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Biomass and Nutrient Distribution and System Nutrient Budget for Western Juniper in Central Oregon.

Abstract

Invasion of western juniper (*Juniperus occidentalis* Hook.) into big sagebrush (*Artemisia tridentata* Nutt.) communities of eastern Oregon implies redistribution of nutrients among ecosystem components, with management implications as stands mature. To assess these effects, we measured biomass and nutrients in juniper trees of five size classes ranging in average age from 36 to 161 yr, and in understory vegetation. Understory was measured at 0.0, 0.5, 1, 2, and 4 canopy radii from the bole and in areas devoid of juniper ("no juniper"). Tree size and distance from boles had no effect on biomass or concentrations and amounts of nutrients in understory vegetation. Above-ground tree biomass increased with maturity from 18.4 kg for size class 1 to 741.4 g for class 5. Biomass accumulated rapidly (22.3 kg/tree/yr) between classes 2 and 3. Foliage comprised 41% of tree biomass in class 1 trees, but decreased to 15% for class 5 trees. Concomitantly, percentage of tree biomass in boles and live branches increased from 29 to 47%. From class 1 to class 5, amounts of nutrients increased as follows: nitrogen (N) from 89 to 2117 kg/tree; phosphorus (P) from 12 to 283 g/tree; and sulfur (S) from 10 to 294 g/tree. In open systems (intercanopy and "no juniper" areas), soil contained 89.9 to 99.8% of the organic carbon (C_{org}), N, P, and S of entire systems. For tree systems (areas occupied by juniper canopies), C_{org}, N, and S in aboveground biomass increased with increasing tree maturity, while P did not change. For the most mature trees, proportions of total system N, S and P allocated to the organic layer and trees was 30, 78, and 5%, respectively. Considering the N and S limited nature of these sites, a conservative harvest management approach that emphasizes retention of organic layers and tree foliage appears prudent.

Introduction

Maintaining adequate levels of essential plant nutrients is important to productivity and stability of any plant community. In central Oregon and northern California, western juniper (*Juniperus occidentalis* Hook.) has been managed largely without regard to the consequences of management activities on nutrient status and potential site productivity. To achieve forage production, wildlife management and watershed improvement goals, juniper trees have been cut, chained, or cabled, and residues piled or windrowed and burned (Valentine 1980, Miller and Wigand 1994, Belsky 1996). Now, significant markets are emerging for western juniper for a variety of wood products (Leavengood and Swan 1998). This could eventually result in western juniper removal from several thousand ha per yr.

If western juniper functions like other shrub and tree species of arid and semi-arid regions,

invasion and development to maturity may be accompanied by transfer of nutrients from intercanopy areas to tree biomass and to organic layers and soil beneath the canopies of juniper trees (Charley 1972, Tiedemann and Klemmedson 1973, Barth and Klemmedson 1978, Barth 1980, Belsky et al. 1989, Rhoades 1997). Western juniper has a wide spreading lateral root system (Young et al. 1984, Tiedemann and Klemmedson 1995) that suggests it may accumulate nutrients from intercanopy areas and sequester them in tree components. Removal of trees results in loss of nutrients from the site that may affect future productivity (Malkonen 1975, Kimmins 1977, Wells and Jorgensen 1979, Tiedemann 1987a, Everett and Thran 1992). Broadcast burning of felled trees and residues has the potential for substantial volatilization losses of some nutrients, especially nitrogen (N) and sulfur (S) (Klemmedson 1976, DeBano and Conrad 1978, Raison et al. 1985, Tiedemann 1987b). Phosphorus (P) losses from the litter may approach 50% (DeBano and Klopatek 1988). Burning piles or windrows of trees also concentrates elements such as P, calcium (Ca), potassium (K), and magnesium (Mg) beneath

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burned piles (DeBano et al. 1987). This may cause a long-term redistribution of these elements from areas occupied by trees to a relatively small portion of the total area. Increased leaching and erosion following treatment may also result in losses of essential plant nutrients (DeBano et al. 1998)

Soil-plant systems of western juniper have not been examined to determine the effect of juniper invasion into big sagebrush (*Artemisia tridentata* Nutt.) communities and development to maturity on distribution of nutrients among mineral soil, organic layers, understory vegetation, and trees of juniper/sagebrush systems. If, as juniper matures, a substantial proportion of the total nutrient capital of a site is contained in the aboveground biomass, care should be exercised to retain as much nutrient capital on the site as feasible in harvesting operations. Productivity concerns may be particularly applicable to semi-arid tree ecosystems such as western juniper (Tiedemann 1987a, Everett and Thran 1992).

The purpose of this study was to quantify accumulation patterns of biomass and nutrients in understory vegetation and trees associated with invasion and development to maturity of western juniper trees. We also compare total system nutrient accumulation patterns for "open systems" (intercanopy and areas devoid of juniper) with those for "tree systems" (areas occupied by juniper tree canopies).

