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Influence of Western Juniper Development on Distribution of Soil and Organic Layer Nutrients

Abstract

The purpose of this study was to determine effects of invading western juniper (*Juniperus occidentalis* Hook.) into big sagebrush (*Artemisia tridentata* Nutt.)/bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. and Smith [now *Pseudoroegneria spicata*]) ecosystems of central Oregon on spatial distribution of nutrients in organic and mineral soil layers. The organic layer and mineral soil from four layers (0-5, 5-15, 15-30, and 30+ cm), were collected beneath juniper trees of five size classes, and one area devoid of juniper on five replicated sites. Samples were taken at five distances (0 to 4 canopy radii) from tree boles into intercanopy areas. The organic layer and mineral soil were analyzed for organic carbon (C_{org}), total nitrogen (N), total phosphorus (P) and total sulfur (S); mineral soil was analyzed for exchangeable calcium (Ca_{ex}), magnesium (Mg_{ex}) and potassium (K_{ex}). Mass of the organic layer and amounts of organic layer nutrients increased with juniper size, and were higher under canopies than in intercanopy and no juniper areas. Concentrations of organic layer N, P, and S declined with distance from tree boles. Tree size, distance and soil layer interacted to affect concentrations of soil C_{org} , K_{ex} , Ca_{ex} and Mg_{ex} . Concentrations of soil N and S increased with tree size. Amounts of soil nutrients, except C_{org} , were not significantly influenced by tree size, but amounts of all soil nutrients, except S and Ca_{ex} , were greater under juniper trees than intercanopy areas. Only Ca_{ex} and Mg_{ex} appeared to have been lost from intercanopy soils compared to no juniper soils.

Introduction

In eastern Oregon and over much of its range, western juniper (*Juniperus occidentalis* Hook.) has encroached into big sagebrush (*Artemisia tridentata* Nutt.)/bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. and Smith [now *Pseudoroegneria spicata*]) communities (Caraher 1978, Eddleman 1987). Recently juniper and pinyon species have increased throughout pinyon-juniper woodlands of the western United States (Miller and Wigand 1994). Tree and shrub invasion in arid and semiarid regions results in formation of "fertile islands" where soil and organic layer properties vary spatially away from plant centers to adjacent interspaces. Development of spatial patterns has been largely attributed to rooting and litterfall patterns of trees or shrubs (Fireman and Hayward 1952, Charley and Cowling 1968, Garcia-Moya and McKell 1970, Tiedemann and Klemmedson 1973, Charley and West 1975, Barth 1980). However, the enriched island effect is complex, and owes its occurrence to many biotic and

abiotic factors and their interactions, induced by presence of trees or shrubs (Leopold 1933, Garcia-Moya and McKell 1970, Tiedemann et al. 1971, Tiedemann and Klemmedson 1973, Balandreau et al. 1976, Tiedemann and Klemmedson 1977, Barth 1980, Tiedemann and Furniss 1985, Belksy et al. 1989, Belsky 1994).

Where roots extend beyond the canopy edge, as in the case of western juniper (Young et al. 1984, Everett et al. 1986), trees or shrubs may exploit moisture and nutrients from interspaces (Klopatek 1987, Bernhard-Reversat 1982). Nonetheless, trees in semi-arid (Bernhard-Reversat 1982), tropical, and subtropical (Belsky 1994) savannas of Africa, and shrubs in the American deserts (Garcia-Moya and McKell 1970, Romney et al. 1978) are thought to be major factors in maintaining soil fertility and productivity of the systems they inhabit.

The rationale for this study was to understand the role of western juniper in nutrient-productivity relations of the ecosystem it dominates just east of the Cascade Range. We examined the influence of invasion of western juniper into the sagebrush/grass system on nutrient status of soil and organic layers of the larger system, i.e. the

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complex of juniper trees and intercanopy areas occupied by sagebrush/grass. In particular, we sought to determine (1) if juniper encroachment changes the spatial distribution of nutrients in juniper and intercanopy areas relative to areas without juniper, and (2) the extent of changes with size (age) of individual juniper trees.

Study Area

The study area was the Three Springs Ranch located about 11 km southwest of Prineville (1110 m elevation) in central Oregon. This area is typical of the community dominated by western juniper on the western edge of the Central Oregon Plateau at the lower boundary of the ponderosa pine zone (Driscoll 1964). Climate is continental with maritime influence from storms originating off the Pacific coast. The region is semiarid with dry, hot summers and cold winters. Precipitation, averaging 26.6 cm annually, occurs as snow during winter and rain during spring and fall. Mean annual temperature at Prineville is 8.5°C; mean January and July temperatures are 0°C and 18.2°C, respectively (National Oceanic and Atmospheric Administration 1995).

