

Impacts of woodchip amendments and soil nutrient availability on patterns of understory vegetation establishment following thinning of a ponderosa pine forest

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ABSTRACT

Mechanical thinning for fire mitigation has become increasingly widespread in recent years throughout the western United States. A common practice in fire mitigation procedures is the conversion of slash into chipped mulch (referred to as “woodchips”) that is spread on-site. Here, we investigated: (1) the effect of woodchip amendments on soil nitrogen availability, and (2) the influence of potential interactions between woodchip amendments and soil nitrogen availability on patterns of native and non-native understory plant establishment in a thinned montane forest in the Front Range of Colorado.

We created a gradient of soil nitrogen availability among experimental plots by applying sugar to reduce plant-available nitrogen and applying ammonium nitrate to increase plant-available nitrogen. Soil and resin bag analyses confirmed the effectiveness of the nitrogen manipulations. Nitrogen manipulations did not affect understory species richness or diversity, but increased nitrogen promoted a disproportionate increase in the cover of non-native forbs.

Woodchip amendments did not alter soil pH, but did increase average soil moisture content. Woodchips did not alter nitrogen availability at ambient levels of soil fertility during the first two years of the study, but were associated with increased soil N availability in the third growing season. Woodchip additions were associated with significantly lower species richness, diversity, and overall plant cover than found in unchipped plots. The observed reduction in plant cover affected native and non-native species similarly, although certain species had distinctive responses to woodchip amendments. On the whole, woodchips excluded more species than they promoted, and the physical effects of woodchips appeared to be more important than soil nitrogen status in influencing the understory composition of this area following thinning. At this site, approximately 60% of the plant cover in the three years following thinning operations was

comprised of non-native plant species. Thus, fire mitigation that employs mulching produced changes in amounts and composition of understory species and therefore can lead to secondary environmental concerns.

KEY WORDS:

Fire mitigation, invasive plants, mulch effects, soil nitrogen,

1. Introduction

The Eastern Slope of the Colorado Front Range is a high-priority area for fire mitigation efforts. Historically, the lower montane zone (1800-2500m) in this region predominantly experienced a mixed-severity fire regime with an average fire-return interval of 10-30 years, which maintained a mosaic of open, park-like woodlands interspersed with even-aged stands of ponderosa pine (Kaufmann et al., 2006; Sherriff and Veblen, 2007). However, fire suppression policies enacted between the 1920s and 1980s led to an expansion of ponderosa pine density and range that exceeds the historical range of variability for the lower montane zone in Colorado, such that current conditions favor severe, stand-replacing fires (Veblen and Brown, 2001; Graham *et al.*, 2004). In an effort to reduce the threat of wildfire to human communities, forest managers have implemented aggressive fire-mitigation strategies, using mechanical thinning to reduce fuel loads in high-risk forested areas.

Since the passage of the Healthy Forests Restoration Act in 2003 (HFRA, 2003), an average of over 20,000 hectares of forest per year has been mechanically thinned for fire mitigation in the state of Colorado alone (USDA/DOI, 2008). Understory saplings are removed while larger, widely spaced, fire-resistant trees are preserved. A large quantity of slash is produced, which is then removed, burned, or chipped and spread on the soil surface. By

convention, machine-chipped whole tree residue is referred to as “woodchip” mulch. The practice of woodchip mulching is a common solution to the problem of disposal of thinned woody biomass because it is economical and has the added benefit of preventing soil erosion after the disturbance of thinning. However, the effects of woodchip amendments on soil nutrient availability and understory vegetation remain largely unstudied. The combination of mechanical thinning, which opens up the forest canopy, and subsequent blanket applications of woodchips to the soil surface is a doubly novel management technique that is likely to affect patterns of vegetation establishment.

A conservation management concern is the susceptibility of thinned forests to non-native plant invasions. The reduction of tree density leads to increased light and space for the establishment of understory plants, both native and non-native. The process of thinning can also introduce plant propagules and disrupt the existing understory plant community. As a result, thinning is commonly associated with a subsequent increase in understory biomass, species richness, abundance, and/or cover (Naumburg and DeWald, 1999; Thomas et al. 1999; Griffis *et al.*, 2001; Metlen and Fiedler, 2006; Moore *et al.*, 2006). In several cases where the establishment of native and non-native plant species has been tracked after thinning operations were completed, thinning was found to facilitate non-native invasions (Scherer *et al.* 2000; Dodson, 2004; Dodson and Fiedler, 2006; Nelson *et al.*, 2008). However, in other studies, thinning was not followed by an increase in non-native plant abundance (Scherer *et al.*, 2000; Griffis *et al.*, 2001;; Fornwalt *et al.*, 2003; Collins *et al.*, 2007; Laughlin *et al.*, 2007).

Variation in patterns of non-native plant invasions has been explained by variation in three main contributing factors: (1) propagule pressure, (2) the characteristics of the invading species, and (3) the characteristics of the recipient ecosystem (Lonsdale, 1999). In the latter case,

the ecosystems that are considered to be most vulnerable to non-native plant invasions are those where physical disturbance (mechanical thinning is one example) co-occurs with unusually abundant resources (Hobbs and Atkins, 1988; Burke and Grime, 1996; Thompson *et al.*, 2001). In North America, nitrogen is the resource that is most commonly limiting to plant growth (Chapin, 1980; Vitousek and Howarth, 1991; Vitousek and Farrington, 1997), and therefore most likely to affect patterns of plant distribution if manipulated. Yet many of the North American forests that are subject to thinning for fire mitigation are located near urban centers that generate chronic inputs of nitrogen into nearby natural areas, due to atmospheric deposition (Fenn *et al.*, 1998). The Eastern Slope of Colorado's Front Range is one such area (Williams *et al.*, 1996; Baron *et al.*, 2000; Rueth and Baron, 2002; Fenn *et al.*, 2003). Furthermore, the need for fire mitigation is generally a result of long periods of fire exclusion (as reviewed in Graham *et al.*, 2004), which is known to contribute to accumulation of plant-available soil nitrogen (Vance and Henderson, 1984). Thus, when the physical disturbance of thinning is performed for fire mitigation near urban areas such as the Front Range, excess nitrogen availability may be a factor that influences non-native plant invasions.

When woodchip mulch is subsequently applied to the soil surface in a thinned forest, it is likely to exert an additional effect on the pattern of plant establishment. Mulch amendments in the form of sawdust or pine bark have been found to provide a competitive advantage to native plant species by disproportionately inhibiting the growth of non-natives (Zink and Allen, 1998; Averett *et al.*, 2004; Perry *et al.*, 2004), although Baer *et al.* (2004) found that sawdust mulch inhibited the growth of native and non-native plant species similarly. Among the few studies that have specifically investigated the impact of woodchips on vegetation establishment, one found that woodchips reduced the absolute cover of vegetation (Greenly and Rakow, 1995), but another

reported that although woodchips were associated with reduced overall plant cover, they did not affect species richness or the relative cover of native and non-native plant species (Wolk and Rocca, 2008). Woodchip applications are common in fire mitigation operations; therefore, their influence on the trajectory of native and non-native vegetation establishment, either directly or in interaction with the level of soil nitrogen availability, deserves more attention.

The goal of the present study was to assess the short-term (three years following thinning) impacts of standard fire mitigation practices at a site that was thinned and mulched with standard, heavy equipment. We hypothesized that this response was strongly mediated by soil fertility; therefore the present study measured the impact of woodchip mulch on plots treated with amendments to alter nitrogen availability (reduced, ambient, and enhanced) on soil characteristics and plant responses.

