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The Influence of Western Juniper Development on Soil Nutrient Availability

Abstract

The objective of the research reported here was to assess the effect of western juniper (*Juniperus occidentalis* Hook.) invasion and tree aging on soil nutrient availability in sagebrush/grass ecosystems of central Oregon. Barley was used as a bioassay test plant to determine availabilities of N, P, K, and S. The surface 15 cm of soil from beneath juniper canopies (canopy soil) and intercanopy areas (intercanopy soil) was collected for five age classes of trees ranging from 36 to 160 y. Nutrient availability determined by bioassy in these soils was compared to an area where juniper had not invaded. Phosphorus availability of intercanopy soils was significantly reduced for the two oldest tree classes. This result suggested an alteration of P availability by the lateral root system of western juniper in the intercanopy areas that is linked to juniper maturity. In canopy soils, juniper did not influence N availability. Advancing juniper maturity was associated with increasing then decreasing P availability with the oldest tree class. The most striking effect of juniper was increased S availability in canopy soils with advancing juniper maturity. Differential responses of N and S availability in canopy soils may reflect the fact that N mineralization is chiefly a biological process whereas S mineralization is both biological and biochemical. Low inherent availabilities of N and S suggest that productivity enhancement measures should include fertilization with these elements.

Introduction

The western juniper (*Juniperus occidentalis* Hook.) vegetation type occupies about 1.2 million ha in central and south-central Oregon (Dealy *et al.* 1978). Over much of its range, western juniper is expanding into the big sagebrush (*Artemisia tridentata* Nutt.)/bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. and Smith) vegetation type (Caraher 1978, Eddleman 1987). This invasion may be accompanied by redistribution of nutrients among biotic and abiotic compartments of these systems (Tiedemann 1987). Shallow lateral roots of juniper that extend well beyond the canopy edge (Young *et al.* 1984, Everett *et al.* 1986) may enable juniper to exploit moisture and nutrients from a much greater area than that within the canopy projection area.

Concern for western juniper invasion and the impact on forage production has resulted in management aimed at reducing the influence of western juniper. Juniper removal is accomplished by burning (Martin 1978), chaining and dozing (Winegar and Elmore 1978), fuelwood harvest (personal observations of the authors), and recently, whole tree harvesting for fuel for electric power generation (personal communication, Dr. Lee Eddleman, Professor, Oregon State University). Chaining, dozing, and fuelwood harvest often are followed by burning of residues. Understanding nutrient accumulation and cycling patterns is an essential step in assessing the consequences of various management strategies on sustainable productivity of semiarid woodlands such as western juniper. If a large proportion of the nutrients on a site are incorporated into aboveground biomass compartments, whole-tree removal or burning of residues could result in large losses of nutrients and may impair future productivity (Tiedemann 1987).

Results reported here are part of a larger study to determine the influence of western juniper invasion and development on nutrient accumulation patterns in sagebrush/grass ecosystems (Cooperative State Research Service grant No. 87-CRSR-2-3116, Influence of Western Juniper Invasion on Nutrient Accumulation in Sagebrush/grass Ecosystems, A. R. Tiedemann and J. O. Klemmedson, Principal Investigators). Hypotheses relevant to the present study are that: 1) the lateral root system of western juniper exploits available nutrients in the intercanopy spaces, and the degree of change is related to the elapsed time of juniper development; and 2) nutrient accumulation by litterfall and a microenvironment more favorable for accumulation and maintenance of organic matter and nutrients (Jenny 1930, Tiedemann and Klemmedson 1986) in the area beneath juniper canopies results in changes in availability of nutrients in that location (Tiedemann and Klemmedson 1973, Barth 1980, Everett *et al.* 1986, Klopatek 1987).

Our objective was to determine changes in availability of N, P, K, and S associated with invasion and development of western juniper over time by using bioassy of soil beneath juniper canopies and in intercanopy areas.

The Study Area

We conducted this study in central Oregon because it has the greatest concentration of western juniper (Driscoll 1964). The study area is at the Three Springs Ranch about 14 km south of Prineville, Oregon, in sections 11, 14, 23, and 27 T16S, R15E.