Soils are young and derived from volcanic ash from the eruption of Mt. Mazama 6845 ± 45 years ago (Bacon 1983). Basalt of local origin underlies the ash (United States Department of Agriculture, Soil Conservation Service 1986). Five soils series occur in the study area: Deschutes, Stukel, Stukmond, Redmond, and Lickskillet (Personal communication, Amanda Moore, Soil Scientist, United States Department of Agriculture, Natural Resources Conservation Service, Redmond, Oregon). Observations of depth, texture, and horizon development during sampling indicated that our sites were primarily in the Stukel series. These soils are well-drained, shallow (25 to 50 cm) loamy, mixed, superactive, mesic Lithic Haploxerolls (United States Department of Agriculture, Natural Resources Conservation Service 1999). No apparent buried soil exists over the basalt bedrock. Outcrops of basalt occur as blisters scattered throughout the gently undulating terrain.

Vegetation of the juniper understory, intercanopy, and areas without juniper is dominated by big sagebrush, rabbitbrush (*Chrysothamnus spp.*), bluebunch wheatgrass, and Idaho fescue (*Festuca idahoensis* Elmer). Cover of juniper

understory, intercanopy, and areas without juniper averages about 25% but is highly variable.

Methods

Conceptual Approach and Site Selection

The general equation of state factors (Jenny 1961):

$$s = f(\text{cl, o, r, p, t}) \quad (1)$$

provided a formalistic approach for the field study. The equation states that magnitude of any soil property (s) is a function of climate (cl), the biotic factor (o), relief (r), parent material (p), and time (t). Revision of the equation as follows:

$$s_n = f(\text{o}_j, \text{cl, o, r, p, t, } \dots) \quad (2)$$

$$s_n = f(\text{t}_j, \text{cl, o, r, p, t, } \dots) \quad (3)$$

provides a conceptual model for site selection and field sampling to determine the influence of western juniper trees (o_j) and their relative size (age) or time of occupancy of a specific site (t_j) on any nutrient property (s_n) of the soil or organic layer.

The remaining state factors in the equations were controlled by selecting study sites so that variation in these factors would have little influence on the dependent variable s_n , compared to that of the variable state factors, o_j and t_j . Climate, topography (2-5% uniform eastward slope), parent material and age of developed soils were uniform among and within sites. Impact of the biotic factor (o), other than juniper trees (i.e., understory vegetation, herbivores, human activity, including fire) appeared to be slight; in no case was distribution of these biotic subfactors related to juniper presence or size. Vegetative cover of shrubs and herbs was sparse, but variable, more so in intercanopy areas and areas without juniper. Although shrubs and herbs may influence distribution of soil and organic layer nutrients (Garcia-Moya and McKell 1970, Tiedemann and Klemmedson 1973, Klemmedson 1983), the scale of this influence is small compared to that of western juniper and was minimized by increasing plot size in the intercanopy area. This portion of Three Springs Ranch showed no evidence of livestock grazing. Length of time the area had been excluded from grazing was not possible to determine. However, there was a well-developed organic layer beneath mature trees and no evidence of livestock trampling or feces. This suggested that grazing had been excluded for a long period of time. Signs of human activity were sparse.

TABLE 1. Ages and physical characteristics of five size classes of western juniper trees sampled in this study.

Size Class	Age (yr)		Height (m)		Basal Diameter (cm)		Canopy Diameter (m)	
	Ave.	Range	Ave.	Range	Ave.	Range	Ave.	Range
1	36	21-58	3.3	2.9-3.8	13	11-17	1.7	1.6-2.2
2	55	37-68	4.8	4.1-6.0	22	17-26	2.5	2.1-3.3
3	62	41-85	7.0	5.7-8.2	37	29-43	4.5	3.2-5.6
4	101	44-154	9.5	8.5-11.7	49	44-53	6.3	5.3-8.7
5	161	108-231	9.9	9.2-10.4	63	58-68	6.7	5.6-7.8

From each of five noncontiguous sites, we located a pool of trees for each of five size classes (Table 1; see Figure 1 in Tiedemann and Klemmedson, 2000), then randomly selected one tree from each class for a total of 25 sample trees. In addition, we randomly selected "no juniper" sampling plots from 5 to 10 ha areas without juniper. Average age for classes 1 through 5 were 36, 55, 62, 101 and 161 years. Average height ranged from 3.3 to 9.9 m and canopy diameters from 1.7 to 6.7 m. Cross-sections from the base of trees were aged by Franco Biondi, Laboratory of Tree Ring Research, University of Arizona.

Sampling

At each sample tree, soil and the organic layer were collected at distances equal to 0, 0.5, 1, 2 and 4 radii of the tree canopy along a transect extending due north of the tree bole. At 0, 0.5, and 1 canopy radii positions the entire organic layer was collected within a 0.093 m² metal frame. At 2 and 4 canopy radii, a 0.5 m² frame was used. Below these, 5 cm diameter soil cores were collected from the 0-5, 5-15, and 15-30 cm soil layers. Two adjacent cores also were taken from the 0 to 5 cm layer for an adequate sample. Because of shallowness and variability in soil depth to the basalt (35 to 65 cm depth), grab samples were taken below 30 cm.

