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Phosphorus Pools in Tree and Intercanopy Microsites of a Juniper–Grass Ecosystem

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ABSTRACT

Gradients of soil-nutrient distribution between trees and intercanopy areas are common in many semiarid woodland ecosystems. To test if microsites under and between canopies influenced P pool distribution in a semiarid woodland dominated by one-seed juniper [*Juniperus monosperma* (Engelm.) Sarg.] and galleta grass [*Hilaria jamesii* (Torr.) Benth.], we compared inorganic, organic, and microbial P pools under trees and intercanopy areas of two Aridisols. Soils collected (5–15 cm depth) under eight tree canopies and in eight intercanopy areas from a Calciorthid and a Camborthid were subjected to a sequential P fractionation scheme. Soils and microsites were significant independent factors determining total soil P, which ranged from 814 μg P g^{-1} soil (SE = 25) to 1123 μg P g^{-1} soil (SE = 21). Resin P was significantly influenced by the interaction of soils with microsite. Organic hydroxide P was the largest organic P fraction and exceeded or equaled the amount of resin P. It differed significantly between the Calciorthid at 10.1 μg P g^{-1} soil (SE = 1.0) and the Camborthid at 22.1 μg P g^{-1} soil (SE = 1.6). Microsite and soil did not significantly affect microbial P, which ranged from 12.9 μg P g^{-1} soil (SE = 2.1) to 17.0 μg P g^{-1} soil (SE = 0.7). Nutrients and microbial activity are usually concentrated under canopies in semiarid and arid ecosystems. This research shows that P pools distribution in the studied ecosystem did not follow this general pattern, and that soils may be more important in determining P pool distribution than microsites.

Pinyon–juniper woodlands are a major vegetation type, occupying ≈325 000 km^2 of the western USA (West, 1984). Despite their large extent, they are poorly characterized with regard to ecosystem function and nutrient-cycling processes. Different physical, chemical, and biological properties of tree and intercanopy microsites suggest that microsites function as distinct ecological units within the overall woodland ecosystem (Barth, 1980; Fresquez, 1990; Breshears et al., 1997). Distinct gradients of soil-nutrient distribution between trees and intercanopy areas are common in semiarid woodland ecosystems and are recognized as an important structural and functional feature in nutrient-cycling dynamics (Schlesinger et al., 1990; Schlesinger and Pilmanis, 1998). Pinyon–juniper woodlands appear to share these horizontal gradients (Barth, 1980; Padien and Lajtha, 1992); however, little information is available on the distribution and dynamics of belowground elements in soils and microsites.

Phosphorus is of particular interest in pinyon–juniper ecosystem–nutrient dynamics because low levels of available soil P (Barth, 1980; Bunderson et al., 1985; Schlesinger et al., 1989) and a high proportion of mycorrhizal plant species (Klopatek and Klopatek, 1987) indicate that P may be a limiting element in these woodlands. It has been suggested that P could be more limiting to plant growth than N in pinyon–juniper ecosystems (Bunderson et al., 1985).

Phosphorus supply and cycling rate act as a fundamental control on C, N, and S dynamics, and P availability limits overall productivity in many natural ecosystems (Vitousek and Howarth, 1991; Chapin et al., 1994). Plants take up inorganic P (P_i) from the soil solution. Solution P makes up only a minimal fraction of total soil P. It is rapidly replenished by P from labile inorganic P minerals and by biochemical mineralization of labile organic P (P_o). Labile P_i and P_o are in exchange with slowly reacting inorganic P minerals, occluded P, and stable organic P (Chauhan et al., 1981; Smeck, 1985; Steward and Tiessen, 1987). The amount of P available to plants is determined by the pool size of labile P_i, the transformation rates between labile and slowly reacting P_i, and the amount and cycling rate of mineralizable P_o (Tiessen, 1991).

We hypothesized that labile, microbial, and total P would be higher under trees than in intercanopy areas because soil nutrients and microbial activity are usually more concentrated under canopies of shrubs and trees in semiarid and arid ecosystems (Barth, 1980; Schlesinger et al., 1996; Schlesinger and Pilmanis, 1998). We used the Hedley et al. (1982) fractionation to measure soil P pools in juniper and intercanopy microsites in two Aridisols in a juniper–grass ecosystem of the Colorado Plateau. The specific objectives were to test if these microsites and soils influenced the distribution of belowground P pools, and to determine the size of labile and moderately labile P_i and P_o, and microbial P pools in this ecosystem, which is slightly more arid than pinyon–juniper woodlands.

MATERIALS AND METHODS

Sites

We collected soils from two 0.45-ha sites in a one-seed juniper/galleta-dominated woodland of the Colorado Plateau in northern Arizona (35°33′ N, 111°28′ W). The sites were located about 45 km northeast of Flagstaff at Wupatki National Monument at an elevation of 1650 m. The climate at Wupatki National Monument is semiarid with 46% of the total annual precipitation occurring during thunderstorms in

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Published in Soil Sci. Soc. Am. J. 63:1901–1905 (1999).

