Plant Establishment and Soil Microenvironments in Utah Juniper Masticated Woodlands

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ABSTRACT

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Juniper (*Juniperus* spp.) encroachment into sagebrush (*Artemisia* spp.) and bunchgrass communities has reduced understory plant cover and allowed juniper trees to dominate millions of hectares of semiarid rangelands. Trees are mechanically masticated or shredded to decrease wildfire potential and increase desirable understory plant cover. When trees are masticated after a major increase in tree population density and associated decrease in perennial understory cover, there is a risk that invasive annual grasses will dominate because they are highly responsive to the increased resource availability that commonly follows removal of the main resource user. To determine if tree mastication increases resource availability and subsequently favors invasive annual or perennial grasses, we compared soil temperature, water, and nutrient microenvironmental conditions and seedling establishment and growth. We used the major rangeland weed, cheatgrass (*Bromus tectorum* L.), to represent invasive annual grasses and Anatone bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve), a natural accession of native bluebunch wheatgrass, to represent the perennial grasses of the sagebrush-bunchgrass plant community. These comparisons were made between and within paired-adjacent masticated and untreated areas at three locations in Utah dominated by Utah juniper (*Juniperus osteosperma* (Torr.) Little). Juniper tree mastication generally increased resource availability with masticated areas having greater soil temperature, soil water availability, and soil N supply rates than untreated areas. Prior to juniper tree mastication litter mounds were not found to be resource islands probably because juniper trees themselves were using subcanopy soil water and nutrients. After juniper tree mastication and elimination of these predominant resource users, litter mounds served as resource islands with greater soil water availability and N supply rates than bare interspaces during the critical time for seedling establishment in spring. Plant growth followed in line with greater resource availability after tree mastication with masticated areas having more productive although fewer invasive-annual and perennial grass seedlings than untreated areas. These results suggest that increases in resource availability and warmer spring temperatures associated with mastication will not necessarily favor invasive annual over perennial grass seedling establishment. Resilience of the sagebrush-bunchgrass community to return to dominance after juniper control will likely be greatly influenced by how much of the sagebrush-bunchgrass community remains following tree control and the intensity of propagule pressure by invasive species. If only invasive annuals remain when the trees are treated then invasive annuals would be expected to dominate the post-treatment plant community especially with their ability to establish inside litter mounds unless they were also controlled and perennial grasses planted at the time of treatment.

Keywords: Anatone bluebunch wheatgrass, carbon, cheatgrass, degree days, fertilizer, Great Basin, mulch, nitrogen, PRS™, rangeland restoration, sagebrush steppe, SageSTEP, seedling establishment, shred, wet days, wet degree days, woodland, woody debris

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ABSTRACT

Millions of hectares of sagebrush (*Artemisia tridentata* Nutt.) and bunchgrass plant communities in the semiarid western U.S. have become dominated by juniper trees (*Juniperus* spp.). Trees are mechanically masticated to reduce the potential for wildfire associated with increased canopy fuel loads and to increase the dominance of pre-encroachment plant species. To determine if tree mastication increases resource availability for potential seedling establishment and residual plant growth, we recorded soil water potential and soil temperature at 1-3, 13-15, and 28-30 cm soil depths hourly throughout the year. We measured paired masticated and untreated areas at three high-density juniper woodlands in Utah. Cumulative seasonal-response variables included degree days (> 0 °C), wet days (> -1.5 MPA), and wet degree days (> -1.5 MPA and > 0 °C). Masticated areas had 32 more degree days ($P = 0.019$), 27 more wet days ($P < 0.001$), and 310 more wet degree days ($P < 0.001$) than untreated areas across soil depths and seasons. Soil not covered by tree litter or masticated debris generally had more degree days than soil covered by tree litter or debris during spring and summer but fewer degree days during fall and winter. Covered soil generally had more wet days and wet degree days than uncovered soil at 1-3 cm soil depths in masticated areas. Increased time of soil water availability while soil temperatures are warm enough for plant growth are expected to support seedling establishment and residual plant growth on masticated areas.

Abbreviations

DD, degree days; WD, wet days; WDD, wet degree days

INTRODUCTION

Juniper trees (*Juniperus* spp.) have encroached on millions of hectares of sagebrush (*Artemisia tridentata* Nutt.) and bunchgrass plant communities in the semiarid western US and generally reduced cover of the understory plant community (Cottam and Stewart, 1940; Johnsen, 1962; West, 1984; Vaitkus and Eddleman, 1987; Miller and Wigand, 1994; Miller and Rose, 1999; Bates et al., 2000; Miller et al., 2000; Albert et al., 2004). Juniper trees reduce the pre-encroachment plant community through resource use and redistribution (Breshears et al., 1997a; Robinson et al., 2010). For example, juniper trees begin transpiration in early spring reducing soil water for understory plant species (Angel and Miller, 1994); juniper roots compete with grass roots for resources (Emerson, 1932); juniper roots move soil water deeper away from the evaporation zone and shallow rooted species (Leffler et al., 2002); and juniper canopies intercept 15-20% of annual precipitation when crown cover is 40% (Evans, 1988).

Increased canopy fuel loads and reduction of pre-encroachment plant cover associated with juniper dominance (West, 1999; Miller and Tausch, 2001) justify juniper tree control. For example, control when trees are small and canopy cover is limited helps prevent extreme canopy wildfires and maintains pre-encroachment plant-communities (Milne et al., 1996; West, 1999; Miller and Tausch, 2001). Juniper tree control also increases resource availability for residual perennial-plant species and allows recovery or reestablishment of pre-encroachment plant communities (Everett and Sharrow, 1985; Miller and Tausch, 2001; Bates et al., 2002; Young et al., in reviewa, in reviewb). It is hoped that a recent type of juniper tree control, mechanical mastication, will increase soil water availability and encourage dominance of the pre-encroachment plant community. Mechanical mastication of woody species is a fuel-reduction treatment consisting of large tractors with spinning spikes that shred tree canopies and trunks.

However, the ecological impacts of tree mastication on soil water and temperature resources and the remaining plant community are largely unknown.

In juniper woodlands, understory seedling establishment and plant growth are influenced by the subcanopy environment of tree-litter mounds and interspaces between the mounds. For example, tree canopies and litter mounds shade the soil and reduce soil temperatures compared to interspaces during spring (Facelli and Pickett, 1991; Lebron et al., 2007; Matsushima and Chang, 2007; Lin, 2010) even though litter insulates and maintains warmer soil temperatures during fall and winter (Breshears et al., 1998). Tree canopies and litter mounds also intercept precipitation and reduce plant-available soil water in subcanopy soils compared to interspaces (Facelli and Pickett, 1991; Breshears et al., 1997a, 1997b). On the other hand, litter cover in general increases soil water availability by reducing evaporation as long as precipitation events are large enough to penetrate litter layers (Facelli and Pickett, 1991). Juniper-tree hydraulic redistribution of soil water from interspaces to subcanopy microsites through roots can also increase litter-mound soil water availability (Newman et al., 2010). Even though litter mounds may have increased water availability compared to interspaces, the physical obstruction of seedling emergence by thick litter layers can impede seedling establishment (Facelli and Pickett, 1991).

While surface soil microenvironments are most important for seed germination and seedling emergence (Roundy et al., 1997; Taylor et al., 2007; Rawlins et al., 2012), subsurface soil conditions are important for long-term establishment and growth of perennial species and plant community dynamics between shallow and deep rooted species (Breshears et al., 1997a). For example, greater soil water content in subsurface and subcanopy microsites support a shift from herbaceous plants with shallow roots to woody species with deep roots (Breshears and

Barnes, 1999). Evapotranspiration and downward hydraulic redistribution of soil water through roots by trees like juniper contribute to the gradient of increasing soil water availability with increasing soil depth (Newman et al., 1997; Leffler et al., 2002; Chambers et al., 2007; Breshears et al., 2009; Ryel et al., 2010). In addition, juniper litter decomposition creates water-repellent soil layers that funnel precipitation, throughfall, and stem flow deeper into the soil profile through preferential flow pathways (Young et al., 1984; Hendrickx et al., 1993; Ritsema and Dekker, 2000; Lebron et al., 2007, Madsen et al., 2008). This gradient requires seedlings to extend root depth fast enough to maintain access to soil water below the soil drying front to avoid desiccation with the onset of a dry season (Abbott and Roundy, 2003). These mechanisms of resource redistribution by juniper trees reduce soil water availability for shallow rooted species, decrease understory vegetation cover in general (Lebron et al., 2007; Robinson et al., 2010), and reinforce juniper tree dominance (Breshears and Barnes, 1999).

An ecological concern following juniper tree control is that increased resource availability will lead to invasion and dominance by annual species like cheatgrass (*Bromus tectorum* L.; Davis et al., 2000; Blank et al., 2007; Chambers et al., 2007). Annual weeds have dominated initially following control of Utah juniper [*Juniperus osteosperma* (Torr.) Little], western juniper (*Juniperus occidentalis* Hook.), and singleleaf piñon trees (*Pinus monophylla* Torr. and Frem.; Barney and Frischknecht, 1974; Tausch and Tueller, 1977; Evans and Young, 1985; Vaitkus and Eddleman, 1987). However, the invasive-annual plant stage could be skipped if perennial understory species dominate following juniper tree control (Barney and Frischknecht, 1974; Bates et al., 2000). Aside from the plant community composition remaining at the time of juniper control, the method used to control juniper influences plant community dynamics. For example, chipping Utah juniper and singleleaf piñon trees increased the density and cover of perennial grasses and decreased the density and cover of invasive-annual grasses (Benson, 2006). Woodchips were considered to have increased perennial grass growth by preserving soil water and to have decreased invasive-annual grass growth by reducing soil inorganic-N availability (Benson, 2006). Mastication of juniper trees could have similar effects.

Woody-species control treatments like mastication could greatly reduce the use of soil water by removing the principle water-user in the community and alter soil-water evaporation rates and soil thermal conditions by removing the canopy and placing masticated debris on the soil surface. The metrics of degree days (DD), wet days (WD), and wet degree days (WDD) are useful in relating the soil microenvironment to plant establishment, growth, and invasibility (Chambers et al., 2007; Roundy et al., 2007; Hardegree et al., 2010). We define DD as the seasonal summation of hourly soil temperatures above 0 °C divided by 24; WD as the seasonal summation of hours when soil water potential is greater than -1.5 MPA divided by 24; and WDD as the seasonal summation of hourly soil temperatures above 0 °C when soil water potential is greater than -1.5 MPA divided by 24. Most plants extract soil water down to about -1.5 MPA, which is considered the wilting point of many species, but some xerophytes (desert-type plants) can extract soil water well below -1.5 MPA (Brady and Weil, 1999). The amount of plant-available soil water remaining below -1.5 MPA is small, roughly 0.1 m^3 water m^{-3} soil in loam soils, and soil water potential quickly decreases with additional water loss (Brady and Weil, 1999). In support of our use of -1.5 MPA as the soil water potential criterion, Rawlins et al. (2012) found that a soil water potential of -1.5 MPA more accurately predicted germination timing for common rangeland species than soil water potentials of -1 or -0.5 in loam soils. Soil taxonomic categorizations of soil moisture regimes are also based on periods of time that the soil water potential is > -1.5 MPA (Soil Survey Staff, 2010). Of course, using a higher or lower water potential cutoff would correspond with a decrease or increase in numbers of calculated wet or wet degree days. The accurate use of DD, WD, and WDD summations to predict specific plant growth responses depends on adequately modeling the linearity or curvilinearity and temperature thresholds of the response (Bonhomme, 2000), as well as accounting for limiting factors besides soil temperature and water availability (Wang, 1960; Idso et al., 1978). Such plant growth models have not been developed for wildland species in sagebrush steppe systems. However, in ecosystems where plant response is highly dependent on short periods of soil water availability and when soil and air temperatures are warm enough for growth, these metrics should indicate soil microenvironmental conditions that generally support plant establishment and growth.

Our major objective was to determine the effects of juniper tree mastication on soil water availability and temperature relative to potential seedling establishment and residual plant growth. We quantified the effects of juniper tree mastication on seasonal DD, WD, and WDD: 1) between masticated and untreated microsites collectively to test the overall effect of juniper tree mastication; 2) across individual microsites inherent to juniper woodlands, created by juniper-tree masticated debris, or manually removed-litter mounds to isolate the effects of litter mounds; and 3) across microsite soil depths relevant to shallow and deep rooted species. We hypothesized that: 1) juniper tree mastication will increase resource availability by increasing DD, WD, and WDD in comparison to untreated areas; 2) microsites covered with juniper canopy litter or masticated debris will have fewer DD during warm periods, more DD during cool periods, more WD throughout the year, and more WDD throughout the year compared to uncovered microsites without litter or debris cover; and 3) DD will decrease with soil depth during warm periods and increase with soil depth during cool periods; WD will increase with soil depths throughout the year; and WDD will increase with soil depths during cool periods.

MATERIALS AND METHODS

Study Locations

We studied the three SageSTEP research locations of Greenville, Onaqui, and Stansbury in western Utah (McIver et al., 2010; www.sagestep.org). High densities of Utah juniper trees or mixed piñon-juniper trees have depleted the previous sagebrush (*Artemisia* spp.) and bunchgrass plant communities. The average elevation at these locations is 1,700-1,900 m. Annual average temperatures at these locations are 9-10 °C with minimum average temperatures of 0-3 °C and maximum average temperatures of 16-19 °C. Annual average precipitation ranged between 193 and 389 mm. Most precipitation comes as snow during winter and rain in spring and fall but summers are mostly dry. Greenville (38° 12′ N, 112° 48′ W), located in Beaver County, is on the north side of the Black Mountains with loamy-skeletal, carbonatic, mesic Typic Calcixerepts (Rau et al., 2011). The dominant vegetation includes Utah juniper trees, two-needle piñon trees (*Pinus edulis* Engelm.), Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young), rabbitbrush [*Chrysothamnus viscidiflorus* (Hook.) Nutt.], bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) A. Löve], needle-and-thread [*Hesperostipa comata* (Trin. & Rupr.) Barkworth], and Indian ricegrass [*Achnatherum hymenoides* (Roem. & Schult.) Barkworth]. Onaqui (40° 13′ N, 112° 28′ W), located in Tooele County, is on the east side of the Onaqui Mountains with loamy-skeletal, carbonatic, mesic, shallow Petrocalcic Palexerolls (Rau et al., 2011). The dominant vegetation includes Utah juniper trees, Wyoming big sagebrush, bluebunch wheatgrass, Sandberg bluegrass (*Poa secunda* J. Presl), and Indian ricegrass. Stansbury (40° 35′ N, 112° 39′ W), located in Tooele County, is on the west side of the Stansbury Mountains with loamy-skeletal, mixed, active, frigid Pachic Haploxerolls (Rau et al., 2011). The dominant vegetation includes Utah juniper trees, Wyoming big sagebrush, antelope bitterbrush [*Purshia tridentata* (Pursh) DC.], bluebunch wheatgrass, Sandberg bluegrass, and cheatgrass.

Treatment Implementation

A Tigercat® M726E Mulcher (Tigercat Industries Inc., Brantford, Ontario) with Fecon® Bull Hog® (Fecon Inc., Lebanon, OH) attachment masticated Utah juniper trees at Onaqui in the fall of 2006 and at Stansbury in the fall of 2007. A skid steer loader with Fecon® Bull Hog® attachment masticated Utah juniper and two-needle piñon trees at Greenville in the fall of 2007. Greenville and Onaqui had 20-ha treatment plots while Stansbury had 5-ha plots.

