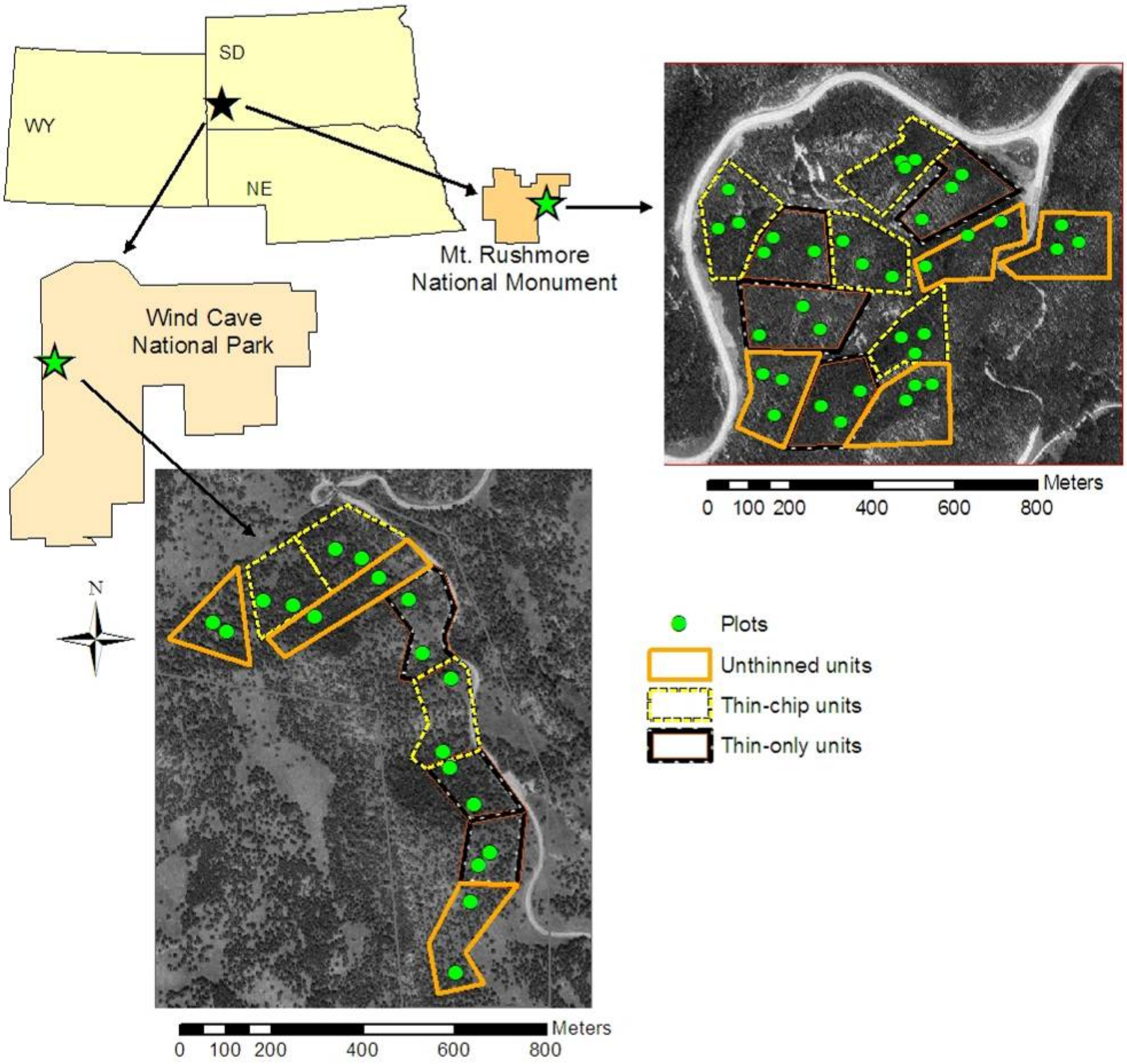

SD
WY
NE
Mt. Rushmore
National Monument
Wind Cave
National Park
Meters
0 100 200 400 600 800
N
Plots
Unthinned units
Thin-chip units
Thin-only units
Meters
0 100 200 400 600 800