Abbreviations: P_i, inorganic P; P_o, organic P.

July, August, and September (National Oceanic and Atmospheric Administration, 1994). The closest weather station is at the visitor center about 9.5 km from the research area at a 1492-m elevation. The long-term average precipitation is 218 mm, and the long-term average temperature is 14.3°C (National Oceanic and Atmospheric Administration, 1994). Both sites had an open stand of widely spaced, mature one-seed juniper, with distinct tree and intercanopy microsites. Vegetation characteristics of the research sites are summarized in Table 1.

Soils at the first site were Winona gravelly loam (loamy-skeletal, carbonatic, mesic Lithic Ustic Haplocalcids) formed in eolian deposits underlain by alluvium derived from limestone and calcareous sandstone (Soil Conservation Service, 1983). Soils at the second site were mapped as Epikom complex (loamy, mixed, superactive, mesic Lithic Haplocambids), developed from alluvial and eolian deposits derived from calcareous sandstone, sandy shale, and pyroclastics (Soil Conservation Service, 1983). Winona soils had a lower pH and a coarser texture than the Epikom soils (Table 2). There were no significant differences in organic carbon, clay content, and field capacity between the soils (Table 2). Both soils are covered with a 2- to 10-cm layer of black cinders, 0.5 to 1 cm in diameter. These cinders were deposited in 1064 AD and originated from the Sunset Crater volcanic field (Nations and Stump, 1981).

Soil Sampling and Phosphorus Fractionation

Within each study site, eight randomly selected mature juniper trees and eight intercanopy areas were used for soil sampling. Half of these juniper trees and intercanopy areas were used for a soil-warming experiment from 23 Aug. to 26 Nov. 1993 (Krämer, 1997). We found no residual treatment effects left in the soils in June 1994. On 3 June 1994, soil was collected from a 0- to-20 cm depth at three randomly located areas underneath each tree and in each intercanopy area with a core sampler lined with a 2.5-cm-diam. butyrate sampling tube. Samples under juniper trees were collected at approximately half the distance between the tree trunk and canopy edge. Sampling tubes were capped, placed on ice to slow microbial activity, and transported to the laboratory. In the laboratory, surface-layer materials and soil from a 0- to 5-cm depth and a 15- to 20-cm depth were discarded, and the 5- to 15-cm core sections were passed through a 2-mm sieve and composited within sample plots to yield 32 samples (2 sites × 2 microsites × 8 replicates). Soils from a 5- to 15-cm depth were used because a preliminary survey indicated that this soil layer contained the largest fraction of grass and fine juniper roots and would therefore be most likely to show differences in P fractions influenced by root activity. Soils were stored at field moisture in polyethylene bottles at −40°C until analysis.

Seven soil P pools were measured with the Hedley et al. (1982) fractionation procedure with the following modifications. We used duplicate samples of 1.0-g field-moist, unground <2-mm soil. To limit P resorption during extraction, we used a soil/solution ratio of 1:30. All extractions were done on a reciprocating shaker. Extracts were centrifuged at 25 000 × *g* for 10 min at 0°C and filtered through 0.4-μm membrane filters. Inorganic P in 0.5 *M* $NaHCO_3$ and 0.1 *M* NaOH was determined after precipitation of organic matter and centrifugation (25 000 × *g* for 10 min at 0°C) (Tiessen and Moir, 1993). After pH adjustment with *p*-nitrophenol as an indicator, P determinations were made spectrophotometrically at 882 nm, according to the Murphy and Riley (1962) method. We calculated microbial P with a *K*p factor of 0.4, which is suggested for soils with pH values ranging from 6.2 to 8.2 (Hedley and Steward, 1982). We did not extract samples with NaOH after sonification, or with HCl as done in Hedley et al. (1982). The residual fraction therefore contains all P_i and P_o not extracted by resin, 0.5 *M* $NaHCO_3$ with and without chloroform fumigation, and 0.1 *M* NaOH. The residual fraction was estimated by oxidation and acid digestion in a hydrogen peroxide (H_2O_2)/sulfuric acid (H_2SO_4) solution. Total P was estimated by separate digestion in a H_2O_2/H_2SO_4 solution; this method does not dissolve all inorganic P and therefore, the true total P of our soils is not known.

Table 2. Chemical and physical characteristics of soils (5- to 15-cm depth) at research sites.