Study Design

We designated paired masticated and untreated (not masticated) plots with similar soils and pretreatment vegetation at each location. We installed a randomized complete block study within each masticated and untreated plot. Sixteen juniper trees in masticated plots and eight juniper trees in untreated plots were grouped into four replicate blocks. We selected trees with at least a 2-m diameter litter mound to allow room to measure the soil microenvironment. For this study, one tree per block was selected on which to measure soil water and temperature. The masticated plots had two more microsite types than untreated plots because juniper tree mastication scatters debris in patches over tree litter mounds and bare interspaces. To separate the effects of litter mounds from masticated debris on soil water and temperature, we designated five microsite types for trees in masticated plots and three microsite types for trees in untreated plots. Masticated-tree microsite types included: 1) juniper litter mounds from old canopy-dropped scales, fruits, and twigs (litter mounds); 2) removed juniper-litter mounds exposing the soil surface (removed-litter mounds); 3) bare interspaces between trees where little vegetation was growing (bare interspaces); 4) bare interspaces covered with masticated juniper debris

(debris-covered interspaces); and 5) juniper litter mounds covered with masticated juniper debris (debris-covered litter mounds). Untreated-tree microsite types included: 1) litter mounds, 2) removed-litter mounds, and 3) bare interspaces. We buried soil water and temperature sensors at 1-3, 13-15, and 28-30 cm soil depths in the microsites of one randomly-selected tree from each block within each treatment plot. The number of microsite experimental units per research location was 32.

Field Measurements

We buried copper-constantan thermocouples (Omega Engineering, Inc., Stamford, CT) to measure soil temperature and gypsum blocks (Delmhorst Instrument Co., Towaco, NJ) to measure soil water potential at Onaqui in October 2007 and at Greenville and Stansbury in July 2008. One of each sensor was buried at 1-3, 13-15, and 28-30 cm soil depths in each microsite of one randomly selected tree per block. We measured soil water and temperature across seasons from the first full season after installation of data loggers through the winter of 2010-2011 at Greenville and Onaqui but only through the spring of 2009 at Stansbury because a wildfire destroyed the study at this location in August 2009. We converted electrical resistance as measured by gypsum blocks to soil water potential using a standard calibration curve (Campbell Scientific, Inc., 1983). CR10X data loggers and AM16/32 multiplexers (Campbell Scientific, Inc., Logan, UT) recorded hourly-average soil water potential and soil temperature using 1-min interval measurements. Soil water potential and temperature were recorded at Greenville from September 2008 through February 2011; Onaqui from December 2007 through February 2011; and Stansbury from September 2008 through June 2009. Onsite air temperature was recorded hourly using a thermistor in a gill shield and precipitation was measured using an electronic tipping-bucket rain gauge at each research location throughout the study.

Data Analysis

Soil water and temperature values were analyzed as the seasonal summations of DD (> 0 °C), WD (> -1.5 MPA), and WDD (> -1.5 MPA and > 0 °C) separately using Proc Mixed (SAS v9.2, SAS Institute, Inc., Cary, NC). The four seasons included spring: 1 March to 30 June; summer: 1 July to 31 August; fall: 1 September to 30 November; and winter: 1 December to 28 February. We combined locations and years for analysis of soil water and temperature. Analysis of variance data requirements were met without transformation of response variables based on evaluation of residual plots. Seasons, treatment plots, microsites, and soil depths were fixed effects and years, locations, blocks, and trees were random effects in mixed-model analysis of variance. Fixed effects were evaluated with F-tests from maximum likelihood estimation. Microsites as the experimental units were nested in trees and trees were nested in years, locations, and blocks. This analysis structure accounted for potential microsite spatial correlation. Season was crossed with years and not nested in years because seasons were the same period of time each year. Season was included as a repeated measures variable to account for potential temporal correlation. We were unable to evaluate interactions between treatments and microsites using a full factorial analysis because masticated plots had more types of microsites than untreated plots, a result of untreated plots not having masticated debris microsites. To evaluate overall treatment comparisons and treatment by microsite interactions, we assigned each treatment by microsite combination to be one of eight levels of the treatment-microsite main effect. These combinations consisted of masticated litter mounds, masticated removed-litter mounds, masticated bare interspaces, masticated debris-covered interspaces, masticated debris-covered litter mounds, untreated litter mounds, untreated removed-litter mounds, and untreated bare interspaces. These combinations allowed us to use linear contrasts to compare the five microsite types in masticated plots with the three microsite types in untreated plots collectively to test the overall treatment effect. We made individual microsite comparisons across and within treatment plots using linear contrasts. For example, we compared untreated bare interspaces with masticated bare interspaces and untreated bare interspaces with untreated litter mounds. We adjusted for false positives from multiple comparisons by using pseudo-Bonferroni with a critical alpha level of 0.001 for individual microsite and soil depth comparisons. Each response variable had 3,628 observations for analysis.

RESULTS

Air Temperature and Precipitation

Annual-average air temperatures were consistent across years but annual precipitation totals varied greatly across years and were generally lower than long-term averages. Greenville and Onaqui had onsite annual-average air temperatures of 9-10 °C with minimum temperatures of 0-2 °C and maximum temperatures of 17-19 °C. Onsite annual air temperature and precipitation data are not available for Stansbury. The long-term annual averages from 1970-2007 at Greenville, Onaqui, and Stansbury for minimum air temperature were 0, 2, and 3 °C and for maximum air temperature were 17, 17, and 16 °C, respectively (PRISM, 2008). Greenville had annual precipitation totals of 193 mm in 2009 and 387 mm in 2010. Onaqui had annual precipitation totals of 259 mm in 2008, 287 mm in 2009, and 370 mm in 2010. The long-term annual precipitation totals from 1970-2007 at Greenville, Onaqui, and Stansbury were 334, 311, and 389 mm, respectively (PRISM, 2008).

Juniper Tree Mastication Effect

The three main effects of treatment-microsite, soil depth, and season and their interactions were always significant for DD, WD, and WDD except for the treatment-microsite by soil depth interaction for DD ($P > 0.001$, Table 1). For the overall treatment effect across all soil depths and seasons, the five microsite types in masticated plots collectively had 32 more DD ($P = 0.019$), 27 more WD ($P < 0.001$), and 310 more WDD ($P < 0.001$) than the three microsite types in untreated plots (Table 2). Considering soil depths and seasons separately across all microsites, masticated plots had 46 more DD than untreated plots at 1-15 cm soil depths during spring and fall ($P < 0.01$, Table 3). Masticated plots had 29 more WD than untreated plots at all soil depths and seasons except there were no differences at 1-3 cm soil depths during summer ($P > 0.001$, Table 4). Masticated plots had 373 more WDD than untreated plots at all soil depths and seasons except there were no differences at 1-15 cm soil depths during winter ($P > 0.001$, Table 5).

Microsite Effect

Uncovered microsites without litter or debris and with no tree canopy cover frequently had more DD than the litter or debris covered microsites during spring and summer. For example, in untreated plots at 1-30 cm soil depths, bare interspaces without tree canopy cover had the most DD followed by removed-litter mounds under tree canopies while litter mounds under tree canopies usually had the fewest DD during spring and summer ($P < 0.001$). In masticated plots at 1-30 cm soil depths, bare interspaces and sometimes removed-litter mounds both without surface or tree canopy cover had the most DD followed by the dark-colored litter mounds during spring and summer ($P < 0.001$). The light-colored, debris-covered interspaces and litter mounds had the least DD during spring and summer ($P < 0.001$).

Covered microsites often had more DD than uncovered microsites during fall and winter even though there were fewer microsite DD differences. In untreated plots, litter mounds and removed-litter mounds under tree canopies had 119 more DD than bare interspaces without surface or tree canopy cover during fall and a similar but non-significant trend during winter at 1-30 cm soil depths ($P > 0.001$). In masticated plots, litter mounds had 84 more DD than interspaces with and without debris cover at 1-3 cm soil depths while there were no microsite DD differences at 13-30 cm soil depths during fall ($P > 0.001$). Debris-covered litter mounds had more DD than removed-litter mounds and bare interspaces during winter at 1-15 cm soil depths ($P < 0.001$).

Covered microsites usually had more WD and WDD than uncovered microsites at 1-3 cm soil depths in masticated plots but there were no clear WD or WDD trends in untreated plots. For example, in masticated plots, litter mounds, debris-covered interspaces, and debris-covered litter mounds had 31 more WD during spring and 305 more WDD during spring and summer than removed-litter mounds and bare interspaces at 1-3 cm soil depths ($P < 0.001$). However at 13-30 cm soil depths, removed-litter mounds had more WDD than debris-covered litter mounds during spring, a trend opposite that at 1-3 cm soil depths in masticated plots ($P < 0.001$). Microsite WDD were also higher for removed-litter mounds and bare interspaces than for debris-covered interspaces and litter mounds at 28-30 cm soil depths during summer ($P < 0.001$).

Soil Depth Effect

Soil depth differences followed a trend of decreasing DD with increasing soil depth during spring and summer but then increasing DD with increasing soil depth during fall and winter. For example, removed-litter mounds and bare interspaces in untreated plots and the five microsites in masticated plots had more DD at 1-3 cm than at 28-30 cm soil depths during spring and summer ($P < 0.001$). Whereas after summer, the three microsites in untreated plots and the five microsites in masticated plots had fewer DD at 1-3 cm than at 28-30 cm soil depths during fall and winter ($P < 0.001$).

Opposite the DD trend across soil depth, uncovered microsite WD in untreated plots increased with soil depth during spring and sometimes summer but then decreased with soil depth during fall and winter. For example, removed-litter mounds had 27 fewer WD at 1-3 cm than at 28-30 cm soil depths in untreated plots during spring and summer ($P < 0.001$). Whereas after summer, removed-litter mounds and bare interspaces during fall and removed-litter mounds during winter had more WD at 1-3 cm than at 28-30 cm soil depths in untreated plots ($P < 0.001$). However, the WD trend in masticated plots was for increased WD with soil depth throughout the year. For example, the following microsites in masticated plots had fewer WD at 1-3 cm than at 28-30 cm soil depths: removed-litter mounds and bare interspaces during all seasons, debris-covered interspaces during summer, litter mounds and debris-covered litter mounds during fall, and litter mounds during winter ($P < 0.001$).

The WDD trend in untreated and masticated plots was for increased WDD with increased soil depth during spring and summer, which was similar to the trend for WD in masticated plots. In untreated plots, the uncovered microsites of removed-litter mounds and bare interspaces had 333 fewer WDD at 1-3 cm soil depths than at 13-30 cm soil depths during spring and removed-litter mounds had 390 fewer WDD at 1-15 cm than at 28-30 cm soil depths during summer ($P < 0.001$). In masticated plots, the uncovered microsites of removed-litter mounds and bare interspaces had 552 fewer WDD at 1-3 cm than at 28-30 cm soil depths during spring ($P < 0.001$). All five microsites in masticated plots had fewer WDD at 1-3 cm than at 28-30 cm soil depths during summer and fall except debris-covered litter mounds did not have fewer WDD at 1-3 cm than at 28-30 cm soil depths during summer ($P > 0.001$).

DISCUSSION

Juniper-Tree Mastication Effect

Masticated plots generally had more DD, WD, and WDD than untreated plots across soil depths and seasons supporting our first hypothesis that juniper tree mastication will increase resource availability. The greater number of DD in masticated than untreated plots was associated with tree canopy removal that allows more solar radiation and warmer soil temperatures (Everett and Sharrow, 1985; Belsky et al., 1989; Breshears et al., 1998; Martens et al., 2000; Breshears, 2006). The greater number of WD in masticated than untreated plots was probably associated with the cessation of juniper tree uptake of soil water. Because both DD and WD were greater in masticated than untreated plots, it follows that WDD would also be higher in masticated plots. The combination of more WDD and soil inorganic-N availability (Young et al., in reviewb) in masticated than untreated plots explain the increased seedling establishment found in a related study (Young et al., in reviewa) conducted on the same microsites as this study. Native perennial and invasive annual aboveground biomass, tillers, and cheatgrass spikelets were higher in masticated than untreated plots (Young et al., in reviewa). The increase in seedling establishment metrics for the invasive annual and perennial grasses suggest that both plant types will increase following mastication rather than one dominating the other assuming both types are present following tree mastication.

Microsite Effect

Microsites covered with litter or debris typically had fewer DD than uncovered microsites without litter or debris during spring and summer but covered microsites frequently had more DD than uncovered microsites during fall and winter. Litter mounds and masticated debris would be expected to maintain cooler soil temperatures in spring by intercepting solar radiation, but maintain warmer soil temperatures during winter by reducing long-wave reradiation from the soil (Breshears et al., 1998; Brady and Weil, 1999; Hillel, 2004). Tree canopies also intercept incoming solar radiation and outgoing reradiation (Barbour et al., 1999; Lin, 2007, 2010). Our results provide an example of this even though we did not measure solar radiation. In untreated plots, removed-litter mounds below tree canopies had fewer DD than bare interspaces without tree canopy cover during spring and summer. In comparison, masticated plots without any tree canopy cover had similar DD between removed-litter mounds and bare interspaces during spring and summer. The cooler soil temperatures under debris than litter seemed to be associated with the lighter color of masticated debris than litter. Darker-colored tree litter would be expected to absorb more radiant energy than light-colored masticated debris (Brady and Weil, 1999). However, masticated debris turns from a tan to a gray color after about a year and may become less reflective over time. Soil cover by debris or litter could delay spring seedling establishment and plant growth through cooler soil temperatures while the lack of soil cover could encourage earlier plant growth through warmer soil temperatures (Brady and Weil, 1999; Chambers et al., 2007; Roundy et al., 2007; Rawlins et al., 2012).

Covered microsites often had more WD and WDD than uncovered microsites at 1-3 cm soil depths in masticated plots while there was no clear trend in untreated plots. As would be expected, litter and debris cover conserved soil water because of the associated reduction in evaporation. Soil cover intercepts solar radiation and decreases the vapor pressure deficit between the soil and atmosphere (Burkhardt and Tisdale, 1976; Duff et al., 1997; Breshears et al., 1997b, 1998; Morecroft et al., 1998; Matsushima and Chang, 2007). The lack of consistent trends among microsite WD and WDD in untreated plots was probably associated with the interactive effects of tree water use, subcanopy shading, temporary shading of bare interspaces

(Lebron et al., 2007; Matsushima and Chang, 2007; Lin, 2010; Robinson et al., 2010), redistribution of precipitation and soil water by tree canopies and roots (Young et al., 1984; Breshears et al., 1997a, 1997b; Leffler et al., 2002; Newman et al., 2010), and other potential tree influences on the microenvironment. Opposite the WDD trend at 1-3 cm soil depths, uncovered microsites frequently had more WDD than covered microsites at 28-30 cm soil depths during spring and summer in masticated plots. This trend was associated with warmer soil temperatures and more DD in uncovered microsites than covered microsites, rather than differences in soil water availability.

More WDD in covered than uncovered microsites at 1-3 cm soil depths in masticated plots should favor increased germination and seedling establishment in juniper-encroached sagebrush steppe because scarcity of soil water and cool spring temperatures limit plant growth in these ecosystems (Lebron et al., 2007; Roundy et al., 2007). Higher soil-N supply rates in litter mounds than interspaces are also expected to increase seedling establishment and plant growth (Young et al., in reviewa, in reviewb) although many other factors influence seedling establishment as well (Harper, 1977). However, when sown invasive annual and native perennial grasses were compared between litter mounds and bare interspaces, few differences in seedling establishment metrics were found (Young et al., in reviewa). Only bluebunch-wheatgrass aboveground biomass was greater in litter mounds than bare interspaces while emergence, tillers, and cheatgrass biomass and spikelets were not different between these microsites (Young et al., in reviewa). This indicates that environmental requirements for seedling establishment were met in both litter mounds and bare interspaces. In a review of the effects of litter cover on plant community dynamics, Facelli and Pickett (1991) reported that thin litter layers can enhance plant establishment by preserving soil water through reduced evaporation; whereas, thick litter layers can limit plant establishment through less solar radiation, cooler soil temperatures, and physical impedance of seeds reaching the soil or seedlings extending coleoptiles up through the cover. The effects of mulches and other seedbed modifications on wildland seedling establishment vary with specific weather conditions during a given year (Hardegree et al., 2011). Mulches or seedbed modifications such as furrowing may increase success on an average year, may not prevent failure in a dry year, and may have little effect in a wet year (Winkel and Roundy, 1991; Roundy et al., 1992; Roundy et al., 1997).