2. Methods

2.1. Site description

The study site is located approximately 18 km northwest of Boulder, CO in a lower montane forest (elevation 2070m; 40°10'28"N, 105°18'29"W) at Heil Valley Ranch, a property of Boulder County Parks and Open Space, a site also described in detail in Wolk and Rocca (2008). The soil is a sandy clay loam, classified as a Pinata series, clayey-skeletal, mixed Typic Eutroboralf. Prior to thinning in 2004, this gently sloping, east-facing montane site was densely covered by an even-aged stand of ponderosa pine (*Pinus ponderosa*), which contained occasional individuals of *Pseudotsuga menziesii* (Douglas fir) and *Juniperus scopulorum* (Rocky Mountain juniper); understory vegetation was minimal to absent throughout. Classified as one a high-priority fire risk by Boulder County Open Space, the site was mechanically thinned for fire

mitigation purposes such that all stems smaller than 18 cm dbh were removed, reducing basal area from ~45 m²/ha to ~24 m²/ha. This activity required the use of heavy equipment that visibly disturbed the soil surface and likely caused compaction of soils.

The semi-arid climate at the research site is characterized by cool, dry winters and warm, dry summers with periodic rain events. Average precipitation at the nearby City of Boulder weather station is 485 mm/y, with the most precipitation falling in April, May and June (monthly means of 53-76 mm) and the least precipitation falling in December, January, and February (monthly means of 18-20 mm). The warmest months are June, July, and August, with average monthly maximum temperatures of 28 to 31°C. The coolest months are December, January, and February, with average monthly minimum temperatures of -5 to -6°C (WRCC, 2008).

2.2. Experimental manipulations

We manipulated nitrogen availability at three levels (increased, ambient, and reduced) and woodchips at two levels (presence and absence). We tested all possible combinations of the soil amendments in the presence and absence of woodchip mulch in a blocked factorial design. For statistical power, we established 5 replicate blocks, with each treatment type randomly assigned to a plot in each block. Plots measured 1.5m x 1.5m square, with a 1m buffer on all sides.

We applied woodchips only once, in May 2005, to an average depth of ~7.5 cm (equivalent to 135,000 kg/ha), in accordance with standard forestry practice. Thereafter, we applied nutrient amendments in three equal monthly amounts, from May through July, in 2005 and 2006. In 2007, we applied nutrient amendments once, in May (in an amount equal to 1/3 the regular annual rate).

To increase inorganic nitrogen, we applied ammonium nitrate fertilizer at a rate of 10 g N/m²/y. Sucrose was applied at a rate of 500 g C/m²/y to reduce inorganic nitrogen. This work was part of a larger experiment that included phosphorus manipulations. Here, however, because phosphorus manipulations produced no measurable effects on plant response, only the portions of the study involving mulch and nitrogen amendments are reported here. Results from plots within blocks that varied only in P amendments, relative to the treatments discussed here, were averaged before statistical tests were applied. The full factorial experiment, including all phosphorus information, is available in Miller (2008).

2.3. Soil analyses

Soil samples were collected prior to thinning in June 2004, to measure baseline values for gravimetric moisture content, pH, KCl-extractable nitrate and ammonium, and resin- and bicarbonate-extractable inorganic P. Following thinning, we recorded the volume of post-thinning organic matter in each plot, using a core with a 2 cm inner diameter and measuring the depth of the organic layer. We also compared soil C:N ratios of soil collected before thinning (June 2004) to soil collected after thinning (May 2005). The CHN analyses were performed by the Colorado State University Soil, Water, and Plant Testing Laboratory using a Leco CHN analyzer (Leco Co., MI). In 2006, we collected soil samples to determine the bulk density of the soils in each plot to assess whether soil compaction varied across the site, a likely outcome of the use of heavy machinery during thinning operations.

From May 2005 to October 2006, we installed three sequential sets of mixed-bed ion-exchange resin bags to monitor the flux of inorganic nitrogen (Binkley and Matson, 1983). The first set was deployed from May through October of 2005 (129 days), the second from October

2005 through May 2006 (211 days), and the third from May through October of 2006 (156 days). During each time period, we used 3 resin bags per plot. Each bag contained 10 g of mixed ion resin (J.T. Baker Mixed Bed Exchange Resin). For each deployment period, we reserved additional resin bags to serve as blanks. These were sealed in double plastic bags until extraction, at which time they were used to correct for background levels of inorganic nitrogen and phosphorus.

Resin bags were installed as close to a depth of 10 cm as possible, depending on rockiness of soils, but no less than 5 cm deep. After collecting resin bags at the end of each deployment period, we air-dried the resin bags for 1 week and homogenized the resin from the three resin bags within each plot. We extracted inorganic nitrogen from resin beads using a ratio of 30 ml of 2N KCl to 8 g air-dry resin. KCl extracts were filtered and then frozen until analysis on Alpkem autoanalyzers (OI Analytical, TX) by soil laboratories at the University of Colorado and Colorado State University.

In May 2006 (prior to inception of nutrient amendments that year) and May 2007 (3 weeks after first application of nutrient amendments that year), we collected soil samples to determine moisture content, pH, and KCl-extractable nitrate and ammonium. On each sampling date, we collected two soil samples from the top 10 cm of mineral soil in each plot, using cores with an inner diameter of 4 cm. We stored samples on ice until sieving/homogenizing with 2 mm sieves. To determine inorganic nitrogen, we kept samples chilled until extracting with KCl (50 ml of 2N KCl to 10 g field-moist soil) within 24 hours of field collection. KCl extracts from soil were analyzed in the same manner as described above for resin bag extracts. We corrected all results for soil moisture content. To determine pH, we used slurries of 10 g soil and 20 ml deionized water and allowed samples to equilibrate for exactly 1 hour before taking the pH

reading using an Orion pH meter (Orion Research, Inc., MA). Gravimetric soil moisture content was measured by drying 10 g field-moist soil at 105°C for 5-7 days. Soil texture was determined by laboratory particle-size analysis at the University of Colorado.

We used a combination of soil samples and buried ion-exchange resin bags from June 2004 through June 2007 to monitor the effects of nutrient and woodchip amendments on plant-available nitrogen. We used soil samples collected in 2006 and 2007 to determine bulk density, gravimetric moisture content, and pH.

To determine if thinning led to a change in total soil nitrogen pools, or if plot-level variations in soil C:N ratios influenced patterns of vegetation establishment, we analyzed soils collected prior to thinning (in 2004) and post-thinning (in 2005, prior to inception of nutrient manipulations) for total soil carbon and total nitrogen.

2.4. Measurement of vegetative response

Prior to thinning, we surveyed the understory species composition of each experimental block. Understory cover at that time was negligible, due to the dense canopy and a thick duff layer. Following thinning, understory plant establishment was abundant. In August of 2005, 2006, and 2007, we used point-intercept sampling of 100 points in the central 1 m² of each of the ninety research plots to determine species composition and the percent cover of each species. Any species that were present in a plot but not captured by the point-intercept sampling method were assigned a cover value of 0.01% for that plot. To determine relative cover of certain species, we calculated the proportion of the total plant cover that consisted of that species or group. Species diversity was calculated using the Shannon index. We also identified the species

that were identified either woodchip plots only or unchipped plots only during the three-year study.

