



Litter decomposition in cut and uncut western juniper woodlands[☆]

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Abstract

The expansion of western juniper (*Juniperus occidentalis* ssp. *occidentalis* Hook.) in the northern Great Basin has resulted in management efforts to reduce juniper by prescribed fire or tree cutting to restore shrub-grassland plant communities. Herbaceous succession following juniper cutting or prescribed fire has been well documented, however, impacts of these disturbances to litter and nutrient cycling is limited in these invasive semi-arid woodlands. This study evaluated the effects of cutting juniper trees on leaf litter decomposition and nitrogen (N) dynamics over a 2-year period in eastern Oregon, USA. Litter bags were used to measure juniper leaf litter decomposition and track litter carbon (C) and N fluxes in cut and uncut juniper woodland treatments. Litter mass loss was 37% greater in the cut treatment compared to the uncut treatment after 2 years. Greater litter inputs, higher litter fall quality, and micro-environmental differences were suggested to have been the main causes for the higher litter decomposition rate in the cut treatment. In both treatments, litter N was released by the second year of decomposition, though N release was greater in the uncut treatment. Retention of juniper debris on site permits storage and release of nutrients through decomposition processes which is likely important in maintaining site productivity.

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1. Introduction

The expansion of western juniper (*Juniperus occidentalis* ssp. *occidentalis* Hook.) and other pinyon-juniper woodlands is of major ecological importance in the western United States (Miller et al., 2005; Van Auken, 2000; West, 1984). Western juniper has increased 9-fold the past 130 years and encompasses an estimated 3.2 million ha in eastern Oregon, southwestern Idaho, and along the northern border of California and Nevada. Woodland dominance reduces productivity and diversity of shrub-steppe communities (Bates et al., 2005; Miller et al., 2005; West 1984), alters the cycling and distribution of soil and litter nutrients (Bates et al., 2002; Doescher et al., 1987; Tiedemann, 1987; Tiedemann and Klemmedson, 1995), and increases soil erosion and runoff (Buckhouse and Mattison, 1980; Miller et al., 2005). The desire by land managers to restore or maintain shrub-steppe grasslands has resulted in large-scale efforts to reduce the expansion of western juniper and other conifer species throughout the western United States. Though plant community succession following juniper cutting or prescribed fire has been well documented (Bates et al., 1998, 2005, 2006; Miller et al., 2005), knowledge of other ecological processes, particularly litter and nutrient cycling is limited in invasive semi-arid woodlands. It is important to evaluate these processes as woodland expansion and associated control measures impact ecosystem carbon and nutrient dynamics (Jackson et al., 2002; Schlesinger et al., 1990).

As woodlands age, nitrogen (N), other nutrients, and carbon (C) accumulate in tree biomass, litter mats, and canopy influenced soils (Doescher et al., 1987; Klemmedson and Tiedemann, 2000; Tiedemann and Klemmedson, 1995, 2000). Surface litter shifts from a composition of herbaceous and shrub detritus to primarily juniper leaf litter. The buildup of litter is characteristic of juniper and other semi-arid woodland expansions indicating increased litter residence times and potentially slower release of plant available nutrients compared to sagebrush steppe grassland (Tiedemann, 1987; Young et al., 1984). Roberts and Jones (2000) measured lower N mineralization and available N fractions in soils under juniper than under grass and sagebrush in central Oregon.

Cutting of juniper woodlands is a common management practice to reduce tree dominance. Because of the limited commercial value attached to juniper in these remote locations, leaving cut trees and debris on site is a common practice and has similarities to forest harvesting which leave substantial amounts of slash. The effects of overstory removal to litter decomposition and nutrient cycling in coniferous forests and woodlands have not produced consistent results among field studies. In boreal and sub-alpine forests litter decomposition and nutrient release may not change or actually decrease following cutting (Feller et al., 2000; Gurlevik et al., 2003; Palviainen et al., 2004; Prescott et al., 2000, 2003). In drier coniferous systems, which are often water limited, there is a tendency for litter decomposition rates and nutrient release to increase in response to overstory cutting (Fahey, 1983; Hart et al., 1992; Klemmedson et al., 1985). In dry conifer forests, increased decomposition may be a result of improved environmental conditions, such as increased soil and litter water content (De Santo et al., 1993). Bates et al. (2000) measured higher soil water content throughout the growing season after cutting western juniper.