Soil Depth Effect

Microsite DD frequently decreased with soil depth during spring and summer but increased with soil depth during fall and winter as expected and stated in our third hypothesis. These DD trends were associated with seasonal differences in solar radiation. In spring and summer, more direct solar radiation at northern latitudes results in greater warming of surface than subsurface soils (Brady and Weil, 1999). Conversely, in fall and winter, less direct solar radiation results in cooler surface than subsurface soils (Brady and Weil, 1999). These types of temperature differences across soil depths have influenced invasive-annual versus native-perennial seedling establishment (Harris, 1967). For example, rapid root elongation after fall germination of invasive annuals like cheatgrass allows roots to penetrate deeper into the soil profile where soil temperatures are warmer during winter (Harris, 1967). Access to deeper soils with warmer temperatures favors winter root growth and spring water uptake by cheatgrass, which gives it an advantage over native-perennial grasses like bluebunch wheatgrass whose seedling roots grow slower than those of cheatgrass at cool temperatures (Harris, 1967).

Uncovered microsite WD often increased with soil depth during spring and summer but decreased with soil depth during fall and winter in untreated plots, a seasonal pattern opposite that of DD. These WD trends suggest that juniper trees deplete much of the plant-available soil water by the end of summer and that the return of precipitation after dry summers likely cause the wetter surface than subsurface soils in fall and winter. However, in masticated plots with no tree water use, WD often increased with soil depth during all seasons as expected in our third hypothesis. With juniper trees being the apparent dominant water-resource user, their removal is expected to influence plant community dynamics by increasing the duration of available soil water for remaining deep-rooted species.

Tree dominance will continue in the absence of disturbance because there is more soil water deeper in the soil profile in these ecosystems (Breshears et al., 2009). The ratio of herbaceous to woody plant biomass is dependent on the ratio of shallow to deep soil water assuming that herbaceous species have more access to shallow soil water than woody species and woody species have sole access to deep soil water (Breshears et al., 1997b). The redistribution of shallow water in bare interspaces to deeper in the soil profile reinforces tree dominance (Breshears and Barnes, 1999) and helps explain why there were more WDD deeper in the soil during spring and summer although other factors like evaporation play a role as well (Hillel, 2004). If pre-encroachment plant communities are to be maintained, juniper tree control is required because the apparent ability of juniper to manipulate resource availability seems to have made it well adapted to encroaching and dominating the sagebrush steppe.

Conclusions

In sagebrush steppe ecosystems invaded by juniper trees, optimum plant growth is restricted to relatively short periods of warm temperatures in spring and early summer when soil water is still available (Chambers et al., 2007; Roundy et al., 2007). However, the increased availability of soil water and warmer temperatures in spring after tree mastication should increase seedling establishment and growth of residual plant species. Time of soil water availability was increased even at the Greenville study site in 2009, when annual precipitation was only 50% of that received in 2010 and 58% of the long-term average precipitation. Seeds under thin litter layers are expected to have a higher probability of successful establishment than those in uncovered microsites due to increased wet degree days. However, thick litter layers may reduce seedling emergence. Seedlings able to emerge through litter mounds should grow and establish well because litter mounds have comparatively long periods of soil water availability and increased soil N availability. In spring, the number of wet days and wet degree days both increased with soil depth, despite the fact that degree days decreased with depth. Longer periods of soil water availability at depth should favor seedling establishment of species with sufficient root extension to stay ahead of the soil drying front. Without tree control or wildfire, juniper trees are expected to continue to dominate sagebrush steppe because they access deeper soil water and can decrease understory plant cover (Miller and Wigand, 1994; Breshears et al., 2009). Degree day, wet day, and wet degree day metrics may prove useful in future research to monitor the effects of global climate change on soil microenvironments that influence seedling establishment and continued plant growth.

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Tables

Table 1-1. Mixed-model analysis of variance and type III F-tests from maximum likelihood estimation for the response variables of degree days, wet days, and wet degree days. We assigned each treatment (trt) by microsite combination as one of 8 levels of the combined main effect of trt-microsite.

	Effect	Num DF†	Den DF‡	F-value	p-value
Degree Days	Trt-microsite	7	3204	60.64	<0.001
	Depth	2	3204	7.28	<0.001
	Season	5	3204	46,783.00	<0.001
	Trt-microsite * Depth	14	3204	1.22	0.250
	Trt-microsite * Season	35	3204	145.73	<0.001
	Depth * Season	10	3204	271.71	<0.001
	Trt-microsite * Depth * Season	70	3204	1.81	<0.001
Wet Days	Trt-microsite	7	3204	37.35	<0.001
	Depth	2	3204	65.47	<0.001
	Season	5	3204	1250.79	<0.001
	Trt-microsite * Depth	14	3204	7.60	<0.001
	Trt-microsite * Season	35	3204	11.39	<0.001
	Depth * Season	10	3204	8.43	<0.001
	Trt-microsite * Depth * Season	70	3204	3.08	<0.001
Wet Degree Days	Trt-microsite	7	3204	58.21	<0.001
	Depth	2	3204	114.49	<0.001
	Season	5	3204	989.83	<0.001
	Trt-microsite * Depth	14	3204	8.54	<0.001
	Trt-microsite * Season	35	3204	13.65	<0.001
	Depth * Season	10	3204	23.95	<0.001
	Trt-microsite * Depth * Season	70	3204	4.40	<0.001

† Num DF, numerator degrees of freedom.

‡ Den DF, denominator degrees of freedom.

Table 1-2. Treatment maximum-likelihood estimates compared between masticated plots with interspace, litter, removed-litter, debris-over-litter, and debris microsites and untreated plots with interspace, litter, and removed-litter microsites across soil depths and seasons.

				1-30 cm		
	Std error†	DF‡	t value	Masticated	Untreated	p-value
Wet Days	1.51	3204	14.90	67	45	<0.001
Degree Days	11.83	3204	2.35	892	865	0.019
Wet Degree Days	13.93	3204	19.42	617	347	<0.001

† Std error, standard error.

‡ DF, degrees of freedom.

Table 1-3. Degree day linear-contrast comparisons among 1) untreated (untrt) and masticated (mast) plots; 2) litter mound (L), removed-litter mound (RL), bare interspace (I), debris-covered interspace (DI), and debris-covered litter mound (DL) microsites (micro); and 3) 1-3, 13-15, and 28-30 cm soil depths. Soils were loamy skeletal at Greenville, Onaqui, and Stansbury in Utah.

		1-3 cm		13-15 cm		28-30 cm	
Season	Micro	Untrt	Mast	Untrt	Mast	Untrt	Mast
Spring	L	*1118*†c‡x§	*1427* b X¶	*1090* c x	*1354* b X	*1085* c x	*1274* b Y
	RL	*1355* b x	*1529* a X	*1250* b y	*1410* ab Y	*1202* b y	*1329* ab Z
	I	1509 a x	1505 a X	1440 a xy	1447 a X	1370 a y	1356 a Y
	DI		1240 c X		1201 c XY		1139 c Y
	DL		1165 c X		1139 c XY		1088 c Y
		1327	*1373*	*1260*	*1310*	1219	1237
Summer	L	*1306* c x	*1557* b X	*1259* c x	*1463* b Y	*1237* b x	*1387* b Y
	RL	*1516* b x	*1676* a X	*1385* b y	*1522* ab Y	*1316* b y	*1443* ab Y
	I	1678 a x	1645 a X	1562 a y	1551 a Y	1494 a y	1481 a Y
	DI		1434 c X		1376 c XY		1314 bc Y
	DL		1327 d X		1295 c X		1246 c X
		1500	1528	1402	1441	1349	1374
Fall	L	1068 a y	1132 a Y	1125 a xy	1191 a XY	1197 a x	1255 a X
	RL	1099 a y	1071 ab Y	1158 a xy	1124 a Y	1225 a x	1208 a X
	I	*947* b y	*1045* b Z	*1014* b y	*1132* a Y	*1119* b x	*1219* a X
	DI		1051 b Y		1125 a XY		1192 a X
	DL		1098 ab Y		1157 a XY		1223 a X
		1038	*1080*	*1099*	*1146*	1180	1220
Winter	L	96 a y	83 ab Y	140 a y	137 ab Y	231 a x	221 ab X
	RL	80 a y	46 b Y	103 ab y	80 b Y	183 ab x	173 ab X
	I	27 a y	50 b Y	61 b y	84 b Y	144 b x	161 b X
	DI		87 ab Y		146 ab XY		214 ab X
	DL		125 a Y		170 a XY		241 a X
		67	78	101	123	186	202

† Within season and soil depth, significant differences between untreated and masticated estimates are underlined and italicized (individual microsite comparisons $P < 0.001$; overall comparisons $P < 0.01$).

‡ Within seasons and columns, individual microsite estimates followed by the same lower-case letter of a, b, or c are not significantly different ($P < 0.001$).

§ Within rows of untreated (Untrt) columns, individual microsite estimates followed by the same lower-case letter of x or y are not significantly different ($P < 0.001$).

¶ Within rows of masticated (Mast) columns, individual microsite estimates followed by the same upper-case letter of X, Y, or Z are not significantly different ($P < 0.001$).

Table 1-4. Wet day linear-contrast comparisons among 1) untreated (untrt) and masticated (mast) plots; 2) litter mound (L), removed-litter mound (RL), bare interspace (I), debris-covered interspace (DI), and debris-covered litter mound (DL) microsites (micro); and 3) 1-3, 13-15, and 28-30 cm soil depths.

		1-3 cm		13-15 cm		28-30 cm	
Season	Micro	Untrt	Mast	Untrt	Mast	Untrt	Mast
Spring	L	*91*†a‡ x§	*114* a X¶	*91* a x	*118* a X	*91* a x	*124* a X
	RL	*67* b y	*86* b Y	*101* a x	*122* a X	*98* a x	*126* a X
	I	81 ab y	86 b Y	*100* a x	*119* a X	*96* a xy	*123* a X
	DI		117 a X		126 a X		128 a X
	DL		121 a X		122 a X		125 a X
		80	*105*	*97*	*121*	*95*	*125*
Summer	L	17 a x	27 a X	19 a x	36 a X	28 ab x	46 a X
	RL	15 a y	14 a Y	24 a xy	29 a XY	37 a x	49 a X
	I	12 a x	11 a Y	10 a x	29 a XY	*9* b x	*49* a X
	DI		18 a Y		36 a XY		42 a X
	DL		28 a X		33 a X		38 a X
		15	20	*18*	*33*	*25*	*45*
Fall	L	*21* a x	*48* a Y	*11* b x	*63* a XY	*15* a x	*73* a X
	RL	23 a x	38 ab Y	*17* ab xy	*56* a X	*4* a y	*67* a X
	I	30 a x	30 b Y	33 a x	46 a XY	*6* a y	*60* a X
	DI		43 ab X		51 a X		59 a X
	DL		45 ab Y		51 a XY		63 a X
		25	*41*	*20*	*53*	*8*	*64*
Winter	L	*45* a x	*67* ab Y	*40* a x	*81* a XY	*34* a x	*90* a X
	RL	52 a x	56 bc Y	*44* a xy	*78* a X	*30* a y	*90* a X
	I	42 a x	47 c Y	54 a x	69 a X	*38* a x	*79* a X
	DI		71 ab X		80 a X		82 a X
	DL		76 a X		82 a X		91 a X
		46	*63*	*46*	*78*	*34*	*86*

† Within season and soil depth, significant differences between untreated and masticated estimates are underlined and italicized (individual microsite and overall comparisons P < 0.001).

‡ Within seasons and columns, individual microsite estimates followed by the same lower-case letter of a, b, or c are not significantly different (P < 0.001).

§ Within rows of untreated (Untrt) columns, individual microsite estimates followed by the same lower-case letter of x or y are not significantly different (P < 0.001).

¶ Within rows of masticated (Mast) columns, individual microsite estimates followed by the same upper-case letter of X, Y, or Z are not significantly different (P < 0.001).

Table 1-5. Wet degree day linear-contrast comparisons among 1) untreated (untrt) and masticated (mast) plots; 2) litter mound (L), removed-litter mound (RL), bare interspace (I), debris-covered interspace (DI), and debris-covered litter mound (DL) microsites (micro); and 3) 1-3, 13-15, and 28-30 cm soil depths.

		1-3 cm		13-15 cm		28-30 cm	
Season	Micro	Untrt	Mast	Untrt	Mast	Untrt	Mast
Spring	L	*699*†a‡x§	*1203* a X¶	*746* a x	*1213* ab X	*765* a x	*1268* ab X
	RL	*527* a y	*809* b Y	*924* a x	*1346* a X	*945* a x	*1357* a X
	I	648 a y	763 b Y	*916* a x	*1318* ab X	*848* a xy	*1319* ab X
	DI		1103 a X		1215 ab X		1198 ab X
	DL		1091 a X		1092 b X		1097 b X
		625	*994*	*862*	*1237*	*853*	*1248*
Summer	L	*209* a x	*526* a Y	*227* a x	*725* a XY	*411* b x	*927* ab X
	RL	178 a y	198 b Z	356 a y	596 a Y	*657* b x	*1035* a X
	I	121 a x	134 b Z	*97* a x	*607* a Y	*82* a x	*1048* a X
	DI		284 ab Y		676 a X		781 b X
	DL		478 a X		581 a X		674 b X
		169	*324*	*197*	*637*	*359*	*893*
Fall	L	*169* a x	*454* a Y	*74* a x	*724* a X	*154* a x	*925* a X
	RL	143 a x	241 ab Z	*162* a x	*563* ab Y	*16* a x	*827* a X
	I	145 a x	169 b Z	211 a x	395 b Y	*-1* a x	*724* a X
	DI		282 ab Y		499 b XY		709 a X
	DL		401 a Y		573 ab XY		782 a X
		152	*309*	*127*	*551*	*78*	*793*
Winter	L	116 a x	132 a X	113 a x	188 a X	121 a x	268 a X
	RL	131 a x	97 a X	107 a x	130 a X	85 a x	209 a X
	I	71 a x	84 a X	103 a x	123 a X	105 a x	184 a X
	DI		146 a X		197 a X		250 a X
	DL		171 a X		209 a X		285 a X
		85	93	108	169	*78*	*239*

† Within season and soil depth, significant differences between untreated and masticated estimates are underlined and italicized (individual microsite and overall comparisons $P < 0.001$).

‡ Within seasons and columns, individual microsite estimates followed by the same lower-case letter of a, b, or c are not significantly different ($P < 0.001$).

§ Within rows of untreated (Untrt) columns, individual microsite estimates followed by the same lower-case letter of x or y are not significantly different ($P < 0.001$).

¶ Within rows of masticated (Mast) columns, individual microsite estimates followed by the same upper-case letter of X, Y, or Z are not significantly different ($P < 0.001$).