Laboratory and Statistical Analyses

Soil and organic layer samples were air-dried. Soil was sieved to remove coarse fragments >2-mm diameter and ground to pass a 0.15-mm sieve. Organic layer samples were ground to pass a 0.425-mm sieve. Samples were analyzed for organic carbon (C_{org}) by dry combustion (Nelson and Sommers, 1982) in a Leco high-frequency induc-

tion furnace (Leco Corp., St. Joseph, MI). Total nitrogen (N) was determined by semi-micro-Kjeldahl (Bremner and Mulvaney, 1982) and total sulfur (S) by dry combustion in the Leco high-frequency induction furnace (Tiedemann and Anderson, 1971). Total phosphorus (P) was determined with ascorbic acid color development (Olsen and Sommers, 1982) following hydrofluoric acid digestion (Bowman, 1988). Exchangeable calcium (Ca_{ex}), magnesium (Mg_{ex}), and potassium (K_{ex}) of soils were determined by inductively coupled plasma emission spectroscopy (Barnes, 1977) following extraction with ammonium acetate (Thomas, 1982).

Because soil bulk density increased markedly with distance from tree boles and with soil depth (0.79 to 1.13 g/cm³), data for both concentration and amounts of nutrients are meaningful here. Statistical analysis for soil nutrient concentration followed a split-split-plot design with size class as the main plot factor, distance from the base of the tree as the sub-plot factor, and soil layer as the sub-sub-plot factor. Amounts of soil nutrients were summed for layers of the upper 30 cm and analyzed as a split-plot with size class as the main plot factor and distance as the sub-plot factor. Analyses of mass, and concentrations and amounts of nutrients in the organic layers were similar to those for soils except there was no sub-sub-plot factor for soil layers. Two statistical analyses [SAS Institute Inc. (1987) analysis of variance] were performed for soil and organic layer nutrient concentrations and amounts for each response variable, and for mass of the organic layer. The first analysis included data for the "no juniper" sites. For this analysis, the least squares (LS) means for size and distance could not be estimated because of missing data caused by the unbalanced

design (i.e., no tree size or distance data for "no juniper" sites). Where the size X distance interaction was significant, the "no juniper" LS mean was tested along with distance means for size classes 1 through 5. The second analysis did not include the "no juniper" sites and was used where the size X distance interaction was not significant. Here the "no juniper" mean could not be compared with the distance means for classes 1 through 5. Separation of means by least significant difference (LSD)(Carmer and Swanson 1971) was performed on differences significant at $P \leq 0.05$ in the analysis of variance.

Results

Organic Layer

Size of trees and location interacted significantly ($P \leq 0.0001$) to influence mass of the organic layer. Mass of the organic layer was greatest at the base of the largest trees (class 5) and declined markedly with tree size and distance to the canopy edge. Size and distance had no effect on organic layer mass beyond tree canopies (Table 2).

The tree size X distance interaction for nutrient concentration of the organic layer was significant only for C_{org} . Wide variation in organic layer C for all tree sizes and at all distances except distance 2 explains this significant interaction. The main effect of tree size had no effect on concentrations of N, P and S in the organic layer, but the main effect of distance from tree boles significantly ($P \leq 0.0001$) influenced each of these organic layer nutrients. The effect of distance on concentrations of N and S was similar (Table 3);

TABLE 2. Mass of organic layer (kg/m^2) as a function of distance from tree boles for six tree size classes, including no juniper (0).

Tree size class	Distance from tree boles (canopy radii)				
	0	0.5	1	2	4
0	0.12 ^{a1}				
1	3.75 ^{cd2}	1.27 ^{ab}	0.21 ^a	0.46 ^a	0.64 ^a
2	4.79 ^{de3}	2.74 ^{bc}	0.49 ^a	0.25 ^a	0.36 ^a
3	5.36 ^{ef}	3.39 ^{cd}	0.56 ^a	0.15 ^a	0.30 ^a
4	8.96 ^f	4.32 ^{cd}	0.69 ^a	0.09 ^a	0.18 ^a
5	9.26 ^f	6.13 ^{cd}	0.88 ^a	0.07 ^a	0.18 ^a

¹Values with the same letters are not significantly different at $P \leq 0.05$.

TABLE 3. Effect of distance from tree boles on concentrations (g/kg) of N, P and S in the organic layer.

Distance from tree bole (canopy radii)	N	P	S
0	11.0 ^{a1}	0.94 ^a	1.13 ^a
0.5	10.8 ^a	0.83 ^b	1.05 ^a
1	7.9 ^b	0.73 ^{bc}	0.83 ^b
2	7.9 ^b	0.66 ^c	0.74 ^b
4	7.8 ^b	0.64 ^c	0.82 ^b
no juniper ²	9.0	0.74	0.89

¹ Within column values with common letters are not significantly different at $P \leq 0.05$.

