Microbial Responses to Coarse Woody Debris in *Juniperus* and *Pinus* Woodlands

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ABSTRACT

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The ecological significance of coarse woody debris (CWD) is usually highlighted in forests where CWD constitutes much of an ecosystem's carbon (C) source and stores. However, a unique addition of CWD is occurring in semi-deserts for which there is no ecological analog. To stem catastrophic wildfires and create firebreaks, whole *Juniperus osteosperma* (Torr.) and *Pinus edulis* (Engelm.) trees are being mechanically shredded into CWD fragments and deposited on soils previously exposed to decades of tree-induced changes that encourage "tree islands of fertility." To investigate consequences of CWD on C and nitrogen (N) cycling, we evaluated microbial metabolic activity and N transformation rates in *Juniperus* and *Pinus* surface and subsurface soils that were either shredded or left untreated. We sampled three categories of tree cover on over 40 tree cover encroachment sites. Tree cover categories (LOW = 0-15%, MID ≥15-45%, HIGH ≥45%) were used to indicate tree island development at time of treatment. In conjunction with our microbial measurements, we evaluated the frequency of three exotic grasses, and thirty-five native perennial grasses to identify links between belowground and aboveground processes. The addition of CWD increased microbial biomass by almost two-fold and increased microbial efficiency, measured as the microbial quotient, at LOW *Juniperus* cover. C mineralization was enhanced by CWD only in *Pinus* soils at the edge of tree canopies. The addition of CWD had little impact on microbial activity in subsurface soils. CWD enhanced the availability of dissolved organic C (DOC) and phosphorus (P) but tended to decrease the overall quality of labile DOC, measured as the ratio of soil microbial biomass to DOC. This suggested that the increase in DOC alone or other environmental factors novel to CWD additions lead to the increase in biomass and efficiency. P concentrations were consistently higher following CWD additions for all encroachment levels. The CWD additions decreased N mineralization and nitrification in *Juniperus* and *Pinus* soils at LOW and MID tree cover but only in surface soils, suggesting that less inorganic N was available to establishing or residual plants. The frequency of native perennial grasses, especially *Elymus elymoides* (Raf.), was at least 65% higher under CWD additions for all categories of tree cover, while the frequencies of exotic annual and perennial grasses were not impacted by CWD. The frequency of all perennial grasses ranged from 10-27%. Our results suggest that CWD enhanced microbial activity even when the quality of C substrates declined requiring microbes to immobilize more N. The reduction in inorganic N may promote the establishment and growth of native perennial grasses. Ultimately, the addition of CWD improved soil conditions for microbes in tree islands of fertility.

Keywords: coarse woody debris; dissolved organic carbon; microbial quotient; nitrogen mineralization; nitrification; phosphorus; Piñon-juniper; soil microbial biomass

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1. INTRODUCTION

Coarse woody debris (CWD) influences microorganisms and ecosystem processes by reducing wind and water erosion and stabilizing soil surfaces (Laiho and Prescott, 2004); capturing and governing the release of nutrients and water essential for microbial metabolic activity and higher plant establishment (Miller and Seastedt, 2009); and determining the storage and release of carbon (C) as soil organic matter or CO_2 to the atmosphere (Spears and Lajtha, 2004). The ecological significance of microbial responses to CWD is usually highlighted in forest ecosystems where CWD may constitute upwards of 10-20% total ecosystem C and regulate microbial biomass and C and nitrogen (N) cycling (Pregitzer and Euskirchen, 2004). However, recently there is an unparalleled addition of CWD occurring in semi-desert ecosystems for which there is no ecological comparison. To stem catastrophic wildfires and create firebreaks in sagebrush/grassland ecosystems (Owen et al., 2009; Ross et al., 2012), thousands of hectares of trees are being mechanically shredded into CWD fragments and translocated to the soil surface. The action of shredding or mastication of desert tree species offers an unprecedented opportunity to understand the impact of CWD on microbial activity in an ecosystem that rarely is exposed to CWD.

In semi-desert ecosystems, "shrub or tree islands of fertility" in contrast to barren plant interspaces (Charley and West, 1975), are chiefly responsible for differences in microbial processes prior to CWD additions. Soils beneath trees are enriched with C and other essential elements (e.g., N, P and Ca) due to litter and root inputs and root translocation of elements from interspace soils (Schlesinger et al., 1996; Schlesinger and Pilmanis, 1998). But even under this enrichment, microbes in tree island soils are often C-limited due to the low quality of pine needle litter. For example, respiration per unit microbial biomass is lower in soils beneath trees than in

adjacent shrub/grassland soils indicating that microbes are less efficient at C mineralization (Liao and Boutton, 2008). Further, despite C-limitation, shrub islands maintain higher levels of microbial biomass than present in interspace soils (Aanderud et al., 2010). Besides metabolic activity, microbial N transformations (e.g., N mineralization and nitrification) are higher beneath tree islands than interspace soils (Schade and Hobbie, 2005). However, the impact of CWD on microbial activity in semi-deserts is relatively unknown and the addition of CWD has the potential to alter soil respiration dynamics and N transformations. For example, in forest soils, additions of CWD stimulate soil respiration in the short-term (i.e., days-year) by releasing labile C substrates, but in the long-term (i.e., year-years) changes in soil respiration are dependent on tree litter chemistry (McClaugherty et al., 1985; Murphy et al., 1998; Resh et al., 2007; Gallo et al., 2009). Further, in forest and desert systems, CWD increases soil moisture, thereby affecting respiration and decomposition rates (Fierer et al., 2003; Lipson and Schmidt, 2004; Crawford et al., 2005; Gottlicher et al., 2006; Monson et al., 2006; Zobitz et al., 2008), net N mineralization (Evans et al., 1998; Perez et al., 2004), and P (Young, 2012). CWD effects on temperate forest inorganic N are mixed. Additions lead to the removal of inorganic N from the soil as the microbes decompose the more recalcitrant tree species (Laiho and Prescott, 2004), or to the accumulation of inorganic N with limited plant uptake of available N (Rhoades et al., 2012). All of these CWD-induced changes occur in relatively shallow soils apart from the impact of dead root biomass in altering microbial processes. Dead root litter has the potential to influence C and N mineralization (Rau et al., 2011b) even though this C source is more diffuse and spread throughout the soil profile compared to concentrated piles of CWD on the soil surface.

Intertwined with effects of CWD additions on desert ecosystem processes are the woody encroachment of the tree species themselves and the invasion of exotic grasses. Tree

encroachment, especially that of *Juniperus osteosperma* (Torr.) Little and *Pinus edulis* (Engelm.), into shrublands and grasslands and the associated accrual of C and N, occurs over one to two centuries (Miller and Rose, 1999; McKinley and Blair, 2008). Microbes may respond differently to CWD depending on the amount of time that the tree has had to alter the soil environment or the quantity and quality of C substrates as the tree ages. For example, the accumulation of nutrients in tree islands, as the trees age, may help microbes overcome the potential C-limitation following the overwhelming addition of CWD or the higher ratio of labile C to recalcitrant C. In relatively younger trees, CWD may stimulate microbial activity more than recalcitrant CWD from older trees. The addition of CWD also has the potential to influence the availability of inorganic N for invading annual exotic grasses (Miller et al., 2000). Unfortunately, if CWD additions alleviate nutrient limitations in ecosystems that are predominantly N-limited and help proliferate exotic grasses, fire control benefits from tree shredding may not be realized as biomass carpets of invading grasses, instead of trees, are substituted as the fuel sources for catastrophic wildfires.

To investigate the influence of CWD on microbial activity and potential for CWD to promote exotic grass invasion, we measured microbial metabolic activity and N transformation rates in surface and subsurface soils where whole *Juniperus* and *Pinus* trees were shredded and CWD deposited on the soil surface. Measurements were made on over 40 sites where trees were shredded 1-8 years previously. Specifically we measured respiration rates, metabolic microbial quotient as a measure of microbial efficiency, the ratio of soil microbial biomass to dissolved organic C ($C_{mic}\,C_{DOC}^{-1}$) as an indicator of organic matter quality (Liao and Boutton, 2008), phosphorus (P), and N mineralization and nitrification rates. Additionally, we evaluated the effects of CWD on these microbial mediated processes in semi-desert microsites and across three

stages of woody tree encroachment. Last, to link CWD-induced changes in microbial activity to plant species distribution we evaluated the frequency of three exotic grasses, and thirty-five native grasses. We hypothesized: (1) CWD will stimulate microbial activity and N transformation rates and the degree of this stimulation will be dependent on increased tree encroachment; (2) microbial activity and N transformations will be higher in surface soils beneath and at the edge of tree canopies where CWD is localized than subsurface soils; and (3) CWD will increase N and P availability for both native and exotic plant species.

2. MATERIALS AND METHODS

2.1 Site Description

We conducted our study at 43 sites throughout the state of Utah, USA over a 2-year period during the summer months (April-August, 2011-2012). The experiment was performed across a gradient of *Juniperus* and *Pinus* encroachment where locations within each site were categorized as low (**LOW**, 0-15% absolute tree cover), mid (**MID**, >15-45% absolute tree cover), and high (**HIGH**, >45-100% absolute tree cover) (Miller and Rose, 1999; Miller et al., 1999; Bates et al., 2011) tree encroachment into sagebrush steppe/semi-desert ecosystems. Tree cover was estimated for these sites using images from the National Agricultural Imagery Program (NAIP) at 1 m spatial resolution (USDA-FSA-APFO Aerial Photography Field Office, Salt Lake City, UT). We used ENVI Zoom version 4.5 (Exelis Visual Information Solutions, Boulder, CO) to classify and select objects into two categories: tree and other. Once the objects were selected the images were opened in ArcMap (ESRI, Environmental Systems Resource Institute, Redlands, CA) and 33 × 30 m subplot squares were placed on the images based on two GPS points that were taken from the field. The tree cover extraction from ENVI Zoom was then

added to ArcMap, where we calculated percent tree cover of potential subplots. From these images, subplots were randomly selected that represented the three tree encroachment categories. Dominant shrub species in the shrub lands included *Artemisia tridentata* Nutt. (ssp. *wyomingensis* Beetle and Young*, tridentata, and vaseyana* [Rydb.] Beetle), *Atriplex canescens* (Pursh) Nutt., *Chrysothamnus viscidiflorus* (Hook.) Nutt., *Ericameria nauseosa* (Pall. ex Pursh) G.L. Nesom and Baird, *Purshia stansburiana* (Torr.) Henrickson, and *Purshia tridentata* (Pursh) DC. Sites had a range of elevation from 1637 - 2512 m.a.s.l., average annual precipitation from 272 - 483 mm, and average annual temperature of 4.5-12 °C (PRISM Climate Group, 2004). A summary of site soil characteristics are shown in Table 1 including EC, %N, %C, % sand, % silt, % clay, precipitation, temperature, and elevation. Soil pastes were made in order to evaluate pH on a Thermo Orion pH meter (model 410, Thermo Scientific Orion, Beverly, MA). Once pH was read, the solution was extracted and read on a Beckman Conductivity Bridge to determine EC (model RC-16C, Beckman Coulter Inc., Brea, CA). Percent C and N analysis was performed on the LECO TruSpec CN Determinator (LECO Corporation, St. Joseph, MI) using the dry combustion method. Soil texture was determined using the hydrometer method.