Chapter 2: Soil nutrients in masticated Utah juniper woodlands

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ABSTRACT

Juniper (*Juniperus* spp.) dominates millions of hectares of previously sagebrush (*Artemisia* spp.) and bunchgrass-dominated land. Juniper mechanical mastication is used to reduce canopy fuel loads and increase cover of understory species, but there are concerns that subsequent increases in resource availability could lead to dominance by invasive species. We quantified the effects of juniper mastication on soil resource availability by comparing total C, total N, C:N ratio, organic matter, Olsen extractable P, sulfate S, and pH using annual soil samples and soil N ($NO_3 + NH_4$) supply rates using ion exchange membranes exchanged at 4-mo intervals. Comparisons were made within and between paired masticated and untreated areas in three juniper-dominated sagebrush-bunchgrass ecosystems in western Utah. Soil N supply rate was 4.7 times higher in masticated than untreated areas across seasons ($P < 0.001$) even though few treatment differences were found for the other nutrients. Within masticated areas, litter mounds of juniper leaf scales, twigs, and berries served as resource islands with 1.9 times higher soil N supply rates, 1.9 times higher total C, 2.8 times higher total N, 3.3 times higher organic matter, and 3.7 times higher sulfate-S than bare interspaces across seasons ($P < 0.01$). Bare interspaces had 3.0-3.4 times higher soil N supply rates than interspaces covered with masticated tree debris (masticated foliage, branches, and trunks) during late-summer through winter even though the debris did not change concentrations of the other nutrients ($P < 0.01$). Soil fertility changes associated with mastication were not considered sufficient to favor establishment of annual over perennial grasses and we expect both life forms to increase in abundance following juniper mastication. Plant community composition at the time of juniper mastication is expected to greatly influence plant community composition following treatment.

Abbreviations

OM, organic matter; PRS™, plant root simulator; IEM, ion exchange membrane; NSR, nitrogen supply rate

INTRODUCTION

Juniper (*Juniperus* spp.) invasion and increased population density in former sagebrush (*Artemisia* spp.) and bunchgrass communities have decreased understory plant cover (Cottam and Stewart, 1940; Johnsen, 1962; Tress and Klopatek, 1987; Vaitkus and Eddleman, 1987; Miller and Wigand, 1994; Miller and Rose, 1999; Bates et al., 2000; Miller et al., 2000; Albert et al., 2004). Overtime, juniper trees move soil nutrients from interspaces between tree canopies to subcanopy litter mounds through roots and litter-fall (fallen foliage, twigs, and berries; Klopatek, 1987; McDaniel and Graham, 1992; Davenport et al., 1996). The increased relative concentrations of soil organic matter, nutrients, and soil microorganism activity in areas below trees result in resource islands (Klopatek, 1987; DeBano and Klopatek, 1988; Kramer and Green, 1999; Neff et al., 2009) and may promote continued tree dominance and reduction of understory vegetation (Doescher et al., 1987; Schlesinger et al., 1990; Schlesinger and Pilmanis, 1998).

Juniper is treated on thousands of hectares annually to reduce fuel loads and high-intensity canopy wildfires and to restore sagebrush-bunchgrass communities. Mechanical mastication is a canopy fuel-reduction treatment that converts the aboveground biomass of woody species into mounds of masticated debris. The ecological and management concern with masticating juniper is that it could increase resource availability and promote dominance by invasive annuals because juniper reduction generally increases resource availability (Bates et al., 2002; Young et al., in reviewb), which reduces plant community resistance and resilience to invasive annuals (Vasquez et al., 2008; D'Antonio et al., 2009). Invasive annuals are highly responsive to soil inorganic N, more competitive than perennials in environments with high N availability (Mangold and Sheley, 2008; Vasquez et al., 2008; Mazzola et al., 2011), and more efficient at N uptake than native perennials (Eckert and Evans, 1963; Young and Clements, 2009).

In contrast, reduced soil N availability reduces the competitive ability of invasive annuals (Beckstead and Augspurger, 2004) more than native perennials (Herron et al., 2001; Mangold 2004; Krueger-Mangold et al., 2006) reducing plant community invasibility (Beckstead and Augspurger, 2004). Perennial grasses perform well with continually low soil N availability with high root:shoot ratios and nitrogen use efficiency with perennial structures and their reallocation of nutrients from senescing leaves to new plant tissue (Grime, 1979; Chapin et al., 1987; Berendse et al., 1992; Tilman, 1988; Monaco et al., 2003). Low soil-N conditions can be induced by adding materials with high organic C and low N content to the soil (Brady and Weil, 1999; Brunson et al., 2010) for example, sucrose and masticated juniper debris. Soil microorganisms immobilize available soil N when these organic-C energy sources do not provide sufficient N for metabolism and growth (Brady and Weil, 1999). Some studies have found C additions to favor the dominance of perennial species whereas other studies have not (Vasquez et al., 2008; Blumenthal, 2009; Brunson et al., 2010; Perry et al., 2010; James et al., 2011). Chipping trees is canopy fuel-reduction treatment similar to masticating trees except the woody species are cut and loaded into a mechanical chipper rather than shredded while standing. The addition of chipped Utah juniper [*Juniperus osteosperma* (Torr.) Little] and singleleaf piñon (*Pinus monophylla* Torr. and Frem.) wood tended to increase perennial grass density and cover and decrease invasive-annual grass density and cover (Benson, 2006). Benson (2006) suggested that the increased perennial grass growth was associated with increased soil moisture under the wood chips and that the decreased invasive-annual grass growth was associated with presumed reduced soil N availability.

Woody species mastication not only has the potential to alter soil nutrient availability, but also affect soil water availability and temperature (Young et al., in reviewb). Soil water and temperature have been suggested to be the primary controls of where the invasive-annual cheatgrass (*Bromus tectorum* L.) can invade and dominate (Chambers et al., 2007). Reasons for this include faster germination and root growth for cheatgrass than native-perennial grasses under cool soil temperatures in winter and early spring in the sagebrush steppe (Harris, 1967; Roundy et al., 2007). This cool-season growth allows cheatgrass to preemptively use soil resources and reduce the amount of soil water remaining later in the growing season for slower establishing native perennials (Harris, 1967). However, juniper mastication has increased the duration of plant-available soil water (Young et al., in reviewb), which may benefit slower establishing native-perennial grasses. So far, it is uncertain how much juniper tree mastication will alter plant community dynamics by altering resource availability.

Our main objective was to determine the effect of juniper mastication on soil nutrient availability relative to potential establishment of invasive annual and native perennial grasses (Young et al., in reviewa). We quantified the effects of juniper mastication on soil nutrient availability by quantifying total C, total N, C:N ratio, organic matter (OM), Olsen extractable P, sulfate S, and pH using soil samples and soil N (NO_3 + NH_4) supply rate using ion exchange membranes. We compared soil nutrient availability: 1) between masticated and untreated areas; 2) among microsites inherent to masticated and untreated juniper woodlands and the modified microsites of removed-litter mounds and debris-covered litter mounds and interspaces between litter mounds to isolate the effects of litter and debris on soil nutrient availability; and 3) across unamended, ammonium-sulfate (N-S) fertilized, and sucrose (C) amended microsites to separate the effects of litter and masticated debris on soil nutrient availability from litter and debris induced changes in soil water availability and temperature (Young et al., in reviewb). We hypothesized that: 1) juniper mastication will increase nutrient availability in comparison to untreated areas, 2) litter mounds will have higher nutrient concentrations than interspaces between tree canopies, and 3) that woody masticated debris will reduce soil N availability by supplying organic C to soil microorganisms encouraging immobilization of available soil N.

MATERIALS AND METHODS

Study Locations

We measured soil nutrients at Greenville (38° 12´ N, 112° 48´ W), Onaqui (40° 13´ N, 112° 28´ W), and Stansbury (40° 35´ N, 112° 39´ W) in western Utah. Our research was conducted on Sagebrush Steppe Treatment Evaluation Project (SageSTEP) sites as part of the larger project quantifying the effectiveness of restoration methods in sagebrush steppe across the Great Basin region (www.sagestep.org). Treatment plots were located in dense stands of Utah juniper [*Juniperus osteosperma* (Torr.) Little] at Onaqui and Stansbury and mixed stands of Utah juniper and two-needle piñon (*Pinus edulis* Engelm.) at Greenville. Sagebrush (*Artemisia* spp.*)* and bunchgrass plant communities previously dominated these locations but at the time of juniper tree mastication little other vegetation remained because juniper trees dominated resource uptake. Greenville elevation ranges from 1,770 to 1,860 m with loamy-skeletal, carbonatic, mesic Typic Calcixerepts (Rau et al., 2011). Onaqui elevation ranges from 1,690 to 1,890 m with loamy-skeletal, carbonatic, mesic, shallow Petrocalcic Palexerolls (Rau et al., 2011). Stansbury elevation ranges from 1,710 to 1,830 m with loamy-skeletal, mixed, active, frigid Pachic Haploxerolls (Rau et al., 2011). Annual average precipitation for Greenville and Onaqui is

350 mm while Stansbury receives 440 mm. A complete description of research locations is located in McIver et al. (2010) and Young et al. (in reviewb).

Treatment Implementation

Trees were masticated in the fall of 2006 at Onaqui and in the fall of 2007 at Greenville and Stansbury. Contractors masticated Utah juniper at Onaqui and Stansbury using a Tigercat® M726E Mulcher (Tigercat Industries Inc., Brantford, Ontario) with Fecon® Bull Hog® (Fecon Inc., Lebanon, OH) masticator. A skid-steer loader with Fecon® Bull Hog® masticator was used to masticate Utah juniper and two-needle piñon at Greenville. These masticators masticate trees similarly.

Study Design

We selected paired masticated and untreated juniper woodlands with similar vegetation and soils within each location. Masticated plots included the overall area within a location where all the trees taller than 0.5 m were masticated. Untreated plots included the overall area within a location where trees were not masticated. We implemented a randomized complete block design within masticated and untreated plots with four replicated blocks in each plot. Each block had four trees in masticated plots and two trees in untreated plots. Only trees that had at least 2-m diameter litter mounds were selected to allow enough room for sampling. We partitioned the area around and under juniper trees into microsites to separate the effects of litter mounds and masticated juniper debris on soil nutrient availability. In masticated plots, two of the four trees per block had five microsites: 1) juniper litter mounds (litter mounds); 2) soil where pre-existing juniper litter mounds were removed (removed-litter mounds); 3) bare interspaces between trees with little remaining vegetation (bare interspaces); 4) masticated debris on former bare interspaces (debris-covered interspaces); and 5) masticated juniper debris covering juniper litter mounds (debris-covered litter mounds; Table 1). The remaining two trees per block in masticated plots were partitioned into six microsites. Three of the six microsites were bare interspaces, debris-covered interspaces, and debris-covered litter mounds where 224 kg ha^{-1} (200 lb ac^{-1}) of N in the form of ammonium-sulfate [$(NH_4)_2SO_4$; 20-0-0] was added each fall. The other three microsites were also bare interspaces, debris-covered interspaces, and debris-covered litter mounds but where 1,100 kg ha^{-1} (981 lb ac^{-1}) of C in the form of sucrose ($C_{12}H_{22}O_{11}$) was added each fall. We applied amendments (i.e., ammonium-sulfate and sucrose) in granular form to the soil surface in bare and debris-covered interspaces and on top of the litter in debris-covered litter mounds to minimize disturbance. In the untreated plots, the two trees per block had the three microsites of bare interspaces, litter mounds, and removed-litter mounds without amendments. The complete number of experimental units (microsites) at each of the three research locations was 112. We combined microsite samples from replicated trees within blocks resulting in 56 samples per sampling date per location.

Measurements

We collected microsite soil samples annually from the top 2 cm of the soil profile because masticated debris would most likely influence the top portion of the soil profile. Soil samples were collected during August at Greenville in 2008-2010, Onaqui in 2008-2010, and Stansbury in 2008 only due to a wildfire in August 2009 (Table 2). We analyzed soil samples for total C and total N (McGeegan and Naylor, 1988) using a LECO TruSpec® CN analyzer (LECO Cor., St. Joseph, MI). Soil sample analyses also included organic matter (OM; Walkley and Black, 1934), Olsen P (Olsen et al., 1954), sulfate S (Williams and Steinbergs, 1964), and pH in a saturated paste (Rhodes, 1982).

We measured in-situ soil N supply rate (NSR), nitrate (NO_3) plus ammonium (NH_4), using plant root simulator (PRS™) probes (Western Ag Innovations Inc., Saskatoon, SK) that we refer to as ion exchange membranes (IEM) in this study. Soil NSR per season represents the N ions available to plant roots during the burial period and includes N that is mineralized during the burial season (Qian and Schoenau, 2002). We buried IEM vertically in the top 12 cm of soil in each of the 112 microsites per location where they remained for 4 months. Ion exchange membranes were exchanged in March, July, and October-November to sample seasons of winter, spring through early-summer, and late-summer through fall. We measured NSR at Greenville in 2009 and 2010, Onaqui in 2008 and 2009, and Stansbury in 2009 (Table 2). After IEM were removed from the soil, we cleaned them with deionized water and shipped them back to Western Ag Innovations for NO_3 and NH_4 analysis.

Data Analysis

We analyzed the response variables of soil total C, total N, C:N ratios, OM, Olsen P, sulfate S, pH, and NSR separately using Proc Mixed (SAS v9.2, SAS Institute, Inc., Cary, NC). The response variables of soil C:N ratios, OM, Olsen P, sulfate S, and NSR were log transformed to make variances more equal prior to analysis and back-transformed to median estimates using exponentiation after data analysis. Mixed-model analysis of variance assumptions were met based on examination of residual plots after log transformation of the response variable where applicable. Masticated plots had more types of microsites than untreated plots with debris-covered litter mounds and debris-covered interspaces. This uneven number of microsite types between treatment plots prevented a full factorial analysis. To allow treatment and microsite comparisons, we assigned each treatment (trt) by microsite (micro) by amendment (amend) combination as one of 14 levels of the combined main effect of trt-micro-amend (Table 1).

Linear contrasts among these 14 levels enabled an overall mastication-treatment effect comparison between the five unamended microsites in masticated plots and the three unamended microsites in untreated plots. Linear contrasts also allowed individual microsite comparisons within and across treatment plots and amended microsite comparisons within masticated plots. We used pseudo-Bonferroni with a 0.01 critical alpha level to adjust for false positives from multiple comparisons. We used maximum likelihood estimation in mixed-model analysis of variance that resulted in F-tests being used to test for fixed effects. We combined the data from multiple locations and years in mixed-model analysis of variance where applicable (Table 2). Soil NSR analysis also included the main effect of season and the interaction between trt-micro-amend and season. Random predictors included location, year, block, and tree. We adjusted for repeated measurements on microsites to account for potential temporal correlation. Potential microsite spatial-correlation was accounted for by nesting microsites in trees and blocks. These smaller-sized random effects were nested in the larger-sized random effects of location and year.

RESULTS

The combined main effect of trt-micro-amend was significant for total C, total N, C:N ratio, OM, Olsen P, sulfate S, and pH in soil samples ($P < 0.001$; Table 3). The main effects of trt-micro-amend and season and the interaction between trt-micro-amend and season were significant for soil NSR that was quantified from IEM ($P < 0.001$).

Mastication Effects

Soil total C, total N, C:N ratios, OM, Olsen P, sulfate S, and pH for the five unamended microsites of litter, removed litter, debris-covered litter mounds, and interspaces with and without debris in masticated plots were not different from the three microsites of litter, removed-litter mounds, and bare interspaces in untreated plots collectively or individually except for P collectively ($P > 0.01$). The five microsites in masticated plots had a median estimate of 7 mg kg^{-1} more P than the three microsites in untreated plots ($P < 0.01$; Table 4). The five microsites in masticated plots consistently had higher NSR than untreated microsites for all seasons ($P < 0.001$; Table 5). Across all seasons, soils in masticated plots had a median estimate of 239 mg m^{-2} 4 mo^{-1} higher NSR than soils in untreated plots ($P < 0.001$).

Litter and Debris Microsite Effects

Litter mounds had more total C, total N, OM, sulfate S, and lower C:N ratios than bare interspaces in both untreated and masticated plots ($P < 0.01$; Table 4). The masticated debris on debris-covered interspaces did not change total C, total N, OM, Olsen P, sulfate S, pH, or C:N ratios from that of bare interspaces ($P > 0.01$). In untreated plots during spring-summer, summer-fall, and all seasons collectively, litter mounds had 26-58 mg m^{-2} 4 mo^{-1} lower NSR than bare interspaces or removed-litter mounds ($P < 0.01$; Table 5). However, in masticated plots, both bare and debris-covered interspaces had lower NSR than litter, removed litter, and debris-covered litter mounds in spring-summer, winter, and all seasons collectively ($P < 0.01$). Debris-covered interspaces also had lower NSR than litter, removed litter, and debris-covered litter mounds in summer-fall ($P < 0.01$). Debris-covered interspaces had 108-168 mg m^{-2} 4 mo^{-1} lower NSR than bare interspaces in summer-fall, winter, and all seasons collectively ($P < 0.01$).