The Study Area

We conducted this study in central Oregon at the Three Springs Ranch about 11 km southwest of Prineville at an elevation of 1110 m. Klemmedson and Tiedemann (2000) provide a complete description of the study area. Briefly, the study area is typical of the community dominated by western juniper on the central Oregon Plateau east of the Cascade Mountains. Climate is continental with maritime influence of storms from the Pacific coast. The area receives 26.6 cm of precipitation annually, mostly in the form of snow. Mean January and July temperatures are 0°C and 18.2°C.

Soils are young, formed in volcanic ash from eruption of Mt. Mazama 6845 ± 45 years ago (Bacon 1983). Five soil series occur in the study area: Stukel, Deschutes, Stukmond, Redmond, and Licksillet (personal communication with Amanda Moore, Soil Scientist, United States Department of Agriculture, Natural Resources Conservation

Service, Redmond, Oregon). Our study sites were primarily on Stukel series soils. 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). Vegetation of the juniper understory, intercanopy, and areas devoid of juniper is dominated by big sagebrush, rabbitbrush (*Chrysothamnus* spp.), bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. and Smith [now *Pseudoroegneria spicata*]), and Idaho fescue (*Festuca idahoensis* Elmer).

Procedures

Site Selection and Field Sampling

We selected five separate, non-contiguous, replicate sites for sampling, all within an area 1 X 8 km. Sample sites were selected for uniformity of climate, topography (2 to 5% eastward slope), parent material, and soil. Except for an occasional tree that had been harvested for fuelwood, the area was undisturbed. 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 disturbance or feces. This suggested that grazing had been excluded for a long time. More detailed information on site selection is provided by Klemmedson and Tiedemann (2000).

At each of the five sites, we selected three trees in each of five size classes and randomly selected one tree in each class for sampling. This resulted in a total of 25 sample trees—five replications of five size class trees (Figure 1 a–e). These are referred to as size classes 1 through 5. Size classes were subjective and based on the distribution of tree sizes on the study area. Individual sample trees were isolated from other trees by 30 to 40 m.

At each of the five sites, we selected a 5 to 10 ha area without juniper that we refer to as "no juniper." Within each "no juniper" area, three plots were established by random distance and direction from a central starting point. One plot was randomly selected from these for sampling.

Understory biomass samples were collected from a 0.5 m² area at the base of each sample tree (distance 0), and at 0.5, 1, 2, and 4 canopy radii due north from the bole of each tree. Biomass



Figure 1. Size distribution of typical western juniper trees used in this study. A through E = size classes 1 through 5.

samples also were collected from “no juniper” sites. Shrubs were separated into foliage and stems.

Each tree was felled (5 cm above ground level) onto large tarpaulins. Tree length was measured and all branches were removed and sorted into two categories: <3 cm and >3 cm based on expected N content. Previous laboratory study had shown that a 3 cm diameter gave the best separation of branches of low versus high N concentration. Boles were cut into 1.0 m sections; 5 cm sample slices were removed from each bole section and from >3 cm branches. Three to five

branches from the <3 cm diameter category were randomly selected from each tree for determination of the proportion of biomass in categories of: foliage; live branches <0.5 cm, 0.5 to 1 cm, and 1 to 3 cm diameter; and dead branches <1 cm and >1 cm diameter. Each branch was then separated by hand into these categories. The proportion of branch weight in each category was used to determine the proportion of total branch weight <3 cm in each category. After field-weighing of all understory biomass components (grass, forb, and shrub) and all tree components, samples

of each component were collected, sealed in double plastic bags, and returned to the laboratory under refrigeration for moisture determination. Field weights of all biomass components were then corrected to oven-dry weight at 70°C. Small samples of each biomass component were collected, air-dried, and ground to 0.25 mm fineness for laboratory analysis of nutrient content.

Dr. Franco Biondi, Tree Ring Laboratory, University of Arizona, Tucson, aged each tree from a slice of the lowermost bole section. Roots of trees and understory vegetation were not collected. Although this omission underestimates the amount of nutrients incorporated into biomass, measuring this biomass component was beyond the objectives of the experiment.

Chemical Analyses

Understory vegetation and tree components were analyzed for total organic C by dry combustion using a high-frequency induction furnace (Nelson and Sommers 1982), total N by the micro-Kjeldahl procedure (Bremner and Mulvaney 1982), total P by dry ashing in the presence of magnesium nitrate followed by vanadate-molybdate yellow color development (Chapman and Pratt 1961), and total S by dry combustion in a high-frequency induction furnace (Tiedemann and Anderson 1971). Nutrient concentrations of bole sections were averaged for statistical analyses.