2.2 Coarse woody debris manipulations and microsites

Mechanical shredding is a wildland fuels control treatment where live trees are shredded or masticated by a Bull Hog® (forest mulcher that uses rotating blades). Shredding places large canopy fuels on the ground as much smaller 1- and 10-hour fuels, which greatly reduces the rate of fire spread and allows fire control crews to more easily contain wildfires. To evaluate the effects of CWD on ecosystem processes and soil microbes, we located unshredded and shredded plots within each site. Where possible, we located three subplots in each of the three tree encroachment categories for both unshredded control and nearby shredded plots. All control and

shredded subplots were 33 × 30 m. Shredding was completed 1-8 years prior to sampling (2003-2010). We sampled specific microsites to determine the contribution of CWD across tree islands in contrast to barren plant interspaces. The two microsites were: tree canopy edge (**EDGE**) and beneath the tree canopy (**CANOPY**) at one-third the distance from the trunk of both *Juniperus* and *Pinus*. All microsites were randomly selected and were from *Juniperus* or *Pinus* trees (estimated from the piles of shredded debris) with a canopy radius of at least 3 m.

2.3 Microbial biomass, soil respiration, and microbial quotient

To determine the effects of CWD on ecosystem processes and microorganisms, we measured soil respiration and microbial biomass in soils beneath CWD manipulations. Soil respiration rates (μg CO_2 g soil^{-1} day^{-1}), microbial biomass (μg C g soil^{-1}), and cumulative CO_2 evolved (μg CO_2 g soil^{-1}) were measured in laboratory incubations on field soils from surface (0-2 cm depth) and subsurface soils (15-17 cm depth). We measured 2 coarse woody debris manipulations × 2 to 3 encroachment categories × 2 microsites × 2 depths × 43 study sites = 1,013 samples. Soils were collected with a soil corer (5 cm diameter and 10 cm in length) and each soil sample represented a composite sample consisting of three subsamples bulked together. Each composited sample was sieved in a 2 mm sieve to remove rocks and roots and stored at 4°C until further analysis. To quantify soil respiration rates and total cumulative CO_2, we sampled and measured the CO_2 four times (0, 1, 3, 6, and 10 days) during a 10-day laboratory incubation at 30°C (Billings et al., 2002; Fierer and Schimel, 2002; Schaeffer et al., 2003; Schaeffer et al., 2007). Briefly, 30 g of soil was weighed into a specimen cup (155 mL), brought to a constant gravimetric water content (0.3 g H_2O g dry soil^{-1}), and placed in a quart-sized mason jar (935 mL). Jars had a gas-tight septum in the lid and contained 10 mL of water to keep samples from drying out during the incubation. At each of the four time intervals (0, 1, 3, 6, and 10 days), 10

mL of air was extracted with a 10 mL gas-tight syringe and CO_2 concentration was measured using an EMG-4 (PP Systems, Amesbury, MA). After each measurement the lid was opened and allowed to equilibrate with ambient CO_2 concentrations (450 - 650 ppm). CO_2 concentrations were converted from PPM to µg using the Ideal Gas Law. Cumulative evolution is presented through rates from the entire incubation.

To investigate the direct effects of CWD on microorganisms, we measured soil microbial biomass (SMB). Active soil microbial biomass (µg C g soil^{-1}) was evaluated using a substrate-induced respiration (SIR) technique (Anderson and Domsch, 1978). The SIR method uses the response of SMB to a readily consumable substrate to indicate the size of the active SMB, but differs somewhat from the commonly used chloroform fumigation procedure in that it is a measure of active rather than total SMB (Bailey et al., 2002). A sucrose solution was added to soil sufficient to provide 4 mg sucrose g soil^{-1} and to bring the soils to field capacity. Briefly, 10 g of soil was weighed into a specimen cup with a gas-tight septum in the lid (155 mL) and 1.121 mL of a 4 M sucrose solution was added to the soil. Respiration rates at 24 and 24.5 hours were measured by capping the cups for 30 minutes and measuring the change in headspace atmospheric CO_2 concentration with CO_2 concentration measured as described above for soil respiration. SIR and SMB was calculated as the difference between the initial and maximum respiration rates in µL CO_2 g soil^{-1} sec^{-1}. Microbial biomass was determined using the equation

$$\text{SMB } (\mu g \text{ C g soil}^{-1}) = (40.04 \times \Delta CO_2) + 0.37 \text{ (Bailey et al., 2002)}$$

where ΔCO_2 is the change in respiration rates in units of µL CO_2 g^{-1} h^{-1} caused by the addition of the sucrose solution. From microbial biomass and respiration rate measurement, we calculated the microbial quotient (µg C-CO_2 g C_{mic} hour^{-1}). Microbial quotient is a measure of microbial efficiency to demonstrate how much carbon was incorporated into the cell structure and how

much was respired by waste. It has an inverse relationship, where an increase of the quotient results in a decrease of the efficiency and vice versa. Meaning, the more carbon a microbe respires, the less efficient it is.

2.4 DOC, $C_{mic}\,C_{DOC}^{-1}$, and P availability

To identify the effects of CWD on soil characteristics and the quality of soil organic matter we evaluated DOC and inorganic P availability. For DOC (μg C g soil^{-1}), soils were extracted via a distilled water extraction (1:2 w/v), passed through a 0.45 μm nylon filter, and measured on a TOC-N analyzer (Shimadzu, Columbia, MD). For P (μg P g soil^{-1}), soils were extracted with 0.5 M $NaHCO_3$ (1:20 w/v) following the Olsen Sodium Bicarbonate method (Olsen et al., 1954; Watanabe and Olsen, 1965; Thomas and Peaslee, 1973). The P concentrations in the supernatant were evaluated colorimetrically (SpectraMax Plus 384, Molecular Devices Corporation, Sunnyside, CA). We calculated $C_{mic}\,C_{DOC}^{-1}$ using microbial biomass and the concentration of DOC ($C_{mic}\,C_{DOC}^{-1}$ %).

2.5 N mineralization, nitrification and inorganic N availability

We measured N transformation rates to identify the impact of CWD on the availability of inorganic soil N. Specifically we measured N mineralization rates (μg N-NH_4^+ g soil^{-1} day^{-1}) and nitrification rates (μg N-NO_3^- g soil^{-1} day^{-1}) as the change in NH_4^+ and NO_3^- over the same 10-day incubation used for soil respiration. For inorganic N concentrations, soils were extracted via a 0.5 M K_2SO_4 (1:2 w/v), centrifuged for 30 minutes at 4,000 rpm, and the N species in the supernatant were determined colorimetrically (SpectraMax Plus 384, Molecular Devices Corporation, Sunnyside, CA) following Forster (1995) for NH_4^+ and Miranda et al. (2001) for NO_3^-.

2.6 Plant responses to coarse woody debris

We evaluated the shifts in individual plant species and functional group to the addition of CWD. We measured 2 to 3 tree cover categories × 2 microsite locations × 23 unseeded plots = 300 samples. We measured the occurrence of every plant species, including shredded tree material using the line-point method as described by McIver et al (2010). We then used python version 2.7.3 (Python Software Foundation, http://www.python.org) to categorize each of the 60 points along five different transects into our microsites (e.g., EDGE and CANOPY) and calculated the average percent frequency of species and functional groups across the five transects, which acted as subsamples. Percent frequency was calculated as the number of times a species/functional group occurred along each transect divided by the total number of microsites in the transect × 100. Specific species of interest included the exotic annual grass *Bromus tectorum* L.*,* native perennial grasses *Elymus elymoides* (Raf.) Swezey, and *Pseudoroegneria spicata* (Pursh) Á. Löve, and exotic perennial grasses *Poa bulbosa* L. and *Poa compressa* L. *Bromus tectorum* is a prolific exotic annual grass that degrades ecosystems by invading and replacing native grass species (Getz and Baker, 2008). It creates a monoculture of continuous fuels causing catastrophic wildfires (Billings, 1990; DiTomaso, 2000; Getz and Baker, 2008; Rau et al., 2011a). Removal of *Juniperus* and *Pinus* in cut and burn management practices has generally aided in the regrowth of native grasses (Rose and Eddleman, 1994; Bates et al., 2007a) such as *Elymus elymoides*, and *Pseudoroegneria spicata,* and we suspect CWD additions will induce similar plant effects. Functional groups generated by our data include exotic perennial grasses, exotic annual grasses, and native perennial grasses.

2.7 Statistical analysis

We tested for the effect of woody debris on our microbial and soil response variables

(e.g., soil respiration, cumulative CO_2 evolution, microbial quotient, N mineralization, Nitrification, inorganic N, DOC, $C_{mic}\,C_{DOC}^{-1}$, and P availability) and plant response variables using two-way ANOVAs by encroachment category and CWD manipulation. ANOVA assumptions were evaluated using the Shapiro-Wilk test for normality and Levene's test for homogeneity of variance. All ANOVAs were run individually by soil depth and microsite location. We used contrast statements in our model since only specific pair-wise combinations were of interest. All analyses were conducted using SAS/STAT (SAS, 2001).