² Because of an unbalanced design, no separation of means could be made for no juniper sites.

concentrations of these nutrients were greatest at 0 and 0.5 distances and significantly lower but similar at the canopy edge and intercanopy distances. Concentration of P in the organic layer declined more rapidly to the canopy edge, and was lower at intercanopy positions than N or S (Table 3). Concentrations of N, P, and S in the organic layer of "no juniper" areas were slightly higher than that of intercanopy areas (Table 3), but differences were not testable for significance because of the unbalanced statistical design.

Size of junipers and distance from tree boles influenced amounts of C_{org} , N, P, and S in the organic layer in similar fashion, but the size X distance interaction also was highly significant ($P \leq 0.0001$). Amounts of these nutrients beneath tree canopies increased with juniper size, especially at distance 0 (Table 4). However, at the canopy edge and beyond, size and distance had no effect on nutrient amounts. Amounts of these organic layer nutrients averaged 14 to 17 times greater near boles than at the canopy edge (Table 4).

Soil

Nutrient Concentrations

Juniper trees influenced nutrient concentration of soils more by spatial effects than by size. The three-way tree size X distance X soil layer interaction was significant ($P \leq 0.01$) for concentrations of C_{org} , Ca_{cx} , Mg_{ex} and K_{cx} . The interactions for C_{org} and Mg_{ex} are easily explained: concentration of C_{org} increased with tree size (Figure 1) beneath canopies, but decreased with soil depth and distance away from tree boles (Figures 1 and

TABLE 4. Amounts (g/m²) of organic C, N, P, and S in the organic layer of juniper as a function of distance from tree boles for six size classes of juniper, including no juniper (0).

Size class	Distance from tree boles (canopy radii)				
	0	0.5	1	2	4
Organic carbon					
0	50 ^{d1}				
1	1032 ^{cd}	399 ^{abc}	89 ^a	106 ^a	313 ^{abc}
2	1712 ^{def}	907 ^{bc}	169 ^a	93 ^a	113 ^a
3	1995 ^{de}	1141 ^{cd}	137 ^a	49 ^a	123 ^a
4	3447 ^h	1801 ^{ef}	191 ^{ab}	28 ^a	71 ^a
5	3195 ^g	2430 ^f	201 ^{ab}	30 ^a	43 ^a
Nitrogen					
0	1.1 ^a				
1	31.3 ^{bc}	10.6 ^{ab}	1.8 ^a	1.8 ^a	9.6 ^{ab}
2	56.4 ^{de}	30.2 ^{bc}	3.7 ^a	1.7 ^a	2.8 ^a
3	63.4 ^{ef}	36.2 ^{cd}	4.0 ^a	1.3 ^a	2.2 ^a
4	107.5 ^g	44.0 ^{de}	5.6 ^a	0.7 ^a	1.6 ^a
5	100.7 ^f	80.8 ^{fg}	7.1 ^a	0.4 ^a	1.6 ^a
Phosphorus					
0	0.09 ^a				
1	2.98 ^{bcd}	0.15 ^a	0.26 ^a	0.90 ^{ab}	0.91 ^{ab}
2	3.60 ^{cd}	1.99 ^{abc}	0.28 ^a	0.17 ^a	0.27 ^a
3	4.76 ^{de}	2.71 ^{bcd}	0.51 ^a	0.12 ^a	0.21 ^a
4	9.73 ^f	3.03 ^{bcd}	0.54 ^a	0.06 ^a	0.15 ^a
5	10.59 ^f	6.36 ^e	0.72 ^{ab}	0.04 ^a	0.12 ^a
Sulfur					
0	0.11 ^a				
1	3.70 ^{cd}	1.26 ^{abc}	0.17 ^a	0.25 ^a	0.82 ^{ab}
2	5.41 ^{ef}	2.78 ^{bcd}	0.42 ^{ab}	0.19 ^a	0.30 ^a
3	6.60 ^{fg}	3.62 ^{cd}	0.46 ^{ab}	0.10 ^a	0.18 ^a
4	10.06 ^{hi}	3.84 ^{de}	0.62 ^{ab}	0.06 ^a	0.17 ^a
5	11.68 ⁱ	8.26 ^{gh}	0.65 ^{ab}	0.04 ^a	0.14 ^a

¹ Values within each nutrient group with the same letters are not significantly different from each other at $P \leq 0.05$.

2). The three-way interaction for Mg_{ex} is explained by the increasing difference in Mg_{ex} concentration among size classes with soil depth (Figure 1) and the decline in Mg_{ex} concentration at intercanopy locations for older trees (Table 5). Both K_{ex} and Ca_{ex} responded similarly to depth and distance. Differences in concentrations of these nutrients in upper soil layers beneath canopies disappeared in lower soil layers at intercanopy

TABLE 5. Concentrations (g/kg) of exchangeable Ca and Mg in the 0–30 cm soil layer as a function of distance from tree boles for six size classes of juniper, including no juniper (0).