Climate is continental with maritime influence from storms originating off the Pacific coast (Driscoll 1964). The semiarid climate is characterized by dry, hot summers and cold winters with most of the precipitation as snow during the winter months and rain during spring and fall. Mean annual temperature at the airport approximately 7 km SW of Prineville is 9.5°C; mean January and July temperatures are 0°C and 19.5°C, respectively (United States Department of Commerce, National Oceanic and Atmospheric Administration 1973). Mean annual precipitation is 25.3 cm.

Soils are derived from Mount Mazama ash and are relatively young. Mount Mazama erupted about 6600 y b.p. (Baldwin 1964) depositing ash over basalt of local origin (United States Department of Agriculture, Soil Conservation Service 1986). Soils are Xerollic Camborthids of the Deschutes Series. Texture is uniformly sandy loam; depth ranges from 30 to 50 cm. The massive nature of the Mazama ash fall has resulted in uniform soil over large areas (United States Deparment of Agriculture, Soil Conservation Service 1986). No apparent buried soil exists over the basalt bedrock. Outcrops of basalt rock (blisters) are scattered throughout the area suggesting that the terrain was gently undulating prior to the Mazama ash fall.

Vegetation of the understory is dominated by big sagebrush, rabbitbrush (*Chrysothamnus spp.*), bluebunch wheatgrass, and Idaho fescue (*Festuca idahoensis* Elmer). Cover of understory vegetation is highly variable, but averages about 25%.

Procedures

Conceptual Approach

Following the state factor approach of Jenny (1961) and Major (1951), the conceptual model for this study,

$$N_{av},\ P_{av},\ K_{av},\ S_{av} = f(o_j,\ t)_{cl,\ o,\ r,\ p}$$

states that availability of N, P, K, and S are a function of juniper invasion (o_j) and time (t) of juniper occupancy of a site, while state factors of climate (cl), biotic factor other than juniper (o), topography (r), and parent material (p) are held constant, or nearly so. Using this model, we carried out field sampling with rigid control of cl, o, r, and p such that their effect would be small relative to the effect of o_j and t.

For the small study area, climate, topography (<5% uniform eastward slope) and parent material were very uniform. Understory vegetation of shrubs and herbs was variable, and the impact of the biotic factor other than juniper (i.e., herbivores, humans, fire) appeared to be slight; in neither case did the distribution of the biotic subfactors appear to be related to juniper presence or size. Although shrubs and herbs may influence distribution of soil and litter nutrients (Garcia-Moya and McKell 1970, Tiedemann and Klemmedson 1973, Klemmedson 1983), the scale of distribution is small relative to that of western juniper and was controlled by sample location.

The study area showed no evidence of recent domestic grazing or disturbance to the area beneath trees. Evidence of firewood removal was sparse.

We selected five separate replicate sites for sampling, all within a distance of 8 km. At each replicate site, we selected three trees in each of five size (age) classes and randomly selected one tree in each size (age) class for sampling. This resulted in a total of 25 sample trees—five replications of five size (age) class western juniper. These are referred to as tree class 1 through 5.

At each of the five sites, we selected a 5 to 10 ha open area with no juniper invasion that we refer to as "No Juniper." Within each open area, three plots were established by random distance and direction from a central starting point. One plot was randomly selected from these for sampling.

Tree ages were determined from sections taken from the butt section of trees cut as part of the larger study. Samples were aged by Franco Biondi, Laboratory of Tree Ring Research, University of Arizona. Average tree age ranged from 36 y for tree class 1 to 160 y for tree class 5 (Table 1). Average height ranged from 3.3 to 9.9 m.

A sample of soil about 30 by 30 cm to 15-cm depth was collected from each of the following locations at each site: a distance of 0.5 canopy radius due north from the base of each western juniper; 4.0 canopy radii due north from the base of each tree (intercanopy); and at the selected sample plot in the open site ("No Juniper").

TABLE 1. Average age and height of 5 classes of western juniper sample trees.