3. RESULTS

3.1 General soil characteristics

All soils were indicative of Great Basin semi-desert aridisols or entisols. Across sites, soil physiochemical characteristics ranged as follows: pH = 6 - 7.5, EC = 0.21 - 1.4 ds/m, total soil C = 0.63-9.44 %, total soil N = 0.08 - 0.27 % (Table 1). Most of the soils (45 %) were loam texture, and the remaining soils ranged from sandy loam to clay loam.

3.2 Microbial metabolic responses to CWD in surface soils

The addition of CWD increased microbial biomass and microbial efficiency for LOW initial *Juniperus* tree cover. Microbial biomass was almost twice as high in *Juniperus* LOW CANOPY and LOW EDGE soils ($P < 0.01$; Fig. 1A, 1B). Microbial quotient decreased 35% (from 53.04 μg C-CO_2 g C_{mic} soil^{-1} to 34.64 μg C-CO_2 g C_{mic} soil^{-1}) in *Juniperus* LOW CANOPY soils, indicating an increase in efficiency (Fig. 1E, 1F). Only in *Pinus* EDGE soils, did the amount of CO_2 evolved in surface soils increase and was 4% higher under CWD additions (800.57 μg CO_2 g soil^{-1}) than in untreated soils (767.99 μg CO_2 g soil^{-1}; Fig. 1G, 1H). Tree

species had only marginal effects on microbial biomass ($F = 3.20$, $P = 0.07$, $df = 1$) and microbial quotient ($F = 3.21$, $P = 0.07$, $df = 1$) following CWD additions.

As tree cover increased, microbial biomass and microbial quotient decreased in surface soils. Microbial biomass and microbial quotient decreased 22% and 14% from LOW to HIGH tree cover under woody additions in *Juniperus* and *Pinus* EDGE (74.52 to 57.78 μg C g soil^{-1} and 58.41 to 50.88 μg C-CO_2 g C_{mic} soil^{-1} respectively; Fig. 1A, 1F). Microbial biomass for *Juniperus* EDGE soils and microbial quotient for *Juniperus* CANOPY, under control conditions demonstrated a similar decline from MID to HIGH and LOW to HIGH tree cover, while biomass in *Juniperus* CANOPY soils in the control treatment increased with increasing tree cover.

3.3 Microbial metabolic responses to CWD in subsurface soils

Opposite of surface soils, the addition of CWD had little impact on microbial activity. However, activity was depressed in subsurface soils. For example, microbial biomass ($F = 195$, $P < 0.0001$, $df = 1$) and cumulative CO_2 ($F = 78$, $P < 0.0001$, $df = 1$) decreased by up to 49% and 14% from surface to subsurface soils. The only difference following CWD additions was in *Juniperus* EDGE soils, where the amounts of CO_2 evolved were 8% lower under debris additions (743.69 μg CO_2 g soil^{-1}) than control conditions (683.13 μg CO_2 g soil^{-1}; Fig. 2G).

The efficiency of microbes increased as tree cover increased as shown through a decrease in microbial quotient. Microbial quotient decreased 12% (41.53 to 47.12 μg C-CO_2 g C_{mic} soil^{-1}) for shredded *Juniperus* from LOW to HIGH initial tree cover for CANOPY soils. Similarly, microbial quotient decreased 10% (65.26 to 58.50 μg C-CO_2 g C_{mic} soil^{-1}) for untreated *Pinus* from LOW to HIGH tree cover soils at the canopy EDGE (Fig. 2E, 2F).

3.4 DOC, C_{mic} C_{DOC}^{-1}, C and P availability following CWD additions

CWD additions enhanced the availability of DOC and P but tended to decrease DOC quality in surface soils. In *Juniperus* MID tree cover CANOPY and LOW tree cover EDGE soils, DOC concentrations increased at least 40% in the shredded treatment (362 and 217 µg C g soil^{-1} respectively) from the untreated control treatment (255 and 128 µg C g soil^{-1} respectively; Fig. 3A, 3B). CWD additions predominantly affected soils associated with *Pinus*. For example, P concentrations were higher in EDGE soils with CWD additions than in untreated soils for all categories of tree cover and also in LOW tree cover CANOPY soils. A similar trend of increasing P following the addition of debris was also apparent for *Juniperus* HIGH tree cover soils, but the difference in P between the treatments was marginal. The quality of DOC decreased following CWD additions in *Juniperus* MID tree cover EDGE surface soils but most surface soils, and especially EDGE soils demonstrated this similar trend. The quality of DOC was influenced by CWD treatments (F = 1.9, P = 0.17, df = 1), tree species (F = 12, P = 0.0007, df = 1), and microsite (F = 173, P = <0.0001, df = 1). In subsurface soils, the CWD-induced reduction was also apparent where C_{mic} C_{DOC}^{-1} decreased between 6 % and 19 % in *Juniperus* EDGE (CWD = 45.29 %, control = 61.97 %) and surface *Pinus* CANOPY and EDGE soils respectively (Fig. 1C, 1D).

DOC remained relatively constant in surface and subsurface soils with increasing tree cover, but P accumulated in subsurface soils beneath *Juniperus* and *Pinus*. Increasing tree cover was associated with increasing P in untreated *Juniperus* and *Pinus* CANOPY soils and untreated *Pinus* EDGE subsurface soils (Fig. 4C, 4D). Soil available P also increased with increasing initial tree cover on shredded plots. For example, soil P was at least two-times higher in HIGH versus LOW tree cover in *Juniperus* CANOPY and *Pinus* EDGE soils. Subsurface P availability

was enhanced by debris additions predominantly in *Pinus* soils. P availability increased almost 100% in *Juniperus* HIGH tree cover CANOPY (CWD= 10.1 μg g soil^{-1}, control = 5.03 μg g soil^{-1}) and *Pinus* HIGH tree cover EDGE debris- addition soils (CWD = 9.59 μg g soil^{-1}, control = 6.4 μg g soil^{-1}; Fig. 4C, 4D). The reduction trend ($P < 0.05$) in C dynamics due to debris was also apparent in *Juniperus* LOW and MID tree cover EDGE soils for C_{mic} C_{DOC}^{-1} (53.27% to 28.54% and 50.15% to 31.42%; Fig. 2C). C_{mic} C_{DOC}^{-1} increased 15% under woody additions for *Pinus* LOW to HIGH tree cover CANOPY soils. The quality of DOC was only marginally affected by tree cover ($F = 0.1$, $P = 0.91$, $df = 2$; Fig 2D).

Subsurface DOC concentrations declined following debris additions but only beneath tree canopies at higher tree covers. DOC concentrations were up to 1.5-times higher in soils of untreated than masticated plots soils regardless of tree species.

3.5 N transformation rates and inorganic N availability in surface and subsurface soils

Coarse woody debris additions decreased N transformations for all categories of tree cover but only in surface soils. N mineralization rates were up to 33% lower under debris additions in LOW tree cover CANOPY (CWD = 0.18 μg N-NH_4^+ g soil^{-1} day^{-1}, control = 0.27 μg N-NH_4^+ g soil^{-1} day^{-1}) and in LOW EDGE soils (CWD = 0.28 μg N-NH_4^+ g soil^{-1} day^{-1}, control = 0.36 μg N-NH_4^+ g soil^{-1} day^{-1}; Fig. 5A). Additionally, nitrification rates ranged from 16% to 21% lower in debris additions than control treatments in LOW EDGE (CWD=0.27 μg N-NO_3^- g soil^{-1} day^{-1}, control=0.34 μg N-NO_3^- g soil^{-1} day^{-1}) and EDGE MID (CWD=0.27 μg N-NO_3^- g soil^{-1} day^{-1}, control=0.32 μg N-NO_3^- g soil^{-1} day^{-1}) and 31% lower in CANOPY LOW (CWD= 0.18 μg N-NO_3^- g soil^{-1} day^{-1}, control=0.26 μg N-NO_3^- g soil^{-1} day^{-1}; Fig 5A, 5C). N mineralization rates ($F = 4.6$, $P = 0.032$, $df = 1$) and nitrification ($F = 4.7$, $P = 0.031$, $df = 1$) declined by at least 55% with depth but there were no differences induced by tree species.

Similar to microbial mediated soil respiration and biomass, N mineralization and nitrification decreased with increasing tree cover and CWD additions greatly influenced N dynamics. For CANOPY in both surface and subsurface soil, nitrification rates in the control treatment decreased 23% and 25% from LOW to HIGH tree cover and 22% under debris additions in subsurface CANOPY soils (Fig. 5C, 5D).

3.6 Plant responses to CWD

The frequency of native perennial grasses, especially *Elymus elymoides*, was enhanced by the addition of CWD for all tree cover categories and microsites, while the frequency of exotic annual or perennial grasses was not impacted by shredding. For example, *Elymus elymoides* frequency was 65% higher in MID tree cover CANOPY and EDGE soils under debris addition than control treatments (Fig. 6A). Percent frequency of other native perennial grasses (e.g., *Achnatherum hymenoides* (Roem. & Schult.) Barkworth*, Hesperostipa comata* (Trin. & Rupr.) Barkworth*, Koeleria macrantha* (Ledeb.) Schult.*, Pascopyrum smithii* (Rydb.) Á. Löve*, Sporobolus cryptandrus* Hitchc.*,* and *Poa secunda* J. Presl) was 74% to 85% higher in LOW tree cover CANOPY and EDGE soils, and in MID tree cover EDGE soils with debris addition from shredding than with no shredding (Fig. 6C). *Pseudoroegneria spicata,* another native perennial grass did not respond to the debris additions but did consistently decrease in frequency with increasing tree cover without shredding (Fig. 6D). There we no apparent changes in exotic annual *Bromus tectorum* or any exotic perennial grass (e.g., *Poa bulbosa*, *Poa compressa*) for any tree cover category or microsite (Fig. 6E).