2.5. Statistical analyses

To determine treatment effects on the patterns of plant establishment, we grouped plants by life form (annual or perennial/biennial), species origin (native or non-native), and functional groups (forb, graminoid, or woody plant). Species classified as “native” plants were those reported as native to Colorado in Weber and Wittmann (2001). For select species of management concern, we separately analyzed the species-level responses to experimental manipulations.

To statistically analyze treatment effect, we used a mixed-model approach to test for repeated measures in SAS version 9.1 (SAS Institute 2002-2004). We selected the appropriate covariance structure for each dataset prior to analysis. All models included *plot* as the repeated subject and *block* as a random factor. The initial model for each analysis included *year*, *nitrogen treatment*, *woodchip treatment*, and all possible interactions of the above. When analyzing the responses of functional groups of vegetation, *species origin* was also included in the original model. Where 3- or 4-way interactions were not significant, those interaction terms were omitted from the final model. We performed post-hoc assessments of individual treatment effects using Tukey tests. For all cases where interactions among treatment effects are significant, we present the results for the highest-level interactions. Where interactions were not significant, we only present the main treatment effects. Finally, to determine if woodchip amendments affected the distribution of locally-rare plants, we utilized the Chi Square Goodness-of-Fit test.

3. RESULTS

3.1. Soil responses

The soil texture at the research site was a sandy clay loam, composed of 55% sand, 25% silt, and 20% clay. Mean post-thinning bulk density at the site was 0.91 g/cm^3 and did not significantly vary by block. The mean soil C:N ratio at the site was 21.82 ± 0.28 , by dry weight ($n=90$) and did not significantly vary before and after thinning (Miller 2008).

Prior to thinning, soil pH at the research site was mildly acidic and varied significantly by block ($F_{2,15}=9.54$, $p<0.01$), from a low of 4.9 ± 0.1 to a high of 5.8 ± 0.2 . Mean pH of the organic layer was 4.9 ± 0.1 ($n=15$). Woodchips did not significantly alter soil pH over the course of the experiment, while the pH of sugar plots exhibited mean values of 5.4 versus 5.6 for control or N-added plots in 2007 ($F_{2,46}=3.60$, $p=0.03$).

Soil moisture varied significantly by block prior to thinning, from a low of $0.17 \pm 0.009 \text{ g}$ water/g dry soil to a high of $0.26 \pm 0.03 \text{ g}$ water/g dry soil ($F_{2,15}=4.27$, $p<0.05$). Among post-thinning soil samples collected in 2006 and 2007, soil moisture was significantly affected by both woodchip and nitrogen manipulations; these treatment effects did not interact with each other or with the sampling date. Mean soil moisture was significantly greater in woodchip plots than in unchipped plots ($0.33 \pm 0.02 \text{ g}$ water/g soil in woodchip plots; $0.27 \pm 0.02 \text{ g}$ water/g soil in unchipped plots) ($F_{1,46}=28.15$, $p<0.0001$). Mean soil moisture was also significantly greater in sugar plots ($0.33 \pm 0.02 \text{ g}$ water/g soil) than in ambient-N or fertilized-N plots ($0.29 \pm 0.02 \text{ g}$ water/g soil in each) ($F_{2,46}=3.69$, $p=0.03$).

Prior to thinning in June 2004, mean KCl-extractable inorganic soil nitrogen (NH_4^+ and NO_3^- combined) did not vary significantly among blocks (mean of $6.3 \pm 0.6 \mu\text{g N/g}$ soil). Following thinning and the inception of nutrient manipulations, we found that our applications of ammonium nitrate fertilizer significantly increased the flux of inorganic nitrogen in all time

periods of resin bag deployment (summer 2005, winter 2005-2006, and summer 2006), but that sugar amendments did not induce the intended reduction in the flux of inorganic nitrogen until the second growing season of the study (year**nitrogen* interaction: $F_{4,72}=9.94$, $p<0.0001$). By 2007, however, the expected pattern was observed (Fig. 1). Soil samples collected in the spring of 2006 and 2007 confirmed the ongoing effectiveness of the soil amendments used to manipulate nitrogen availability, but we found that woodchip amendments temporarily interacted with this effect. In 2006, we collected soil cores prior to application of nutrient amendments that year and found that plots that had been fertilized with nitrogen the previous year still had significantly more plant-available nitrogen than ambient or sugar-treated plots, but that this effect was reduced where woodchips were present (*nitrogen*woodchip* interaction: $F_{2,20}=312.76$, $p<0.02$) (Fig. 2). In contrast, we collected the 2007 soil cores three weeks after applying the first nutrient amendments of the year. At that time, we found that the first nutrient amendments of the season had already reestablished the gradient of nitrogen availability ($F_{2,20}=41.67$, $p<0.0001$) (Fig. 3a). Furthermore, we found approximately 33% more inorganic nitrogen, overall, in woodchip plots than unchipped plots ($F_{1,20}=11.64$, $p<0.003$) (Fig. 3b). These effects did not interact in 2007. The overall difference in mean inorganic soil nitrogen in 2006 and 2007 is within the expected range of variability for different sampling dates.

3.2. Vegetation response

The diversity of understory plant species at the site was low in the three years following thinning. Variation in diversity was not explained by plot-level variation in soil moisture, bulk density, or litter depth. Woodchip amendments were associated with significantly lower understory species diversity than found in unchipped plots ($F_{1,72}=41.33$, $p<0.0001$). This trend

did not vary by year; the annual mean Shannon diversity value for woodchip plots was 0.7 ± 0.06 , as compared to 1.1 ± 0.06 in unchipped plots. Nitrogen manipulations did not affect understory species diversity.

Shannon Diversity is a combined measure of species richness and evenness; in this case, the lower diversity in woodchip plots can be attributed to low species richness. Evenness of species distributions did not vary by treatment type. On average, woodchip plots contained less than half the number of plant species as unchipped plots, with a three-year mean of $9.0 (\pm 0.4)$ species in unchipped plots but only $4.4 (\pm 0.4)$ species in woodchip plots ($F_{1,156}=147.88$, $p<0.0001$). Richness was not affected by nitrogen manipulations.

In agreement with the finding that the species richness of woodchip plots was significantly lower than that of unchipped plots, we found that ~24% of the species present at the site were entirely excluded from woodchip plots during the three-year study. Out of a total of 63 species, 15 species were never found in woodchip plots (Table 1). Of those, the majority were native forbs and native graminoids. In contrast, only two species, both non-natives, were present only in woodchip plots over the three-year study period. Although the species that were entirely excluded from either woodchip or unchipped plots tended to be those that were locally infrequent (66% of the species excluded from either woodchip or unchipped plots were present in experimental plots only one year out of the three years of the study), the distribution of those infrequent species was skewed toward exclusion from woodchip plots to a degree that is unlikely to occur by chance (Chi Square Goodness of Fit test: $p<0.002$, $\chi^2=9.94$, $df=1$).

Plant cover in all plots increased over time, but this trend was primarily driven by an increase in non-native plant cover; the mean annual cover of native plants did not significantly change from 2005 to 2007 (year*origin interaction: $F_{2,156}=5.19$, $p<0.01$) (Fig. 4). Nitrogen

manipulations and woodchip amendments interacted to affect overall plant cover: fertilization was associated with greater mean plant cover than found in ambient plots, but sugar treatments did not affect plant cover. Furthermore, the presence of woodchip amendments was associated with significantly lower plant cover within each level of nitrogen availability (nitrogen*woodchip interaction: $F_{2,72}=3.97$, $p=0.02$) (Fig. 5). In fact, the presence of woodchips completely inhibited the increased plant cover that was otherwise associated with nitrogen fertilization.