Size class	Distance from tree boles (canopy radii)				
	0	0.5	1	2	4
Ca_{ex}					
0	1.66				
1	1.50 ^{cd}	1.72 ^b	1.70 ^b	1.83 ^b	1.41 ^{bcd}
2	1.60 ^d	1.44 ^{b-c}	1.39 ^{bcd}	1.41 ^{bcd}	1.52 ^{bcd}
3	1.61 ^{cd}	1.49 ^{b-c}	1.45 ^{b-c}	1.44 ^{b-c}	1.33 ^{abc}
4	1.96 ^e	1.68 ^b	1.45 ^{b-c}	1.38 ^{bcd}	1.28 ^a
5	1.98 ^e	1.64 ^b	1.30 ^{ab}	1.21 ^a	1.29 ^{ab}
Mg_{ex}					
0	0.38				
1	0.31 ^{cde}	0.31 ^{cde}	0.29 ^{abc}	0.30 ^{bc}	0.30 ^{bc}
2	0.37 ^{ab}	0.35 ^{efg}	0.34 ^{d-g}	0.34 ^{d-g}	0.32 ^{cde}
3	0.33 ^{def}	0.34 ^{d-g}	0.35 ^{efg}	0.35 ^{efg}	0.32 ^{cde}
4	0.40 ^f	0.36 ^{fg}	0.32 ^{cde}	0.32 ^{c-f}	0.29 ^{abc}
5	0.34 ^{d-g}	0.31 ^{cde}	0.27 ^{ab}	0.26 ^a	0.26 ^a

¹ Because of an unbalanced design, no separation of means could be made for the no juniper age class (0).

² Values within each nutrient group with common letters are not significantly different at $P \leq 0.05$.

locations (Figure 2), while responses to depth among size classes displayed an erratic pattern for both nutrients (Figure 1). Concentrations of Ca_{ex} and Mg_{ex} for most size classes in intercanopy soils (distances 1, 2 and 4) and some canopy locations, tended to be lower than that of no juniper soils (Table 5). However, this effect, which would suggest nutrient redistribution by juniper roots, could not be tested because of the unbalanced design for this part of the study.

Concentrations of N, P and S responded significantly ($P \leq 0.0001$) to the distance X soil layer interaction. In the upper soil layer, concentrations of these three nutrients declined markedly with distance from tree boles into intercanopy space (Figure 2). With depth, however, differences among locations disappeared. The tree size X soil layer interaction was significant for concentrations of N and S. Concentration of N in surface soils declined with size of junipers (Figure 1), but with increasing soil depth this difference in N concentration disappeared. The S concentration response was similar to that for N for the upper three soil layers, but unexplained differences among trees sizes occurred in the lower soil layer (Figure 1).