4. DISCUSSION

4.1 Impact of CWD on microbial activity and tree islands

Contrary to our hypothesis the addition of CWD did not stimulate C mineralization or N mineralization. Although, microbial biomass and the efficiency of this biomass increased under CWD, there was no visible enhancement of the total amount of CO_2 evolved following CWD additions. The increase in biomass was potentially induced by an increase in microbial C substrate (e.g., DOC) availability or other environmental factors novel to CWD additions. Soil under CWD additions often experienced increased temperature and soil moisture in the spring and summer months (Young, 2012) that may promote microbial activity. We did find a trend with tree encroachment, where as tree cover increased, microbial biomass and microbial quotient decreased in surface soils. Although we did not age trees in this study to quantify encroachment phases, we chose encroachment study sites using the indicators of Tausch et al. (2009). Within the encroachment areas, we consider that greater tree cover is associated with increasing encroachment, although understory cover may be lost at widely different ranges of tree cover depending on the site (Roundy et. al., Unpublished resultsb). Microbial biomass decreased by 22% while microbial efficiency increased by 14% as encroachment level increased in our semi-arid deserts. This decrease in biomass but increase of efficiency was not expected since Liao and Boutton (2008) found an increase of biomass and decrease of efficiency in woody plant soils than in adjacent shrub/grassland soils. They attribute this finding to lower quality organic matter and higher resistance to decay in woodland soils. In general, microbes have a harder time degrading more recalcitrant CWD that contains complex plant polymers such as lignin and as a result produce more CO_2 per unit biomass (Liao and Boutton, 2008). Our measured decrease in biomass may be attributed to a possible decline in tree litter chemistry and the resulting CWD as

trees become older and have a higher percentage of their biomass as lignin. Further, our findings were contrary to McCulley et al. (2004), which found that microbes were less efficient at converting available C into biomass during the encroachment of woody *Prosopis glandulosa* Torr. in a subtropical savannah. Since we found an increase in microbial efficiency and our C_{mic} C_{DOC}^{-1} generally remained constant, we believe that the microbial community becomes more carbon use efficient as tree cover increases in our woodlands. Powlsen et al. (1987) demonstrated that soil microbial biomass and C_{mic} C_{DOC}^{-1} ratio can provide an effective early warning of the deterioration of soil quality. Ultimately, the addition of CWD decreased the quality of C substrates but improved soil conditions enough for microbes to enhance their activity in tree islands of fertility.

The poor quality DOC in our study may have led to the reduction in N mineralization and nitrification in surface *Juniperus* and *Pinus* soils during the increase from low to mid tree cover. Our results are similar to Zaady et al (1996) who did not find increased C availability, but found that increased soil moisture beneath CWD stimulated microbial biomass activity. Young (2012) and Roundy et al. (Unpublished resultsa) found that tree reduction greatly increased time of available water during the spring growing season in sagebrush steppe communities encroached by *Juniperus* and *Pinus* trees. Longer periods of available water are associated with longer periods of nutrient dissipation and potential uptake by residual species (Ryel et al., 2010; Leffler and Ryel, 2012). Further, we found that N mineralization rates decreased up to 22% and nitrification rates decreased up to 23% as tree cover increased. Others have found the same reduction in nitrification rates as forest ecosystems (mixed conifer, and lodgepole pine [*Pinus contorta* Douglas ex Loudon]) mature in sub-humid climates (Selmants et al., 2008) and semi-arid climates (Selmants and Hart, 2010; Vitousek et al., 1989; Frazer et al., 1990; Binkley et al.,

1995). We also noted a decline in N mineralization rates up to 33% and nitrification rates decreased up to 21% in soils treated with CWD. A similar reduction in N transformation rates was evident in *Juniperus* woodland soil exposed to CWD in field study done by Bates et al. (2002). The implication of this decline in organic N availability is a microbial biomass that is immobilizing more organic N from litter and CWD or inorganic N from the soil environment.

The tree island of fertility effect is the process of nutrients being recycled under trees in otherwise relatively infertile soils (Schlesinger and Pilmanis, 1998). The nutrients are deposited over time from tree litter or from the roots gathering nutrients from interspace soils (Klopatek, 1987; McDaniel and Graham, 1992). The tree islands are capable of storing moisture for longer periods of time (Schade and Hobbie, 2005), especially when shredded due to reduced tree water use (Young, 2012), and were thought to create ideal environments for microbial activity. This was not the case with our results. If anything, CWD increased fertility in tree island patches for many soil components except N, but microbial activity was not always benefitted. For example, the addition of CWD did elevate DOC and P availability, but it created more impoverished C substrates as noted in a 15% decrease in C_{mic} C_{DOC}^{-1} under CWD in *Pinus* soils. The differences in DOC were more apparent in subsurface soils suggesting that DOC from the CWD on the soil surface are either flowing to deeper soils (Cross and Schlesinger, 1999; Abrahams et al., 1994) or decomposing roots are also creating C-limited microbial substrates. Tree roots in semi-deserts account for 25-40% of total biomass (Cairns et al., 1997; Miller et al., 1990) and could quite easily alter soil conditions independently of aboveground CWD piles, especially once the tree has been shredded. Unfortunately, we did not measure root biomass, but root decomposition may contribute to the higher levels of DOC following CWD additions.

4.2 Surface and subsurface soil differences

In agreement with our hypothesis, most of the impact of CWD on microbial activity occurred in surface soils instead of subsurface soils. Surface soil to subsurface soil comparisons for every microbial response variable was extremely significant ($P<0.0001$). This was expected due to concentrated CWD directly influencing microbial processes. Piles of CWD are not incorporated into the soil due to high rock content and act as a moisture trap (Miller and Seastedt, 2009), reducing evaporation (Young, 2012) and potentially supporting microbial activity longer into the warm summer months. Further, the wetter and warmer conditions may have promoted our measured decreases in N mineralization and nitrification (Bottner, 1985; Kieft et al., 1987). The decline in nutrients and microbial activity with depth is common (Zaady et al., 1996; Spears and Lajtha, 2004) but we found no real differences in microbial C mineralization between soils at the edge of tree canopy and the soils directly below the tree canopy. Microbial biomass, microbial efficiency, and cumulative CO_2 evolved were not significantly impacted by microsite location. However, N transformations and soil characteristics such as DOC, DOC quality, and P availability were consistently higher under canopy soils in both surface and subsurface soils regardless of CWD treatment. Thus, the soils beneath the canopy, instead of soils at the tree canopy edge, still remained the area of microbial and nutrient hotspots even after addition. Miwa and Reuter (2010) noted that there is a steep gradient of nutrient dynamics under *Juniperus* canopy, with the highest concentrations closest to the bole of the tree and decreasing concentrations as distance from the bole increases. We thought that microbial activity at the edges of CWD piles would really change since the CWD was in direct contact with the soil surface instead of being separated by a layer of pine needles but our results demonstrated otherwise. Young (2012) also found that tree litter had a more pronounced effect

on soil nutrients than CWD, allowing for more microbial activity in litter due to lower C:N ratios in litter than in CWD. This points to the conclusion that many of the changes that we found in microbial C and N cycling may be due to the decomposition of pine needles and juniper litter instead of CWD.

4.3 Impact of CWD on native and exotic grasses

We found that CWD-induced changes to soil properties promoted the frequency of native grasses over the exotic annual grass, *Bromus tectorum*. Contrary to our hypothesis, the increase in P and the decrease in N mineralization and nitrification rate increased the frequency of native perennial grasses. For example, the frequency of perennial grasses, especially *Elymus elymoides*, was at least 65% higher under CWD additions for all categories of tree cover, while the frequency of perennial exotic grasses was not impacted by CWD. As tree cover increases with encroachment, *Juniperus* and *Pinus* generally utilize nutrients and water, suffocating out other plants (Selmants and Hart, 2010). Once these trees are removed the subsequent nutrients in the tree island and tree biomass begin to become available to plants and soil moisture increases during the spring and summer months as found by Young (2012). Other researchers (Bates et al., 2007a; Ross et al., 2012) also found an increase of native plants, especially perennial plants, occurring at least two years after CWD treatments, and these grasses have the ability to increase in cover with each passing year (Eddleman, 2002). Klemmedson and Tiedemann (2000) found an increase of soil nutrients and litter mass on soil surface with increased age and size of *Juniperus*. As tree cover increases, so will biomass of trees. Once shredded this leaves more biomass on the ground allowing more plant available nutrients to become available. Miwa and Reuter (2010) found that more exotic invasions occurred with higher tree cover and fewer invasions occurred with lower tree cover due to fewer tree islands. We found a similar trend

where the exotic *Bromus tectorum* did increase in frequency under CWD treatment in mid categories of tree cover. In general, however, the frequency of *Bromus tectorum* decreased with the addition of CWD and this trend is apparent in other studies (Wicks, 1997; Wolk and Rocca, 2009) where mulch additions inhibited the growth of the exotic annual *Bromus tectorum.* This decrease in *Bromus* tectorum could be due to seedlings being light-limited under CWD (Andersson et al., 2002). In a similar study by Young (2012), less *Bromus tectorum* was observed in shredded sites, but when it did grow, it grew in with more tillers and aboveground biomass, taking advantage of increased available soil nutrients. A decrease in inorganic N availability does not seem to affect the growth of native perennials in a negative way (Lowe et al., 2003), but the increase in P may have had a positive effect in the increase of native perennials (Tomassen et al., 2004). P levels are generally extremely low in *Juniperus* and *Pinus* woodlands and the addition of more P may allow native perennial grasses to proliferate.

5. CONCLUSIONS

N mineralization and nitrification rates decreased in *Juniperus* and *Pinus* woodland soils treated with CWD. The decline in N mineralization and nitrification rates is due to a microbial biomass that is immobilizing more organic N from litter and CWD or inorganic N from the soil environment. Microbial quotient decreased, meaning that efficiency increased with the addition of CWD. Increased efficiency coincided with increased microbial biomass in CWD treatments and these changes in microbial activity are most likely due to the increase in DOC or other environmental factors novel to CWD additions like increases in soil temperature and moisture. Microbial biomass, microbial quotient, N mineralization and nitrification rates decreased as encroachment progressed. Decreases in microbial biomass and quotient suggest that as encroachment progresses, even though organic matter quality decreases, microbial communities

are still finding a way to become more efficient. A further study is needed to understand why this occurred. Most microbial activity occurred in surface soils rather than subsurface soils which was expected due to direct soil contact with CWD. CWD increased fertility in tree island patches for DOC and P in surface and subsurface soils. These increases were mostly seen in canopy microsites rather than canopy edge microsites and possibly aided in the increase of native grasses.