3.3. Post-Thinning Patterns Plant Establishment by Functional Group

Overall, the study plots tended to contain slightly more non-native plant species than native plant species, with annual means of 6.1 (± 0.4) native plant species and 7.23 (± 0.4) non-native species per plot. Sixty-three species of plants became established in the experimental plots at Heil Valley Ranch during the three years after thinning (Miller 2008; data not shown). Many of these species occurred infrequently; 85% of the mean annual plant cover was comprised of just twelve species during the three-year study. The majority of the understory plants that became established in the three years after thinning had a perennial or biennial life form. Neither woodchip nor nutrient amendments affected the relative cover of annuals to perennials/biennials. On all sampling dates, annuals comprised less than 5% of the understory cover.

Since most species were present at low levels of mean annual cover, we grouped species according to species origin (native and non-native) and functional group (forbs, graminoids, and woody plants) in order to analyze responses to nitrogen and woodchip manipulations. For two non-native forb species that were especially common at the site, we also analyzed the species-level responses to experimental manipulations. Both species were present in over half of the

experimental plots each year and are classified as noxious weeds in the state of Colorado: *Cirsium arvense* (Canada thistle) and *Verbascum thapsus* (common mullein).

Native and non-native graminoids attained similar levels of cover within each year, with overall graminoid cover increasing from a mean of 8.9% (± 2.0) of the plot area in 2005 to a mean of 23.0% (± 2.8) in 2007 ($F_{2,156}=11.68$, $p<0.0001$). The species with the greatest mean annual relative cover at the site (17% of the vegetation) in the three years following thinning was a non-native graminoid, *Poa pratensis* (Kentucky bluegrass).

Woodchips significantly inhibited the establishment of graminoid cover throughout the three-year study: the annual mean cover of graminoids in unchipped plots was 22.7% (± 2.0), as compared to 6.9% (± 2.0) in woodchip plots ($F_{1,156}=51.54$, $p<0.0001$). There was no difference in the response of native and non-native graminoids to woodchip amendments, and nitrogen manipulations did not affect the cover of native or non-native graminoids in any year.

Fertilizer significantly increased the mean annual cover of forbs, but this effect was lost if woodchips were present (nitrogen*woodchip: $F_{2,156}=4.39$, $p=0.01$). Mean annual forb cover in unchipped, fertilized plots was 22.4% (± 2.9) of the plot area. Among all other treatment types, mean forb cover was less than 11% of the plot area per year and did not significantly vary over time or in response to woodchip and/or nitrogen manipulations during the three years of the study. The observed increase in forb cover in response to nitrogen fertilization was driven by the non-native forbs. Native forbs were present only at low levels of cover during the three years after thinning and did not exhibit changes in mean annual cover in response to nitrogen manipulations.

Within all nitrogen manipulation types, the non-native forb group (analyzed without including *Cirsium arvense*) was present at significantly greater levels of cover than that of native

forbs, but the mean annual cover of non-native forbs was especially great in nitrogen-fertilized plots (nitrogen*origin: $F_{2,156}=8.75$, $p=0.003$) (Fig. 6). These trends did not significantly change over time.

Woodchip amendments significantly inhibited the cover of non-native forbs: their mean annual cover was 24.7% (± 2.7) in unchipped plots but only 14.6% (± 2.7) in woodchip plots (woodchip*origin: $F_{1,156}=8.81$, $p=0.004$). Native forb cover was consistently low in all treatment types and was not significantly affected by woodchip amendments.

When the response of the noxious weed, *Cirsium arvense*, was analyzed, we found that the cover of *C. arvense* increased strongly in response to nitrogen fertilization by the second year of the study. In the first growing season after thinning (2005), the mean cover of *C. arvense* was similar in all nitrogen treatment types (less than 3% cover in each). However, in each of the following two years, the mean cover of *C. arvense* was significantly greater in nitrogen-fertilized plots (10.1% (± 1.8) in 2006 and 8.6% (± 1.8) in 2007) than in ambient and sugar plots (mean annual cover of less than 5% in each) (year*nitrogen: $F_{2,72}=2.69$, $p<0.04$). Conversely, the cover of *C. arvense* was not affected by sugar amendments.

Although increased plant cover is an expected response to fertilization, the increase in *C. arvense* was disproportionately greater than that of other species. Its relative cover in ambient and sugar-treated plots was less than 7% of the total plant cover, whereas it comprised 17.1% (± 2.4) of the total plant cover in fertilized plots ($F_{2,72}=12.28$, $p<0.0001$, data not shown).

The absolute cover of *C. arvense* was unaffected by woodchip treatments, which translated into significantly greater relative cover of *C. arvense* in woodchip plots over time (year*woodchip: $F_{2,72}=3.34$, $p=0.04$) (Fig.7a), since woodchips tended to inhibit the development

of plant cover for most other species. Among unchipped plots, the relative cover of *C. arvensis* remained consistent over time.

In contrast, the relative cover of the other locally-common noxious weed, *Verbascum thapsus*, was unaffected by nitrogen manipulations but disproportionately inhibited by woodchip amendments, although the magnitude of that response varied over time (year*woodchip: $F_{2,72}=4.46$, $p<0.02$) (Fig. 7b). The greatest relative cover of *V. thapsus* was found in unchipped plots in the first two years after thinning, where it comprised ~19% of the total plant cover in each year. By the second year, the relative cover of *V. thapsus* in woodchip plots was very low, close to 1%.

The woody plants that became established at the site, including ponderosa pine seedlings, were all native species. As a group, the native woody species attained significantly greater relative cover in fertilized woodchip plots than in all other treatment types, with annual mean cover values of 2.1% (± 0.5) of the plot area in fertilized woodchip plots over the three-year study, as compared to less than 1% in all other treatment types ($F_{2,72}=4.72$, $p=0.01$; data not shown). This effect did not significantly vary over time. However, the percentage of plots that contained ponderosa pine seedlings did increase over time ($F_{2,72}=15.67$, $p<0.0001$). Ponderosa seedlings were not observed in the first growing season after thinning, but were found in 13% of plots in 2005 and 24% of plots in 2006. Neither woodchip nor nitrogen manipulations affected the pattern of ponderosa seedling germination.

4. Discussion

Our study overlapped with the work of Wolk and Rocca (2008) who measured the vegetation response of this area during three to five growing seasons post-thinning. That study

differed from ours in comparing thin+woodchips, thin only, and unthinned stands whereas here we focus only on the first three growing season responses of thinned areas that varied in wood chip cover and soil fertility status. The two studies were consistent in reporting declines in vegetation cover with the addition of woodchips, but differed in some species-specific responses reported here. Our work also contributes to an understanding of the specific mechanism(s) whereby woodchips affect the vegetation response.

Woodchips did not alter nitrogen availability at ambient levels of soil fertility during the first two year of the study as measured by buried ion-exchange resin bags. However, woodchips prompted immobilization of a portion of the excess nitrogen applied to nitrogen-fertilized plots, suggesting that woodchips selected for a microbial community that was more effective at utilizing excess incoming inorganic nitrogen than at utilizing inorganic nitrogen in the soil. By the spring of the third growing season of the study, woodchips were associated with increased soil nitrogen availability across all treatment types. Woodchips did not alter soil pH, but did increase average percent soil moisture. Woodchip amendments had profound effects on patterns of understory plant establishment at the site: woodchips were associated with significantly lower species richness, diversity, and overall cover than found in unchipped plots in the three years after thinning. On the whole, woodchips excluded more species than they promoted.