In this study, we examined juniper leaf litter mass loss, litter decomposition rates, and litter C and N dynamics in cut and uncut western juniper woodland in southeast Oregon over a 2-year period. Because the cut junipers were left on site, dead trees provided a continual source of litter fall that was expected to be greater and of higher quality than

uncut woodlands. Additions of fresh litter of higher quality increases decomposition rates of older litters (Dalenburg and Jager, 1981; Melillo et al., 1982; Sorensen, 1974). Thus, the decomposition of juniper leaf litter was expected to increase following cutting as a result of greater deposition of higher quality litter and a more favorable micro-environment. Nitrogen in conifer litters often increases in early stages of decomposition and may take longer than 2 years for N to be released (Klemmedson et al., 1985; Yavitt and Fahey, 1986). Therefore, we expected N to accumulate in leaf litter of both cut and uncut juniper treatments.

2. Methods

2.1. Site description and experimental design

The study was located on Steens Mountain in southeast Oregon, approximately 9.5 km south of the town of Diamond (118°37'W, 47°55'N). The site was on a west-facing slope at an elevation of 1500 m and was dominated by an 80-year-old western juniper woodland. Prior to juniper dominance, the site was a basin big sagebrush/Thurber's needlegrass association (*Artemisia tridentata* spp. *tridentata* Nutt./*Stipa thurberiana* Piper). Juniper canopy cover was about 24% and the density of mature trees averaged 220 trees ha⁻¹. Understory canopy cover was less than 5% and bare soil exceeded 97% in the interspace (area between tree canopies). Long-term precipitation (October 1–September 30) from the nearest recording station located 25 km to the northwest averages 249 mm annually. The majority of precipitation falls between November and late May. Soils were described to the subgroup level and were primarily Typic Vitrixerands with inclusions of Typic Durixerolls. Soil pH (0–10 cm) in the interspace was 7.5 and under tree canopies was 7.8. Organic matter in the top 10 cm of the soil profile averaged 3.1% in the interspace and 5.1% under tree canopies.

The study was conducted as a randomized complete block design, with cut and uncut juniper woodland treatments. Eight, 0.9 ha blocks were placed in a contiguous fashion (north–south) along the ridge slope in June 1991. In August 1991 junipers on one half of each block were felled using chainsaws. Cut junipers were left in place. A buffer zone of 5 m separated treatment plots within each block.

2.2. Juniper leaf litter decomposition and litter floor measurements

Decomposition trials began in September 1991 and were concluded in September 1993. The litter bag method (Bocock and Gilbert, 1957) was used to measure decomposition dynamics of juniper leaf litter. Litter bags, measuring 10 × 20 cm, were constructed from nylon screening with a mesh size of 1 mm². Litter used in the study consisted of juniper leaves gathered from live trees and both treatments utilized the same litter material for the decomposition trials. Initial N content and C/N ratio of the litter were 0.45% and 115:1, respectively. Twenty-five grams of dried juniper leaf litter was placed in each litter bag. Numbered aluminum tags were placed in bags for identification purposes. Openings were sealed by sewing the ends with nylon thread.

Forty-eight litter bags were placed on each block (24 on each cut and 24 on each uncut plot, 192 litter bags per treatment) in September 1991. Litter bags were placed in areas receiving the most litter inputs. In the cut treatment, litter bags were placed on the soil

surface beneath the cut trees. In the uncut treatment, litter bags were placed on the 0i horizon under tree canopies midway between the drip-line and tree bole. Litter bags were nailed to the ground to prevent bags from being moved by rodents and/or overland flow events. Bags were lightly camouflaged by the same leaf material as was placed in the litter bags. Nonetheless, 3% of the litter bags (5–6 bags per treatment) were destroyed by rodents during the 2-year study.

Three to four bags were collected from each treatment plot on six dates (April, 23; July, 16; September, 22) in 1992 and 1993. Litter was dried at 48 °C to a constant weight and then weighed to determine mass loss. Litter samples were ground in a Cyclone Sample Mill (UDY Corp., Fort Collins, CO).¹ Carbon and N content of the litter subsamples (1.5–2.5 mg) were determined using a Perkin-Elmer 2400 Series II CHNS/O analyzer. Litter subsamples (2–3 g) were combusted at 500 °C for 8 h to correct for ash content. Juniper leaf litter decomposition rate constants (k) were calculated using the negative, single exponential equation from [Olsen \(1963\)](#);

$$k = -\ln X/X_0,$$

where k is the decomposition constant (yr^{-1}), X the mass of litter at time t , and X_0 the initial litter mass at time zero.