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Table 1. Ecosystem and soil characteristics of our 43 semi-desert sites. Data (mean ± SEM) are from the composite soil samples from surface soils (*n* = 3) Mean annual elevation, mean annual temperature, and mean annual precipitation data was collected from the Oregon State PRISM website (PRISM Climate Group, 2004). Mean temperature and precipitation were generated over a 30-year period.

Site	pH	EC	% N	% C	% Sand	% Silt	% Clay	Elev	Temp	Precip
		ds/m						m	ºC	mm
Anderson Mountain	6.3 ± 0.13	0.29 ± 0.06	0.10 ± 0.01	1.3 ± 0.28	51 ± 5.8	31 ± 3.0	19 ± 2.5	1914	9.7	348
Augusi	7.1 ± 0.06	1.0 ± 0.30	0.25 ± 0.04	8.3 ± 0.76	45 ± 3.9	28 ± 3.1	28 ± 6.5	2298	7.3	445
Black Dragon	7.5 ± 0.07	0.61 ± 0.02	0.27 ± 0.02	11 ± 0.65	37 ± 4.0	37 ± 4.0	26 ± 0.09	2512	4.5	483
Blue Valley	6.7 ± 0.24	0.72 ± 0.12	0.17 ± 0.01	2.9 ± 0.46	42 ± 2.2	31 ± 0.52	27 ± 1.7	1967	9.5	340
Bowery sagebrush	7.4 ± 0.07	0.35 ± 0.08	0.13 ± 0.01	4.4 ± 1.0	29 ± 11	23 ± 1.0	50 ± 10.3	2011	6.8	315
Bowery Springs	7.1 ± 0.14	0.44 ± 0.05	0.15 ± 0.03	3.9 ± 1.1	42 ± 3.4	27 ± 7.0	32 ± 9.3	2082	6.8	330
Chokecherry	6.6 ± 0.12	0.48 ± 0.04	0.15 ± 0.01	1.8 ± 0.33	46 ± 5.9	31 ± 3.4	24 ± 2.9	1835	8.2	300
Columbia	7.1 ± 0.03	0.54 ± 0.13	0.15 ± 0.01	7.2 ± 0.25	48 ± 1.1	29 ± 1.4	24 ± 2.5	1860	9.5	297
Cook Canyon	6.8 ± 0.14	0.46 ± 0.06	0.22 ± 0.04	3.9 ± 1.25	41 ± 2.3	39 ± 2.6	21 ± 0.42	1799	7.1	322
Eight Mile Bench	6.1 ± 0.10	0.22 ± 0.01	0.11 ± 0.02	1.4 ± 0.51	53 ± 2.2	28 ± 2.1	20 ± 3.7	1894	11.8	474
Goslin	6.6 ± 0.31	0.55 ± 0.06	0.18 ± 0.04	4.2 ± 1.5	49 ± 3.9	32 ± 3.2	19 ± 1.1	2034	6.8	333
Government Creek	7.2 ± 0.02	0.57 ± 0.02	0.25 ± 0.05	5.9 ± 1.2	34 ± 2.9	42 ± 4.3	24 ± 2.9	1768	10	406
Grantsville	7.3 ± 0.05	0.47 ± 0.10	0.23 ± 0.01	3.9 ± 0.42	39 ± 1.3	33 ± 3.5	28 ± 2.7	1746	11	470
Greenville	7.2 ± 0.30	0.52 ± 0.14	0.17 ± 0.04	3.8 ± 1.9	45 ± 1.3	31 ± 3.2	24 ± 3.3	1786	10	338
Hiawatha	7.4 ± 0.07	1.3 ± 0.35	0.20 ± 0.07	5.1 ± 3.3	62 ± 1.1	19 ± 6.7	19 ± 7.8	1896	7.8	282
Hwy 56 black sagebrush	7.4 ± 0.13	0.49 ± 0.08	0.16 ± 0.03	5.3 ± 1.9	49 ± 1.1	27 ± 0.39	24 ± 1.5	1682	12	351
Hwy 56 big sagebrush	7.2 ± 0.05	0.39 ± 0.04	0.13 ± 0.02	4.9 ± 0.40	48 ± 1.4	27 ± 2.9	25 ± 2.3	1682	12	351
Hyatt Springs	6.2 ± 0.28	0.23 ± 0.04	0.13 ± 0.01	2.4 ± 0.58	58 ± 1.2	24 ± 3.8	18 ± 2.0	1822	12	411
Indian Springs	6.5 ± 0.40	0.79 ± 0.26	0.26 ± 0.05	8.1 ± 1.9	22 ± 3.8	47 ± 2.4	30 ± 5.7	2320	6.5	462
James Ranch	7.1 ± 0.06	0.45 ± 0.02	0.15 ± 0.00	5.1 ± 0.26	29 ± 4.4	40 ± 4.7	31 ± 1.6	1653	10	351
Keg Springs	7.2 ± 0.03	0.51 ± 0.06	0.22 ± 0.01	6.3 ± 1.3	34 ± 2.3	37 ± 2.2	28 ± 1.1	1774	7.7	305
Muddy Creek	6.3 ± 0.22	0.21 ± 0.04	0.08 ± 0.00	0.6 ± 0.05	75 ± 6.4	13 ± 5.0	12 ± 2.2	1766	11	386
Natural Bridges	7.5 ± 0.03	1.5 ± 0.95	0.17 ± 0.03	3.7 ± 1.5	57 ± 5.5	29 ± 3.3	13 ± 2.5	1856	13	292
Natural Bridges 2	7.4 ± 0.05	0.49 ± 0.07	0.17 ± 0.03	4.3 ± 2.7	50 ± 3.1	28 ± 3.4	22 ± 1.6	1856	13	292
Onaqui	7.5 ± 0.06	0.81 ± 0.35	0.26 ± 0.09	6.6 ± 2.8	39 ± 1.5	37 ± 3.2	24 ± 3.3	1709	10	348
Ray Mesa	6.7 ± 0.20	0.46 ± 0.10	0.21 ± 0.04	4.2 ± 0.94	45 ± 3.6	42 ± 3.2	15 ± 0.82	2271	10	442
Sand Hollow	7.0 ± 0.03	1.1 ± 0.33	0.19 ± 0.03	4.8 ± 1.2	53 ± 8.0	25 ± 7.0	22 ± 4.5	1915	9.8	335
Scipio	7.3 ± 0.02	0.41 ± 0.07	0.17 ± 0.02	9.4 ± 1.5	46 ± 0.96	32 ± 1.9	22 ± 1.9	1728	11	381
Sharpes Valley	7.1 ± 0.04	0.58 ± 0.03	0.21 ± 0.03	6.9 ± 1.9	35 ± 2.5	39 ± 3.2	27 ± 1.5	1879	9.0	404
South Beaver	6.6 ± 0.17	0.70 ± 0.15	0.15 ± 0.02	2.3 ± 0.39	45 ± 6.5	32 ± 2.4	24 ± 5.2	2058	8.4	354
South Creek	6.0 ± 0.10	0.27 ± 0.06	0.13 ± 0.01	2.4 ± 0.32	57 ± 4.4	22 ± 2.2	22 ± 5.7	2247	4.9	368
South Hills	6.2 ± 0.26	1.4 ± 0.20	0.16 ± 0.03	3.2 ± 1.2	57 ± 4.4	28 ± 2.7	15 ± 1.9	2016	9.1	438
Stansbury	6.9 ± 0.18	0.54 ± 0.05	0.19 ± 0.02	3.0 ± 0.63	37 ± 1.9	37 ± 0.49	26 ± 1.8	1748	11	437

Steinaker	6.7 ± 0.71	0.65 ± 0.13	0.09 ± 0.02	1.2 ± 0.35	74 ± 3.3	15 ± 3.6	11 ± 0.47	1867	7.7	272
Terra East	7.4 ± 0.05	0.61 ± 0.06	0.19 ± 0.02	3.9 ± 0.89	35 ± 1.2	36 ± 2.2	29 ± 2.2	1637	11	376
Unit B	6.7 ± 0.29	0.83 ± 0.03	0.15 ± 0.02	3.1 ± 0.48	56 ± 3.6	27 ± 2.6	17 ± 1.5	1991	9.5	338
West Carbon	7.1 ± 0.03	0.54 ± 0.04	0.22 ± 0.04	7.8 ± 1.6	57 ± 4.1	28 ± 4.5	15 ± 0.50	2004	8.8	353
West Oakbrush	7.1 ± 0.06	0.51 ± 0.05	0.26 ± 0.03	4.6 ± 0.88	36 ± 0.97	40 ± 1.4	25 ± 1.7	1748	9.9	406
West Onaqui sagebrush	7.3 ± 0.06	0.55 ± 0.05	0.20 ± 0.02	8.2 ± 1.1	32 ± 4.2	38 ± 4.6	31 ± 2.4	1719	10	368
West Onaqui Mid	7.2 ± 0.02	0.60 ± 0.10	0.26 ± 0.05	9.4 ± 2.2	29 ± 2.1	46 ± 2.7	24 ± 2.3	1848	10	419
West Onaqui Upper	7.3 ± 0.07	0.61 ± 0.16	0.22 ± 0.04	7.5 ± 0.77	21 ± 1.4	43 ± 3.8	35 ± 2.9	1848	10	419
Winter Springs Low	7.3 ± 0.12	0.43 ± 0.09	0.16 ± 0.00	2.5 ± 0.36	44 ± 1.3	31 ± 2.4	26 ± 3.3	1653	11	330
Winter Springs High	6.9 ± 0.07	0.38 ± 0.05	0.25 ± 0.03	5.3 ± 1.4	29 ± 8.5	42 ± 7.2	29 ± 1.8	1850	10	417

Table 2. ANOVA results for microbial metabolic activity, N transformations, and soil characteristics by tree species, tree cover category, coarse woody debris (CWD) treatment, and microsite tree island location. The major effects include: depth = 0-2 cm and 15-17 cm below the soil surface; tree species = *Juniperus* and *Pinus*; three tree cover encroachment categories of *Juniperus* and *Pinus* cover; microsite = beneath the tree canopy edge and the tree canopy; CWD treatment = the addition of CWD to the soil surface or no addition.