Applications of ammonium nitrate fertilizer immediately increased the flux of plant-available nitrogen, whereas sugar amendments did not induce a measurable reduction in the flux of plant-available nitrogen until the second growing season of the study. We found that nitrogen manipulations did not affect species richness or diversity of the understory plants that became established in the three years after thinning. However, nitrogen fertilization did promote increased plant cover. This response was primarily driven by an increase in non-native forb

cover. In contrast, the cover of native forbs, native graminoids, and non-native graminoids was unaffected by nitrogen manipulations in either direction. The abundant establishment of non-native forbs at the site is a management concern and is likely due, in part, to high propagules pressure from nearby meadows, which experienced heavy grazing in the past. However, the presence of woodchip amendments inhibited the establishment of non-native forb cover in all three years of the study, even in the presence of nitrogen fertilization.

Both native and non-native graminoids became well-established at the site in the three years after thinning. From a management standpoint, this outcome may be a desirable one, as graminoids are thought to be the historically dominant understory vegetation type (Veblen and Brown, 2001). Other studies have reported a strong response by native graminoids to thinning operations (Scherer *et al.*, 2000; Dodson and Fiedler, 2006; Nelson *et al.*, 2008), but in this study, native and non-native graminoids responded similarly to experimental manipulations. Native and non-native graminoids exhibited similarly reduced mean annual cover in response to woodchip amendments in each of the three years of the study and the relative abundances were unaffected by nitrogen manipulations.

Overall, nearly 60% of the plant cover in the thinned forest was comprised of non-native species. The three species that attained the greatest mean relative cover at the site were all non-native perennial species: *Poa pratensis*, *Cirsium arvense*, and *Verbascum thapsus*. The first, *Poa pratensis*, was similarly found to dominate thinned forest sites at nearby Rocky Mountain National Park (Dodson, 2004). The latter two are state-listed noxious weeds. The dominance of these species may be a temporary response to the availability of resources that will diminish over time, or may be indicative of a lasting trajectory; at this time, the long-term outcome is impossible to predict.

In each of the three years after thinning, over 95% of the plant cover was comprised of species with a perennial or biennial life form. Neither woodchip nor nitrogen manipulations affected the ratio of the relative cover of annuals to perennials/biennials. In other studies, annual and perennial species responded differently to nitrogen manipulations; perennials tend to be particularly well-adapted to habitats with low nutrient availability (Carson and Barrett, 1988; Lowe et al., 2003), and several studies have reported that annuals were disproportionately inhibited by reduced levels of plant-available nitrogen (McLendon and Redente, 1992; Paschke *et al.*, 2000; Prober *et al.*, 2005; Eschen *et al.*, 2007). Conversely, nitrogen enrichment has been found to promote the dominance of annual species (Carson and Barrett, 1988; Paschke *et al.*, 2000). However, those studies investigated the effects of nitrogen manipulations in established herbaceous communities. In this study, we tested the effects of nitrogen manipulations during the first three years of plant establishment after thinning of a forest largely lacking an understory vegetation. Thus, the difference in results may be due to the difference in the importance of competition between establishing and well-established plant communities. Another study performed in a thinned Arizona ponderosa pine forest similarly found that perennials were initially the most dominant life form after thinning, but reported a large pulse in the biomass of annual plants 5 years after thinning (Moore et al., 2006).

Nitrogen manipulations did not affect the species richness or diversity of the establishing understory plant community. This response was unexpected because a number of other studies have found that nitrogen fertilization was associated with reduced species richness due to the strong growth response of a few, dominant species (Huston, 1997; Foster and Gross, 1998; Huenneke *et al.*, 1990; ;Wilson and Tilman, 1991; Tilman, 1993; Stevens *et al.*, 2004). A 2005 meta-analysis of the relationship between nitrogen availability and species diversity found that

nitrogen fertilization is frequently associated with the loss of species richness in a variety of terrestrial ecosystems (Suding et al., 2005). Specifically, nitrogen fertilization was found to exclude rare plants in general but also plants that are better adapted for belowground competition (for nitrogen) than aboveground competition (for light); i.e., plants of native origin, nitrogen fixers, perennials, and plants with short stature.

In this study, we did not find that that nitrogen fertilization affected species richness or the proportion of annual to perennial/biennial plants. However, we investigated patterns of plant establishment in the first three years after thinning, so competition (for either nutrients or light) was unlikely to have yet become a strong driver of patterns of plant distribution. Nevertheless, we did find that nitrogen manipulations altered the proportion of native and non-native understory species that became established. In this study, the absolute cover of native graminoids and forbs remained similar across all levels of nitrogen availability. This result suggests that the resident native plants, as a group, were constrained in their ability to respond to nitrogen fertilization. Likewise, non-native graminoid cover was similar at all levels of nitrogen availability, a result that contrasts with the findings of several other studies that found that nitrogen enrichment specifically favored non-native grasses (Bobbink and Willems, 1987; Huenneke *et al.*, 1990; ; Lowe *et al.*, 2003; LeJeune *et al.*, 2006). Non-native forbs, especially *Cirsium arvense*, were tolerant of reduced levels of nitrogen availability yet were able to readily respond to increases in nitrogen availability by increasing in cover. Clearly, reductions in nitrogen availability did not provide a competitive advantage to native plants in this system.

Although several studies have reported that carbon amendments (primarily sugar, sawdust, or a mixture of the two) provided a competitive advantage to native plants by reducing nitrogen availability (Morgan, 1994; Zink and Allen, 1998; Paschke *et al.*, 2000; Blumenthal *et*

al., 2003; Perry *et al.*, 2004; Averett *et al.*, 2004; Prober *et al.*, 2005), others found that carbon amendments inhibited native and non-native plants similarly (McLendon and Redente, 1992; Seastedt *et al.*, 1996; Alpert and Maron, 2000; Baer *et al.*, 2004; Eschen *et al.*, 2006; Kulmatiski and Beard, 2006; Lowe *et al.*, 2002; Paschke *et al.*, 2000;) and yet others found that carbon amendments did not inhibit either natives or non-natives at all (Wilson and Gerry, 1995; Reeve-Morghan and Seastedt, 1999; Cione *et al.*, 2002; Corbin and D'Antonio, 2004; Huddleston and Young, 2005). The current study falls in with the latter. Apparently, carbon addition promotes the relative success of natives in some ecosystems but not others.

The successful use of carbon addition as a restoration tool to promote the establishment of native species likely depends on a number of factors. As suggested by Blumenthal *et al.* (2003), not only must nitrogen be the limiting nutrient in the system and the carbon additions great enough to overcome the nitrogen-storage capacity of the soil, but also the non-native species must be more nitrophilic than the native species. Although a large number of native North American plants have undoubtedly evolved under low nutrient conditions, not all native plants are constrained in their ability to respond to increased availability of resources, and not all non-native invaders are fast-growing nutrient-lovers (Padgett and Allen, 1999; Lowe *et al.*, 2002; Thomsen *et al.*, 2006; Funk and Vitousek, 2007). Furthermore, not all invasions are governed by nutrient availability; a number of other factors are important components of non-native plant invasion success, such as reproductive rate, dispersal ability, and escape from natural enemies (Rejmanek and Richardson 1996; Lonsdale, 1999; Keane and Crawley, 2002; Shea and Chesson, 2002). It is not surprising that there are cases where experimental reduction of nitrogen availability does not provide a competitive advantage to the native plants.