Tree class	Age — yr		Height — m	
	Average	Range	Average	Range
1	36	21-58	3.3	2.9-3.8
2	52	36-68	4.8	4.1-6.0
3	62	41-85	7.0	5.7-8.2
4	81	44-135	9.5	8.5-11.7
5	160	108-231	9.9	9.2-10.4

Bioassay Trial

A bioassay trial (Jenny *et al.* 1950) was used to determine availabilities of individual nutrients N, P, K, and S. Soils were air-dried, mixed thoroughly, and sieved to remove particles larger than 4 mm. The five field sites served as replications for the greenhouse bioassay trial. Soil (400 g) was weighed into plastic pots to which the following nutrient treatments were applied:

TREATMENT	NUTRIENTS ADDED
Control	No added nutrients
No nitrogen (N_0)	P, K, S
No phosphorus (P_0)	N, K, S
No potassium (K_0)	N, P, S
No sulfur (S_0)	N, P, K,
Full nutrient treatment	N, P, K, S

Nitrogen was added at a rate of 134 mg.kg^{-1} as ammonium nitrate; phosphorus at 89 mg.kg^{-1} as calcium dihydrogen phosphate; potassium at 45 mg.kg^{-1} as potassium chloride; and sulfur at 45 mg.kg^{-1} as magnesium sulfate. These sources of P and S offer little risk of confounding with Ca and Mg, which are rarely deficient in western soils, with some exceptions such as serpentine soils and highly leached, acid soils (Bohn et al., 1979).

Barley seeds were sown into the pots, thinned to three plants per pot, and grown in a controlled environment chamber with 12-hour photoperiod with full spectrum, high output fluorescent lamps at 24°C daytime and 19°C nighttime temperatures. Relative humidity was maintained at about 70% during the growth period. After 8 weeks, plants were harvested, oven-dried at 70°C and weighed.

Study design was a split-split plot with trees (tree classes 1 through 5) and "No Juniper" as a main effect, location (canopy, intercanopy) as the subplot effects and nutrient treatments as sub-subplot effects in the SAS Institute Inc. (1987) analysis of variance. Mean separation was by the least significant difference (LSD) procedure (Carmer and Swanson 1971).

Results

Analysis of variance showed no significant differences among tree classes (including No Juniper) or for the interaction of tree classes X location (Table 2). The following were significant at $p<0.005$: location (canopy, intercanopy), bioassay nutrient treatments and the interactions of nutrient treatments X tree class (including No Juniper), location X nutrients, and tree class (including No Juniper) X location X nutrient treatment.

TABLE 2. Analysis of variance (SAS) for bioassay nutrient trial.

Source	df	Probability >F
Site (replications)	4	–
Tree class (TC)	5	.3513
Site x TC	20	–
Location (L)	1	.0049
TC x L	4	.1232
Site x TC x L	20	–
Nutrient treatment (N)	5	.0001
TC x N	20	.0023
L x N	5	.0001
TC x L x N	20	.0052

Comparison of yields between the control and full nutrient treatments averaged among tree classes, "No Juniper" and canopy/intercanopy locations revealed that availability of one or more nutrients was significantly reduced (Table 3). Average yield for the control treatment for all tree classes, "No Juniper," and soil locations was 1.21 g compared to 5.82 g for the full nutrient treatment. Examination of yields of individual treatments shows that yields of N_0 and S_0 (1.49 and 2.46 g, respectively) were significantly less than those of the full nutrient treatment and, thus, were chiefly responsible for low fertility of these soils as indicated by the control treatment (Table 3). The average yield for the P_0 treatment (5.22 g) was significantly less than that of the full treatment, but the difference was not as substantial as that for N and S. The K_0 and full treatment yields did not differ significantly.

TABLE 3. Barley yields for 6 nutrient treatments averaged across tree classes and locations.

Yields (g)					
Control	N_o	P_o	K_o	S_o	Full
1.21^E	1.49^D	5.22^B	5.63^A	2.46^C	5.82^A

Values with the same letter are not significantly different at $p < 0.05$.

Relative yields (yield of any individual nutrient treatment X_0 divided by the yield of the full nutrient treatment X 100) for N ranged from 19% in soil from "No Juniper" sites to 31% in canopy soil (Table 4). Relative yields for S ranged from 27% in "No Juniper" soil to 58% in canopy soil. By contrast, relative yield for P and K exceeded 83% for all locations.