Mean residence time (R_t) of leaf litter in each treatment was estimated by the inverse of k calculated ([Waring and Schlesinger, 1985](#)):

$$R_t = 1/k.$$

Leaf litter fall in the cut and uncut treatments were estimated based on the mass of juniper leaves prior to cutting (cut treatment) and the mass of the woodland floor (uncut treatment). Leaf biomass was estimated using an equation developed by [Miller et al. \(1987\)](#) that relates basal circumference of western juniper to leaf biomass. Prior to cutting, juniper leaf biomass (dry matter) averaged about 6600 kg ha⁻¹ in the cut areas ([Table 1](#)). Although cutting resulted in the deposition of large amounts of leaves on the ground surface, initially, the majority of juniper leaf detritus remained suspended above ground. Visual inspection provided an estimate of the percentage of suspended juniper leaves that were deposited on the ground annually. Categories for suspended litter that had fallen were 0%, 25%, 50%, 75%, and 100%. Estimates were multiplied by juniper leaf biomass values to provide approximate litter fall in the cut treatment. We tended to be conservative in our approximations, thus, it was likely that litter fall from cut trees was underestimated. Each year in September, suspended litter was collected and analyzed for C and N content.

In the uncut treatment, leaf litter fall was estimated using a steady-state mass balance technique described in [Waring and Schlesinger \(1985\)](#) that relates litter fall inputs to the decomposition coefficient and the mass of litter on the woodland floor;

$$\text{Litter fall (kg/yr)} = k(\text{Litter floor mass(kg)}),$$

where k is the decomposition coefficient (yr^{-1}).

Mass of the woodland floor was measured by sampling beneath 20 randomly selected junipers. Litter was collected to mineral soil at the edge, middle, and next to the bole, in the four cardinal directions, inside 0.2 m² frames (12 samples per tree). Litter mass beneath trees was calculated based on zonal area and then averaged for the 20 trees measured.

¹Mention of trade names does not indicate endorsement by USDA-ARS.

Table 1

Treatment comparisons for litter mass dynamics, and litter floor, and litter fall values

Response variable	Cut	Uncut
Litter mass dynamics		
Mass loss (%) (Sept 1991–Sept 1993)	27.0 ± 1.2 b	16.9 ± 0.9 a
C loss (%) (Sept 1991–Sept 1993)	25.1 ± 1.1 b	15.0 ± 0.9 a
k (yr ⁻¹)		
210 days (Sept 1991–May 1992)	-0.188 ± 0.007 a	-0.162 ± 0.005 b
365 days (Sept 1991–Sept 1992)	-0.154 ± 0.005 a	-0.101 ± 0.007 b
730 days (Sept 1991–Sept 1993)	-0.159 ± 0.007 a	-0.093 ± 0.004 b
Residence time (R_t , yr)	6.4 ± 0.01 a	10.8 ± 0.02 b
Litter floor and litter fall		
Litter floor (kg ha ⁻¹ , 1991)	9861 ± 1751	10,225.0 ± 1832
Leaf biomass (kg ha ⁻¹ , 1991)	6570 ± 510	6927 ± 480
Litter fall (kg ha ⁻¹ , 2 years)	4507 ± 375 b	1940 ± 268 a
Litter fall N (%)		
Sept 1991	0.94 ± 0.06 b	0.45 ± 0.02 a
Sept 1992	0.70 ± 0.19 b	0.43 ± 0.02 a
Sept 1993	0.65 ± 0.12 b	0.46 ± 0.01 a
Litter fall C:N		
Sept 1991	48.2 ± 1.2 a	115.0 ± 5.2 b
Sept 1992	75.2 ± 4.2 a	114.4 ± 6.4 b
Sept 1993	77.6 ± 6.2 a	112.0 ± 4.7 b

Different lower case letters indicate significant treatment differences ($P > 0.05$).

Woodland floor mass (kg ha⁻¹) was estimated by multiplying tree density by the litter mass average. Interspaces were largely bare of juniper litter and were not sampled. The assumptions of the steady-state approach are that k and woodland floor mass are constant through time which probably is not the case, especially for k which is often calculated based on short-term measurements of decomposition. There is the potential for litter fall to be over-estimated using this method.

Gravimetric soil moisture (0–10) cm was measured biweekly from late March until November each year. Because of different soil textures under cut juniper (interspace soil–clay loam) and uncut treatment tree canopies (loam), soil water contents were converted to soil water potentials (Ψ_{soil}). Soil surface temperatures were measured bi-weekly during the growing season but did not differ between the cut and uncut treatments and are not presented.