Woodchip amendments significantly reduced species richness and, correspondingly, species diversity in each year of the study. This effect did not vary by year, with woodchip plots consistently containing about half the number of species as unchipped plots. Overall, we found that woodchips excluded more species than they promoted. Only two species [both non-native and one (*Linaria dalmatica*) a Colorado noxious weed,] were found only in woodchip plots during the three year study. In contrast, 15 species were found only in unchipped plots. Most of the species showing these patterns of exclusion were locally infrequent, but woodchips nevertheless appear to reduce local plant diversity by excluding certain species entirely.

Plant cover was significantly lower in woodchip plots than unchipped plots in all years. One noxious weed species of management concern, *Verbascum thapsus*, was strongly inhibited by woodchip amendments. Wolk and Rocca (2008) reported a similar finding for the invasive annual grass, *Bromus tectorum*. However, not all species were inhibited by woodchips. The absolute cover of *Cirsium arvense* was unaffected by woodchip treatments, which translated into significantly greater relative cover in woodchip plots for that species. *Cirsium arvense* likely benefits from its ability to spread vegetatively, and this weed also benefited from additional nitrogen from fertilizer or (in year three) woodchips. Individuals that become established in a gap with bare soil can spread into woodchip-covered areas that provide greater soil moisture. Another local study reported that plants capable of vegetative reproduction were found more frequently in woodchipped areas than in unchipped areas (Wolk and Rocca 2008). Woodchip amendments did not affect the mean annual cover of native forbs, which were present at low levels of cover in all treatment types (although woodchips did exclude several species of native forbs altogether, as discussed previously). Likewise, native woody plants were present at low levels of cover, but exhibited greater cover in fertilized woodchip plots. Presumably, these

species are large enough to survive burial by woodchips and benefit from the increased soil moisture associated with woodchip plots. Ponderosa pine seedlings were present in an equal number of woodchip and unchipped plots within each year. However, this study was not able to assess long-term survivorship. This topic is one that deserves further investigation, as the goal of forest mitigation projects is to reduce tree density. Any impact of woodchip amendments on ponderosa pine regeneration, either positive or negative, would be an important management consideration.

5. Conclusions

Mechanical forest thinning for fire mitigation is a fact of life for land managers throughout the western United States. However, the physical disturbances of mechanical thinning create conditions that are associated with a subsequent increase in understory species richness and cover. At this site, approximately 60% of the mean annual plant cover in the three years following thinning operations was comprised of non-native plant species. Thus, thinning for fire mitigation can lead to secondary environmental concerns.

We found that woodchips did not reduce plant-available soil nitrogen at ambient levels of fertility, but present a physical barrier that influenced patterns of plant establishment. Propagules either could not germinate in or could not survive the environment created by the mulch. Here, we showed that woodchip amendments significantly reduced the richness and cover of understory plant species. In fact, woodchips excluded certain species altogether, especially locally-uncommon, native herbaceous plants. In contrast, native shrubs attained greater relative cover where woodchips were applied, as did the noxious weed *Cirsium arvense*.

The application of woodchip amendments in fire mitigation operations does not appear to affect soils in ways that strongly affect nutrient availability, but it does reduce local species richness and plant cover, at least initially. Several local species demonstrated particularly strong responses to woodchip amendments. Thus, where the dual management concerns of fire mitigation and weed management coexist, the decision to apply woodchip mulch needs to consider impacts on understory species richness and composition.

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Table 1. Species present on plots but not found in woodchip plots or only found in woodchip plots. Parentheses following the species name indicate functional group (f=forb, g=graminoid) and life form (a=annual, p=perennial, b=biennial).

	Not found on woodchip plots	Only found on woodchip plots
Native	<i>Agaloma marginata</i> (f, a)	[none]
	<i>Artemisia frigida</i> (f, p)	
	<i>Corallorhiza maculata</i> (f, p)	
	<i>Geranium caespitosem</i> (f, p)	
	<i>Koeleria macrantha</i> (g, p)	
	<i>Maianthemum stellatum</i> (f, p)	
	<i>Potentilla effusa</i> (f, p)	
	<i>Potentilla fissa</i> (f, p)	
	<i>Senecio intergerrimus</i> (f, p)	
	<i>Senecio spartioides</i> (f, p)	
	<i>Stipa viridula</i> (g, p)	
Non-Native	<i>Solanum physalifolium</i> (f, a)	<i>Linaria dalmatica</i> (f, p)
	<i>Solanum triflorum</i> (f, a)	<i>Phleum pratense</i> (g, p)
	<i>Tragopogon dubius</i> (f, b)	
	<i>Verbena bracteata</i> (f, p)	

Figure legends

Figure 1. Mean inorganic N amounts captured per gram of resin per day in sugar-amended, control, and N-added plots (n=30 per year). Different letters indicate significantly different mean values for log-transformed values.

Figure 2. Inorganic N concentrations of soils of sugar, control, and N-added plots with and without woodchips in 2006. The immobilization potential of wood chip additions were evident in the N-added plots but showed no impacts in other treatments.

Figure 3. Reversal of woodchip effects on inorganic N concentrations of soils. Immobilization effect of woodchips observed in 2006 (figure 3a) changes to an apparent N enrichment effect of woodchips in 2007 (figure 3b).

Figure 4. Native and non-native plant cover for all plots during first three years following thinning.

Figure 5. Effect of woodchips and nutrient manipulations on plant cover following thinning.

Figure 6. Relative abundance of native and non-native forbs (herbaceous dicots, excluding Canada thistle) as a function of soil treatments, averaged over the first three years following thinning.

Figure 7. Effects of woodchips on the relative abundance of two noxious weeds of Colorado.

Figure 7a. Canada thistle (*C. arvensis*) shows ability to become a relatively abundant in woodchip plots. Figure 7b Common mullen (*V. Thapsus*) exhibits a negative response to woodchip additions.

Fig. 1

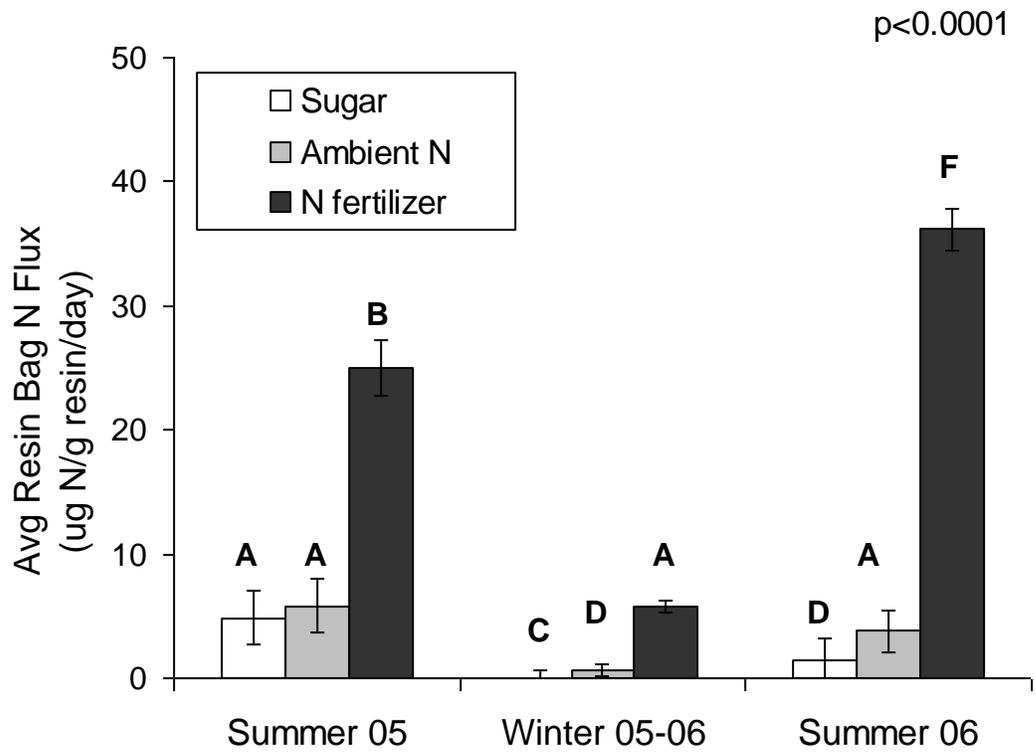


Fig 2.