Source	df	*F value*	*P*
Microbial metabolic characteristics			
Microbial biomass (C_{mic}, μg C g soil^{-1})			
Depth	1	195.14	<0.0001
Tree species	1	3.2	0.0742
Tree cover category	2	0.02	0.9841
Microsite	1	1.16	0.2827
CWD treatment	1	0	0.9859
Depth × CWD treatment	1	5.38	0.0206
Tree species × CWD treatment	1	1.86	0.1734
Tree cover category × CWD treatment	2	4.89	0.0077
Microsite × CWD treatment	1	0	0.9943
Microbial quotient (μg C-CO_2 g C_{mic}^{-1} hour^{-1})			
Depth	1	28.25	<0.0001
Tree species	1	3.21	0.0733
Tree cover category	2	1.74	0.1753
Microsite	1	7.59	0.006
CWD treatment	1	0.74	0.3887
Depth × CWD treatment	1	0	0.9988
Tree species × CWD treatment	1	1.9	0.1685
Encroachment level × CWD treatment	2	2.44	0.088
Microsite × CWD treatment	1	1.86	0.1726
Microbial biomass to dissolved organic C ratio (C_{mic} C_{DOC}^{-1}, %)			
Depth	1	16.04	<0.0001
Tree species	1	5.28	0.0218
Tree cover category	2	2.7	0.0679
Microsite	1	117.64	<0.0001
CWD treatment	1	7.49	0.0063
Depth × CWD treatment	1	0.07	0.787
Tree species × CWD treatment	1	0.04	0.8434
Encroachment level × CWD treatment	2	2.36	0.0948
Microsite × CWD treatment	1	15.55	<0.0001
Cumulative CO_2 evolution (μg C-CO_2 g soil^{-1})			
Depth	1	78.3	<0.0001
Tree species	1	0.15	0.6953
Tree cover category	2	0.69	0.5004
Microsite	1	26.14	<0.0001
CWD treatment	1	0.15	0.6996
Depth × CWD treatment	1	1.96	0.1623
Tree species × CWD treatment	1	2.47	0.1166
Encroachment level × CWD treatment	2	0.52	0.5939
Microsite × CWD treatment	1	0.03	0.8726

Soil characteristics			
Dissolved organic C (μg C g soil^{-1})			
Depth	1	105.45	<0.0001
Tree species	1	11.58	0.0007
Tree cover category	2	0.1	0.9079
Microsite	1	173.36	<0.0001
CWD treatment	1	1.88	0.1709
Depth × CWD treatment	1	11.08	0.0009
Tree species × CWD treatment	1	2.04	0.1539
Encroachment level × CWD treatment	2	3.24	0.0394
Microsite × CWD treatment	1	3.55	0.0597
P availability C (μg P g soil^{-1})			
Depth	1	337.67	<0.0001
Tree species	1	5.84	0.0258
Tree cover category	2	3.47	0.0314
Microsite	1	31.3	<0.0001
CWD treatment	1	28.75	<0.0001
Depth × CWD treatment	1	4.78	0.0291
Tree species × CWD treatment	1	1.92	0.1664
Encroachment level × CWD treatment	2	3.68	0.0255
Microsite × CWD treatment	1	0.38	0.5367
N transformations			
N mineralization rate (μg N-NH_4^+ g soil^{-1})			
Depth	1	427.09	<0.0001
Tree species	1	1.67	0.197
Tree cover category	2	3.71	0.0248
Microsite	1	46.02	<0.0001
CWD treatment	1	4.64	0.0315
Depth × CWD treatment	1	15.78	<0.0001
Tree species × CWD treatment	1	0.04	0.8447
Encroachment level × CWD treatment	2	1.2	0.3002
Microsite × CWD treatment	1	0.89	0.3464
Nitrification rate (μg N-NO_3^- g soil^{-1} day^{-1})			
Depth	1	448.47	<0.0001
Tree species	1	1.58	0.2097
Tree cover category	2	5.44	0.0045
Microsite	1	41.83	<0.0001
CWD treatment	1	4.66	0.0312
Depth × CWD treatment	1	15.02	0.0001
Tree species × CWD treatment	1	0.05	0.8277
Encroachment level × CWD treatment	2	0.99	0.3701
Microsite × CWD treatment	1	1.45	0.2293

Figure 1. Microbial metabolic responses to CWD additions in surface soils beneath tree canopy edges and canopies (microsites) during *Juniperus* and *Pinus* encroachment. Data (mean ± SEM) are based on composite soil samples (*n* for *Juniperus* = 653, *Pinus* = 360). Increasing tree cover categories indicate increasing tree encroachment (low, LOW = 0-15 %; MID = 15.01-45 %, and, HIGH = 45.01-100 %). Asterisks indicate significance differences (* = $P < 0.05$, ** = $P < 0.01$) between CWD treatments by microsites and encroachment level, and different letters indicate significant differences ($P < 0.05$) within encroachment levels for a given CWD treatment.

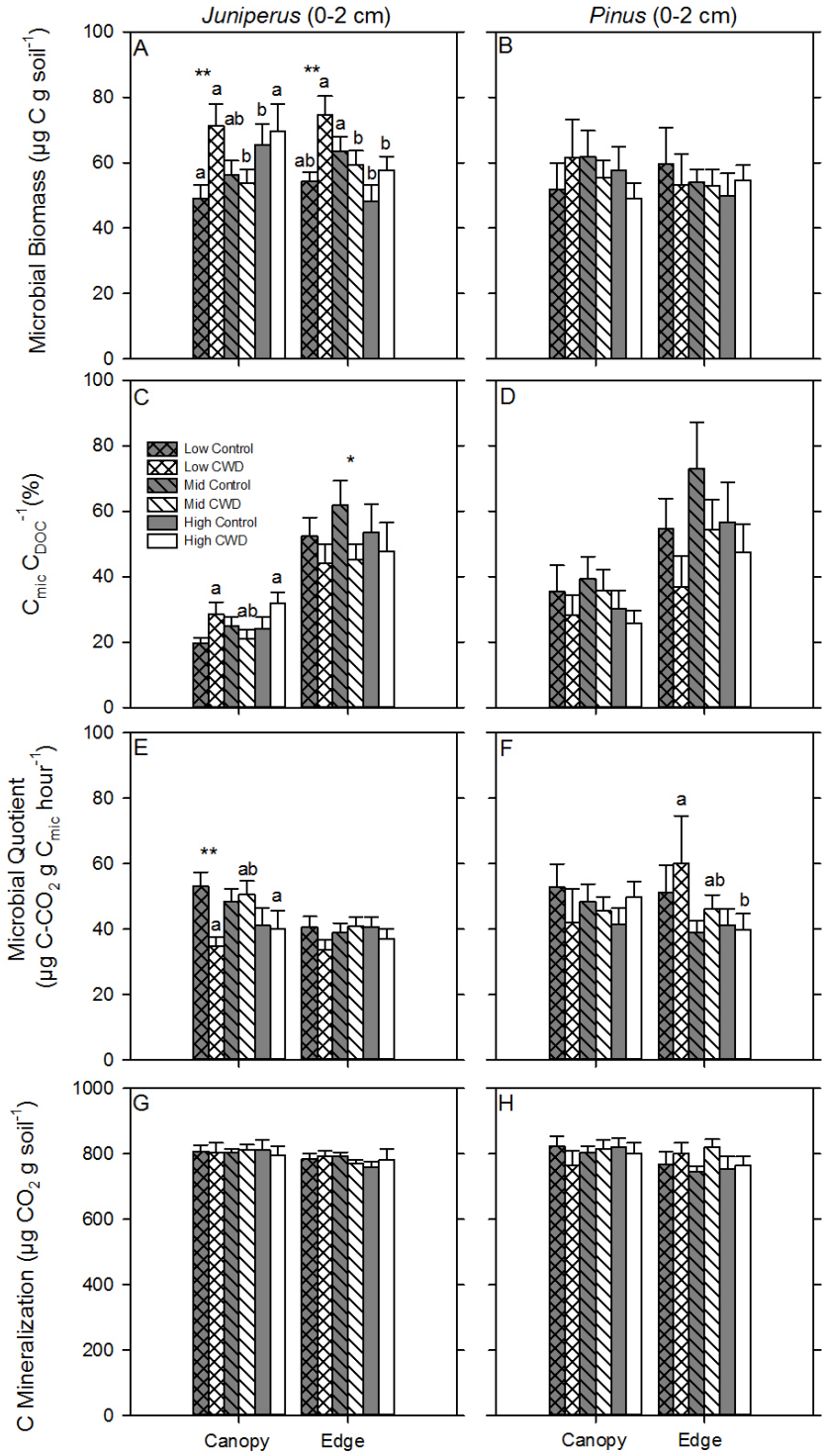

Figure 2. Microbial metabolic responses to CWD additions in subsurface soils beneath tree canopy edges and canopies (microsites) during *Juniperus* and *Pinus* encroachment. Data (mean ± SEM) are based on composite soil samples (*n* for *Juniperus* = 653, *Pinus* = 360). Tree cover categories, CWD treatments, and significant differences are as explained for Fig. 1.