2.3. Statistical analysis

Leaf litter mass loss, decomposition constants (k), residence times (R_t), litter fall, litter N and C content, litter C/N ratios, and soil water potential were analyzed using a repeated measures analysis of variance (ANOVA) with time and treatment as main effects. The response variables often interacted with time, thus we also analyzed by sampling date using a one-way ANOVA to assist in explaining treatment differences. The general linear model (GLM) procedure was used to compensate for missing data (rodents destroyed some bags). Regression analyses were conducted to determine the influence of soil moisture content

and time on litter decay rates. Statistical significance of all tests was set at $P < 0.05$. Unless noted leaf litter mass, N, and C are expressed as a percent of their original quantity and content.

3. Results

3.1. Litter decomposition

Leaf litter mass loss was significantly greater in the cut treatment than in the uncut treatment on all measurement dates following litter bag placement (Fig. 1; Table 1). There was a significant time by treatment interaction resulting from increasing differences in remaining leaf litter mass between cut and uncut treatments during the course of the study. By the end of the study, leaf litter k values were 1.7 times more negative in the cut than the uncut treatment (Table 1). Mean residence time of juniper leaf litter was 4.4 years longer in the uncut treatment than in the cut treatment. In both treatments leaf litter k values were significantly more negative in the initial 210 days (September 1991–April 1992) of decomposition than during the balance of the study (April 1992–September 1993). Although decomposition rates decreased after April 1992 (Table 1), the percentage of leaf litter mass remaining was relatively linear in both treatments over the course of the study (Fig. 1). Simple regressions with time (days) as the independent variable and percentage of initial leaf litter mass remaining as the dependent variable fit the data well for both treatments.

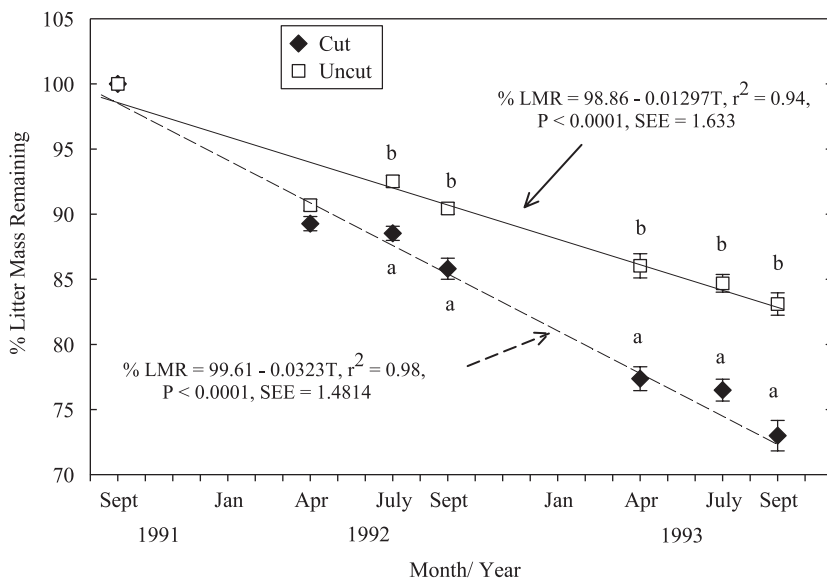


Fig. 1. Percent litter mass remaining (LMR) of juniper leaf litter and regressions correlating litter remaining with time (T , in days), September 1991–September 1993. Data are in means + one SE. Different lower case letters indicate significant treatment differences ($P > 0.05$). Regressions show relationship of dry mass remaining of leaf litter (%) and date of decomposition (1992, day: 210, 295, 365 and 1993, day: 575, 660, 730).

3.2. Litter N and C dynamics

Juniper leaf litter N content varied over time in both treatments. In the cut treatment, leaf litter N content increased during the first year and was greater than the uncut treatment by the second year of the trial (Fig. 2A). As a percentage of original litter N, the