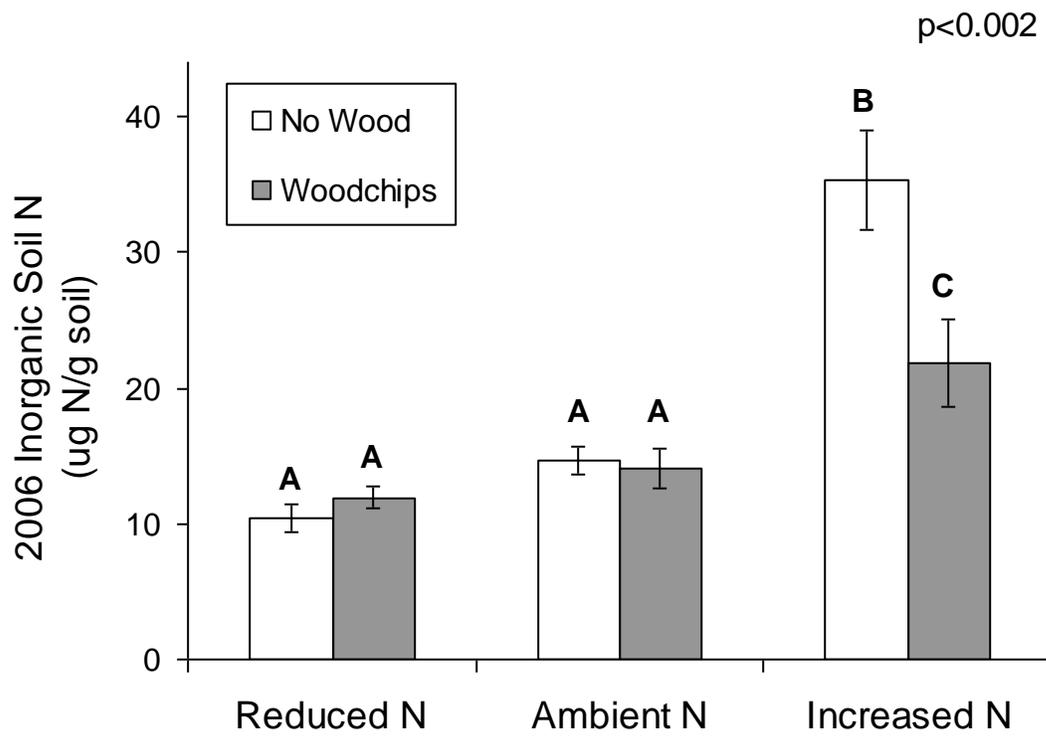


Fig 3a

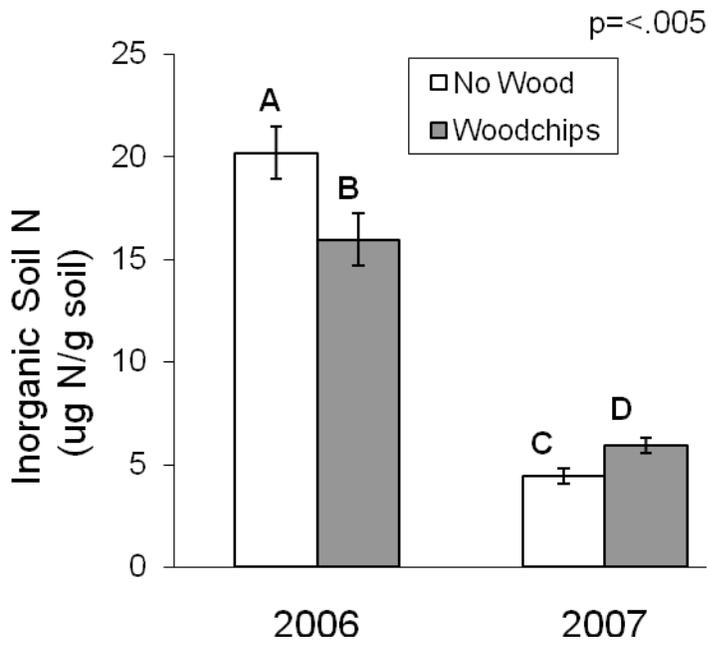
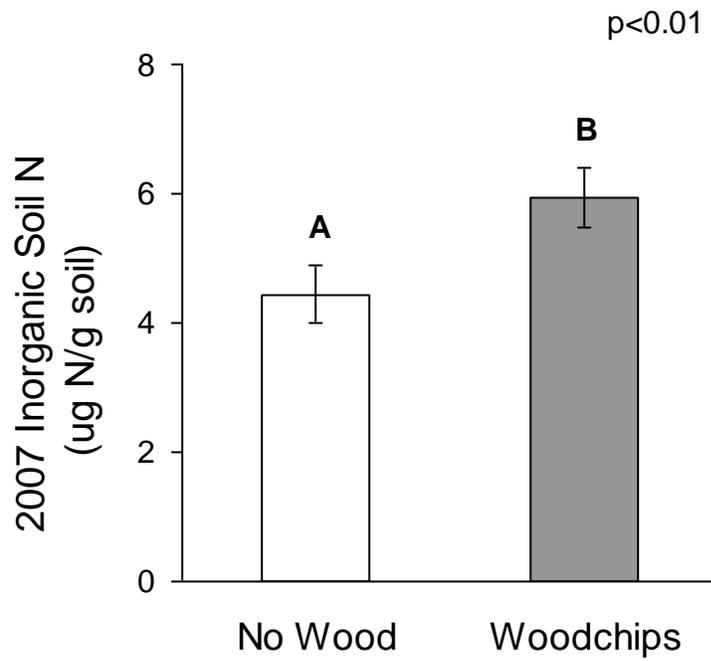