Figure 2

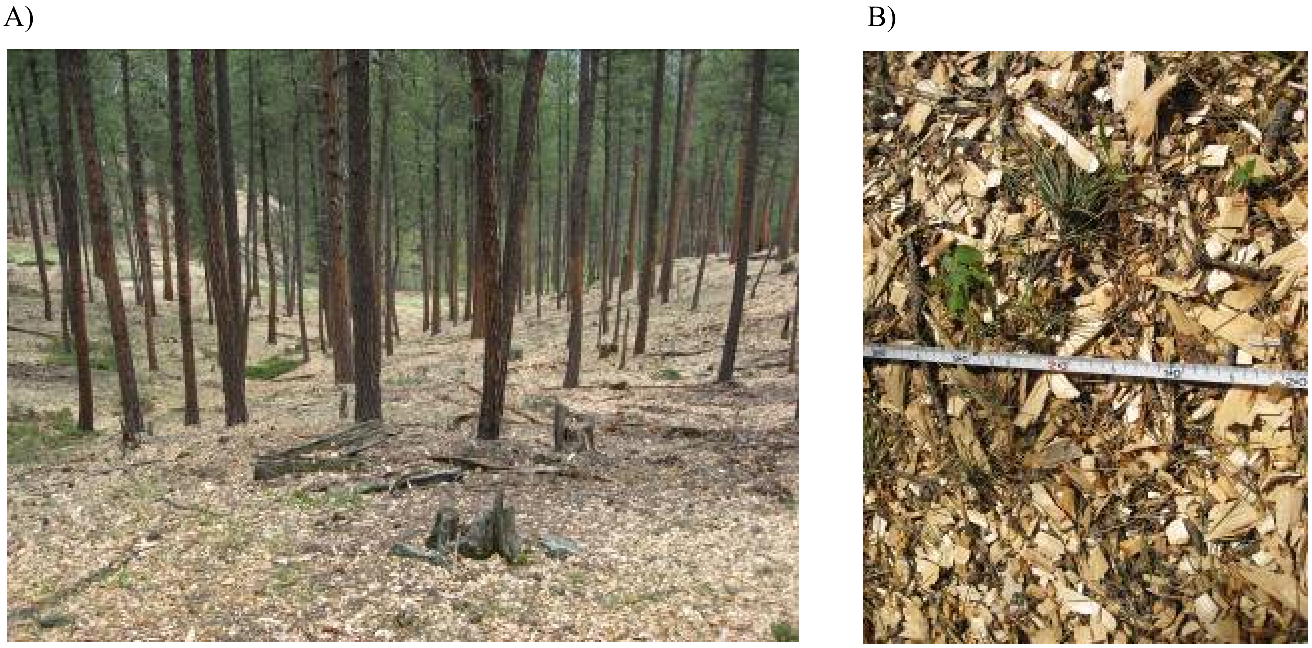
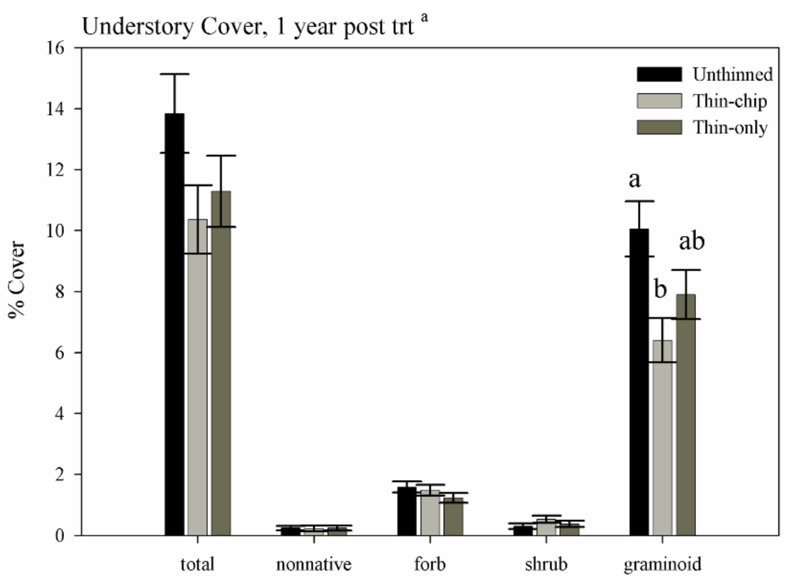
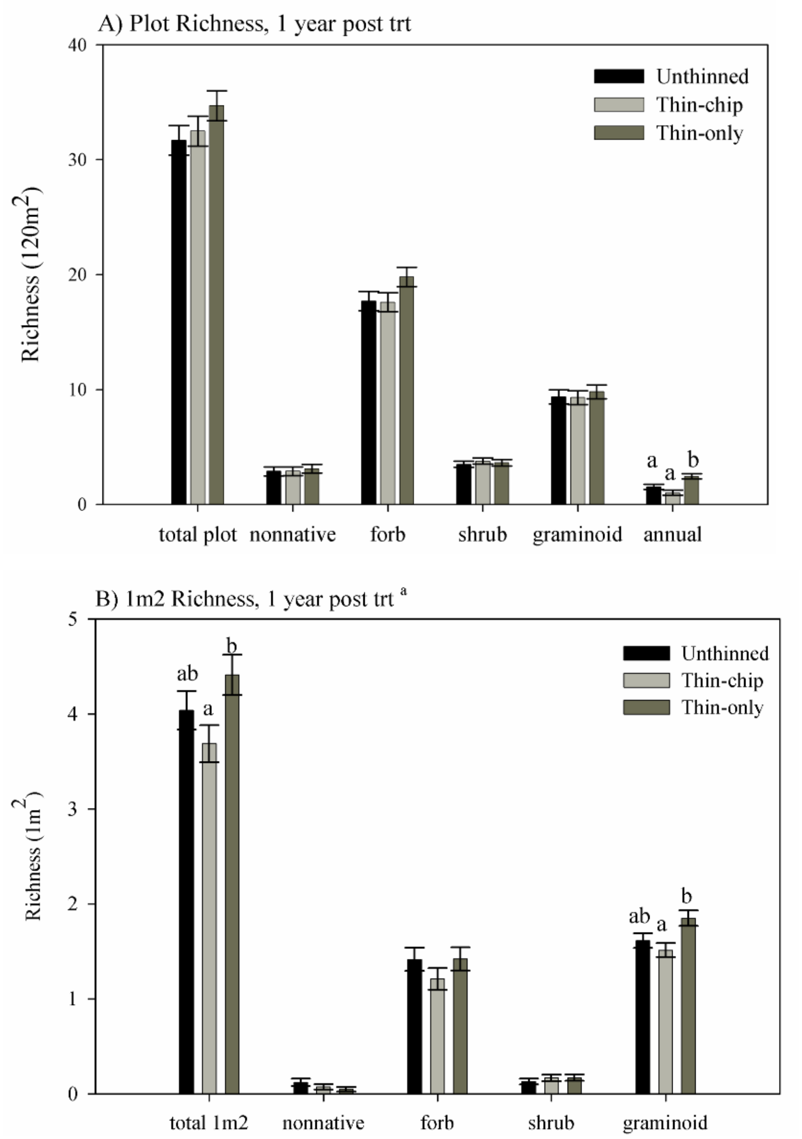