Statistical Analyses

Data for understory biomass and contained nutrients (concentrations and amounts) were analyzed as a randomized complete block with sites as blocks and size class (including "no juniper") and distances as main effects [SAS Institute Inc. (1987) analysis of variance]. Biomass, concentrations of nutrients, and nutrient amounts by tree component were analyzed as a randomized complete block with sites as blocks and size class as the main effect. Tree component was treated as a split-plot. The LSD test ($P \leq 0.05$) was used for determination of differences among means for main effects, split-plot effects, and interactions significant at $P \leq 0.05$ (Carmer and Swanson 1971).

Development of a Complete System Nutrient Budget

Biomass and nutrient accumulation data were expressed on a kg/m² or g/m² basis for mineral soil, organic layers, understory vegetation, and

trees for open systems (intercanopy and "no juniper" areas) and for tree systems (areas occupied by juniper canopies). For tree systems, nutrient accumulation is expressed on the basis of crown occupancy area. Organic layer and soil data are from Klemmedson and Tiedemann (2000). Weighted average values for the organic layer and soil for each tree were determined from amounts of nutrients calculated for three concentric bands (each one-third canopy radius in width) from nutrient data for the 0, 0.5, and 1 canopy radii locations representing inner to outer bands, respectively. Data for the three bands were then summed and divided by canopy area to obtain g/m² values for each nutrient, for each tree size class. No statistical analyses were performed on nutrient budget values.

Results and Discussion

Biomass and Concentrations and Amounts of Nutrients in Understory

Biomass, nutrient concentrations, and amounts of nutrients in understory vegetation were unaffected by size class (including "no juniper"), distance from tree boles, and the size class X distance interaction. Biomass of understory vegetation averaged 163 g/m² (1630 kg/ha). Concentrations of C_{org}, N, P, and S in understory vegetation averaged 425, 8.2, 1.3, and 1.0 g/kg; amounts of C_{org}, N, P, and S in understory averaged 69.8, 1.12, 0.20, and 0.15 g/m², respectively.

Lack of differences in biomass of understory vegetation between areas under tree canopies, intercanopy, and areas without juniper was contrary to observations of other semi-arid woodlands (Clary and Morrison 1973, Bedell and Bunch 1978, Tiedemann and Klemmedson 1977, Belsky et al. 1989, Belsky 1994). Understory biomass has generally been shown to be greater beneath canopies of trees than in adjacent openings. In some cases, differences between these locations were primarily the result of higher cover and production of perennial grasses under tree canopies (Clary and Morrison 1973, Tiedemann and Klemmedson 1977). We did not measure differences in plant composition between canopy and intercanopy areas.

Physical Characteristics of Sample Trees

Average tree age ranged from 36 yr for class 1 to 161 yr for class 5 (Table 1). The youngest tree was 21 yr; the oldest 231 yr. Average height among

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

TABLE 2. Distribution of biomass (kg) among tree components.

Size Class	Component							Total	
	Boles	Foliage	Live Branches				Dead Branches		
			>3 cm	1-3 cm	0.5-1 cm	<0.5 cm	>1 cm		<1 cm
1	4.7 ^{a1}	7.6 ^a	0	3.5 ^a	0.8 ^a	0.9 ^a	<0.1 ^a	0.1 ^a	18.4 ^a
2	15.4 ^b	19.3 ^a	0	14.8 ^a	2.3 ^a	2.8 ^a	<0.1 ^a	0.2 ^a	56.4 ^a
3	55.5 ^c	50.2 ^b	20.9 ^a	55.5 ^b	7.7 ^a	6.6 ^a	3.8 ^a	1.3 ^a	212.3 ^b
4	146.6 ^c	91.4 ^c	71.9 ^a	86.2 ^c	12.9 ^a	15.0 ^a	8.9 ^a	2.1 ^a	433.6 ^c
5	238.5 ^d	113.9 ^c	130.1 ^c	156.5 ^d	18.3 ^a	20.8 ^a	14.7 ^a	5.2 ^a	741.4 ^d

¹ Values in a column with the same lower case letter are not significantly different at $P \leq 0.05$.

classes ranged from 3.3 to 9.9 m but overall height (irrespective of size class) ranged from 2.9 to 10.4 m. Basal diameter for class 1 averaged 13 cm, which for size class 5 was nearly 5 times greater (63 cm). Canopy diameters ranged from 1.7 m to 6.7 m.

Biomass of Trees and Tree Components

Tree biomass increased markedly with size class from 18.4 kg for class 1 to 741.1 kg for class 5 (Table 2); differences among larger classes (2 - 5) were all significant.

Because the size class X tree component interaction for biomass was highly significant, we focus here on explaining the interaction, and note differences among size classes for individual components. These comparisons relate directly to study objectives. Biomass of boles, foliage, and live branches >3 cm and 1 to 3 cm diameter increased significantly with size class. By contrast, tree size had no influence on smaller live branches (<1 cm) or dead branches, hence the significant interaction (Table 2). For classes 1 and 2, foliage comprised the greatest part of the tree biomass (41.3 and 34.2%). Foliage, boles, and live branches 1 to 3 cm diameter, were roughly equal in biomass

for class 3. As trees matured (class 5), boles, live branches 1 to 3 cm diameter, and live branches >3 cm diameter became the major tree components.