Nitrogen-Sulfur and Carbon Amendment Effects

Interspaces with and without debris and debris-covered litter mounds were compared as groups collectively and individually among unamended, N-S fertilized, and C amended microsites within masticated plots. The N-S fertilized microsites collectively had a median estimate of 54 mg kg^{-1} more sulfate S than unamended or C amended microsites ($P < 0.01$; Table 4). Nitrogen-sulfur fertilized interspaces with and without debris had a 0.2-0.4 lower pH than the respective unamended microsites but the addition of N-S fertilizer was not found to change total C, total N, C:N ratios, OM, or Olsen P ($P > 0.01$). Similarly, C amendments were not found to alter these variables except Olsen P was 15-17 mg kg^{-1} lower in interspaces with and without debris cover than in debris-covered litter mounds after C additions ($P < 0.01$). Nitrogen-sulfur fertilized microsites collectively had a median estimate of 436 mg m^{-2} 4 mo^{-1} higher NSR than unamended microsites whereas C amended microsites collectively had a median estimate of 74 mg m^{-2} 4 mo^{-1} lower NSR than unamended microsites across seasons ($P < 0.001$; Table 5). The N-S fertilization had less effect on NSR in winter than other seasons and did not significantly increase NSR on debris-covered litter mounds during late-summer through winter ($P > 0.01$).

DISCUSSION

Masticating juniper trees increased NSR and had no effect on soil total C, total N, C:N ratios, OM, sulfate S, and pH in surface soil samples 1-3 yr after treatment. Nitrogen supply rates were usually two to five times higher in masticated plots than in untreated plots throughout the year whether collectively comparing all unamended microsites between masticated and untreated plots or individually comparing microsites between treatment plots. Our experiments were conducted on areas of advanced juniper invasion where trees were the dominant resource users and there was limited cover of understory shrubs and herbaceous plants. Cessation of resource uptake by juniper trees following mastication best accounts for the increased NSR compared to untreated plots. Similarly, cessation of soil-water use by trees after mastication resulted in longer durations of plant-available soil water in masticated than untreated plots during spring through fall (Young et al., in reviewb). The greater availability of water probably helped increase NSR because IEM adsorption of nutrient ions is largely dependent on nutrient diffusion through the soil solution from areas of high to low concentration (Qian and Schoenau, 2002). The increased NSR and plant-available soil water resulted in greater annual and perennial-grass seedling growth following planting in masticated plots compared to untreated plots (Young et al., in reviewa).

The lack of a mastication effect on soil total C, total N, OM, sulfate S, and pH was likely a result of slow plant material decomposition. Slow decomposition of juniper would be expected due to the aridity of the environment, the high C:N ratio of the woody debris, and limited incorporation of debris into the soil (Brady and Weil, 1999). Future sampling is needed to determine long-term decomposition effects on soil nutrient concentrations. Techniques to better incorporate masticated debris into the soil could increase total soil C in the short-term as was found with sawdust from unspecified species that had a C:N ratio of 122 (Baer et al., 2003). Lyons and McCarthy (2010) found a mass-loss decay constant (k) of 0.176 yr^{-1} based on annual mass loss of Ashe juniper (*Juniperus ashei* J. Buchholz) wood during the 2 yr following chipping on the Edwards Plateau in Texas. Our locations had an annual average temperature about 10 °C cooler and an annual average precipitation about half of that at Edwards Plateau (Lyons and McCarthy, 2010; Young et al., in reviewb).

Tree mounds with and without masticated debris and removed-litter mounds had higher concentrations of total C, total N, and OM than adjacent bare or debris-covered interspaces. Nitrogen supply rate also followed this trend in masticated plots. High soil fertility in juniper mounds compared to interspaces is a well-known phenomenon (Brotherson and Osayande, 1980; DeBano and Klopatek, 1988; McDaniel and Graham, 1992; Evans and Ehleringer, 1993; Davenport et al., 1996; Kramer and Green, 1999). Juniper trees develop nutrient islands as their roots mine resources from interspaces and drop nutrients under their canopies in the form of leaf scales, fruits, and twigs over decades (Klopatek, 1987; McDaniel and Graham, 1992; Davenport et al., 1996).

High NSR in litter mounds and interspaces after mastication could favor dominance of invasive annuals over native perennials. Increased soil N has been shown to increase aboveground tissue-N concentrations, growth, growth rates, and competitive ability of annual grasses, as well as to encourage dominance of invasive annuals over perennials (Wilson et al., 1966; Bazzaz, 1979; Tilman, 1982, 1987; McLendon and Redente, 1992; Redente et al., 1992; Paschke et al., 2000; Monaco et al., 2003). This potential increase in invasive annuals would most likely occur in litter mounds where soil N availability is abundant and where the duration of available soil water is high following tree control (Young et al., in reviewb). However, higher NSR did not result in a general increase in seedling establishment of sown annual or perennial grasses in litter mounds compared to interspaces (Young et al., in reviewa). This may be due to reduced light penetration and seedling emergence under litter (Facelli and Pickett, 1991) or because soil N availability may have been sufficient for plant growth even in interspaces.

The redistribution of nutrients and the increased size of nutrient islands that occur during woody plant encroachment may serve as a positive feedback mechanism (Schlesinger et al., 1990; Schlesinger and Pilmanis, 1998). This feedback may encourage the continued dominance of woody plants as soil and nutrients are lost in the interspaces through wind and water erosion further increasing desertification (Schlesinger et al., 1990; Schlesinger and Pilmanis, 1998). This process may make it more difficult for the pre-encroachment plant community and former distribution of resources to return after disturbance (Schlesinger et al., 1990; Schlesinger and Pilmanis, 1998), pushing the system to assume a new state by weakening the resilience of the pre-encroachment state.

Even though resource islands do eventually dissipate with time since tree control (Schlesinger and Pilmanis, 1998) many years are required as resource islands can last for 15 yr after cutting juniper as a result of deep litter layers (Miwa and Reuter, 2010). As nutrient concentrations in old litter mounds are reduced over time, nutrient islands become smaller, nutrients become more evenly distributed, and the resilience of the pre-encroachment plant community may be strengthened (Schlesinger and Pilmanis, 1998; Ravi et al., 2009). Restoring the appropriate scale of resource patchiness through anthropogenic means or fire has been suggested as an important step in the reestablishment of pre-encroachment plant communities (Boeken and Shachak, 1994; Schlesinger and Pilmanis, 1998; Ravi et al., 2009). A more rapid return of pre-encroachment sized resource islands and distribution is especially important in these systems because invasive annuals or regenerating trees will likely dominate the masticated site before tree resource islands naturally dissipate if perennial grasses and shrubs are missing. More research is needed to fully understand the potential for mechanical or fire induced manipulation of the size of resource patches to encourage reestablishment of the pre-encroachment plant community.

Although higher NSR in litter and removed-litter mounds than interspaces with or without debris cover in masticated plots illustrated the nutrient-island distribution pattern, litter mounds had less NSR than removed-litter mounds and interspaces in untreated plots. Ion exchange membranes in litter mounds may have adsorbed less N than in interspaces in untreated plots because of potentially more intense competition for soil N from a higher concentration of juniper fine-feeder roots in litter mounds than interspaces (Everett et al., 1986). The higher NSR in removed-litter mounds and interspaces than litter mounds in untreated plots may also have been due to warmer soil temperatures in removed-litter mounds and interspaces during spring and summer (Young et al., in reviewb). High soil temperatures can reduce juniper root activity (Williams and Ehleringer, 2000) and thereby reduce competition for soil N near the surface allowing more N ions to be adsorbed on IEM in removed-litter mounds and interspaces. In agreement with less NSR and cooler soil temperatures in untreated plots, seeded invasive-annual and perennial grasses had less emergence and fewer tillers and invasive annual grasses also had fewer spikelets in litter mounds than interspaces (Young et al., in reviewa). However, these plant responses also could have been depressed by litter mounds physically obstructing seedling emergence. Other tree influences also could have limited subcanopy plant growth including canopy interception of precipitation, canopy shading of subcanopy areas, and soil-water repellant layers under litter mounds (Breshears et al., 1997; Lebron et al., 2007; Matsushima and Chang, 2007; Lin, 2010), but we did not measure these factors.

The unamended microsites in masticated plots collectively had more Olsen P than the microsites in untreated plots. This result may have been due to the end of P uptake by masticated juniper, longer durations of plant-available water during spring allowing more mineralization of P, and P potentially being released into the soil solution through microorganism mineralization of organic P from decomposing roots (Brady and Weil, 1999). Within masticated plots, litter mounds had more Olsen P than removed-litter mounds. This result may have been due to the longer durations of plant-available soil water in litter mounds than removed-litter mounds in masticated plots. As low P availability has been suggested as a limiting factor of plant growth in juniper woodlands (Bunderson et al., 1985; Tiedemann, 1987; Kramer and Green, 2000), the slight increase in Olsen P with juniper mastication may lead to increased plant production. Plants currently growing on the site that do not have to migrate into the area may benefit more from increased P availability as Olsen P can quickly react with calcium in alkaline soils and become less available to plants in the form of calcium phosphate (Brady and Weil, 1999).

Soil Nutrient versus Water Effects

Because juniper mastication, litter mounds, and debris cover can change both soil nutrient concentrations and the duration of soil water we made specific microsite comparisons to separate the effects of nutrient concentrations from soil water on seedling establishment. These comparisons include references to companion research papers (Young et al., in reviewa; Young et al., in reviewb) that evaluated soil water and temperature and seedling establishment on many of the same microsites and during the same time as our study. We compared microsites that allowed us to evaluate whether soil nutrients, especially available N, or soil water was more limiting of plant growth. Seedling establishment is influenced by many factors but we focused our comparisons on soil N and water because they are commonly regarded as the most limiting resources in arid to semi-arid environments. An increase in the most limiting resource should produce the greatest increase in plant growth according to the law of the minimum by Liebig (Brady and Weil, 1999).

Comparing unamended removed-litter mounds with bare interspaces in untreated and masticated plots separately provided a comparison of the effects of soil nutrient concentrations on seedling establishment without changes in the duration of plant-available soil water. Removed-litter mounds had more soil total C, total N, OM, and sulfate S than interspaces in untreated plots and removed-litter mounds had more total C, total N, OM, and NSR than interspaces in masticated plots. However, these greater nutrient concentrations in removed-litter mounds than bare interspaces were not found to increase plant emergence, aboveground biomass, number of tillers, or number of cheatgrass spikelets in either untreated or masticated plots

(Young et al., in reviewa). These results suggest that soil fertility was adequate for plant growth in these microsites before and after juniper tree mastication.

Similar NSR between unamended bare and debris-covered interspaces during spring, a critical season for seedling establishment, suggests that our third hypothesis may have been incorrect even though debris-covered interspaces had less NSR during late-summer through winter. We had expected woody masticated debris with a high C:N ratio to lower NSR in debris-covered interspaces because soil microorganisms need organic C sources with C:N ratios no higher than 25:1 for metabolism, otherwise they use available soil N to support their decomposition of high C:N ratio plant material (Brady and Weil, 1999). Western juniper (*Juniperus occidentalis* Hook.), a species similar to Utah juniper, has wood C:N ratios of 240:1 (Bates et al., 2002). If masticated debris had lowered NSR during spring, then we would have expected a negative effect on invasive-annual seedlings compared to perennial grass seedlings. Lower successional, invasive annuals tend to be replaced by more competitive perennial species over time as nutrient availability decreases, even though the annuals generally grow rapidly under conditions of high resource availability after disturbance (Grime and Hunt, 1975; Tilman, 1993). When continually low soil-N availability is maintained for several years, reductions in the growth, tillering, and seed production of invasive annuals like cheatgrass may allow dominance of established perennials on semiarid lands (Redente et al., 1992; Paschke et al., 2000; Monaco et al., 2003). In addition, reductions in soil N availability are thought to reduce the invasibility of plant communities (Beckstead and Augspurger, 2004) and therefore should strengthen the resistance and resilience of pre-encroachment plant communities to invasive annuals.

Nitrogen-sulfur applications increased sulfate S in debris-covered interspaces compared to unamended debris-covered interspaces and N-S fertilized bare interspaces. This increase in sulfate S was associated with longer durations of plant-available soil water during winter and spring in debris-covered interspaces than bare interspaces as was found among respective unamended microsites (Young et al., in reviewb). These results also may have resulted from cooler soil temperatures in debris-covered interspaces during spring and summer (Young et al., in reviewb) with cooler temperatures reducing S volatilization and loss from the soil (Brady and Weil, 1999). Increased concentrations of sulfate S can increase plant growth when soil N, P, and water are not limiting (Tiedemann and Klemmedson, 1995), but sulfate S probably did not limit plant growth in masticated juniper woodlands because N-S applications did not increase seedling emergence or aboveground biomass (Young et al., in reviewa). Nitrogen-sulfur applications also influenced soil ph. The trend of lower pH in N-S fertilized microsites relative to unamended and C amended microsites was likely due to the hydrogen ions released during oxidation of ammonium-sulfate (Brady and Weil, 1999). Even though we found significant differences in soil pH related to N-S fertilization, the slight changes in pH are not expected to alter seedling establishment.

To answer the question of whether soil water was more or less limiting of seedling establishment and growth than soil NSR, we refer to the comparison of the five unamended microsites in masticated plots with the three unamended microsites in untreated plots in Young et al. (in reviewa) and Young et al. (in reviewb). Mastication of juniper trees generally increased seedling aboveground biomass and number of tillers of invasive-annual and perennial grasses (Young et al., in reviewa). These results were associated with masticated plots having longer durations of plant-available soil water than untreated plots during fall through spring (Young et al., in reviewb) but confounding the effect of soil water availability on seedling establishment, NSR also was higher in masticated plots. However, the increase in NSR after juniper tree mastication was less than half the increase in NSR after N-S fertilization and this greater increase in NSR did not increase seedling aboveground biomass or number of tillers. Therefore, the evidence suggests that soil water availability rather than N availability was most limiting seedling establishment and growth on our study sites.

Conclusions

Mastication improves growing conditions for residual plants by increasing NSR and by increasing the duration of plant-available soil water (Young et al., in reviewb). We did not find convincing evidence that altered resource availability following juniper mastication would strongly favor invasive annual or perennial life-history strategies. The abundance of residual perennial species compared to the abundance and propagule pressure of invasive annual species will greatly affect which life form benefits the most from increased resource availability following tree control (Miller and Wigand, 1994; Foster and Dickson, 2004; Bates et al., 2005; Mazzola et al., 2011). Whether invasive annuals or perennials dominate given the increased resource availability following juniper mastication remains to be seen. Monitoring of restoration projects will play an important role in assessing the long-term impacts of juniper mastication on plant community dynamics. Maintenance of vigorous and diverse pre-encroachment vegetation should limit the resources available to invasive annuals and may be the most effective form of weed control (Turner et al., 1963; Chambers et al., 2007; Vasquez et al., 2008). Hence, it is imperative to masticate trees when desirable perennials are still abundant enough to use the increased resource availability following juniper control and limit resources available to invasive annuals.

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Tables

Table 2-1. Study design implemented in each of four blocks in paired masticated and untreated juniper plots at Greenville, Onaqui, and Stansbury in Utah. Our three amendment categories included: no amendment, ammonium-sulfate [$(NH_4)_2SO_4$] applied in granular form at 224 kg ha^{-1} N, and sucrose ($C_{12}H_{22}O_{11}$) applied in granular form at 1,100 kg ha^{-1} C. Bare interspace, debris-covered interspace, and debris-covered litter mound microsites were amended at Greenville in October 2008 and November 2009, Onaqui in October 2007 and October 2008, and Stansbury in October 2008.