Because the three-way interaction of tree class X location X nutrient treatment was significant (Table 2), it is appropriate to discuss the source of that interaction at the outset using Table 5. We first compare yields for soils of canopy and intercanopy locations for tree classes 1 through 5. For the control and full treatments, barley yields for canopy and intercanopy locations did not differ among tree classes. Similarity of yields for the full treatment between locations and for all tree classes indicated that the full treatment provided an adequate supply of N, P, K, and S under conditions of this bioassay trial.

TABLE 4. Relative yields [1] (percent) for N, P, K, and S for open, intercanopy, and canopy soils—average of tree classes.

	N	P	K	S
No Juniper	19	95	93	27
Intercanopy	22	83	95	31
Canopy	31	96	99	58

[1] Relative yield = $\frac{\text{Xo treatment yield (g)}}{\text{Full nutrient treatment yield (g)}}$ X 100

Table 5 shows that the N_0 yields did not differ between the two locations for any tree class. This

TABLE 5. Comparisons of barley yields between western juniper canopy (C) and intercanopy (IC) locations for 6 nutrient treatments.

	Treatment											
	Control		N_o		P_o		K_o		S_o		Full	
	Location											
	C	IC	C	IC	C	IC	C	IC	C	IC	C	IC
Tree Classes	g/pot											
1	1.141	1.130	1.231	1.136	5.101	5.167	4.383*	5.508	2.375	1.692	5.522	5.341
2	1.242	.878	1.356	1.307	5.438	4.928	6.395	5.54	2.332	1.832	6.029	5.486
3	1.186	.949	1.797	1.364	5.595	5.364	5.899	6.306	2.825	1.793	5.723	6.017
4	1.387	.914	1.473	1.349	6.524*	4.494	5.839	5.722	4.358*	1.684	5.404	6.419
5	1.353	.987	2.023	2.339	4.246	4.523	5.330	5.572	4.417*	2.037	5.488	6.134

LSD = 1.046 for comparison of differences between locations for each tree and nutrient treatment.

* Denotes a significant yield difference ($p \leq 0.05$) between canopy and intercanopy soil for an individual tree class and treatment.

LSD = 1.123 for comparisons among tree classes, nutrients, and locations.

suggests that invasion and development of western juniper has had no influence on availability of N. The P_0 barley yields show that P was significantly more available in canopy than intercanopy soil, but only for tree class 4. The response of K was in sharp contrast to that of P. The K_0 yield for canopy soil was significantly less than that for intercanopy soil for tree class 1; for other tree classes, there were no location differences in K supply. The effect of location on S supply was marked; canopy soil was much higher in available S than intercanopy soil for tree classes 4 and 5 (Table 5).

We now compare yields for canopy and intercanopy soils for tree classes 1 through 5 and "No Juniper" areas. This comparison provides an indication of the long-term influence of western juniper invasion and development on availability of individual nutrients in each location. For the intercanopy location, juniper invasion has affected only the supply of P; in the intercanopy soil it was significantly less for tree classes 2, 4, and 5 than for soil from "No Juniper" areas.

Juniper had a greater influence on canopy than on intercanopy soils; differences among tree classes were evident for the P_0, K_0, and S_0 treatments (Figure 1). Yields for the P_0 treatment were the same among "No Juniper" through tree class 3, but P supply was significantly higher for soil of tree class 4 than that of tree class 1; P supply for soil of tree class 5 was lower than that of all other tree classes. Yields of the K_0 treatment declined between "No Juniper" and tree class 1 (Table 2) indicating reduced availability with tree establishment. However, K_0 yields then increased and remained constant through tree class 5, indicating that K availability increased after the initial decline. Yields