Figure 2 portrays the percentage of tree biomass in each tree component for each size class. The most striking change with increasing tree maturity was for foliage. Between class 1 and 5, percentage of total tree biomass in foliage declined from 41 to 15. This was not unexpected; Rodin and Bazilevich (1967) reported that young trees generally have a greater proportion of biomass allocated to foliage than mature trees. Foliage biomass, as a proportion of tree biomass, however, was comparable to that measured by Gholz (1980) for western juniper (20%) and for 90- and 350-year old one-seeded juniper (*Juniperus monosperma* Sarg.) in northern Arizona (22% and 12%, respectively) determined by Grier et al. (1992). However, the high mean percentage of biomass in foliage (26%) and the high proportion of foliage in mature junipers (15% for class 5) was substantially greater than that (3 to 9%) normally allocated to foliage in conifers (Rodin and Bazilevich (1967).

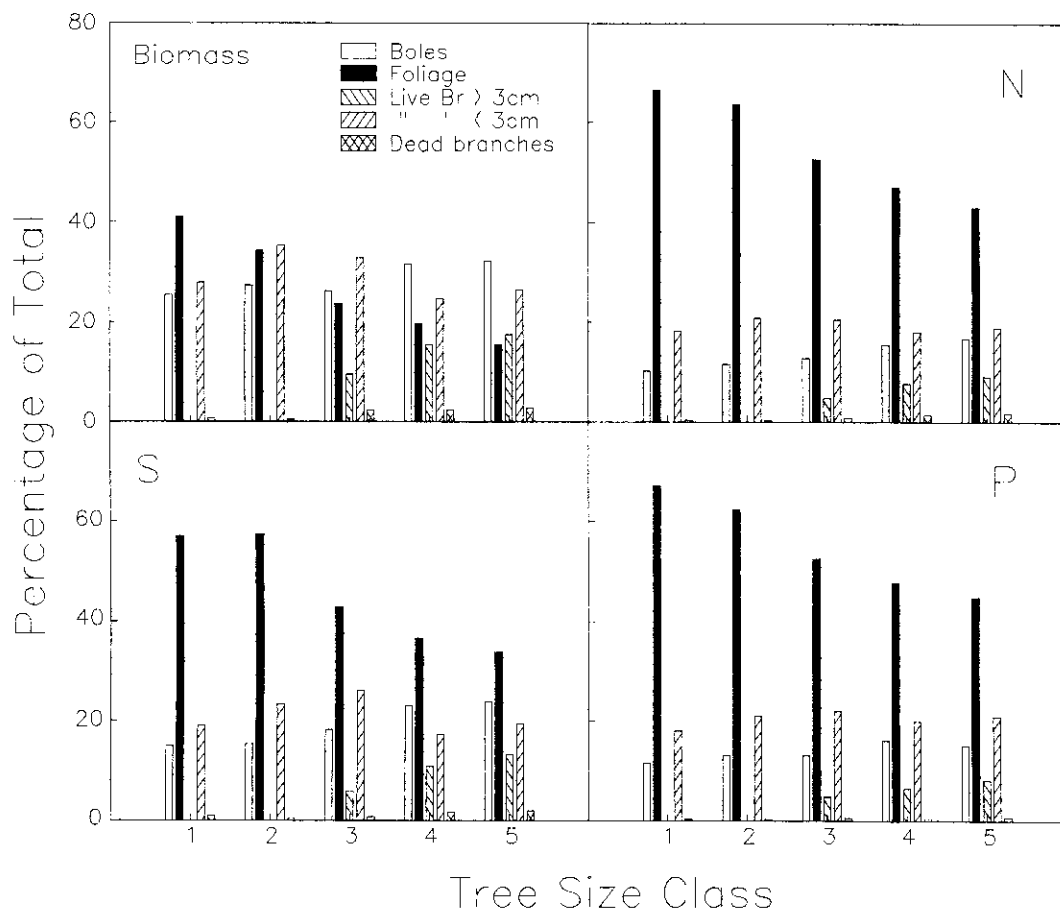


Figure 2. Percentage distribution of tree biomass, N, S, and P among tree components for five size classes of western juniper.

Large live branches (>3 cm diameter) was the only other tree component that changed markedly with increasing tree size, from 0 to 17% between class 2 and 5 (Figure 2). Changes in proportions of other tree components among classes were minor.

Live and dead branches were important components of western juniper; they comprised 29 to 47% of tree biomass. This is not unusual for juniper. Gholz (1980) found that live and dead branch biomass comprised 38% of tree biomass in western juniper. Grier et al. (1992) reported that branches comprised 57 to 62% of tree biomass for 90- and 350-year old one-seeded juniper in northern Arizona.