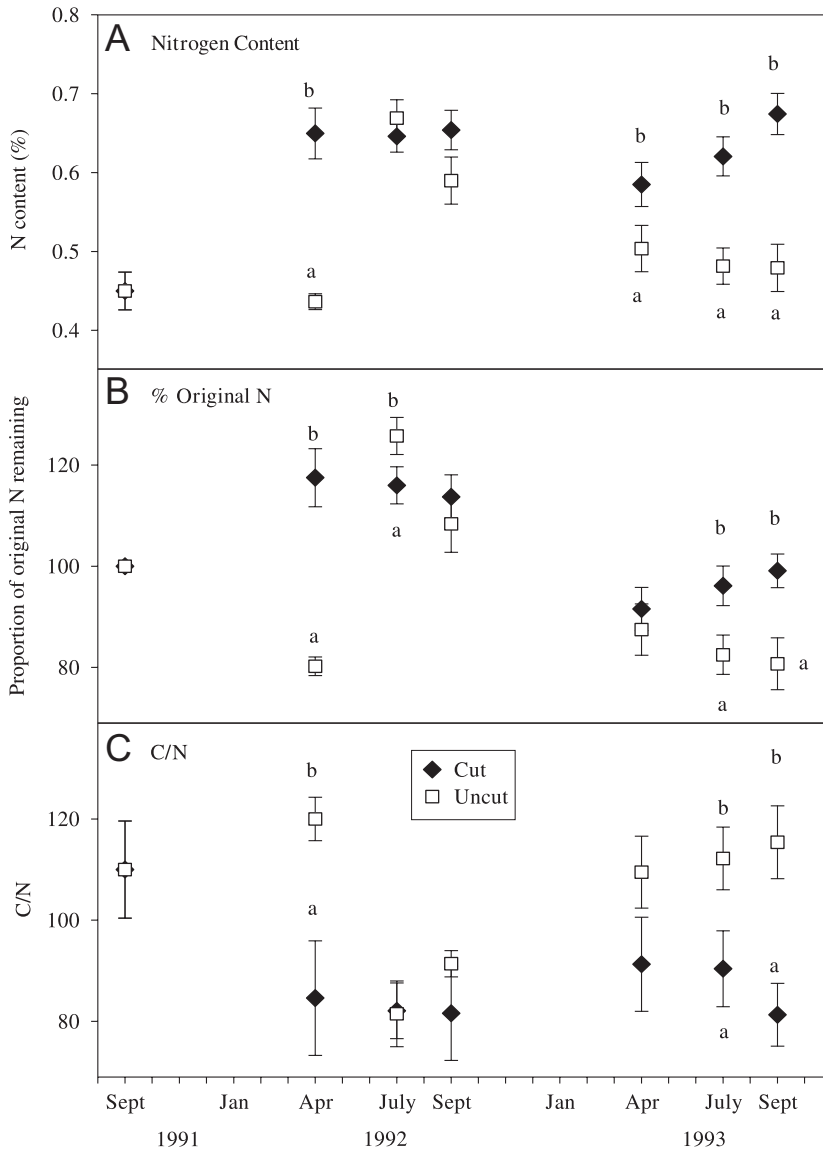


Fig. 2. Treatment comparisons of juniper leaf litter for; litter N content (%), proportion of original N remaining, and C:N ratios. Data are in means + one SE. Different lower case letters indicate significant treatment differences ($P > 0.05$).

cut treatment showed no change at the end of the study while the uncut treatment released about 20% of original leaf litter N (Fig. 2B). Carbon losses in leaf litter followed patterns similar to dry matter losses, thus, greater amounts of carbon were mineralized in the cut treatment compared to the uncut treatment. Carbon as a percentage of dry matter, however, did not change over time, remaining, on average, about 54% (ash-free weight basis) in both treatments. Litter C/N ratios were significantly lower in the cut treatment than the uncut treatment (except for September 1991 and July 1992–May 1993) (Fig. 2C). In both treatments, litter C/N ratios decreased during periods of N accumulation and increased during periods of N decrease.

3.3. Litter fall estimates

Leaf litter fall and N concentration were both greater in the cut treatment. It was estimated that about 75% of suspended juniper leaves had been deposited on the ground 2 years after cutting. Thus, 4500 kg ha⁻¹ of juniper leaf litter was deposited on the ground in the 2 years following cutting (Table 1). In the uncut treatment, litter mass of the woodland floor was 10,225 kg ha⁻¹ (Table 1). By multiplying the mass of leaf litter accumulated in the woodland floor by k , annual litter fall in the uncut treatment was estimated to be 970 kg ha⁻¹ yr⁻¹. From these estimates, leaf litter fall was about 2.3 times greater in the cut treatment compared to the uncut treatment. Litter fall in the cut treatment was also of higher quality (higher N content and lower C/N ratio) than the uncut treatment (Table 1). Nitrogen content in leaf litter fall in the cut treatment was 1.2–2 times greater than the N content of litter fall in the uncut treatment. This treatment difference may have resulted from a lack of N resorption from juniper leaves following tree cutting.