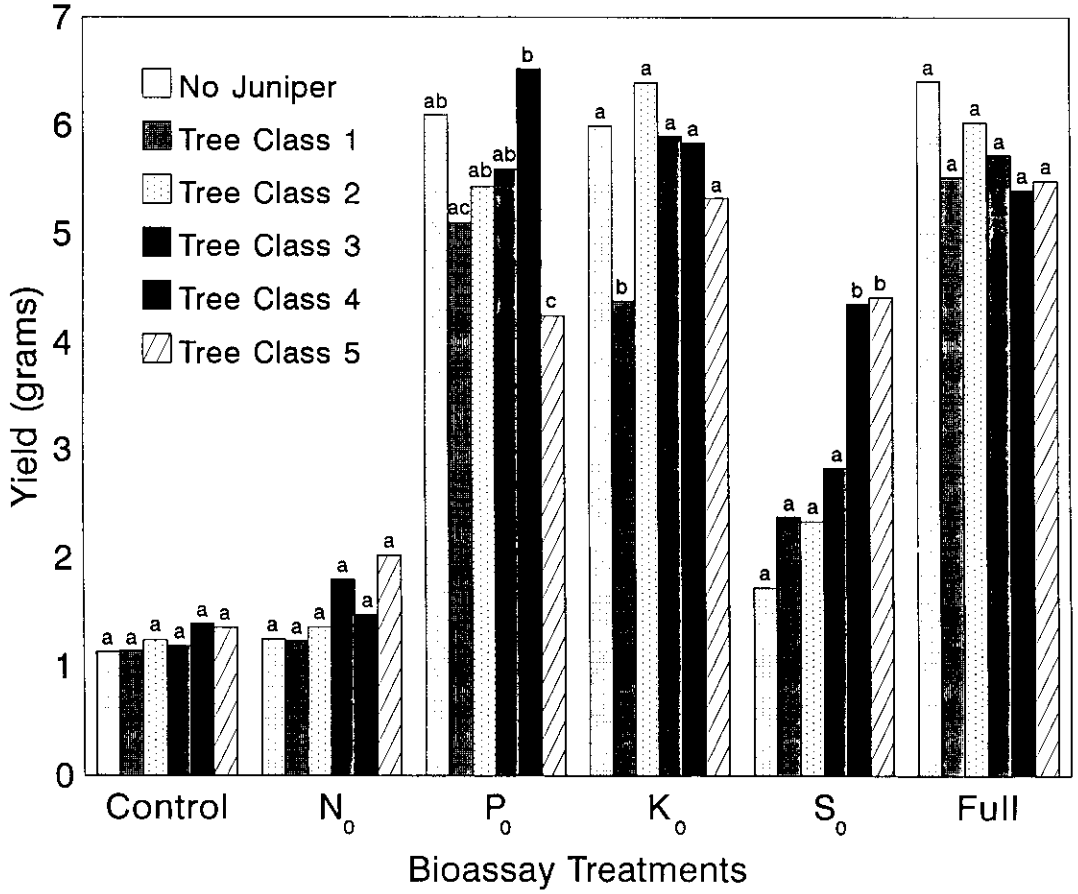

Figure 1. Comparisons of canopy soil barley yields among the 5 tree classes and "No Juniper" for 6 nutrient treatments. Bars with the same letter are not significantly different (p=0.05) within an individual treatment. LSD = 1.123

for S were most definitive and showed distinct trends with advancing juniper maturity. There were no differences in S_0 yield between "No Juniper" and the first three tree classes. However, S availability increased markedly for the two older tree classes (Figure 1).

Discussion

The similarity of available N in "No Juniper," intercanopy, and canopy soils was an unexpected result. Most studies of canopy/intercanopy soil nutrient availability have shown differences for available N between canopy and intercanopy locations. In our studies with mesquite (*Prosopis juliflora* Swartz. DC) using the same bioassay technique, available N in soil from beneath tree canopies was 15 times greater than in soil from intercanopy areas (Tiedemann and Klemmedson 1973). Barth (1980) found a 2.4-fold greater nitrate-N concentration in soil under old (540 y) pinyon pine compared to adjacent shrub-dominated areas. Moreover, nitrate-N concentration in soil from beneath pinyon canopies was positively related to tree age from 15 to 540 y. Klopatek (1987) examined available N (NH_4-N and NO_3-N) in the 2- to 10-cm soil layer for two sites with mature pinyon-juniper trees 300 to 400 y of age. At one site, the available N was comparable between canopy and intercanopy areas. At another site, available N was 2X greater in soil beneath canopies than in the interspaces. We observed no similar response with increasing tree age.

Differences in N mineralization potential may explain low availability of N in canopy soils of western juniper. Klopatek and Klopatek (1987) provide evidence that nitrifying bacteria are substantially lower in soils beneath canopies of pinyon-juniper trees than intercanopy soil. Possible reasons for low availability of N in canopy soils include leaching of nitrate-N, uptake of available N ions by the fine root system of juniper, high organic C/N ratios, and inhibition of microbial processes by volatile oils from juniper foliage.