The highest rate of tree biomass accumulation (22.3 kg/tree/year) occurred between classes 2 and 3, an interval of 7 years (Table 3). Yearly increment patterns indicate that the growth pattern of

TABLE 3. Annual rates of accumulation of biomass and nutrients in western juniper as a function of tree size class.

Size Class	Elapsed Years	Biomass (kg/yr)	N (g/yr)	P (g/yr)	S (g/yr)
1	36	0.5	2.5	0.3	0.3
2	19	2.0	7.3	1.0	0.8
3	7	22.3	69.7	9.4	10.6
4	39	5.7	17.7	2.5	2.3
5	60	5.1	11.8	1.4	1.7

TABLE 4. Concentrations of nutrients (g/kg) in tree components of western juniper (average of size classes).

Tree Component	Nutrient			
	C _{ORG}	N	P	S
Foliage	505 ^a	7.67 ^c	1.06 ^d	0.80 ^e
Live Branches <0.5 cm	476 ^a	3.76 ^d	0.53 ^c	0.42 ^b
Live Branches 0.5-1 cm	480 ^{ab}	2.88 ^c	0.40 ^c	0.35 ^a
Live Branches 1-3 cm	489 ^a	2.18 ^c	0.30 ^b	0.33 ^a
Live Branches >3 cm	491 ^a	1.51	0.19	0.28
Boles	488 ^a	1.80 ^a	0.27 ^b	0.32 ^a
Dead Branches <1 cm	483 ^{ab}	2.81 ^c	0.28 ^b	0.40 ^{ab}
Dead Branches >1 cm	481 ^{ab}	2.09 ^b	0.13 ^a	0.33 ^a

^a Values in a column with the same lower case letter are not significantly different at $P \leq 0.05$.

^b No LSD test for this category because there were no samples for Size Classes 1 and 2.

western juniper trees followed an S-shaped growth curve, confirming results of Eddleman (1987).

Nutrient Concentrations in Tree Components

Concentrations of N, P, and S (averaged among tree size classes) were greater ($P \leq 0.05$) in foliage than in other tree components (Table 4) and declined to low levels in dead branches and boles.

Although concentration of C_{org} was highest in foliage, it varied little among components.

Concentration of N in foliage of western juniper trees (average 7.7 g/kg) was near the lower end of the range for coniferous forests worldwide (Rodin and Bazilevich 1967), whereas concentrations of P and S were in the middle of the range.

Accumulation of Nutrients in Tree Components

Accumulation of nutrients for individual tree components was directly related to accumulation of biomass, i.e., increase in tree size (Table 5). This was especially so for C_{org}, where the correspondence between C_{org} and biomass was near 1:1, i.e., concentration of C_{org} varies <3% among tree components (Table 4). For that reason, we have not included data for C_{org} in Table 5. The analysis of variance showed that the interaction of size class X tree component significantly ($P \leq 0.0001$) influenced amounts of C_{org}, N, P, and S. Two factors appear responsible for the significant interaction. First, there were no live branches >3 cm diameter for classes 1 and 2 (Table 5). Secondly, accumulation of C_{org}, N, P, and S among size classes was much greater for boles, foliage, and live

TABLE 5. Distribution of nutrients (g) among tree components by tree size class.

Nutrient	Size Class	Tree component								Total
		Boles	Foliage	Live Branches				Dead Branches		
				>3 cm	1-3 cm	0.5-1 cm	<0.5 cm	>1 cm	<1 cm	
Nitrogen	1	9.1 ^a	59.4 ^a	0	9.6 ^a	2.8 ^a	3.9 ^a	<0.1 ^a	0.4 ^a	89.4 ^a
	2	26.3 ^a	145.1 ^a	0	30.0 ^a	6.6 ^a	10.8 ^{ab}	0.1 ^{ab}	0.6 ^a	228.0 ^a
	3	89.9 ^b	375.4 ^b	34.1 ^a	101.2 ^{bc}	20.9 ^{bc}	24.6 ^b	4.2 ^{bc}	2.4 ^a	715.8 ^b
	4	217.1 ^c	661.4 ^c	109.0 ^a	173.5 ^c	30.9 ^c	49.1 ^c	16.9 ^c	3.5 ^a	1408.4 ^c
	5	355.0 ^d	906.1 ^c	193.6 ^b	287.9 ^c	42.9 ^c	70.1 ^c	30.4 ^d	8.6 ^b	2116.8 ^d
Phosphorus	1	1.4 ^d	8.2 ^a	0	1.3 ^b	0.4 ^a	0.5 ^c	0	<0.1 ^c	12.2 ^a
	2	4.0 ^d	19.2 ^a	0	4.0 ^a	1.0 ^{bc}	1.5 ^{cd}	0	0.1 ^c	30.8 ^a
	3	12.6 ^c	50.7 ^b	4.6 ^a	14.9 ^{ab}	3.0 ^{bc}	3.6 ^b	0.3 ^a	0.3 ^a	96.8 ^a
	4	31.2 ^c	92.1 ^c	12.4 ^{ab}	26.4 ^{bc}	4.4 ^{cd}	7.6 ^c	0.6 ^a	0.3 ^a	193.3 ^b
	5	42.9 ^d	127.0 ^d	23.0 ^b	41.8 ^c	6.1 ^d	11.3 ^d	1.9 ^b	1.2 ^b	283.5 ^d
Sulfur	1	1.5 ^a	5.7 ^c	0	1.4 ^b	0.4 ^a	0.4 ^a	0	0.1 ^a	10.0 ^a
	2	4.1 ^a	15.2 ^{ab}	0	4.2 ^{ab}	0.9 ^a	1.1 ^a	0	0.1 ^a	26.5 ^a
	3	18.4 ^b	43.2 ^{bc}	5.9 ^a	21.0 ^b	2.3 ^b	3.0 ^{ab}	0.5 ^a	0.3 ^a	100.7 ^b
	4	44.0 ^b	69.8 ^{cd}	20.3 ^{ab}	22.4 ^b	5.1 ^{cd}	5.5 ^b	2.7 ^{ab}	0.7 ^{ab}	190.6 ^c
	5	70.2 ^d	99.7 ^d	38.9 ^b	43.6 ^c	4.7 ^c	8.8 ^c	4.8 ^c	1.3 ^b	294.2 ^c