Figure 3



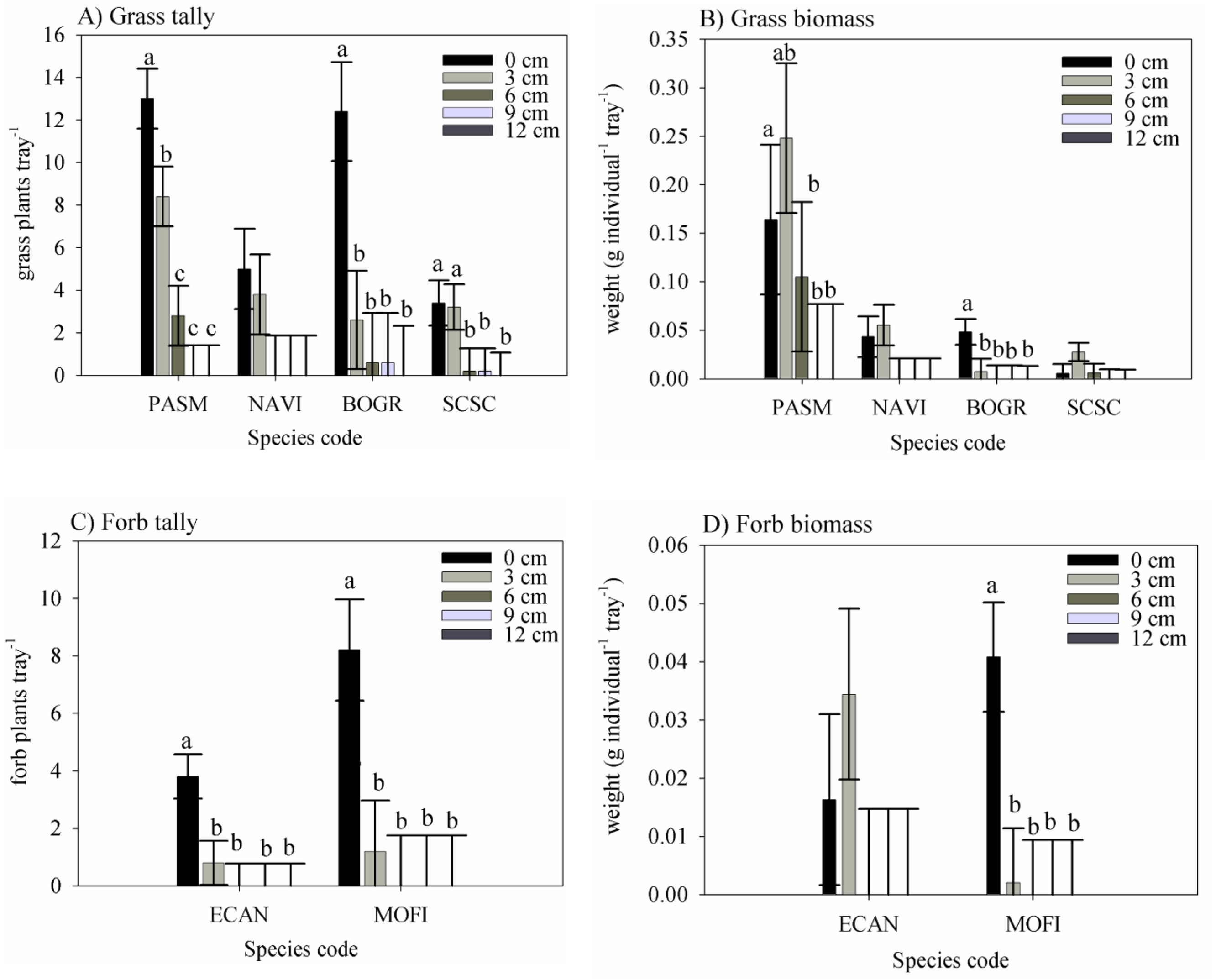
[a] Analysis was performed on square root transformed data. Back-transformed means (± SE) are presented. See methods for details.