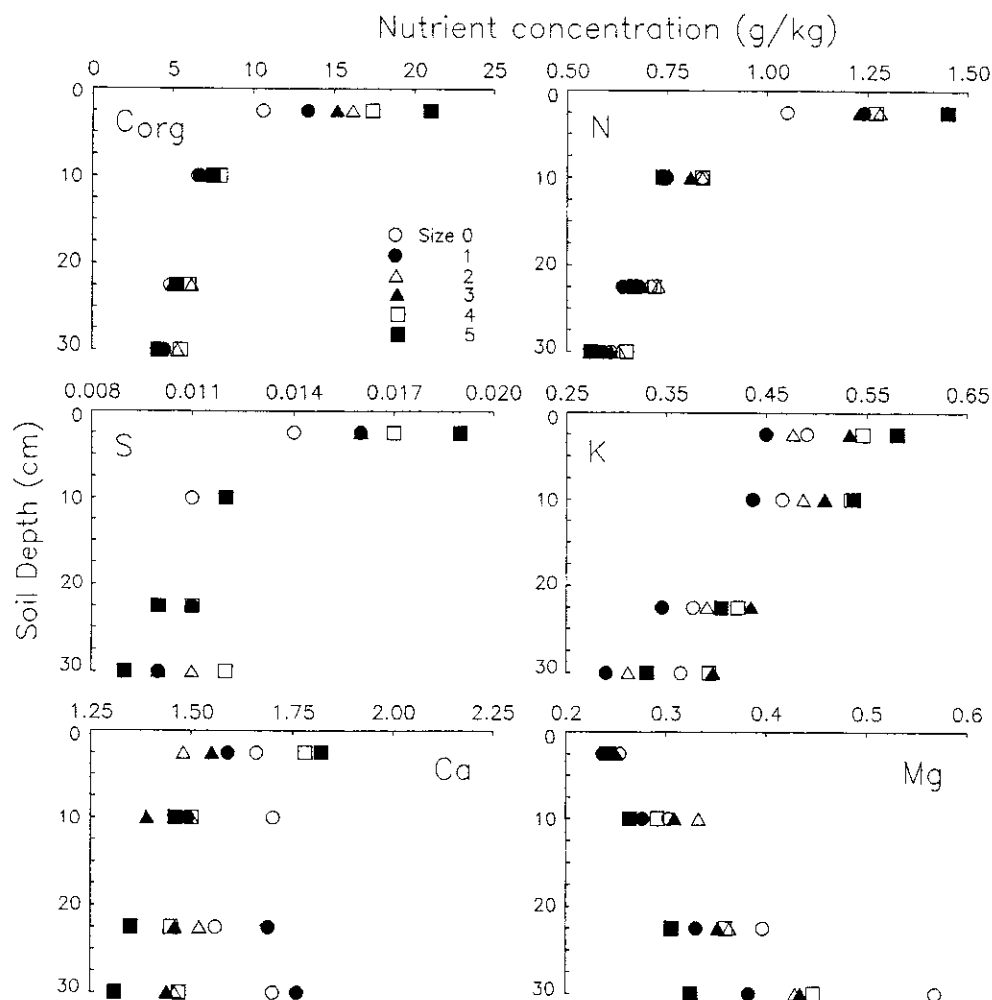


Figure 1. Concentrations of C_{org} , N, S, K_{ex} , Ca_{ex} and Mg_{ex} (averaged over distances from 0 to 4 canopy radii) as a function of soil depth for six size classes of juniper, including no juniper (0).

Interestingly, P was the only soil nutrient that did not respond to tree size, either as the main effect or as an interaction.

Nutrient Amounts

Amounts of nutrients (except S and Ca_{ex}) in the upper 30 cm of soil were significantly influenced by distance, but not by juniper size. The size X distance interaction was significant only for C_{org} ($P \leq 0.0119$). Amounts of soil C_{org} were greater for all sizes of juniper at the 0 distance and for classes 3–5 at the 0.5 distance than that for no juniper sites (Table 6), and increased with tree size. At the canopy edge and beyond, tree size had no effect on amount of soil C_{org} .

TABLE 6. Amount of organic C (kg/m^2) in the 0–30 cm soil layer as a function of distance from tree boles for six size classes of juniper, including no juniper (0).

Size class	Distance from tree boles (canopy radii)				
	0	0.5	1	2	4
0	1.88 ^{abc}				
1	2.55 ^{d-h}	2.03 ^{a-d}	2.17 ^{a-e}	1.91 ^{abc}	1.99 ^{a-d}
2	3.09 ^b	2.61 ^{e-h}	2.37 ^{c-g}	2.34 ^{a-c}	2.19 ^{a-c}
3	2.80 ^{g-h}	2.02 ^{a-d}	1.85 ^{ab}	2.03 ^{a-d}	2.02 ^{a-d}
4	3.59 ^j	2.91 ^{gh}	2.41 ^{c-d}	1.99 ^{a-d}	1.90 ^{abc}
5	3.62 ⁱ	3.08 ^h	2.12 ^{a-e}	1.81 ^a	1.79 ^a

Values with common letters are not significantly different at $P \leq 0.05$.