^a Values in a column with the same lower case letter are not significantly different at $P \leq 0.05$.

^b Total tree values do not equal the sum of individual components because the "debris" category is not shown in the table.

branches 1 to 3 cm diameter than for the other components.

As implied above, tree amounts of C_{org} increased in parallel fashion to biomass (Table 2), from 9 kg for class 1 to 368 kg for class 5. Tree N increased from 89 to 2117 g between classes 1 and 5. Although amounts of P and S accumulated were about one-tenth the amount of N, rates of increase between classes 1 and 5 were similar to those for N. Tree accumulations of C_{org} , N, P, and S were not significantly different for classes 1 and 2, but these two classes differed significantly from all larger size classes, and they from each other (Table 5).

Nutrient accumulation proceeded slowly for all tree components for young trees (classes 1 and 2), but accelerated as trees increased in size and accumulated biomass. Nutrient accumulation among size classes was most pronounced in boles, foliage, and live branches 1 to 3 cm and 0.5 to 1 cm diameter (Table 5). For these components (with exception of S in live branches 1 to 3 cm diameter), nutrient amounts were significantly greater in classes 4 and 5 than in classes 1 and 2. The other consistent aspect of the data for all nutrients and tree components was significantly greater nutrient amounts for class 5 than for class 3.

Annual rates of accumulation of biomass and all nutrients increased with tree size, reaching a maximum in class 3, then declined with maturity in classes 4 and 5 (Table 3).

Foliage was the predominant component home for N, P, and S in western juniper throughout the life of the trees (Figure 2). However, as size (age) increased, the percentage of each of these nutrients residing in foliage declined, reaching a minimum of about 43-45% of the tree total for N and P, and 34% for S. Concurrently, the relative amount of N and S increased slightly in boles and live branches >3 cm diameter. Live branches <3 cm diameter were the second most important component for accumulation of N, P, and S in western juniper, containing about 20% of the total.

Nutrient Budget for Soil, Organic Layer, Understory, and Trees

Nutrient Accumulation Patterns in Open Systems

Accumulations of C_{org} , N, P, and S in soil, organic layer, and understory vegetation were similar at intercanopy distances 2 and 4 for all size classes

(Klemmedson and Tiedemann 2000). In the organic layer, amounts of N for "no juniper" sites tended to be lower, but not significantly so, than that for intercanopy locations. Amounts of C_{org} , P, and S in the organic layer did not differ among "no juniper" and intercanopy locations.

We were unable to make statistical comparisons of mineral soil among intercanopy and "no juniper" areas because of the unbalanced experimental design. However, amounts of C_{org} , N, P, and S in soil for "no juniper" areas were within the range of values for intercanopy distances 2 and 4 and, hence, would not likely have differed significantly (Klemmedson and Tiedemann 2000). Total accumulations of C_{org} , N, P, and S in open systems were 2176, 243.9, 228.5, and 4.1 g/m², respectively (Table 6). Most (89.9 to 99.8%) of the C_{org} , N, P, and S in these systems was contained in the soil. Aboveground amounts of these nutrients in open systems were about equally allocated between the organic layer and understory vegetation.