Figure 4



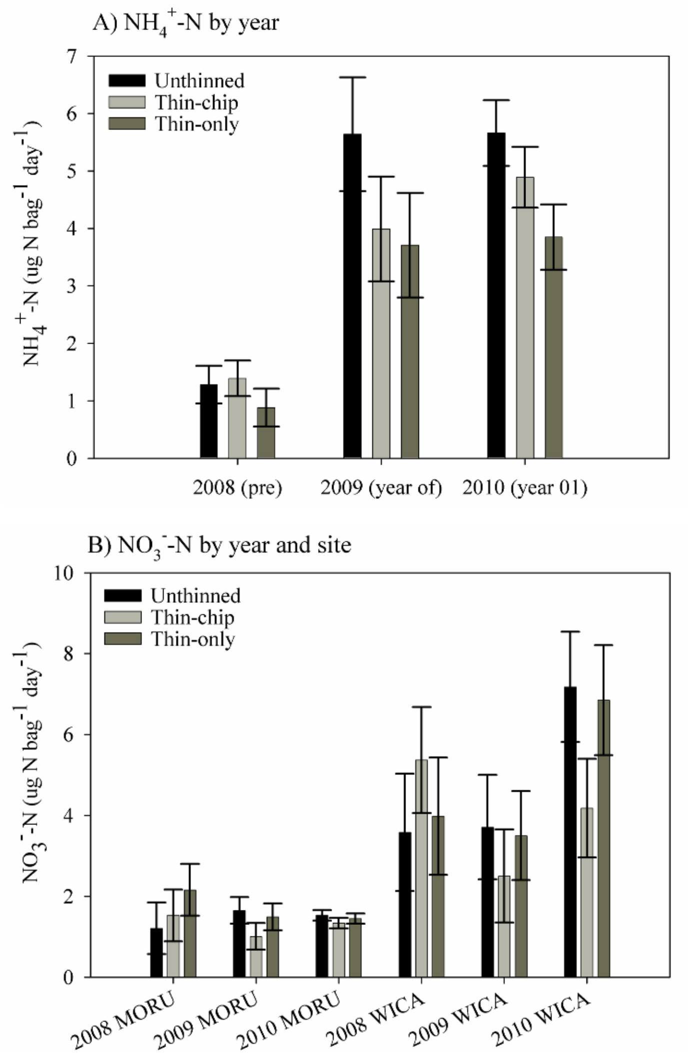
[a] Analysis on $1m^2$ richness was performed on square root transformed data. Back-transformed means (± SE) are presented. See methods for details.

Figure 5



A) Grass tally
16
14
12
10
8
6
4
2
0
grass plants tray^{-1}
a
b
c
c c
a
b
b b
b
a a
b b
b
0 cm
3 cm
6 cm
9 cm
12 cm
PASM
NAVI
BOGR
SCSC
Species code
B) Grass biomass
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
weight (g individual^{-1} tray^{-1})
ab
a
b
bb
a
b
bb
b
0 cm
3 cm
6 cm
9 cm
12 cm
PASM
NAVI
BOGR
SCSC
Species code
C) Forb tally
12
10
8
6
4
2
0
forb plants tray^{-1}
a
b
b
b b
a
b
b b b
0 cm
3 cm
6 cm
9 cm
12 cm
ECAN
MOFI
Species code
D) Forb biomass
0.06
0.05
0.04
0.03
0.02
0.01
0.00
weight (g individual^{-1} tray^{-1})
a
b
b b b
0 cm
3 cm
6 cm
9 cm
12 cm
ECAN
MOFI
Species code

Figure 6



A) NH_4^+-N by year

B) NO_3^--N by year and site