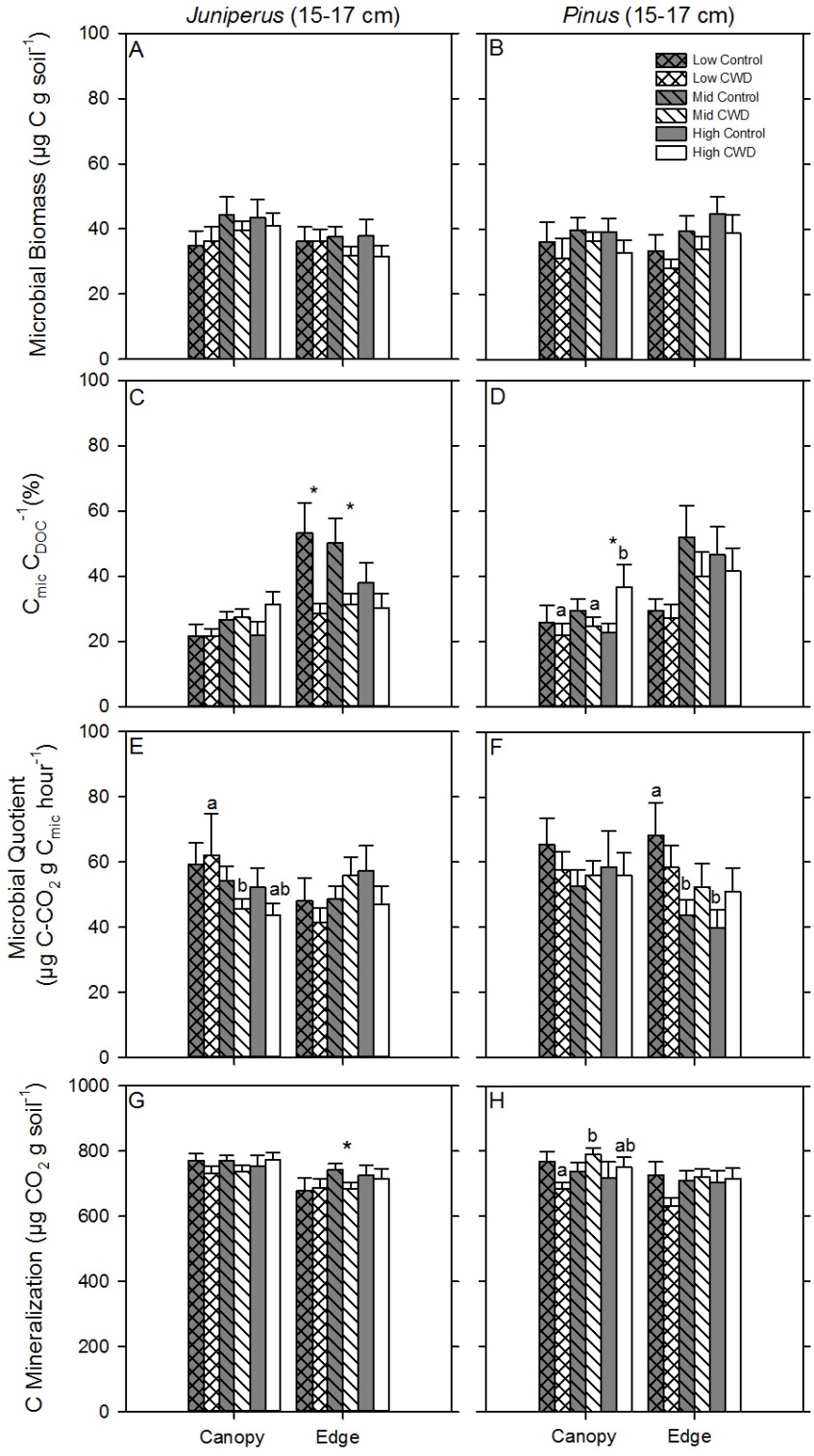

Figure 3. DOC and P availability responses to CWD additions in surface soils beneath tree canopy edges and canopies (microsites) during *Juniperus* and *Pinus* encroachment. Data (mean ± SEM) are based on composite soil samples (*n* for *Juniperus* = 653, *Pinus* = 360). Tree cover categories, CWD treatments, and significant differences are as explained for Fig. 1.

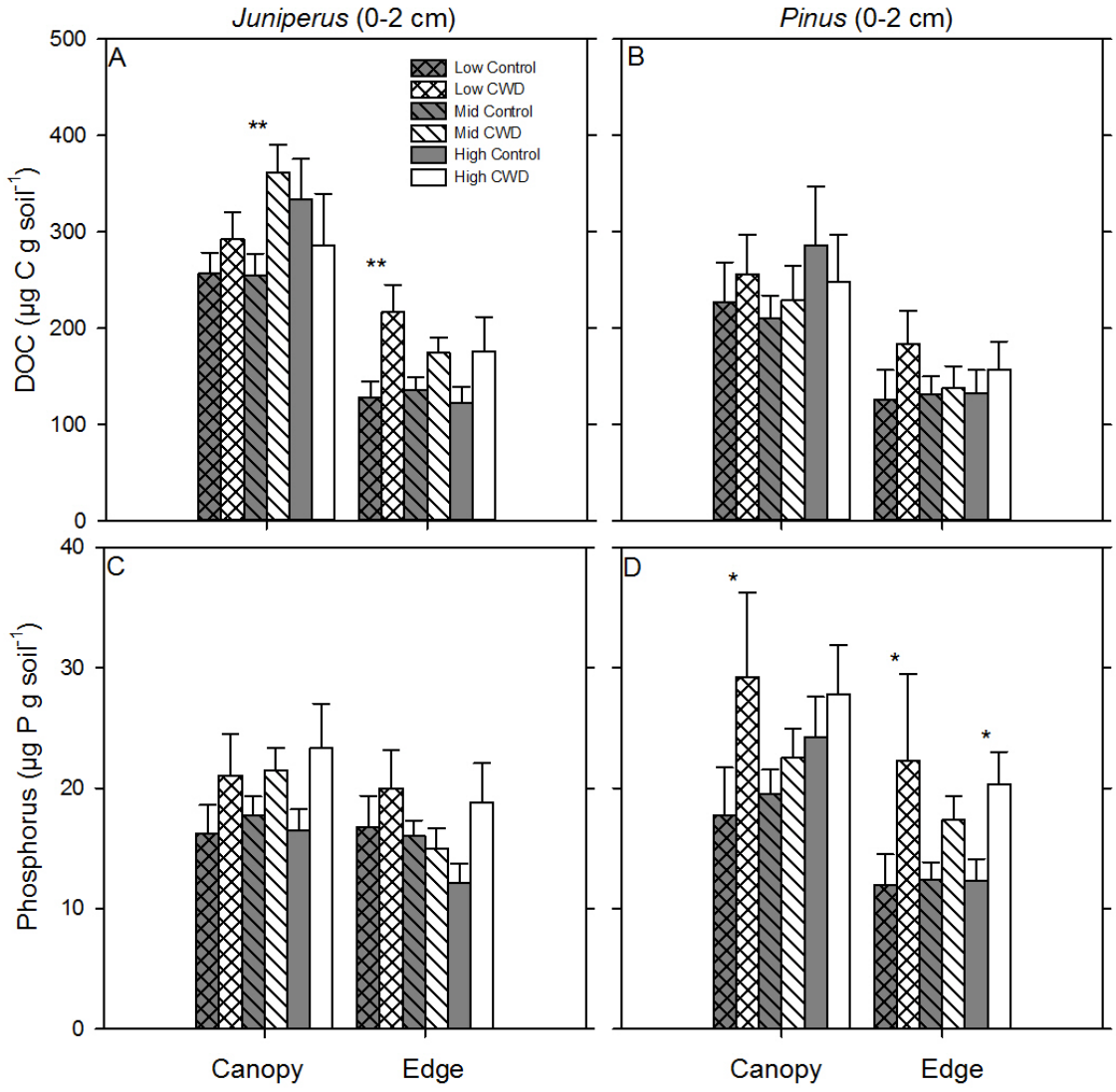

Figure 4. DOC and P availability responses to CWD additions in subsurface soils beneath tree canopy edges and canopies (microsites) during *Juniperus* and *Pinus* encroachment. Data (mean ± SEM) are based on composite soil samples (*n* for *Juniperus* = 653, *Pinus* = 360). Tree cover categories, CWD treatments, and significant differences are as explained for Fig. 1.