Nutrient Accumulation Patterns in Tree Systems

The largest proportion of total system C_{org} (61 to 69%) was contained in trees (Table 6). Between classes 1 and 5, C_{org} increased 2.4 times, i.e., at the same rate as biomass. In the organic layer, C_{org} increased five-fold between classes 1 and 5; i.e., from 303 to 1503 g/m² of system C_{org} . While C_{org} increased from 2125 to 2697 g/m² in the mineral soil between classes 1 and 5, the percentage of total system C_{org} declined from 33 to 20% (Table 6).

Most of the N in this system (70 to 84%) was contained in mineral soil. Amounts of soil N increased with increasing tree size, but the proportion contained in the soil declined from 84 to 70% from class 1 to 5. The most salient result of the N budget was that by the time trees reached maturity (class 5), 30% of N was contained in trees and organic layers.

Phosphorus resided primarily in the mineral soil and the proportional distribution (95 to 97%) did not change with tree size (Table 6). By contrast, P accumulation (g/m²) in the organic layer increased 6-fold from class 1 to 5 (Table 6). Most of the aboveground P was contained in tree biomass, but amounts accumulated were similar, regardless of tree size, except for the largest trees.

TABLE 6. Distribution of carbon, nitrogen, phosphorus, and sulfur in open-intercanopy and western juniper systems as a function of tree size class.

Nutrient	Tree Size Class ¹	System Component								Total	
		Trees		Understory		Organic Layer		Mineral Soil			
		g/m ²	%	g/m ²	%	g/m ²	%	g/m ²	%	g/m ²	%
Carbon	Open	0	0	96	4.4	93	4.3	1987	91.3	2176	100.0
	1	3882	61.0	49	0.8	303	4.8	2125	33.4	6359	100.0
	2	5263	62.1	45	0.5	634	7.5	2537	29.9	8479	100.0
	3	6310	69.1	71	0.8	753	8.2	1994	21.8	9128	100.0
	4	6938	63.5	46	0.4	1199	11.0	2736	25.1	10919	100.0
	5	9390	68.9	32	0.2	1503	11.0	2697	19.8	13622	100.0
Nitrogen	Open	0.0	0.0	1.58	0.7	2.26	0.9	240	98.4	243.9	100.0
	1	38.5	13.3	0.90	0.3	8.05	2.8	243	83.7	290.5	100.0
	2	43.8	13.2	0.50	0.2	20.23	6.1	268	80.6	332.5	100.0
	3	43.5	14.3	1.10	0.4	23.81	7.8	236	77.5	304.4	100.0
	4	42.9	12.1	0.80	0.2	31.18	8.8	280	78.9	354.9	100.0
	5	59.8	16.2	0.50	0.1	49.82	13.5	258	70.1	368.1	100.0
Phosphorus	Open	0.0	0.0	0.31	0.1	0.22	0.1	228	99.8	228.5	100.0
	1	5.2	2.3	0.12	0.1	0.71	0.3	224	97.4	230.0	100.0
	2	5.7	2.4	0.09	<0.1	1.34	0.6	226	96.9	233.1	100.0
	3	5.9	2.6	0.14	0.1	1.88	0.8	220	96.5	227.9	100.0
	4	5.9	2.5	0.10	<0.1	2.36	1.0	230	96.5	238.4	100.0
	5	8.0	3.4	0.08	<0.1	4.16	1.8	225	94.8	237.2	100.0
Sulfur	Open	0.0	0.0	0.20	4.9	0.21	5.2	3.66	89.9	4.1	100.0
	1	4.2	47.2	0.12	1.3	0.94	10.6	3.63	40.8	8.9	100.0
	2	5.1	46.7	0.10	0.9	1.91	17.5	3.82	34.9	10.9	100.0
	3	6.1	50.2	0.14	1.2	2.42	19.9	3.48	28.7	12.1	100.0
	4	5.7	45.0	0.10	0.8	2.82	22.2	4.06	32.0	12.7	100.0
	5	8.3	47.9	0.08	0.5	5.14	29.7	3.79	21.9	17.3	100.0

¹ Values shown for "open" are the average of values for "no juniper" and intercanopy sites (distances 2 and 4 for tree size classes 1-5)

The pattern of S distribution among ecosystem components and size classes differed distinctly from that of N and P in most respects. Most of the S (59 to 78%) was in trees and the organic layer, with the largest amount in trees. Although the amount of S in trees almost doubled between classes 1 and 5, the proportion of system total remained fairly constant (45 to 50%). Most of the distributional difference of S among classes occurred in the organic layer, as in the case of P; the amount of S increased 5-fold from class 1 to 5 while proportion of total system S increased 3-fold. Amounts of soil S were relatively constant among classes (3.5 to 4.1 g/m²), but the proportion of total declined from 41 to 22% between class 1 and 5 (Table 6).