The observed similarity of available P in canopy and intercanopy soils (Table 5) for the oldest and largest trees (class 5) presented a contrast to pinyon-juniper woodland studies. These studies (Barth 1980, Everett *et al.* 1986, and Klopatek 1987) indicate improved P availability in soil beneath tree canopies (300 to 540 y old) compared to adjacent interspaces. However, our results do agree with those of Doescher *et al.* (1987). They found no difference in available P (sodium bicarbonate extractable) in soil beneath canopies of juvenile (<40 y) or mature (>80 y) western juniper compared to interspaces. Average age of class 4 trees, which exhibited greater P availability in canopy than intercanopy soils, was 81 y. Our results suggest there may be a period of time during the development of western juniper between 44 and 135 y that P availability is enhanced in the canopy soil compared to intercanopy soil.

Observed differences in available P between canopy and intercanopy soils (Barth 1980, Klopatek 1987, and Everett *et al.* 1986) for pinyon pine and Utah juniper (*J. utahensis* (Engelm.) Lemmon.)) has led to speculation that the lateral root system affects nutrient status of open area soils. There is evidence, including our observations, that juniper roots extend well beyond the canopy edge (Young *et al.* 1984). We found western juniper lateral roots at a distance of 4 canopy radii at a depth of about 30 cm in several sample holes.

Reduced availability of P in intercanopy soils compared to "No Juniper" soils with increasing juniper maturity (tree classes 4 and 5) suggests that lateral roots of western juniper have influenced nutrient capital of the areas between trees. Our results also suggest that the degree of alteration is related to age of western juniper. None of the studies cited above have examined P availability as a function of tree age for intercanopy soils.

Reduced K availability in tree class 1 canopy soils compared to intercanopy soils and "No Juniper" areas (Table 5, Figure 1) may reflect high K demand in young trees for nutrients as they allocate a large part of their resources to roots and foliage (Miller *et al.* 1990).

Results of this study on S supply, especially compared to results for N, are noteworthy. Generally, differences reported in SO_4-S between canopy and intercanopy soils have been greater than those for NH_4-N and NO_3-N. Barth (1980), for example, found 16X and 7.5X more SO_4-S in the 0- to 10-cm and 10- to 40-cm layers of canopy soil, respectively, than intercanopy soils. By contrast, Barth's canopy soils contained only 2.4X and 4.1X more NO_3-N at those depths than intercanopy soils. Others (Klopatek 1987, Thran and Everett 1987) have reported NO_3-N up to 10 times higher in canopy than intercanopy soils. In Klopatek's study, NH_4-N comprised most of the available N, but the canopy-intercanopy difference was only about twofold.

Mineralization of soil N and S are in some respects similar and in some respects different (Starkey 1966, McGill and Cole 1981). Nitrogen is mineralized by biological mineralization, whereas S is mineralized by biological and biochemical mineralization processes (McGill and Cole 1981). That S has a dual mineralization system in contrast to the single system for N may help explain the inconsistent relation between N and S mineralization noted by Biederbeck (1978) and the difference in N and S supply noted here. Presumably, biochemical reactions in the S mineralization system would be relatively insensitive to volatile oils present in the canopy environment of this study.

Conclusions

Low P_0 barley yields for intercanopy soils with advancing tree age suggests that the lateral root system of western juniper may have transported significant amounts of P from open areas to the tree and canopy area. This result would seem to support our hypothesis (1) that the lateral root system exploits available nutrients in the intercanopy spaces. Without mass balance data, however, it is uncertain whether reduced P availability in the intercanopy area is a consequence of P export by juniper roots or altered conditions as a consequence of the presence of the lateral roots. Our data from the larger part of this study on mass balance of nutrients should shed light on the question of nutrient transport.