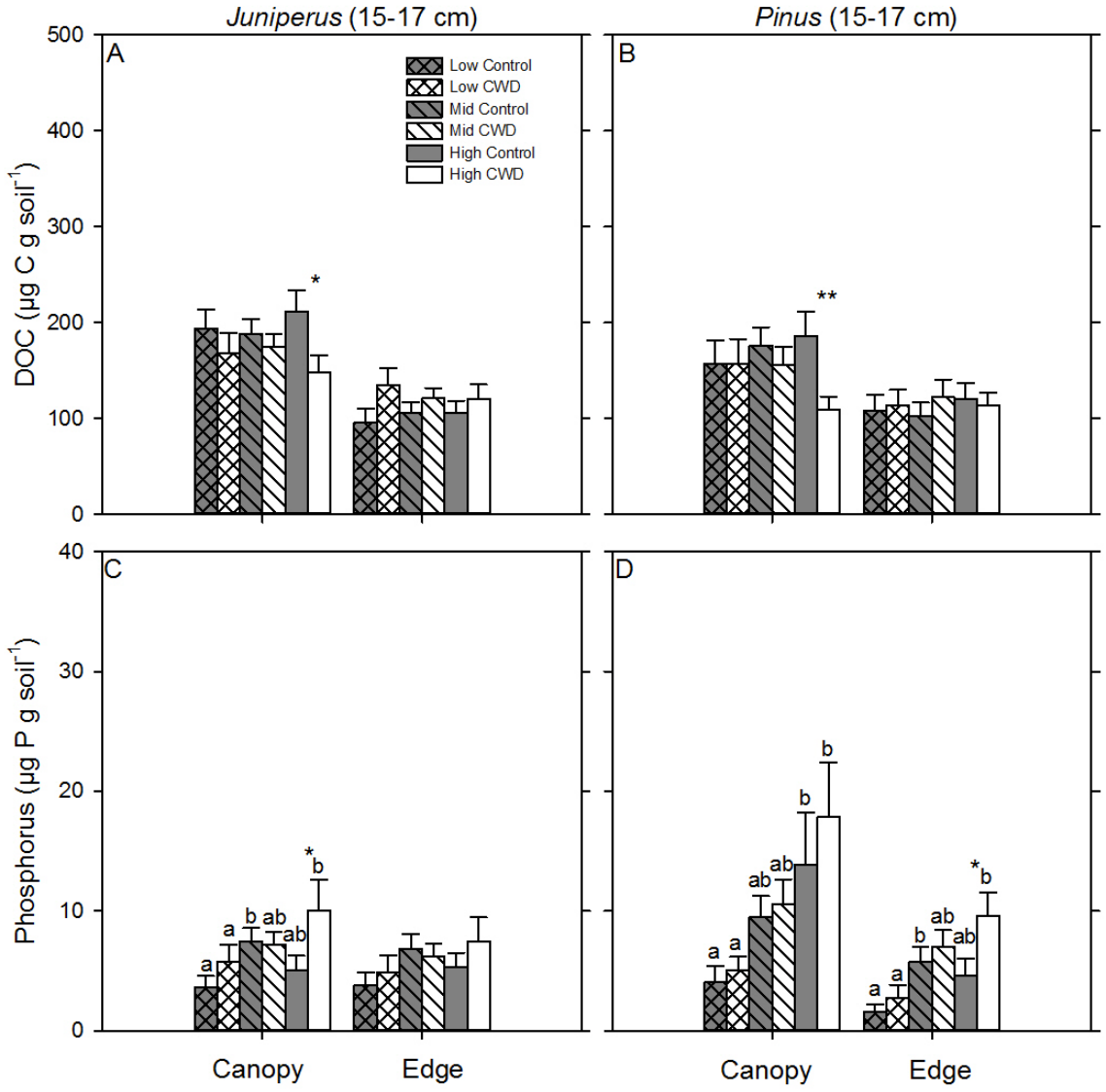

Figure 5. N mineralization and nitrification rates in surface and subsurface soils beneath tree canopy edges and canopies (microsites) during *Juniperus* and *Pinus* encroachment. Data (mean ± SEM) are based on composite soil samples from both tree species (n = 1013). Asterisks indicate significance differences (* = $P < 0.05$, ** = $P < 0.01$) between CWD treatments by microsites and tree cover categories, and different letters indicate significant differences ($P < 0.05$) within encroachment levels for a given CWD treatment.

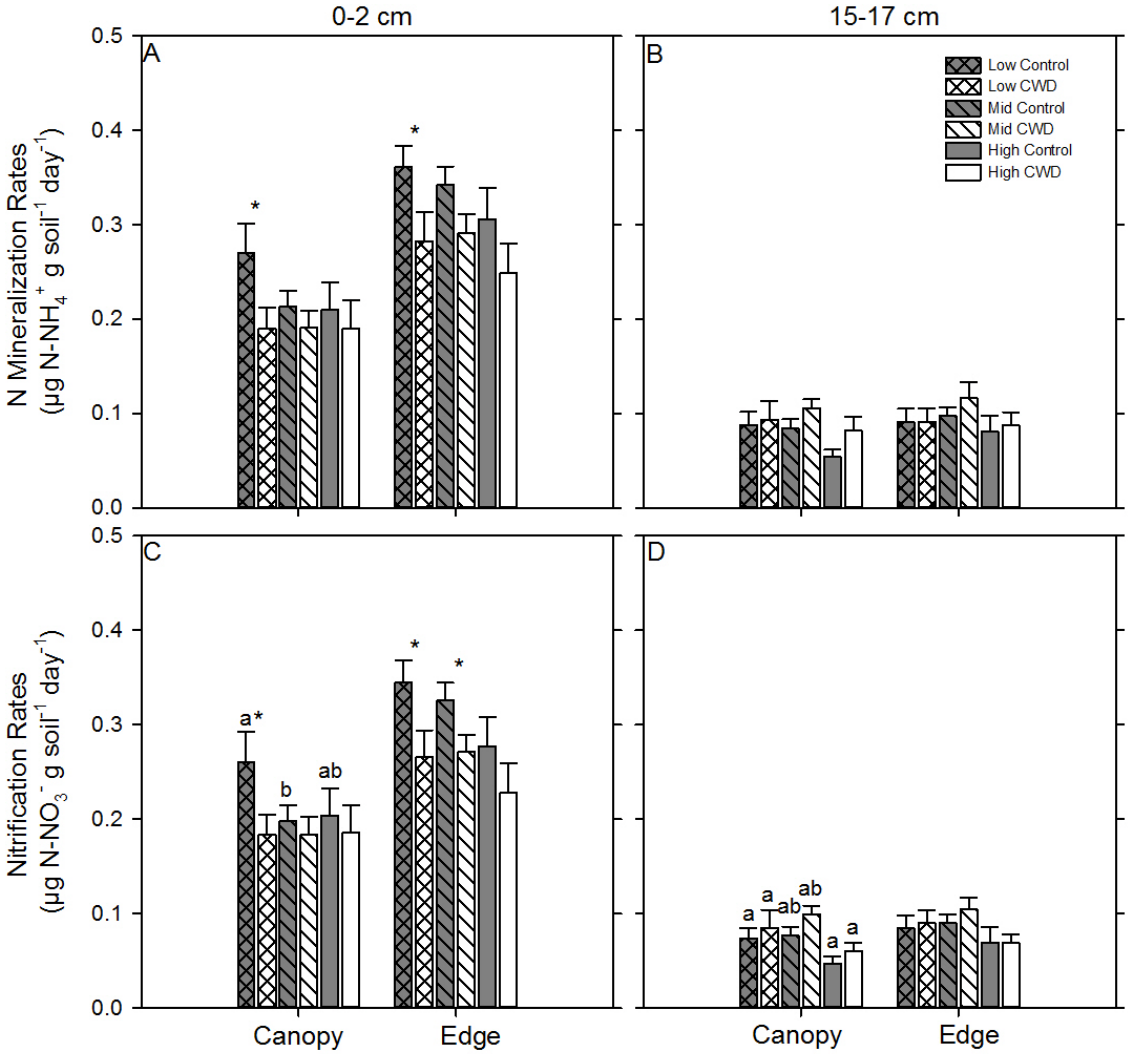
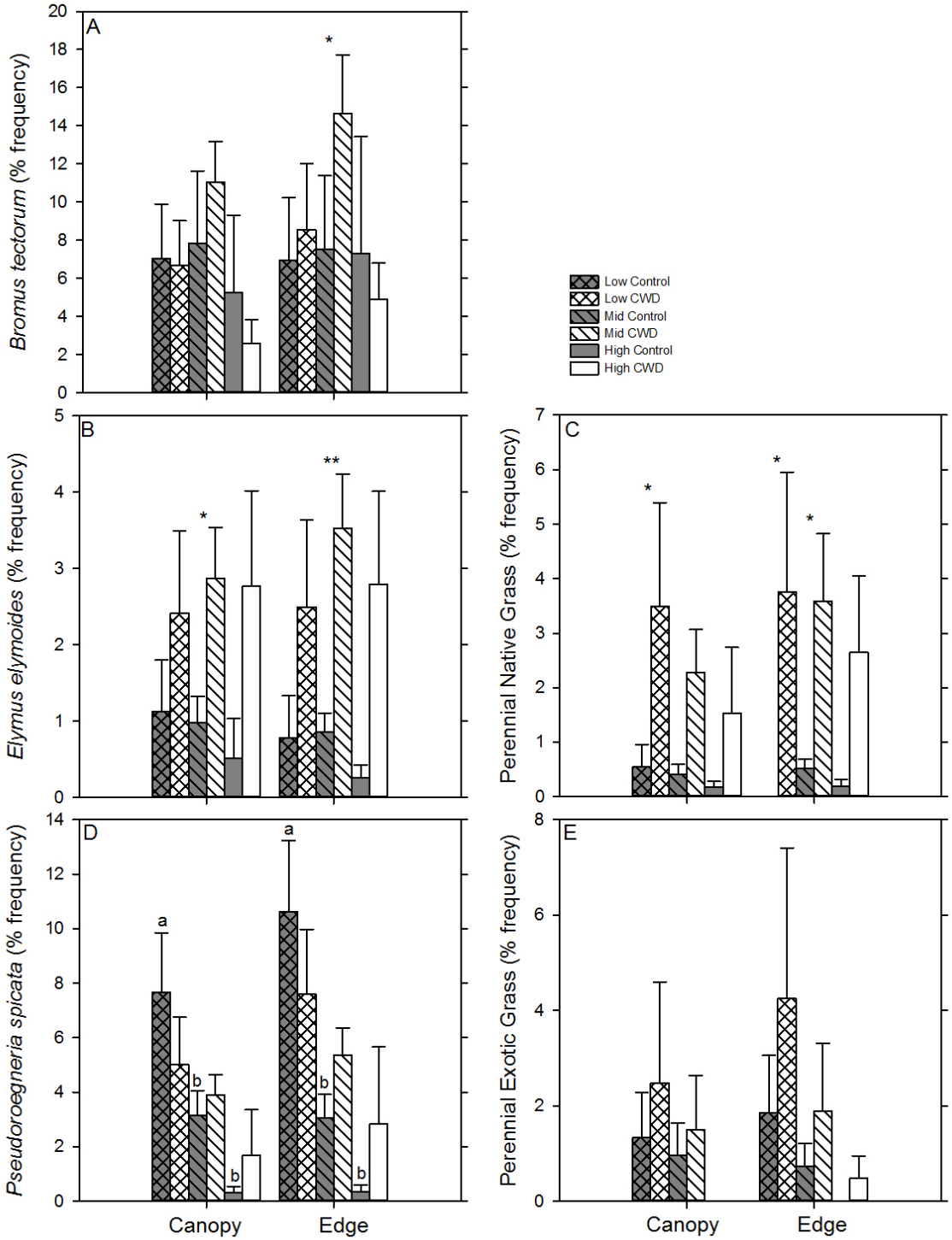
Figure 6. Exotic invasive *Bromus tectorum* and native perennial grass species shifts following CWD additions during *Juniperus* and *Pinus* encroachment. Data (mean ± SEM) are % frequencies for each species or functional group from line-intercept measurements (*n* for *Juniperus* = 653, *Pinus* = 360). Asterisks indicate significance differences (* = $P < 0.05$, ** = $P < 0.01$) between CWD treatments by microsite and tree cover categories, and different letters indicate significant differences ($P < 0.05$) within encroachment levels for a given CWD treatment.