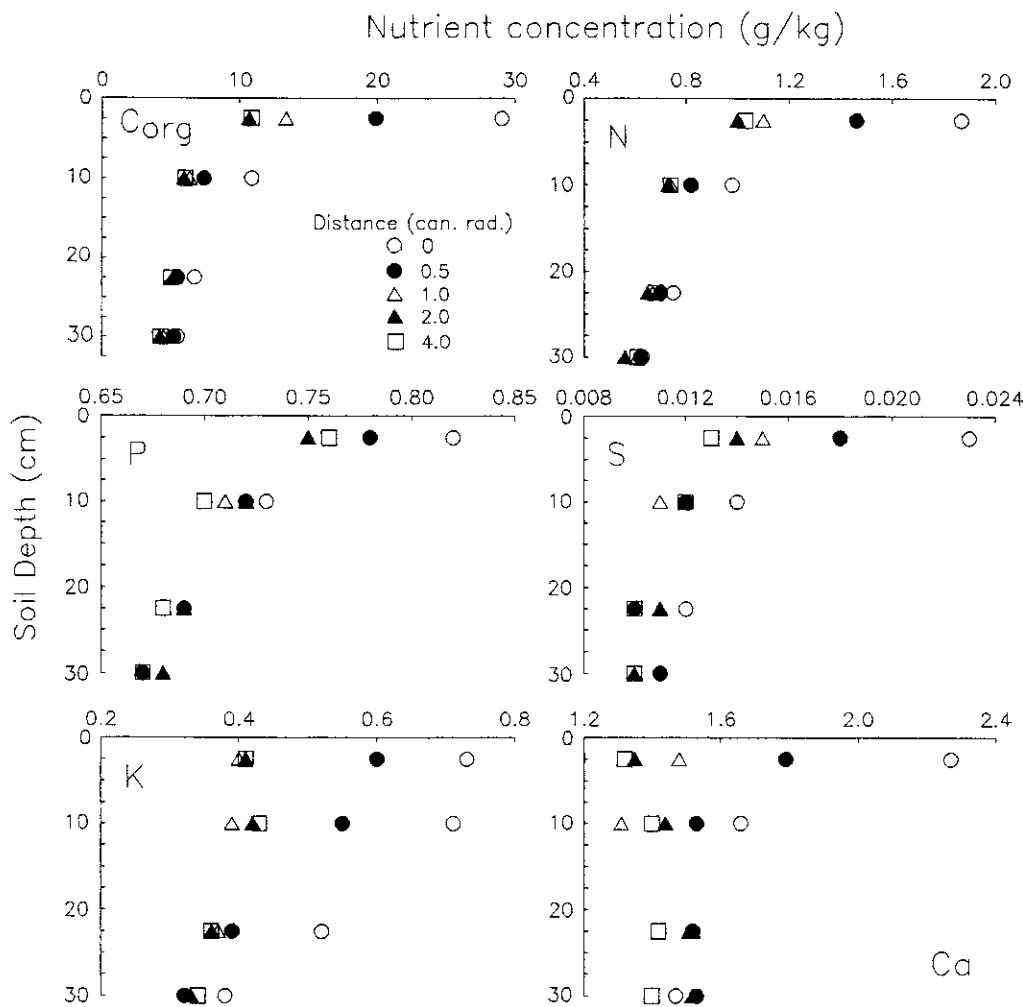


Figure 2. Concentrations of C_{org} , N, P, S, K_{ex} and Ca_{ex} (averaged over juniper size classes 1–5) as a function of soil depth for distances of 0 to 4 canopy radii from tree boles.

The distance main effect significantly influenced amounts of N, P, K_{ex} and Mg_{ex} in the 0- to 30-cm soil layer (Table 7). Amounts of N, K_{ex} and Mg_{ex} were all greater under juniper canopies, while amount of P was lower at the 0 distance than at all other distances.

Discussion and Conclusions

Juniper invasion in the sagebrush/grass ecosystem distinctly altered the spatial distribution of nutrients in the organic layer and soil. Moreover, tree size intensified this effect. Nutrient gains under juniper (exceptions noted below) were not matched with equal losses from intercanopy areas. Because

TABLE 7. Amounts (g/m^2) of total N and P, and exchangeable K and Mg in the 0–30 cm soil layer as a function of distance from tree boles.

Distance	N	P	K_{ex}	Mg_{ex}
0	277.2 ^{b1}	209.8 ^b	174.7 ^b	100.1 ^c
0.5	266.2 ^b	224.3 ^b	148.1 ^a	104.0 ^c
1	243.9 ^a	228.5 ^a	123.2 ^a	99.1 ^{bc}
2	236.1 ^a	231.2 ^a	126.2 ^a	97.3 ^{ab}
4	243.0 ^a	227.1 ^a	127.9 ^a	92.4 ^a
no juniper ²	242.4	217.6	130.7	106.9

¹ Within column values with common letters are not significantly different at $P \leq 0.05$.

² Because of an unbalanced design, no separation of means could be made for no juniper sites.

the organic layer and soil are integral parts of the same system, they are influenced by the same external factors. Hence, we expect similar patterns of nutrient accumulation, as observed here. However, the organic layer and soil differ in position, composition, and in chemistry among nutrients. These differences account for differences in accumulation patterns observed between the organic layer and soil, and among nutrients.

The pattern of nutrient accumulation under juniper trees was that of "islands of fertility" described earlier for a variety of tree and shrub species (Fireman and Hayward 1952, Zinke 1962, Garcia-Moya and McKell 1970, Barth 1980, Belsky et al. 1989). The large increases in mass of the organic layer and nutrients beneath canopies with juniper size is largely attributable to the effect of accumulating biomass with size (age) (Bernhard-Reversat 1982, Tiedemann and Klemmedson 2000) and slow decomposition of juniper litter. Steepness of the gradients from boles to canopy edge (60- to 120-fold greater than in intercanopy and no juniper areas), even in the smallest size class, reflects large differences in litter production and accumulation, litter quality (Kittredge 1948, Klemmedson 1992), and microclimate (radiation, temperature, moisture) of the contrasting juniper and intercanopy sagebrush/grass environments (Tiedemann and Klemmedson 1977, Belsky et al. 1989). The steep horizontal organic layer gradients reported here contrast sharply with essentially flat gradients observed for litter under mesquite (*Prosopis juliflora* (Swartz) DC) and palo verde (*Cercidium floridum* Benth.) in the Sonoran desert (Barth and Klemmedson 1978).

Decline in concentrations of N, P and S in juniper organic layers (Table 3) with distance from bole to canopy edge is likely explained by the change in litterfall composition and decomposition environment with distance to the canopy edge.