Treatment	Amendment	Microsite
Masticated	none	Litter mound
		Removed-litter mound
		Bare interspace
		Debris-covered interspace
		Debris-covered litter mound
	Sucrose (C)	Bare interspace
		Debris-covered interspace
		Debris-covered litter mound
	Ammonium-sulfate (N-S)	Bare interspace
		Debris-covered interspace
		Debris-covered litter mound
Untreated	none	Litter mound
		Removed-litter mound
		Bare interspace

Table 2-2. Soil-sampling schedule for soil nutrients. Soil nutrients other than soil N availability were sampled using soil cores from the top 2 cm of soil in August of each summer. Soil N availability was sampled using PRS™ probes buried in the top 12 cm of soil. Sampling seasons for soil N availability were winter (November-February), spring-summer (March-June), and summer-fall (July-October).

Soil Nutrient	Location	Season	Year
Total C, Total N, C:N, OM	Greenville, Onaqui, Stansbury	Summer	2008
Total C, Total N, C:N, OM	Greenville and Onaqui	Summer	2009, 2010
Olsen P, SO_4-S, pH	Greenville and Onaqui	Summer	2010
Soil N (NO_3+NH_4) availability	Greenville	Winter, Spring-Summer, Summer-Fall	2009, 2010
Soil N (NO_3+NH_4) availability	Onaqui	Winter, Spring-Summer, Summer-Fall	2008, 2009
Soil N (NO_3+NH_4) availability	Stansbury	Winter, Spring-Summer	2009

Table 2-3. Mixed-model analysis of variance and type III F-tests from maximum likelihood estimation for soil nutrient response variables. We assigned each treatment (trt) by microsite (micro) by amendment (amend) combination as one of 14 levels of the combined main effect of trt-micro-amend. Soil N availability had the additional main effect of season.

Response Variables	Effect	Num DF†	Den DF‡	F-value	p-value
Total C%, 2008-2010	trt-micro-amend	13	121	21.60	<0.001
Total N%, 2008-2010	trt-micro-amend	13	121	27.52	<0.001
Total C:N ratio, 2008-2010	trt-micro-amend	13	121	6.55	<0.001
OM%, 2008-2010	trt-micro-amend	13	121	41.62	<0.001
Olsen P, mg kg^{-1}, 2010	trt-micro-amend	13	77	3.19	<0.001
SO_4-S, mg kg^{-1}, 2010	trt-micro-amend	13	77	8.58	<0.001
pH, 2010	trt-micro-amend	13	77	7.43	<0.001
NSR§ 2008-2010	trt-micro-amend	13	109	56.53	<0.001
	season	2	477	8.09	<0.001
	trt-micro-amend * season	26	462	16.41	<0.001

† Num DF, numerator degrees of freedom.

‡ Den DF, denominator degrees of freedom.

§ NSR, nitrogen supply rate.

Table 2-4. Soil nutrient linear-contrast comparisons from the top 2 cm of microsite soils compared among 1) untreated (untrt) and masticated (mast) plots; 2) litter mound (L), removed-litter mound (RL), bare interspace (I), debris-covered interspace (DI), and debris-covered litter mound (DL) microsites (micro); and 3) unamended (unamend) microsites, ammonium-sulfate [$(NH_4)_2SO_4$] fertilized microsites with 224 kg ha^{-1} N, and sucrose ($C_{12}H_{22}O_{11}$) amended microsites with 1,100 kg ha^{-1} C. Soils were loamy skeletal at Greenville, Onaqui, and Stansbury in Utah. Numerically-different estimates between the two "Unamend Mast" columns result from conducting separate analyses for treatment and soil amendment effects.

		Treatment Effect		Amendment Effect		
		Unamend	Unamend	Unamend	$(NH_4)_2SO_4$	$C_{12}H_{22}O_{11}$
Nutrient	Micro	Untrt	Mast	Mast	Mast	Mast
Total C% 2008-2010	L	6.32 a†	7.07 a			
	RL	5.19 a	6.23 a			
	I	3.12 b	3.70 b	4.15 b X‡	4.05 b X	4.34 b X
	DI		4.44 b	4.92 b X	4.51 b X	4.71 b X
	DL		7.61 a	8.18 a X	9.18 a X	8.77 a X
		4.88	5.81	5.75 X	5.91 X	5.94 X
Total N% 2008-2010	L	0.26 a	0.28 ab			
	RL	0.21 a	0.24 b			
	I	0.11 b	0.10 c	0.10 b X	0.08 b X	0.11 b X
	DI		0.16 c	0.16 b X	0.13 b X	0.12 b X
	DL		0.32 a	0.32 a X	0.33 a X	0.31 a X
		0.19	0.22	0.19 X	0.18 X	0.18 X
Total C:N ratio 2008-2010	L	24.55 b	24.95 b			
	RL	25.81 b	25.76 b			
	I	33.20 a	41.12 a	42.73 a X	52.62 a X	47.78 a X
	DI		31.02 ab	32.86 ab X	35.36 b X	40.01 ab X
	DL		23.43 b	24.65 b X	27.27 b X	29.78 b X
		27.85	29.26	33.41 X	38.42 X	39.19 X
OM% 2008-2010	L	5.98 a	6.53 a			
	RL	4.41 a	5.82 a			
	I	1.79 b	1.95 b	1.59 c X	1.37 c X	1.50 c X
	DI		2.56 b	2.53 b X	2.29 b X	2.62 b X
	DL		7.45 a	8.29 a X	8.03 a X	7.59 a X
		4.06	4.86	4.14 X	3.90 X	3.90 X
Olsen P, mg kg^{-1} 2010	L	21.14 a	33.99 a			
	RL	14.65 a	20.39 b			
	I	21.02 a	22.65 ab	22.65 a X	30.59 a X	21.06 b X
	DI		26.02 ab	26.02 a X	27.65 a X	22.52 b X
	DL		26.66 ab	26.66 a X	31.56 a X	37.65 a X
		18.94§	*25.94*	25.11 X	29.93 X	27.08 X
SO_4-S, mg kg^{-1} 2010	L	38.32 a	31.21 a			
	RL	30.92 a	12.54 abc			
	I	4.82 b	8.33 bc	8.33 ab XY	18.58 b X	3.14 b Y

	DI		3.63 bc	3.63 b Y	139.59 a X	4.47 b Y
	DL		16.45 ab	16.45 a X	33.09 b X	23.31 a X
		24.69	14.43	9.47 Y	63.75 X	10.31 Y
pH	L	7.62 a	7.63 b			
2010	RL	7.70 a	7.78 a			
	I	7.70 a	7.68 ab	7.68 a X	7.51 a Y	7.61 a XY
	DI		7.67 ab	7.67 a X	7.28 b Y	7.63 a X
	DL		7.67 ab	7.67 a XY	7.59 a Y	7.73 a X
		7.67	7.69	7.67 X	7.46 Y	7.66 X

† Within nutrients and columns, individual microsite estimates followed by the same lower-case letter are not significantly different ($P < 0.01$).

‡ Within nutrients and rows of the amendment effect columns, amendment estimates followed by the same upper-case letter are not significantly different (individual microsite comparisons $P < 0.001$; overall comparisons $P < 0.01$).

§ Within nutrients, significant differences between untreated and masticated estimates without amendments are underlined and italicized ($P < 0.01$).

Table 2-5. Soil N ($NO_3 + NH_4$) supply rate multiple comparisons sampled in the top 12 cm of microsite soils using PRS™ probes. Soil N availability was compared among 1) untreated (untrt) and masticated (mast) plots; 2) litter mound (L), removed-litter mound (RL), bare interspace (I), debris-covered interspace (DI), and debris-covered litter mound (DL) microsites (micro); and 3) unamend (unamend) microsites, ammonium-sulfate [$(NH_4)_2SO_4$] fertilized microsites with 224 kg ha^{-1} N, and sucrose ($C_{12}H_{22}O_{11}$) amended microsites with 1,100 kg ha^{-1} C. Soils were loamy skeletal at Greenville, Onaqui, and Stansbury in Utah.

		Treatment Effect		Amendment Effect		
		Unamend	Unamend	Unamend	$(NH_4)_2SO_4$	$C_{12}H_{22}O_{11}$
Season	Micro	Untrt	Mast	Mast	Mast	Mast
		------------------------ mg m^{-2} 4 mo^{-1} ------------------------				
Spring-Summer	L	*25*†b‡	*416* a			
	RL	*60* a	*437* a			
	I	*51* a	*158* b	158 b Y§	1082 a X	35 b Z
	DI		146 b	146 b Y	943 a X	59 b Z
	DL		397 a	397 a Y	898 a X	470 a XY
		45	*311*	234 Y	974 X	188 Z
Summer-Fall	L	*22* b	*322* ab			
	RL	*59* a	*500* a			
	I	*80* a	*238* b	238 a Y	1042 a X	90 b Z
	DI		70 c	70 b Y	471 b X	46 b Y
	DL		334 ab	334 a X	580 ab X	305 a X
		53	*293*	214 Y	698 X	147 Z
Winter	L	*98* a	*402* a			
	RL	*153* a	*498* a			
	I	*102* a	*203* b	203 b X	365 a X	11 b Y
	DI		67 c	67 c Y	362 a X	13 b Z
	DL		413 a	413 a X	622 a X	378 a X
		117	*317*	228 Y	450 X	134 Z
All Seasons	L	*38* b	*377* a			
	RL	*81* a	*477* a			
	I	*75* a	*197* b	197 b Y	744 a X	33 b Z
	DI		89 c	89 c Y	544 a X	33 b Z
	DL		380 a	380 a Y	687 a X	379 a Y
		65	*304*	222 Y	658 X	148 Z

† Within seasons, significant differences between untreated and masticated estimates without amendments are underlined and italicized (individual microsite comparisons $P < 0.01$; overall comparisons $P < 0.001$).

‡ Within seasons and columns, individual microsite estimates followed by the same lower-case letter are not significantly different ($P < 0.01$).

§ Within seasons and rows of the amendment effect columns, amendment estimates followed by the same upper-case letter are not significantly different ($P < 0.01$).

Chapter 3: Plant Establishment in Masticated Utah Juniper Woodlands

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ABSTRACT

Juniper (*Juniperus* spp.) encroachment into sagebrush (*Artemisia* spp.)/bunchgrass communities has reduced understory cover on millions of hectares of semiarid rangelands. Mechanical masticators shred trees to restore desirable vegetation and reduce the potential for catastrophic wildfire. Mechanical mastication where tree density is high and perennial grass cover is low brings a risk of invasive weed dominance unless perennial species are sown. To determine whether tree mastication favors annual or perennial grass establishment, we compared seedling emergence, tillers, and aboveground biomass of cheatgrass (*Bromus tectorum* L.) and Anatone bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve). Comparisons were made among hand-planted rows below and between juniper canopies of masticated and adjacent untreated areas at three locations in Utah. Bluebunch wheatgrass had 16% (95% CI 11, 21) and cheatgrass had 10% (95% CI 5, 15) fewer seedlings emerge per row in masticated than untreated areas ($P < 0.001$). However, bluebunch wheatgrass had 3.2 (95% CI 2.0, 5.2) times more tillers and 1.9 (95% CI 1.6, 2.2) times more aboveground biomass per row in masticated than untreated areas ($P < 0.001$). Similarly, cheatgrass had 2.3 (95% CI 1.5, 3.8) times more tillers, 2.0 (95% CI 1.7, 2.4) times more aboveground biomass, and 11.4 (95% CI 6.3, 20.7) times more spikelets per row in masticated than untreated areas ($P < 0.001$). This increased seedling growth on masticated areas was associated with increased soil temperatures, durations of soil water availability, and inorganic nitrogen availability compared to untreated areas. Because mastication improves growth of both annual and perennial grass seedlings, it potentially could support dominance of either life form. To avoid annual grass dominance where perennial understory cover is limited and annual-grass propagule pressure is high, mastication should be accompanied by planting perennial grasses and applying selective-herbicides or other measures to control annual grasses.

Key Words

Anatone bluebunch wheatgrass, carbon, cheatgrass, Great Basin, mulch, nitrogen, rangeland restoration, sagebrush, SageSTEP, shred, woody debris

INTRODUCTION

Juniper (*Juniperus* spp.) encroachment into sagebrush (*Artemisia* spp.) and bunchgrass communities has reduced understory plant cover and resulted in juniper dominating millions of hectares of semiarid rangelands (Cottam and Stewart 1940; Johnsen 1962; Tress and Klopatek 1987; Vaitkus and Eddleman 1987; Miller and Wigand 1994; Miller and Rose 1999; Bates et al. 2000; Miller et al. 2000; Albert et al. 2004). Over time, juniper trees move soil nutrients and water from interspaces between trees to subcanopy litter mounds through roots and canopy-dropped leaf scales, fruits, and twigs (Klopatek 1987; McDaniel and Graham 1992; Davenport et al. 1996; Newman et al. 2010). The higher concentrations of soil organic matter, nutrients, and microorganism activity in subcanopy litter mounds than interspaces result in resource islands (Klopatek 1987; DeBano and Klopatek 1988; Kramer and Green 1999; Neff et al. 2009) that help trees reduce understory vegetation and maintain resource dominance (Doescher et al. 1987; Schlesinger et al. 1990; Schlesinger and Pilmanis 1998).

Some juniper-tree encroached lands are treated to return the plant community back to sagebrush-bunchgrass dominated systems and to reduce the potential for canopy wildfire by reducing canopy fuel loads (Miller and Tausch 2001). A recent control method for woody species is mechanical mastication that shreds canopies, branches, and trunks into masticated surface debris. It is unknown how the mastication method of juniper tree control influences plant community dynamics. In general, juniper control reduces competition for resources necessary for plant growth (Bates et al. 2000), increases resource availability for remaining plant species (Bates et al. 2002; Young et al. in reviewa, in reviewb), and increases understory plant productivity (Everett and Sharrow 1985).

One life form sometimes dominates another following tree reduction. For example, burning, chaining, and cutting juniper trees have initially resulted in annual plant dominance at some locations (Barney and Frischknecht 1974; Tausch and Tueller 1977; Quinsey 1984; Evans and Young 1985; Vaitkus and Eddleman 1987) but not at other locations (Barney and Frischknecht 1974; Quinsey 1984; Bates et al. 2000). It may not be clear why invasive annuals sometimes dominate after woody species control but increased resource availability is thought to increase the invasibility of plant communities and reduce plant community resistance and resilience to weed invasion (Vasquez et al. 2008; D'Antonio et al. 2009). Other influences like the composition of vegetation at the time of woody plant control also greatly influence plant community composition after control (Miller and Wigand 1994).

High soil inorganic-N availability can enable greater competitiveness in invasive annual grasses over perennial grasses (Mangold and Sheley 2008; Vasquez et al. 2008; Mazzola et al. 2011). For example, increased soil N availability increases invasive-annual grass growth more than perennial grass growth (Monaco et al. 2003). Rapid invasive-annual grass growth also reduces resource availability for slower-growing perennial grasses, which can reduce perennial grass vigor (Young and Evans 1978; Melgoza et al. 1990; Smith and Nowak 1990; Berendse et al. 1992; van der Werf et al. 1993a, 1993b; Monaco et al. 2003). Higher soil N availability following juniper tree mastication could lead to invasive-annual grass dominance especially in litter mounds where soil N availability is greatest (Young et al. in reviewa). However, traits that endow plants with the ability to grow rapidly in conditions of high resource availability may reduce their ability to thrive in conditions of low resource availability (Grime and Hunt 1975).