3.4. Litter environment

Soil water potentials were significantly less negative in the cut treatment (except November 1991) than in the uncut treatment in the first year of decomposition (Fig. 3). During the second year of decomposition there were no differences in Ψ_{soil} until late June 1993. From late June to September 1993, Ψ_{soil} was greater in the cut treatment. However, no significant correlation was found between litter decomposition and Ψ_{soil} .

4. Discussion

4.1. Litter decomposition and litter fall

After 2 years of *in situ* exposure leaf litter mass loss was greater in the cut juniper treatment compared to the uncut treatment. This result was expected as litter decomposition rates frequently increase following overstory cutting in dry coniferous forests (Fahey, 1983; Hart et al., 1992; Klemmedson et al., 1985). We attributed the increase in juniper leaf litter decomposition in the cut treatment to greater inputs of higher quality litter (e.g. lower C/N ratio) than the uncut treatment, litter bag placement, and favorable micro-environmental conditions. In other studies, the addition of fresh litter of higher quality increases decomposition rates of older litters (Dalenburg and Jager, 1981; Melillo et al., 1982; Sorensen, 1974).

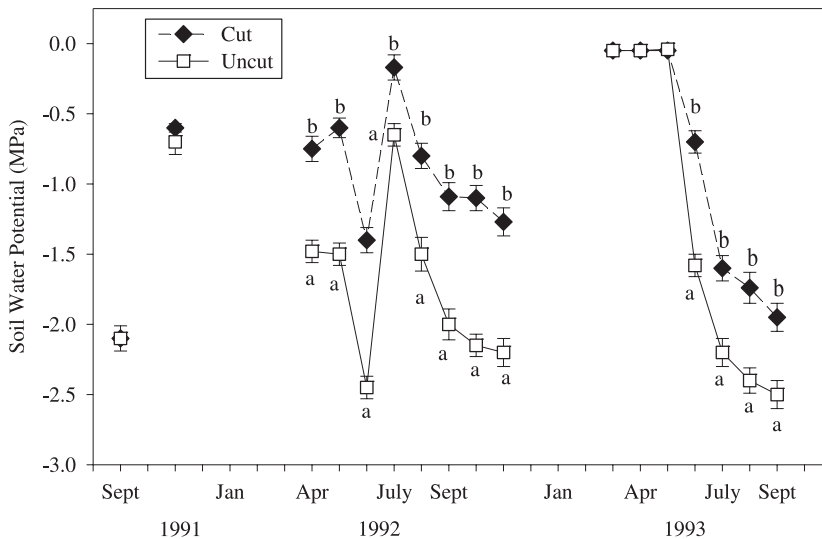


Fig. 3. Soil water potential (MPa), 0–10 cm, in cut and uncut woodland treatments. Data are in means + one SE. Different lower case letters indicate significant treatment differences ($P > 0.05$).

Juniper leaf litter mass loss followed a pattern that is typically reported for other plant litters. Faster rates of juniper leaf litter mass loss were measured during the initial 210-day stage of decomposition followed by a relatively steady rate of mass loss. Plant litters tend to have higher initial decomposition rates as more labile compounds (e.g., soluble carbohydrates, proteins) are decomposed relatively quickly (Moro and Domingo, 2000; Parsons et al., 1990; Schlesinger, 1985). In later stages of decomposition litter disappearance is reduced because more recalcitrant litter materials (e.g., lignin and cellulose) are decomposed at slower rates (Parsons et al., 1990; Schlesinger, 1985). Although time was a good predictor of litter mass remaining in our 2-year study (Fig. 1), these relationships may not serve as good predictors in the long term. Long-term studies have noted that short-term litter decay rates are not good predictors of long-term decomposition rates (Aber et al., 1990; Prescott et al., 2000).

Decomposition rates of western juniper needle litter in both cut and uncut treatment treatments were among the lowest that have been reported for semi-arid and temperate forest tree and shrub species (Table 2). Comparable litter decomposition constants have been measured in ponderosa pine (*Pinus ponderosa*) forests in California (Hart et al., 1992) and Californian chaparral systems (Schlesinger, 1985). Leaf litter decomposition in big sagebrush (*Artemisia tridentata*) systems are relatively rapid ($k \leq -0.60$), with most litter disappearing within 2 years following leaf abscission (Comaner and Staffeldt, 1979; Murray, 1975). If the reported litter decomposition coefficients are representative of western juniper and sagebrush communities, this suggests that litter and nutrient cycling becomes less dynamic as trees invade and replace sagebrush-grassland. This conclusion is supported by biomass and nutrient accumulations reported for western juniper woodlands (21–231 years in age) by Klemmedson and Tiedemann (2000) and Tiedemann and Klemmedson (2000). As trees age, biomass and nutrients accumulate in litter horizons beneath tree canopies at the expense of intercanopy areas.