Availability of N and K in soil beneath canopies of western juniper was not greatly enhanced by invasion and development of the tree. Thus, for these nutrients, we reject our hypothesis (2) that nutrient availability beneath the canopy is improved by litterfall accumulation and a microenvironment improved for accumulation and maintenance of organic matter and nutrients. Phosphorus availability in canopy soil was enhanced for class 4 trees (81 y average age) but then sharply reduced for the oldest tree class (161 y). Sulfur availability was significantly improved in canopy soils with the two oldest tree classes compared to the other tree classes and open soils. Volatile oils in western juniper litter may influence N and S mineralization in several ways, such as to affect net mineralization. However, S availability may be less influenced than N availability because biochemical process reactions are a dominant avenue for production of SO_4-S.

Relative yields indicate that all locations were N deficient to the point that fertilization may be a viable option for enhancing production of vegetation (Jenny *et al.* 1950). Furthermore, relative yields for S indicate that this nutrient is deficient to the extent that any fertilization should include this element. Moisture is certainly limiting in these habitats, but any management strategy aimed at reducing moisture competition for vegetation production should be coupled with nutrient amelioration.

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Literature Cited

Baldwin, E. M. 1964. Geology of Oregon. University of Oregon Cooperative Book Store, Eugene. 165 p.

Barth, R. C. 1980. Influence of pinyon pine on soil chemical and physical properties. Soil Sci. Soc. Am. J. 44:112-114.

Biederbeck, V. O. 1978. Soil organic sulfur and fertility. *In*: M. Schnitzer and S. U. Khan (eds.). Soil organic matter. Develop. Soil Sci. 8:273-310. Elsevier, Amsterdam.

Bohn, H. L., B. L. McNeal, and G. A. O'Connor. 1979. Soil Chemistry. John Wiley and Sons, New York.

Caraher, D. L. 1978. The spread of western juniper in central Oregon. *In*: R. E. Martin, J. E. Dealy, and D. L. Caraher (eds.). Proceedings of the Western Juniper Ecology and Management Workshop; Bend, Oregon: January 1977. USDA For. Serv. Gen. Tech Rep. PNW-74. Pacific Northwest For. and Range Exp. Sta., Portland, Oregon. Pp. 3-7.

Carmer, S. G., and M. R. Swanson. 1971. Detection of differences between means: a Monte Carlo study of five pairwise multiple comparison procedures. Agron. J. 36:40-945.

Dealy, E. J., J. M. Geist, and R. S. Driscoll. 1978. Communities of western juniper in the intermountain Northwest. *In*: R. E. Martin, J. E. Dealy, and D. L. Caraher (eds.). Proceedings of the Western Juniper Ecology and Management Workshop; Bend, Oregon; January 1977. USDA For. Serv. Gen. Tech Rep. PNW-74. Pacific Northwest For. and Range Exp. Sta., Portland, Oregon. Pp. 11-29.

Doescher, P. S., L. E. Eddleman, and M. R. Vaitkus. 1987. Evaluation of soil nutrients, pH, and organic matter in rangelands dominated by western juniper. Northwest Sci. 61:97-102.

Driscoll, R. S. 1964. Vegetation-soil units in the central Oregon juniper zone. USDA For. Serv. Res. Pap. PNW-19. Pacific Northwest For. and Range Exp. Sta., Portland, Oregon. 60 p.

Eddleman, L. E. 1987. Western juniper in central Oregon. *In*: R. L. Everett, (compiler). Proceedings, Pinyon-Juniper Conference; 13-16 Jan. 1986; Reno, Nevada. USDA For. Ser. Gen. Tech. Rep. INT-215. Intermountain Res. Sta., Ogden, Utah. Pp. 255-259.

Everett, R. L., S. H. Sharrow, and D. F. Thran. 1986. Soil nutrient distribution under and adjacent singleleaf pinyon crowns. Soil Sci. Soc. Am. J. 50:788-792.

Garcia-Moya, E., and C. M. McKell. 1970. Contribution of shrubs to the nitrogen economy of a desert shrub community. Ecology 51:81-88.

Jenny, H. 1930. A study of the influence of climate upon nitrogen and organic matter content of the soil. Missouri Agric. Exp. Sta. Res. Bull. 152.

________. 1961. Derivation of state factor equations of soils and ecosystems. Soil Sci. Soc. Am. Proc. 25:385-388.

Jenny, H., J. Vlamis, and W. E. Martin. 1950. Greenhouse assay of fertility of California soils. Hilgardia 20:1-8.