As N is usually the most limiting mineral resource (Sylvia et al. 2005), reducing soil N availability with C additions has been shown to reduce the biomass, density, and competitiveness of invasive annual grasses like cheatgrass (*Bromus tectorum* L.; McLendon and Redente 1991; Hardegree et al. 2000; Paschke et al. 2000; Beckstead and Augspurger 2004). Adding C in the form of masticated woody debris to bare interspaces reduced soil N availability by 108-168 mg m^{-2} 4 mo^{-1} during late-summer through winter and adding sucrose to the bare interspaces reduced soil N availability by 123-192 mg m^{-2} 4 mo^{-1} during all seasons (Young et al. in reviewa). These types of C additions can reduce soil N availability because soil microorganisms use available soil N when the organic C energy source does not provide sufficient N for microorganism metabolism and growth (Brady and Weil 1999). Just how long masticated debris reduces soil N availability and how this affects plant community composition is not known. However, low soil N levels over time might favor dominance of perennial, rather than annual grasses (Monaco et al. 2003).

The control of juniper trees, the main resource users in densely-populated juniper stands where few other plants remain, not only increases soil N availability but also increases soil water availability and soil temperature during spring (Young et al. in reviewa, in reviewb), a critical time for seedling establishment (Hardegree et al. 2003; Bradford and Lauenroth 2006; Roundy et al. 2007). For example, litter mounds in masticated areas had 23 more days of available soil water than untreated (not masticated) areas during spring (Young et al. in reviewb), which may have helped increase the soil N availability found in masticated areas by increasing soil solution and nutrient diffusion (Leffler and Ryel 2012). The availability of soil water in masticated areas later in spring may benefit perennials more than invasive annuals because perennial grass roots like those of bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve) grow slower than annuals like cheatgrass especially during cool seasons (Harris 1967). Chipping trees is similar to mastication except trees are cut and fed into a chipper rather than shredded while standing. Increased soil water availability and presumed lower soil N availability after tree chipping were associated with increased perennial and decreased annual grass density and cover under woody debris (Benson 2006). Such outcomes are dependent on pre-treatment plant-community composition and residual perennial cover, which may be limited where trees have long-term and extensive dominance (Miller and Wigand 1994; Koniak and Everett 1982).

Land managers need to know if mastication will favor desirable plant dominance and if they should plant perennial grasses in combination with juniper tree mastication where increased tree population density has reduced desirable perennials. To address these questions, our main objective was to determine if juniper tree mastication favors invasive-annual or perennial-grass seedling establishment and growth. Our secondary objective was to determine microenvironmental effects on seedling establishment and growth associated with masticated and untreated juniper woodlands. This objective included making seedling comparisons among naturally occurring microsites of litter mounds, bare interspaces between litter mounds, and masticated debris on litter mounds and on bare interspaces. We removed part of the litter mounds by hand down to the soil to isolate the effects of litter on seedling establishment and growth. Our tertiary objective was to determine the isolated effects of soil N availability on seedling establishment and growth using N-S applications of ammonium-sulfate and C applications of sucrose because we expected juniper tree mastication to alter soil N availability in combination with altering soil water availability and temperature. Seedling establishment and growth were evaluated using the metrics of seedling emergence, tillers, aboveground biomass, and spikelets in hand-planted rows of Anatone bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve) and cheatgrass. We hypothesized that: 1) juniper tree mastication would generally increase grass establishment because of increased resource availability following juniper tree mastication; 2) litter mounds consisting mainly of leave scales with typically lower C:N ratios than woody debris would favor invasive annual grasses over perennial grasses because of greater soil N and water availability in masticated areas; 3) high C:N-ratio woody debris would favor perennial grass establishment by reducing soil N availability while increasing the duration of soil water availability; 4) N fertilization would increase invasive-annual grass establishment over perennial grasses; and 5) C amendments added to the soil would increase perennial grass establishment over invasive-annual grass establishment.

MATERIALS AND METHODS

Study Locations

We measured field-planted seedling establishment and growth at Greenville (38° 12′ N, 112° 48′ W), Onaqui (40° 13′ N, 112° 28′ W), and Stansbury (40° 35′ N, 112° 39′ W) in western Utah. These locations were part of the Sagebrush Steppe Treatment Evaluation Project (SageSTEP) evaluating sagebrush-steppe restoration methods in the Great Basin region (www.sagestep.org). Utah juniper (*Juniperus osteosperma* [Torr.] Little) in densely populated stands dominates our research areas at these three locations that were historically dominated by sagebrush-bunchgrass plant communities. Greenville also supports two-needle piñon (*Pinus edulis* Engelm.) in combination with Utah juniper. Few naturally-occurring understory plants have remained due to competition with juniper trees in pre-masticated areas. Soils at the three locations are loamy skeletal. Greenville soils are carbonatic, mesic Typic Calcixerepts (Rau et al.

2011). Onaqui soils are carbonatic, mesic, shallow Petrocalcic Palexerolls (Rau et al. 2011). Stansbury soils are mixed, active, frigid Pachic Haploxerolls (Rau et al. 2011). We conducted our research at 1 700 to 1 900 m in elevation across all three locations. Annual precipitation totals during 1970-2007 averaged 334 mm at Greenville, 311 mm at Onaqui, and 389 mm at Stansbury (PRISM, 2008). A full description of the SageSTEP locations can be found in McIver et al. (2010) and Young et al. (in reviewb).

Treatment Implementation

A Tigercat® M726E Mulcher (Tigercat Industries Inc, Brantford, Ontario) with Fecon® Bull Hog® (Fecon Inc, Lebanon, OH) masticated trees in fall 2006 at Onaqui and in fall 2007 at Stansbury. A skid steer loader with Fecon® Bull Hog® masticated trees in fall 2007 at Greenville. These two machines masticate trees similarly.

Study Design

We studied paired masticated and untreated plots with similar soil and vegetation at each of the three locations. A masticated plot refers to the general area where all juniper trees taller than 0.5 m were masticated. An untreated plot refers to the general area where none of the juniper trees were masticated. We implemented a randomized complete block design within treatment plots. Each plot had four replicate blocks with two trees in untreated blocks and four trees in masticated blocks. We used juniper trees with litter mounds at least 2 m in diameter to allow room for planting. We divided the area around trees into microsites like slices of a pie. This allowed us to make microsite comparisons that isolated the effects of debris and litter mounds on seedling establishment in our study and on soil nutrients, water, and temperature in related studies (Young et al. in reviewa, in reviewb).

The number of microsite experimental units was 112 at each of the three locations. In untreated plots, the two trees per block had three microsite types that included: 1) juniper litter mounds consisting of dead scales, fruits, and twigs (litter mounds), 2) exposed soil after hand removal of litter mounds (removed-litter mounds), 3) interspaces between trees where little vegetation was growing (bare interspaces). In masticated plots, two of the four trees per block each had five microsite types that included: 1) litter mounds, 2) removed-litter mounds, 3) bare interspaces, 4) former bare interspaces covered with juniper debris following mastication (debris-covered interspaces), and 5) juniper litter mounds covered with juniper debris following mastication (debris-covered litter mounds). The other two trees per block in masticated plots had two sets of bare interspaces, debris-covered interspaces, and debris-covered litter mounds per tree. One set of these three microsite types per tree received 1 100 kg · ha^{-1} (981 lb · ac^{-1}) of C applied in the form of sucrose ($C_{12}H_{22}O_{11}$). The other set received 224 kg · ha^{-1} (200 lb · ac^{-1}) of N applied in the form of ammonium-sulfate ($[NH_4]_2SO_4$) that we refer to as N-S fertilizer. We amended the soil to determine the effects of an extreme range of soil N availability on plant growth isolated from confounding changes in soil water and temperature because juniper tree mastication alters soil N, water, temperature, and cover simultaneously and it was unknown how much juniper mastication and masticated debris affected soil N availability. We applied N-S and C amendments at Greenville in October 2008 and November 2009, Onaqui in October 2007 and October 2008, and Stansbury in October 2008.

We temporarily removed the debris on half of the debris-covered microsites long enough to count seedlings emerged from the soil but not through the debris and compared this with the number of seedlings emerged from the soil in bare interspaces to evaluate the effects of debris on seedling emergence from the soil. These results were compared with the number of seedlings emerged through the debris far enough to be visible without moving the debris, which allowed us to quantify how much debris physically impeded seedling emergence through the debris. The exception was at Onaqui in 2008 when debris was moved on all debris-covered microsites to count seedling emergence.

In every microsite, 40 seeds of Anatone bluebunch wheatgrass and cheatgrass were planted in separate 0.5-m rows during October-November. Anatone bluebunch-wheatgrass seed was purchased from the Granite Seed Company in Lehi, UT. The cheatgrass seed planted at Onaqui and Stansbury was hand collected from Skull Valley, UT in June 2007 and the cheatgrass seed planted at Greenville was collected from the same area in June 2008. From hand sown seeds, seedling emergence, tillers, aboveground biomass, and cheatgrass spikelets were measured at Greenville in 2009 and 2010 and at Onaqui in 2008 and 2009 except tillers were not counted at Onaqui in 2008. Only seedling emergence was measured at Stansbury in 2009 because a wildfire ended our study at this location in August 2009. Wire netting with 2.5-cm openings was placed around rows with seedlings at Greenville in 2010 to prevent abnormally high wildlife browsing.

Field Measurements

We counted seedling emergence at approximately three week intervals during the first spring and early-summer following fall planting. We counted tillers per row during summer before August harvest because many plants became intermingled and indistinguishable as individual plants. Cheatgrass tillers were collected as their seed heads became ripe but bluebunch wheatgrass did not produce seed the first growing season. We harvested all remaining aboveground biomass within 0.5 cm of the soil in August and oven dried it at 60 °C for at least 72 hr. When preparing hand-collected cheatgrass seed for fall planting, we found that the first floret in each spikelet was usually the only filled seed. So, after harvesting planted rows we counted the number of spikelets per row to represent cheatgrass seed production.

Data Analysis

We analyzed the response variables of seedling emergence, tillers, aboveground biomass, and spikelets separately using mixed-model analysis of variance in Proc Glimmix (SAS v9.2, SAS Institute, Inc, Cary, NC) with location, year, block, and tree as random effects. Potential spatial correlation among microsites was adjusted for by nesting microsites in trees and blocks that were nested in locations and years. All available years and locations were analyzed together. Seedling emergence, tiller counts, aboveground biomass, and cheatgrass spikelets had 1 120, 456, 584, and 292 observations for data analysis, respectively. Seedling emergence values did not need to be transformed to meet the distribution requirements for analysis of variance based on examination of residual plots. Tiller counts, aboveground biomass, and cheatgrass spikelets were log transformed prior to analysis and back-transformed by exponentiation for presentation. Masticated plots had more microsite types than untreated plots because of the debris-covered microsites and N-S and C amended microsites in masticated plots. This uneven number of microsite types between treatment plots prevented a full factorial analysis. To allow an overall treatment effect comparison, we assigned each treatment (trt) by microsite (micro) by amendment (amend) combination to be one of 20 levels for emergence and one of 11 levels for tillers, aboveground biomass, and cheatgrass spikelets for the combined main effect of trt-micro-amend. The number of levels among response variables differed because moved debris-covered interspaces and litter mounds were not analyzed for tillers, aboveground biomass, or spikelets. Removing and then replacing debris on half of the debris covered microsites to count seedlings emerged from the soil did not allow these seedlings sufficient time to grow through the debris to full sunlight where greater photosynthesis and growth may have prevented their desiccation. Linear contrasts allowed us to compare the five unamended-microsite types in masticated plots with the three microsite types in untreated plots. We also used linear contrasts to compare individual microsite types within and across treatment plots. We adjusted for false positives from multiple comparisons using pseudo-Bonferroni with a critical alpha level of 0.01 for 30 or fewer comparisons and 0.001 for more than 30 comparisons. A species main effect and the interaction between species and trt-micro-amend allowed us to compare seedling establishment differences between Anatone bluebunch wheatgrass and cheatgrass. The maximum likelihood estimation method used for mixed-model analysis of variance resulted in an F-test for testing the significance of the fixed effects.

RESULTS

The combined trt-micro-amend main effect was significant for emergence, tillers, aboveground biomass, and spikelets ($P < 0.001$; Table 1). The species effect was significant for emergence and tillers ($P < 0.001$). The trt-micro-amend by species interaction was significant for emergence ($P < 0.001$).

Juniper Tree Mastication Effect

Masticated plots had fewer but more productive seedlings than untreated plots. For example, bluebunch wheatgrass had 16% (95% CI 11, 21) and cheatgrass had 10% (95% CI 5, 15) fewer seedlings emerge per row in unamended masticated plots than untreated plots ($P < 0.001$; Table 2). However, bluebunch wheatgrass had 3.2 (95% CI 2.0, 5.2) times more tillers and 1.9 (95% CI 1.6, 2.2) times more aboveground biomass per row in unamended masticated plots than untreated plots ($P < 0.001$). Similarly, cheatgrass had 2.3 (95% CI 1.5, 3.8) times more tillers, 2.0 (95% CI 1.7, 2.4) times more aboveground biomass, and 11.4 (95% CI 6.3, 20.7) times more spikelets per row in unamended masticated plots than untreated plots ($P < 0.001$).

Litter Mound Effect

Litter mounds had fewer and less productive seedlings than uncovered microsites in untreated plots. For example, bluebunch wheatgrass had 17% (95% CI 8, 25) and cheatgrass had 23% (95% CI 14, 31) fewer seedlings emerge per row in litter mounds than bare interspaces in untreated plots ($P < 0.001$). Bluebunch wheatgrass had 3.2 (95% CI 1.5, 7.2) times and cheatgrass had 4.7 (95% CI 2.1, 10.3) times fewer tillers per row and cheatgrass had 4.4 (95% CI 1.6, 12.3) times fewer spikelets per row in litter mounds than bare interspaces ($P < 0.01$). Following the same trend, litter mounds had fewer and less productive seedlings than removed-litter mounds in untreated plots. However, in masticated plots, litter mounds had little effect on seedling establishment in unamended microsites. Bluebunch wheatgrass and cheatgrass emergence, tiller counts, and aboveground biomass and cheatgrass spikelets were not different among litter mounds, removed-litter mounds, or bare interspaces except that bluebunch wheatgrass had 1.4 (95% CI 1.1, 1.9) times more aboveground biomass per row in litter mounds than bare interspaces in masticated plots ($P < 0.01$).

Debris Effect

Debris increased seedling emergence from the soil but reduced seedling emergence through the debris. For example, in debris-covered interspaces where the debris was repeatedly moved during spring to count emerged seedlings, bluebunch wheatgrass had 19% (95% CI 9, 29) more seedlings emerge than in bare interspaces even though cheatgrass emergence was not significantly different across these microsites ($P > 0.001$). However, in debris-covered interspaces where the debris was not moved and seedlings had to emerge through the debris to be counted, bluebunch wheatgrass had 25% (95% CI 14, 37) and cheatgrass had 27% (95% CI 15, 38) fewer seedlings emerge than in bare interspaces ($P > 0.001$). The movement of debris to count seedling emergence in moved-debris-covered microsites and the combined depth of debris and litter in debris-covered litter mounds prevented sufficient seedling survival for collection and analysis of aboveground biomass, tillers, and spikelets. The seedling establishment trends among unamended microsites in masticated plots were similar among N-S and C amended microsites.

Species Effect

Most species comparisons were not significant but of the significant comparisons, bluebunch wheatgrass had more seedling establishment than cheatgrass. For example, bluebunch wheatgrass had 12% (95% CI 8, 16) more seedlings emerge per row than cheatgrass across all microsites in untreated plots ($P < 0.01$). Likewise, bluebunch wheatgrass had 6% (95% CI 3, 9) more seedlings emerge per row than cheatgrass across all microsites in unamended masticated plots with a similar trend among N-S and C amended microsites ($P < 0.01$). Bluebunch wheatgrass seedling emergence was most notably higher than cheatgrass in litter mounds of both untreated and unamended masticated plots. In line with these results, bluebunch wheatgrass had 1.9 (95% CI 1.3, 2.6) times more tillers per row across microsites in unamended masticated plots and 2.4 (95% CI 1.3, 4.3) times more tillers per row in litter mounds than cheatgrass ($P < 0.01$).