Table 2
Comparison of litter decay constants (k) of tree and shrub species in semi-arid and temperate ecosystems

Species/location	Study period (yr)	k (yr ⁻¹)	Reference
<i>Juniperus occidentalis</i>			
Oregon, USA			
Cut treatment	2	-0.16	This study
Uncut treatment	2	-0.09	
<i>Populus tremuloides</i>			
Alberta, Canada	1.4–6.3	-0.48 to -0.11	Louiser and Parkinson (1976)
<i>Pinus ponderosa</i>			
Arizona, USA			Klemmedson et al. (1985)
Clearcut	2.8	-0.37	
Forest	2.8	-0.17	
California, USA			Hart et al. (1992)
Young forest	2	-0.19	
Old forest	2	-0.08	
<i>Pinus contorta</i>			
Wyoming, USA	2–7	-0.35 to -0.12	Yavitt and Fahey (1986)
<i>Pinus pinaster</i>			
Almeria Province, Spain	2	-0.12	Moro and Domingo (2000)
<i>Pinus nigra</i>			
Almeria Province, Spain	2	-0.17	Moro and Domingo (2000)
<i>Artemisia tridentata</i>			
Washington, USA	2	-0.60	Murray (1975)
Nevada, USA	1	-0.69	Comaner and Staffeldt (1979)
<i>Larrea tridentata</i>			
New Mexico, USA	1	-0.80	Whitford et al. (1986)
<i>Salvia mellifera</i>			
California, USA	1–3	-0.34 to -0.06	Schlesinger (1985)

4.2. Leaf litter nitrogen

In both treatments, N accumulated in juniper leaf litter by the end of the first year. This pattern was expected as N accumulation in litter, particularly in the early stages of decomposition, has been reported elsewhere (Klemmedson et al., 1985; McClaugherty et al., 1985; Moro and Domingo, 2000; Yavitt and Fahey, 1986). The accumulation of N in litter in the cut treatment and the uncut treatment was speculated to have resulted from micro-flora importation of N from surrounding substrates. When N is limiting during litter decomposition, microbes and fungi not only immobilize N in litter but may import N from surrounding litter substrates. Nitrogen transport between litter substrates by micro-flora was measured in ponderosa pine forests in California (Schimel and Firestone, 1989). We did not quantify the micro-flora community, however, an extensive network of fungal hyphae was observed inside litter bags and within juniper litter mats.

By the second year, leaf litter N was released in both treatments, with the release being greater in the uncut treatment. We had expected that if N was released it would be greater

in the cut treatment because of greater rates of litter decomposition than the uncut treatment. These results were also surprising because in other coniferous ecosystems it often requires more than 2 years before N is exported from recently deposited litter. In lodgepole pine forests the release of N from decomposing needle litter was reported to take as long as 5 years after abscission (Yavitt and Fahey, 1986). Nitrogen accumulated in recently deposited ponderosa pine litter for 2–3 years prior to release (Hart et al., 1992; Klemmedson et al., 1985). In our study, N was released from litter in the uncut treatment at relatively high C/N ratios (>110:1), while in the cut treatment N was released at lower C/N ratios (<80:1). Berg and Ekbohm (1983) concluded that there is no fixed C/N ratio for determining N release or immobilization in litters. Berg and Ekbohm (1983) also reported that N was released at higher C:N ratios in a mature forest compared to a forest clearcut.

Nitrogen release in the second year has two potential explanations; microbial transfers of N to soil or fresh litter substrates and/or leaching of litter N in snowmelt and rain. In 1993, soil inorganic N levels and mineralization rates (0–10 cm) were lower than 1992 and perhaps increased demand for N by micro-flora in soils or litter (Bates et al., 2002). Precipitation and snow accumulation in the winter and early spring of 1992–93 were above average, thus potentially leaching N from leaf litter into the soil. Yavitt and Fahey (1986) measured significant movement of litter N via snowmelt in a lodgepole pine forest. We measured small increases in soil N content (0–10 cm) in the uncut treatment but not in the cut treatment (Bates et al., 2002). Thus, in the cut treatment, N transfers from leaf litter contained in bags may have been moved by micro-flora to other litter substrates.