Results of Everett and Thran (1992), who looked at nutrient distribution in entire stands of singleleaf pinyon (*Pinus monophylla* Torr. & Frem.) in

Nevada, are not directly comparable with this study, but nonetheless worth noting. They found 53% of the site N incorporated in trees and organic layers, about three-fourths of which was in the organic layer. Our oldest trees had 30% of the system N incorporated about equally in trees and organic layers. Although P was stored primarily in soil in both western juniper and singleleaf pinyon systems, the difference in distribution (96% versus 85%) is noteworthy. Sulfur distribution presented a major contrast between the two studies. We found 59 to 78% of S in aboveground components compared to only 13% in singleleaf pinyon tree systems (Everett and Thran 1992).

Comparisons of Open and Tree Systems

Comparing storage of C_{org}, N, P, and S in open systems with that in the tree system reveals much about change in nutrient status of this sagebrush/

grass system as western juniper invades and grows to maturity. Even for the youngest trees, the amount of C_{org} in the tree system was three times greater than that of open systems. For class 5, this difference was more than 6-fold. Even the smallest (youngest) tree system (class 1) contained 16% (47 g/m²) more N than the open systems. Class 5 had accumulated 51% more N (124 g/m²) than open systems.

System P, in contrast to N, was reasonably comparable between open and tree systems. However, S accumulation differed more between tree and open systems than N. Amount of S accumulated in the tree system was 2- to 4-fold greater than open systems, depending on tree size.

Comparisons of tree with open systems indicate that western juniper effectively accumulates C_{org} , N, and S. Lack of noticeable accumulation of P by juniper systems may be due to the high soil P status prior to juniper invasion. Sources of N and S accrued to the tree system were not ascertained, but these additions apparently were not at the expense of intercanopy soils. Several sources, both biotic and abiotic, could account for net accrual of these nutrients to tree systems without a significant loss from intercanopy areas. These sources of nutrient accrual to "fertile islands" are described in the introduction to the companion paper (Klemmedson and Tiedemann 2000).

As the state of the system changes with growth to maturity of junipers, cooler understory temperatures and a moister microenvironment (Tiedemann and Klemmedson 1977) will promote higher steady state levels of soil organic matter and associated nutrients (Jenny 1930, Tiedemann and Klemmedson 1986). These conditions should lead to improved decomposition and mineralization, lower losses of soil C and N by volatilization and denitrification (West 1981, 1991) and more efficient cycling of nutrients in the juniper system than in the sparse vegetation of open systems (Odum 1969).

Conclusions

Biomass of juniper understory (1630 kg/ha) reflected the sparse appearance of this western juniper/big sagebrush/bluebunch wheatgrass ecosystem. As a consequence, understory vegetation was also a minor compartment of the soil/plant system for accumulation of nutrients.

Salient features of biomass distribution among tree components were: the decline in percentage of biomass in foliage (41 to 15%) with increasing tree size from class 1 to 5, the high mean percentage of biomass allocated to foliage (26%), and the high proportion of tree biomass allocated to live and dead branches 29 to 47%. Miller et al. (1990) noted high biomass allocation to foliage in young western juniper (<40 yr) and concluded this enabled western juniper to optimize photosynthetic capacity. Our observations suggest that this adaptive feature also may be important to mature trees in these warm, semi-arid environments.

Comparisons of tree and open systems indicate that western juniper plays a dominant role in capture and retention of nutrients in these semi-arid habitats. This role of juniper appears directly related to the time of occupancy. Nutrient accumulation patterns that we document for western juniper reinforces the importance Romney et al. (1978) ascribe to shrubs in desert ecosystems. They suggest that if fertile islands created by shrubs did not exist, fertility present in them would be dispersed over the entire area. For plants not capable of N-fixation, deficiency for that element would be present over the entire area.

Results of comparisons made here do not lead directly to answers to questions about effects of management of western juniper on future site productivity. Nonetheless, our results signal caution in the way western juniper is managed that will help avoid degradation of productivity. At these sites, availability of soil N and S are inherently low (Tiedemann and Klemmedson 1995) and levels of total N and S are below the range for interior Pacific Northwest volcanic ash soils (Tiedemann and Klock 1977, Geist and Strickler 1978). Even for the nutrient enriched tree system, levels of N and S are still at the low end of the range for interior Pacific Northwest volcanic soils. In tree systems, 59 to 78% of system S and 16 to 30% of system N are incorporated into organic layer and tree components. This, coupled with the nutrient-limited status of soils of these western juniper systems, suggests that retention of as much of the accumulated aboveground nutrient capital as possible is a prudent management strategy. Retention of tree foliage (i.e., lop and scatter) and the organic layer would be particularly important. An error on the conservative side can be corrected in the future. If residues and the organic layer are burned, only time can compensate

for volatilization loss of nutrients and for associated effects on productivity. West's (1991) review and results from Everett and Thran (1992) support this conclusion. West indicates that in habitats where shrubs or small trees contain a substantial part of the nutrient pool, fire may be more disruptive to nutrient cycles than livestock grazing. Further, West (1991) states that savannas and shrub-steppes "need careful management to maintain them since it is very difficult to re-establish the original structure once they are degraded."

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