Soil Amendment Effect

Most amendment comparisons were not significant. Still, bluebunch wheatgrass and cheatgrass in moved debris-covered interspaces had 15% (95% CI 4, 26) more seedlings emerge from the soil in C amended than N-S fertilized microsites in masticated plots ($P < 0.01$). Also, bare interspaces and unmoved debris-covered interspaces collectively had 1.5 (95% CI 1.1, 2.0) times more cheatgrass aboveground biomass per row in unamended microsites than C amended microsites ($P < 0.01$).

DISCUSSION

Juniper Tree Mastication Effect

Masticated plots generally had fewer bluebunch wheatgrass and cheatgrass seedlings emerge than untreated plots. Thick cover from masticated tree debris best accounts for the lower number of emerged seedlings in masticated plots. Deep soil cover is known to physically limit seedling emergence, intercept light necessary for germination and seedling development, and lower soil temperatures that can slow plant growth (Facelli and Pickett 1991). For example, cheatgrass germination has been reduced to 0% germination in complete darkness (Andersson et al. 2002). On the other hand, those seedlings that did emerge in masticated plots generally had more aboveground biomass and tillers and cheatgrass had more spikelets per row than in untreated plots in support of our first hypothesis that juniper tree mastication would increase seedling establishment. The increased productivity of both the invasive annual and perennial grasses were associated with more soil inorganic-N availability (Young et al. in reviewa), warmer soil temperatures, and longer durations of soil water availability during spring in masticated plots (Young et al. in reviewb) among other potential influences. This increased growth of both the invasive annual and perennial grasses suggests that both types of plants when present will increase following woody species mastication.

Litter Mound Effect

Litter mounds had less bluebunch wheatgrass and cheatgrass emergence and tillers and cheatgrass spikelets per row than removed-litter mounds and interspaces in untreated plots. This lower seedling establishment has been associated with less soil N availability (Young et al. in reviewa); greater competition from juniper roots (Emerson 1932); reduced solar radiation and spring soil temperatures below tree canopies and litter mounds (Facelli and Pickett 1991; Lebron et al. 2007; Matsushima and Chang 2007; Lin 2010); and physical impedance of seedling emergence by litter mounds (Facelli and Pickett 1991; Horman and Anderson 2003). However, juniper tree mastication changed the microsite plant-establishment pattern from that of untreated plots. In masticated plots, litter mounds had little effect on seedling establishment even though litter mounds had more soil N availability than interspaces as expected of resource islands (Brotherson and Osayande 1980; Padien and Lajtha 1992). This result is contrary to our second hypothesis that higher soil N availability in litter mounds would favor invasive-annual grass establishment. Seedling establishment was more similar between litter mounds and bare interspaces in masticated than untreated plots. Removal of the live tree-canopy cover and discontinued interception of precipitation and solar radiation likely benefited seedling establishment after mastication (Evans 1988; Barbour et al. 1999; Lin 2007, 2010). Without tree canopy cover, litter mounds had longer periods of soil water availability and higher soil temperatures during spring, as well as more soil N availability (Young et al. in reviewa, in reviewb). These improved environmental conditions during the critical spring growth period probably compensated for some of the physical impedance of seedling emergence by litter mounds.

Because we planted seeds in our experiments, our interpretations apply to potential seedling establishment from an existing or sown seedbank, and do not account for effects of treatments and microsites on seed dispersal, catchment, or potential seed location. Species with wind-dispersed seeds capable of establishing inside plant litter may dominate litter mounds initially following juniper tree mastication. For example, we observed unplanted cheatgrass seedlings growing with seeds suspended in litter mounds, roots extending down into the soil, and leaves growing up through litter. Plant litter has been shown to modify both soil water and temperature conditions in favor of increased cheatgrass germination and seedling establishment (Young and Evans 1975; Evans and Young 1984). The ability to germinate and extend roots into the soil below litter mounds also gives invasive annuals access to the greater soil N and water availability we found in the soil below these litter mounds post-mastication (Young et al. in reviewa, in reviewb). Litter mounds on masticated areas apparently serve as resource islands for at least some wind-dispersed species. In general, increased resource availability, especially increased soil N, is expected to increase the invasibility of plant communities and reduce their resistance and resilience to invasive annuals (Vasquez et al. 2008; D'Antonio et al. 2009).

Debris Effect

The greater number of seedlings that emerged from the soil under debris in moved debris-covered interspaces than bare interspaces was associated with longer durations of soil water availability during spring, as well as moderated soil temperatures (Young et al. in reviewb). For example, debris-covered interspaces were cooler than bare interspaces during spring but warmer during winter (Young et al. in reviewb). The lesser number of seedlings that emerged through the debris in unmoved debris-covered interspaces compared to bare interspaces was probably associated with physical impedance of seedling emergence by the debris. However, the few seedlings that did emerge through the debris produced as much biomass and as many tillers and spikelets per row as seedlings growing in bare interspaces. This increased growth per plant was associated with longer durations of soil water availability in debris-covered interspaces during spring (Miller and Seastedt 2009; Young et al. in reviewb) and not soil N availability because soil N availability was lower in debris-covered interspaces during late-summer through winter

(Young et al. in reviewa). The overall similarity in seedling establishment between both the invasive annual and perennial grasses suggests that debris will not favor perennial grass establishment over invasive annual grasses as we had hoped.

Species Effect

Most species comparisons between the invasive annual and perennial grasses were not significant but when they were, bluebunch wheatgrass had more seedling emergence in masticated and untreated plots and more tillers in masticated plots than cheatgrass. The greater emergence and number of bluebunch wheatgrass tillers were associated with the establishment characteristics of Anatone bluebunch wheatgrass. Anatone was selected in part for its fast germination rate at cold temperatures and strong seedling emergence, establishment, and vigor; traits thought to help Anatone compete with invasive annual grasses like cheatgrass (Monsen et al. 2004). These results and characteristics suggest that Anatone, where adapted, would be a good choice when planting perennial grasses in rangeland restoration projects. However, Anatone should not be expected to outcompete cheatgrass at the seedling stage. Even though cheatgrass sometimes had fewer seedlings per row than bluebunch wheatgrass, it produced similar aboveground biomass per row. This result indicates that cheatgrass produced more aboveground biomass per plant than bluebunch wheatgrass during the first growing season. Cheatgrass and other invasive annuals have high relative growth rates and specific leaf area in both high and low nutrient conditions (James 2012). In addition, cheatgrass produced seed the first growing season following planting whereas Anatone did not produce seed until the second growing season. These findings suggest that if perennial grasses have been severely weakened or lost over decades of tree dominance and cheatgrass is dominant on the project site, cheatgrass will need to be controlled to allow time and resources for residual or planted species such as Anatone to fully establish.

Soil Amendment Effect

We had hypothesized that N fertilization would increase invasive-annual grass establishment and growth over perennial grasses and that C amendments applied to the soil would increase perennial grass establishment and growth over invasive annual grasses because of the highly-responsive nature of invasive annuals to soil N availability (Monaco et al. 2003; Mazzola et al. 2011). However, we found that N-S and C amendments had little effect on seedling establishment and first year growth even though N-S fertilization increased soil N availability by two to four times the increase in soil N availability resulting from juniper tree mastication (Young et al. in reviewa). Even so, the lower soil N availability in C amended microsites (Young et al. in reviewa) did result in less cheatgrass aboveground biomass compared to unamended microsites. Bluebunch wheatgrass followed the same trend as cheatgrass but with less and nonsignificant decreases in aboveground biomass with lower soil N availability in C amended microsites. However, the lack of plant response to increased soil N availability and the similarity in response between the invasive annual and perennial grasses to lower soil N availability suggest that changes in soil N availability induced by tree mastication are not sufficient to favor one species or life form over the other, at least in the short-term. Perennial and annual plant seedling responses to nutrient manipulations have been mixed, but manipulations are much more likely to favor established perennials than seedlings of perennials (James 2012). In the long-term as plant succession progresses, soil nutrients like soil N availability tend to become more limited and perennials adept to growing in low nutrient environments may be favored (McLendon and Redente 1991). Under continually low nutrient environments, the slower growth rates, greater root:shoot ratios, greater N use-efficiency with perennial structures, and nutrient reabsorption from senescing leaves generally found in perennial grasses may help them eventually dominate invasive annuals (Chapin 1980; Chapin et al. 1987; Monaco et al. 2003; Vasquez et al. 2008).

Implications

Woody species encroachment should be controlled before perennial grasses are weakened or lost. If woody species already dominate, mastication will likely result in increased invasive-annual and perennial grass seedling establishment and growth due to increased resource availability in the form of soil water and N availability (Young et al. in reviewa, in reviewa). In line with plant community resilience and resistance theory (D'Antonio et al. 2009), we expect areas with dominant perennial grass cover before woody species mastication to have a strong perennial grass component after mastication. If perennial grasses have been lost during decades of juniper dominance, then vigorous perennial grasses like Anatone bluebunch wheatgrass will need to be sown. Dominant invasive annuals with their fast growth rates will need to be controlled for example, with selective herbicides to allow time and resources for the slower growing perennial grasses to establish (James 2012). Where possible, maintaining healthy, perennial vegetation before weedy species dominate may be the most effective way to limit invasive-annual species dominance (Turner et al. 1963; Chambers et al. 2007; Roundy et al. 2007). Once perennials are established, maintaining low soil nutrient availability will help perennial grasses with nutrient-conserving perennial structures compete with invasive annuals (James 2012). In the long-term, monitoring of masticated areas will improve post-mastication expectations for invasive annual and perennial grass dynamics.

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Tables

Table 3-1. Mixed-model analysis of variance and type III F-tests from maximum likelihood estimation for the plant establishment response variables quantified during the spring and summer following the fall planting of 40 seeds of Anatone bluebunch wheatgrass and cheatgrass in separate 0.5-m rows. We assigned each treatment (trt) by microsite (micro) by amendment (amend) combination as one of 20 levels for emergence and one of 11 levels for tillers, aboveground biomass, and cheatgrass spikelets for the combined main effect of trt-micro-amend.

	Effect	Num DF[1]	Den DF[2]	F-value	p-value
Emergence (%)	Trt-micro-amend	19	286	21.92	<0.001
	Species	1	727	55.26	<0.001
	Trt-micro-amend * Species	19	727	2.91	<0.001
Tillers (No.)	Trt-micro-amend	10	109	6.71	<0.001
	Species	1	281	18.61	<0.001
	Trt-micro-amend * Species	10	281	1.07	0.389
Aboveground biomass (g)	Trt-micro-amend	10	122	12.65	<0.001
	Species	1	415	0.11	<0.741
	Trt-micro-amend * Species	10	415	0.28	0.985
Cheatgrass Spikelets (No.)	Trt-micro-amend	10	138	10	<0.001

[1] Numerator degrees of freedom.

[2] Denominator degrees of freedom.

Table 3-2. Seedling establishment linear-contrast comparisons among 1) untreated (untrt) and masticated (mast) plots; 2) unamended (unamend) microsites (micro), ammonium-sulfate ($[NH_4]_2SO_4$) microsites fertilized with 224 kg · ha^{-1} N, and sucrose ($C_{12}H_{22}O_{11}$) microsites amended with 1 100 kg · ha^{-1} C; 3) litter mounds (L), removed-litter mounds (RL), bare interspace (I), debris-covered litter mounds with debris moved to count seedling emergence from the litter under debris (DLm), debris-covered litter mounds with debris unmoved to count emergence through the litter and debris (DLum), debris-covered interspaces with debris moved to count emergence from the soil under debris (DIm), and debris-covered interspaces with debris unmoved to count emergence through the debris (DIum); and 4) Anatone bluebunch wheatgrass and cheatgrass planted in separate 0.5-m rows using 40 seeds of each species. Tillers, aboveground biomass, and spikelets were log transformed for analysis and back-transformed by exponentiation for presentation.

		Treatment Effect		Amendment Effect		
		Unamend	Unamend	Unamend	$(NH_4)_2SO_4$	$C_{12}H_{22}O_{11}$
	Micro	Untrt	Mast	Mast	Mast	Mast
Bluebunch Emergence (%)	L	33[1] b[2]R[3]	36 b R	—[4]	—	—
	RL	53 a R	37 b S	—	—	—
	I	50 a R	37 b S	37 X[5]	34 a X	31 b X
	DLm	—	22 bc	22 X	17 b X	14 bc X
	DLum	—	4 c	4 X	3 b X	3 c X
	DIm	—	56 a	56 XY	42 a Y	57 a X
	DIum	—	12 c	12 X	13 b X	23 bc X
		45 R	29 S	26 X	22 X	26 X
Cheatgrass Emergence (%)	L	16 b R	22 ab R	—	—	—
	RL	46 a R	43 a R	—	—	—
	I	39 a R	33 a R	33 X	36 a X	28 ab X
	DLm	—	12 bc	12 X	9 c X	6 c X
	DLum	—	3 c	3 X	1 c X	1 c X
	DIm	—	42 a	42 X	27 ab Y	42 a X
	DIum	—	7 bc	7 X	9 bc X	14 bc X
		33 R	23 S	19 X	16 X	18 X
Bluebunch Tillers (No.)	L	2 b S	28 a R	—	—	—
	RL	9 a S	30 a R	—	—	—
	I	9 a R	21 a R	21 X	7 a X	8 a X
	DIum	—	11 a R	11 X	7 a X	7 a X
		7 S	22 R	16 X	7 X	7 X
Cheatgrass Tillers (No.)	L	1 b S	11 a R	—	—	—
	RL	11 a R	20 a R	—	—	—
	I	6 a R	10 a R	10 X	6 a X	7 a X
	DIum	—	6 a R	6 X	3 a X	4 a X
		6 S	12 R	8 X	4 X	5 X
Bluebunch Aboveground	L	0.05 a S	1.49 a R	—	—	—
	RL	0.14 a S	1.35 ab R	—	—	—

Biomass (g)	I	0.09 a S	0.73 b R	0.73 X	0.41 a X	0.30 a X
	DIum	—	0.78 ab R	0.78 X	0.91 a X	0.38 a X
		0.09 S	1.09 R	0.76 X	0.66 X	0.34 X
Cheatgrass Aboveground Biomass (g)	L	0.02 a S	1.50 a R	—	—	—
	RL	0.14 a S	1.54 a R	—	—	—
	I	0.10 a S	0.79 a R	0.79 X	0.35 a XY	0.19 a Y
	DIum	—	0.95 a R	0.95 X	0.63 a X	0.34 a X
		0.08 S	1.19 R	0.87 X	0.49 XY	0.27 Y
Cheatgrass Spikelets (#)	L	1 b S	58 a R	—	—	—
	RL	9 a S	121 a R	—	—	—
	I	6 a S	36 a R	36 X	20 a X	9 a X
	DIum	—	32 a R	32 X	7 a X	9 a X
		5 S	62 R	34 X	14 X	9 X

[1] Within response variables and columns, significant differences between bluebunch and cheatgrass estimates are underlined and italicized (individual microsite and overall comparisons $P < 0.01$).

[2] Within response variables, species, and columns, individual microsite estimates followed by the same lower-case letter of a, b, or c are not significantly different (emergence $P < 0.001$; tillers, aboveground biomass, and spikelets $P < 0.01$).

[3] Within rows of treatment effect columns, estimates followed by the same upper-case letter of R or S are not significantly different (individual microsite comparisons $P < 0.01$; overall comparisons $P < 0.001$).

[4] —, nonexistent microsite type.

[5] Within rows of amendment effect columns, estimates followed by the same upper-case letter of X or Y are not significantly different (individual microsite and overall comparisons $P < 0.01$).