4.3. Influence of litter environment

The lack of correlation between Ψ_{soil} and leaf litter decay rates was not expected. Klopatek et al. (1995) determined that litter decomposition in northern Arizona pinyon-juniper woodlands was influenced by moisture conditions. In other coniferous systems increased soil or litter water content resulted in greater litter decomposition rates (De Santo et al., 1993; Jansson and Berg, 1985). Our results suggest that litter decomposition in juniper woodlands may be relatively independent of moisture conditions. The greatest rates of leaf litter decomposition occurred during the initial 210-day period, characterized by dry soil conditions, and decay rates did not increase in response to greater soil water content in the winter and spring of 1992–93. Results from other studies in arid lands indicate that litter decomposition may be less dependent on soil water conditions and more dependent on the availability of litter substrates (MacKay et al., 1987; Whitford et al., 1986). In our study, the quality and amount of litter fall inputs appears to have been important for explaining differences in leaf litter decomposition in cut and uncut treatments.

However, measurement of water content within litter bags may have provided a better predictor of moisture influences on litter decay rates in our study. De Santo et al. (1993) determined that decay rates of coniferous litter were highly correlated with litter water content. In the cut treatment, litter bags were placed in direct contact with the soil surface beneath the cut trees. The soils directly under litter bags in the cut treatment remained moist during the study. The direct contact between litter bags and moist surface soils may have maintained more mesic conditions, which were conducive to increased decomposer activity and greater litter decomposition. In contrast, litter bags in the uncut treatment

were placed in the Oi horizon beneath juniper canopies, which have low water holding capacities (Larsen, 1993). Except in the early spring of 1993, the Oi horizon remained dry during the study in the uncut treatment.

5. Conclusions

The results were useful in comparing short-term juniper leaf litter decomposition and N dynamics between the two treatments. However, because of the study's short-term nature and slow decomposition rates of juniper leaf litter, results were of limited value in determining impacts of the cut treatment to site fertility. A difficulty common in short-term decomposition studies is that results may not be good predictors of long-term litter mass and nutrient dynamics (Prescott, 2005). For instance, total soil N content in the uncut treatment increased but did not change in the cut treatment which may indicate that litter N was being immobilized in aboveground substrates. Greater N immobilization in soils beneath cut trees was indicated when measuring soil N dynamics (Bates et al., 2002). Soil inorganic N pools and N mineralization rates were lower under juniper debris than interspace and canopy soils of the cut treatment and were more comparable to N dynamics measured in the uncut treatment. Therefore, it appears that an increase or change in soil N under cut juniper trees will take longer than 2 years.

There was an increase in soil C under cut trees (Bates et al., 2002). The source of this C likely originated from decomposing juniper litter substrates and/or from the increase in the productivity of the herbaceous component (Bates et al., 2000). However, we did not determine how carbon pools were affected on site or by treatment. Ecosystem C pools have been demonstrated to decrease with woodland encroachment in wetter environments and increase in drier semi-arid sites (Goodale and Davidson, 2002; Jackson et al., 2002). The C cycle in Great Basin juniper woodlands has not been evaluated; however, C accumulations and losses are likely to vary considerably depending on location because juniper invades a wide range of sites from dry, lower elevation communities to wetter, higher elevation shrublands and riparian communities (Miller et al., 2005).

There is increasing debate of the impacts that juniper treatments have on site nutrient capital and C pools, particularly when trees are removed for commercial energy production or when juniper debris is burned after cutting. The removal of juniper debris has the potential to reduce nutrient pools which may impact site productivity (Tiedemann and Klemmedson, 2000). The retention of juniper debris on site permits storage and release of nutrients through decomposition processes and may be important in maintaining long-term site productivity.

It is also important to evaluate litter and nutrient dynamics in relation to other ecosystem processes such as plant succession, particularly after disturbance. Bates et al. (2006) and Evans and Young (1985) measured large increases of invasive annual grasses into areas of juniper litter deposition about 5 years following woodland cutting. Both of these studies suggested that litter areas may provide ideal micro-sites for invasive annuals to establish because of greater soil water availability and higher soil fertility that enhance plant growth. Evans and Young (1985) reported that it took 4–5 years after juniper cutting for soil nitrogen to increase in litter deposition areas which coincided with the increase in annual grass. Bates et al. (2005) and Miller et al. (2005) suggested that management of juniper litter in recently controlled woodlands may be important in reducing the threat of invasive weeds when restoring shrub-steppe grasslands. Large-scale and long-term

assessments of C, nutrient dynamics, and their influence on successional dynamics in invasive juniper woodlands are needed to provide managers with the consequences and alternatives of retaining or removing debris following juniper control.

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