Klemmedson, J.O. 1983. State of dry matter and nutrients in soil-plant systems of Arizona fescue and mountain muhly. J. Range Manage. 36:558-564.

Klopatek, C. C., and J. M Klopatek. 1987. Mycorrhizae, microbes, and nutrient cycling processes in pinyon-juniper ecoystems. *In*: R. L. Everett (compiler). Proceedings, Pinyon-Juniper Conference; 13-16 Jan. 1986; Reno, Nevada. USDA For. Ser. Gen. Tech. Rep. INT-215. Intermountain Res. Sta., Ogden, Utah. Pp. 360-364.

Klopatek, J. M. 1987. Nitrogen mineralization and nitrification in mineral soils of pinyon-juniper ecosystems. Soil Sci. Soc. Am. J. 51:453-457.

Major, J. 1951. A functional, factorial approach to plant ecology. Ecology 32:392-412.

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Martin, R. E. 1978. Fire manipulation and effects in western juniper (*Juniperus occidentalis* Hook.). *In*: R. E. Martin, J. E. Dealy, and D. L. Caraher (eds.). Proceedings of the Western Juniper Ecology and Management Workshop; Bend, Oregon; January 1977. USDA For. Serv. Gen. Tech. Rep. PNW-74. Pacific Northwest For. and Range Exp. Sta., Portland, Oregon. Pp. 121-136.

McGill, W. B., and C. V. Cole. 1981. Comparative aspects of cycling of organic C, N, S, and P through soil organic matter. Geoderma 26:267-286.

Miller, P. M., L. E. Eddleman, and S. Kramer. 1990. Allocation patterns of carbon and minerals in juvenile and small-adult *Juniperus occidentalis*. Forest Sci. 36:734-747.

SAS Institute Inc. 1987. SAS/STAT Guide for personal computers, version 6 ed., Gary, NC.

Starkey, R. L. 1966. Oxidation and reduction of sulfur compounds in soils. Soil Sci. 101:297-306.

Thran, D. F., and R. L. Everett. 1987. Soil nutrient changes following tree harvest. *In*: R. L. Everett (compiler). Proceedings, Pinyon-Juniper Conference; 13-16 Jan. 1986; Reno, Nevada. USDA For. Ser. Gen. Tech. Rep. INT-215. Intermountain Res. Sta., Ogden, Utah. Pp. 387-390.

Tiedemann, A. R. 1987. Nutrient accumulations in pinyon-juniper ecosystems—managing for future site productivity. *In*: R. L. Everett (compiler). Proceedings, Pinyon-Juniper Conference; 13-16 Jan. 1986; Reno, Nevada. USDA For. Ser. Gen. Tech. Rep. INT-215. Intermountain Res. Sta., Ogden, Utah. Pp. 352-359.

Tiedemann, A. R., and J. O. Klemmedson. 1973. Nutrient availability in desert grassland soils under mesquite (*Prosopis juliflora*) trees and adjacent open areas. Soil Sci. Soc. Am. Proc. 37:107-111.

________. 1986. Long-term effects of mesquite removal on soil characteristics: I. Nutrients and bulk density. Soil Sci. Soc. Am. J. 50:472-475.

United States Department of Commerce. National Oceanic and Atmospheric Administration. 1973. Climatological Data, Oregon, Annual Summary 79 (13):1-9.

United States Department of Agriculture, Soil Conservation Service. 1986. General Soil Map, State of Oregon. General Soils 4-R-39694. USDA Soil Conservation Service, Forest Service, and United States Department of the Interior, Bureau of Land Management. One page map.

Winegar, H., and W. Elmore. 1978. Mechanical manipulation of western juniper—some methods and results. *In*: R. E. Martin. J. E. Dealy, and D. L. Caraher (eds.). Proceedings of the Western Juniper Ecology and Management Workshop; Bend, Oregon; January 1977. USDA For. Serv. Gen. Tech. Rep. PNW-74. Pacific Northwest For. and Range Exp. Sta., Portland, Oregon. Pp. 107-119.

Young, J. A., R. A. Evans, and D. A. Easi. 1984. Stem flow on western Juniper (*Juniperus occidentalis*) trees. Weed Sci. 32:320-327.