Thus, litter quality changes as the proportions of juniper and herbaceous litterfall change near the canopy edge and as the microclimate changes, thereby hastening decomposition. Spatial distribution of litterfall is a possible explanation for under-canopy nutrient gradients. Zinke (1962) reported that bark litter of several forest trees, found in rings next to boles, differed in pH and element composition from leaf litter that dominated an outer ring extending to the canopy edge.

We observed no distinct accumulations of bark under junipers, but did not sort litterfall for composition. However, based on Zinke's (1962) data, we probably would have found different nutrient patterns in juniper organic layers and soils had there been a distinct zone of accumulating bark litter.

We have no explanation for the significant tree size X distance interaction displayed for C_{org} concentration in the organic layer and conclude it is an aberration in the data. That C_{org} concentration of the organic layers did not follow the pattern for N, P and S discussed above is attributed to the relative supply of these elements to decomposer organisms and their fate during early stages of decomposition. Carbon is abundant in organic layers, while N, P and S are usually limited (Swift et al. 1979). As mineralization-immobilization proceeds, excess C is evolved continuously as CO_2 while N, P, and S are retained in immobilized form.

The significant effect of distance on amounts of organic layer nutrients is a straightforward result of the distance effect on organic layer mass (Table 2) and nutrient concentration (Table 3). The change in composition of litterfall along the distance gradient has a bearing on both of these variables.

Although the horizontal pattern of soil nutrient accumulation in the juniper-intercanopy system was similar to that for the organic layer, the magnitude of distance gradients was markedly flatter. Soil nutrient concentrations ranged from 1.18- to 1.76-fold higher at tree boles than at canopy edge and intercanopy areas, except for P (1.02-fold) and Mg_{ex} (1.12-fold). In the same locale, Doescher et al. (1987) found concentrations of soil organic matter, N, Ca_{ex} , and K_{ex} under mature western juniper 1.1- to 1.6-fold higher than in the intercanopy areas. Barth (1980) found organic matter and extractable K about 3.4-fold higher, but P an unusual 20-fold higher under 490-yr-old pinyon pine (*Pinus edulis* Engelm.) than in the intercanopy areas. Tiedemann and Klemmedson (1973) reported 3.0- and 2.6-fold tree-intercanopy differences for N and S for mesquite-grass systems in Arizona.

Our findings are generally consistent with the literature regarding the mosaic pattern of nutrient distribution found in savannas, or in grasslands and shrublands invaded by trees or shrubs. However, we differ in some respects on source

of nutrient gains. Some authors (Charley and West 1975, Barth 1980, Klopatek 1987) have concluded or implied that enrichment of canopy area soils means a loss from intercanopy areas. That does not necessarily follow. In our study, all nutrients except Ca_{ex} and Mg_{ex} were enriched in soils beneath junipers. However, only Mg_{ex} and Ca_{ex} , and possibly N, displayed significant loss from the intercanopy area compared with no juniper areas. This is not to say that gains of other nutrients (C_{org} , P, S, and K_{ex}) in canopy soils did not come, in some measure, from intercanopy soils. However, other sources may have been important to canopy soil and organic layer gains of these nutrients. The question remains as to where Ca and Mg absorbed from intercanopy areas resides, since canopy soils showed no accumulation of these nutrients. Logically it appears these nutrients were absorbed and stored in the tree biomass.

Although not measured here, temperature probably contributed significantly to spatial distribution of soil and organic layer nutrients of juniper-intercanopy systems. The widely reported influence of trees and shrubs on soil and litter properties (Muller 1887, Harradine 1958, Zinke 1962, Garcia-Moya and McKell 1970) has focused chiefly on plant to soil nutrient transfers. Although the general effects of tree and shrub canopies on understory temperatures are universally understood, the spatial effects of understory temperatures on nutrient accumulation have been scarcely recognized (Tiedemann and Klemmedson 1986). Along transects from juniper boles to intercanopy areas, the state of the system (Jenny 1961) and its microenvironment changes with growth to maturity of junipers. In turn, decomposition and mineralization processes, and status of nutrients associated with litter and organic matter, change along these gradients. The role of temperature on

soil and organic layer nutrient accumulation in juniper-intercanopy systems should be studied.

The juniper-sagebrush/grass system, of course, is not static. Once junipers are harvested or removed, the plant biotic factor is again changed. Nutrient availability may be improved in former juniper soils and productivity of herbaceous vegetation increased for a period of years (Thran and Everett 1987, Rose and Eddleman 1994). Following harvest of junipers, however, total soil nutrients should seek the old steady state conditions of the sagebrush/grass system, probably within a short period of time for organic-based nutrients (C_{org} , N, S, and P), based on findings of Tiedemann and Klemmedson (1986), but probably a much longer time for Ca_{ex} and Mg_{ex} (Adams and Boyle 1982).

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