Fig 3b



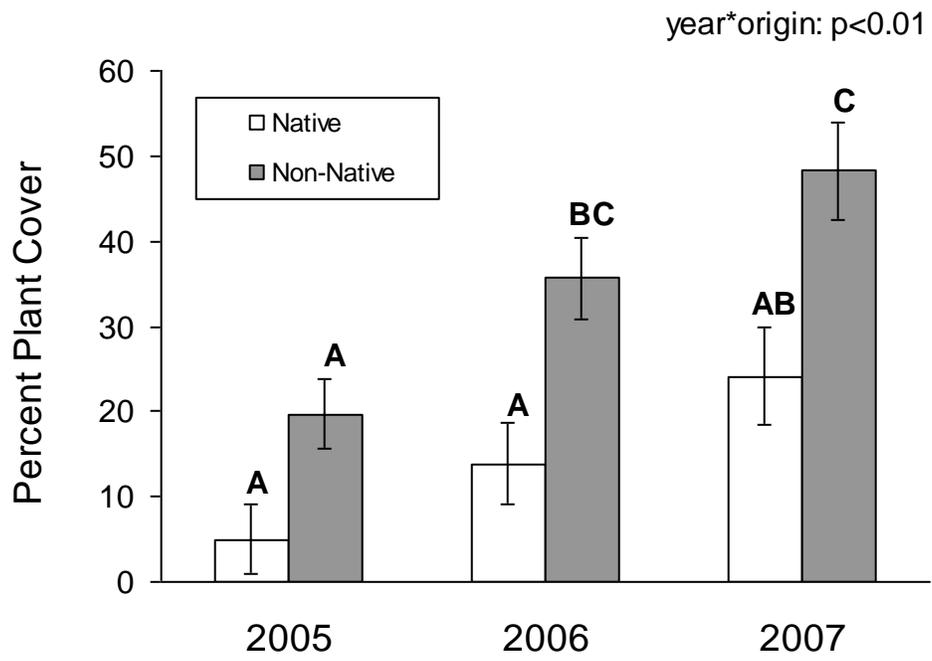


Fig. 4

Fig. 5

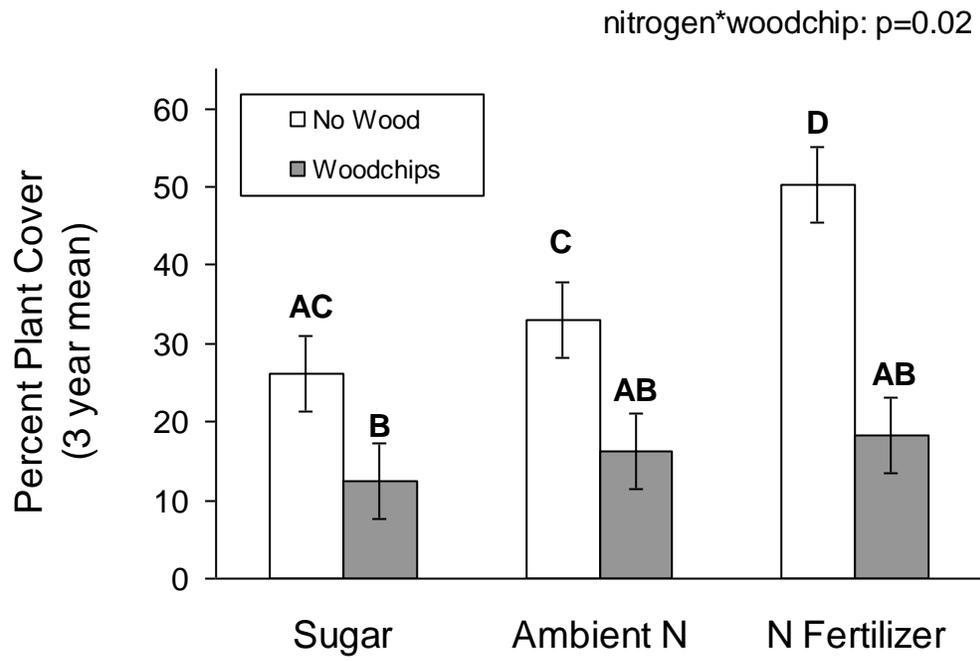


Fig 6

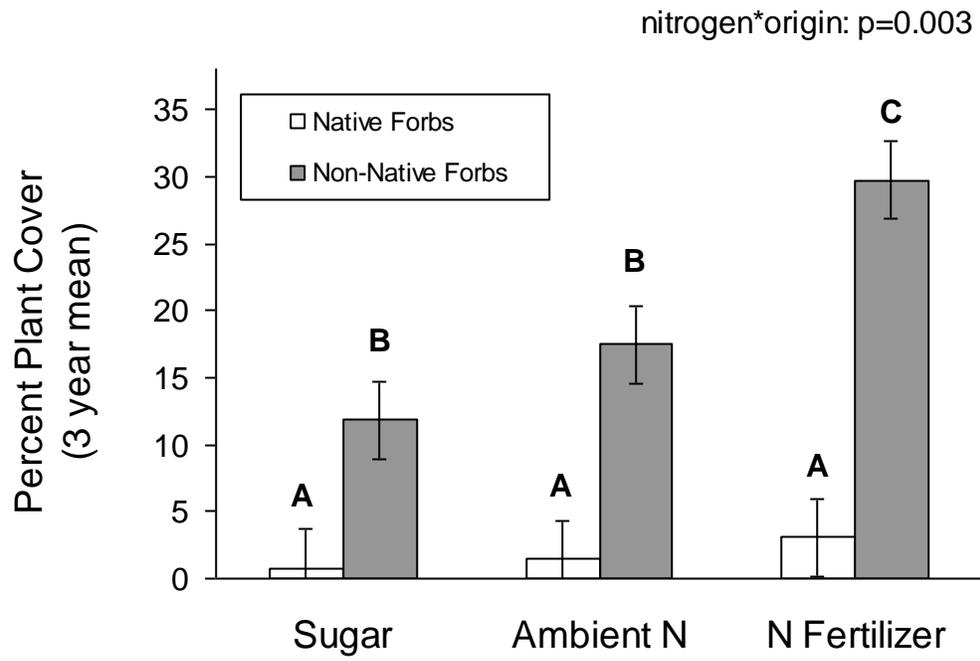


Fig. 7a

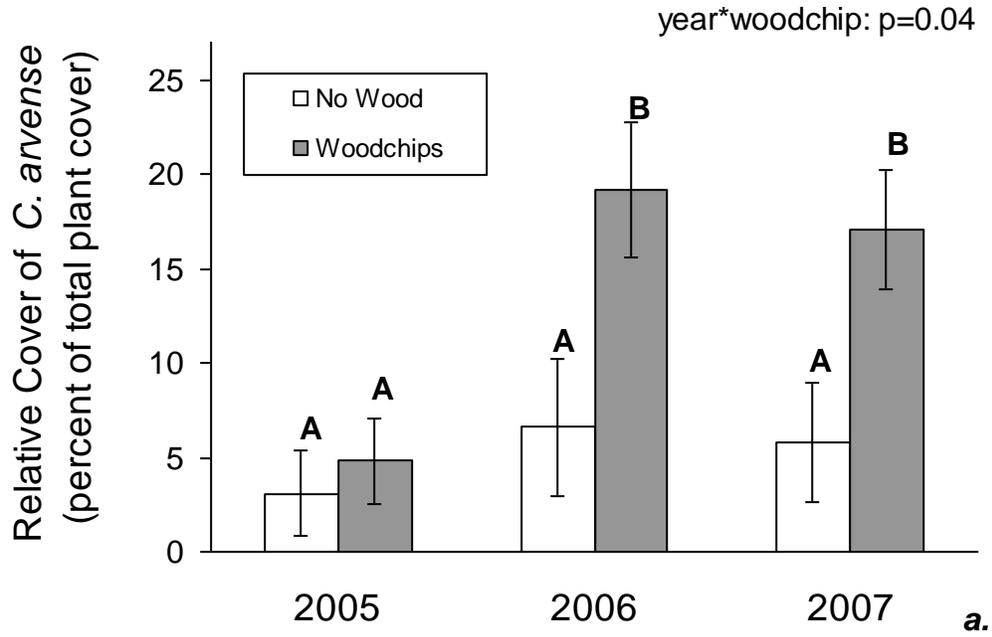


Fig 7b