Soil characteristic	Winona soil site		Epikom soil site	
	Intercanopy	Juniper	Intercanopy	Juniper
pH†	7.4 *a*1††	7.9 *b*1	7.9 *a*2	8.0 *b*2
Organic carbon, %‡	0.7	1.11	0.7 *a*	1.02 *b*
Textural class	Sandy loam	Sandy loam	Loam	Loam
Sand, %§	54.3 *a*1	63.6 *b*	48.2 *2*	50.7
Clay, %§	20.1	14.2	21.4	20.3
Field capacity (g/g)¶	0.28	0.29	0.30	0.32
Cinder/litter depth (cm)#	3.2 *a*1	8.6 *b*1	1.6 *a*2	4.3 *b*2

† 1:1 soil/$CaCl_2$ (McLean, 1982).
‡ Walkley-Black wet oxidation (Nelson and Sommers, 1982).
§ Bouyoucos hydrometer (Gee and Bauder, 1986).
¶ Sand tension table 10 cm deep (Reeve and Carter, 1991).
# Measured at three random locations in each plot used for soil collection.
†† Lower-case letters indicate significant differences (*t*-test, $P \leq 0.05$, $n = 3$) in intercanopy or juniper soils between research sites.

Statistical Analyses

To test the influence of two microsites (juniper and intercanopy), two soils (Winona and Epikom), and their interactions on soil P pools, we designed the study as a factorial experiment. Soils from individual trees and intercanopy areas were the experimental units. We used the balanced ANOVA procedure in MINITAB for Windows version 10.1 (MINITAB, 1994) for data analyses. Treatment means for significant interactions ($P \leq 0.1$) were separated with linear contrasts

Table 1. Average cover of dominant plant species at research sites.

Species	Cover	
	Winona soil site	Epikom soil site
	%	
One-seed juniper [*Juniperus monosperma* (Engelm.) Sarg.]†	8.2	3.5
Galleta [*Hilaria jamesii* (Torr.) Benth.]‡	7.0a§	4.5b
Sand dropseed [*Sporobolus cryptandrus* (Torr.) Gray.]‡	<0.5	<0.5
Arizona three-awn (*Aristida arizonica* Vassy.)‡	<0.5	0
New Mexican feathergrass [*Stipa neomexicana* (Thrub.) Scribn.]‡	<0.5	0
Squirrel tail [*Sitanion hystrix* (Nutt.) J.G. Smith.]‡	0	<0.5

† Estimated with spherical densiometer (Lemmon, 1956).
‡ Estimated along 5, 30 m transects at 1-m intervals in 20 by 50 cm plots based on cover classes (Daubenmire, 1968).
§ Values followed by different letters are significantly different (*t*-test, $P \leq 0.05$, $n = 10$ for tree canopy cover, $n = 5$ for grass cover) between research sites.

Table 3. Phosphorus pools (and SE in parentheses, $n = 8$) in 5- to 15-cm depth of intercanopy and juniper microsites of Winona and Epikom soils.

P pool†	Winona soil		Epikom soil		Main effects	
	Intercanopy	Juniper	Intercanopy	Juniper	Soil	Microsite
	μg P g^{-1} soil					
Extractable P_i						
Resin P_i	21.5 (5.8)‡§	11.7 (2.1)§	5.3 (0.2)	7.5 (0.6)	NS	NS
$NaHCO_3$-P_i	3.7 (1.1)‡§	2.0 (0.4)	1.3 (0.2)	1.8 (0.4)	NS	NS
NaOH-P_i	7.4 (1.4)‡§	4.3 (0.6)§	0.3 (0.1)	0.7 (0.3)	NS	NS
Extractable P_o						
$NaHCO_3$-P_o	1.4 (0.1)‡§	1.9 (0.3)§	1.9 (0.1)	1.7 (0.2)	NS	NS
NaOH-P_o	22.1 (1.6)	18.8 (1.5)	10.1 (0.8)	10.1 (1.0)	*	NS
Other						
Microbial P	13.7 (1.5)	13.5 (1.0)	17.02 (0.1)	12.9 (2.1)	NS	NS
Residual P	937.1 (28.3)	945.0 (24.9)	830.4 (27.6)	785.5 (28.8)	*	NS
Total P#	1123.3 (21.12)	1069.2 (30.8)	867.4 (16.8)	813.6 (25.2)	*	†

* and † Significant at 0.05 and 0.1 probability levels, respectively; NS = not significant.
† P_i is inorganic P; P_o is organic P.
‡ Difference between microsite within Winona soil at the 0.1 probability level.
§ Difference between soils within intercanopy microsite or within juniper microsite at the 0.1 probability level.
# By separate digestion.

(Petersen, 1985). Data are reported as means ± their standard errors (SE).

RESULTS

Microsite and soil were both significant independent factors in determining concentrations of total P (Table 3). Total P_o, NaOH P_o, and residual P concentrations were independent of microsites, but were significantly affected by soil. Microsites influenced the P pools significantly only in interaction with soil. Microbial P was the only P pool not affected by either microsite or soil.

Total P ranged from 813 to 1123 μg g^{-1} (Table 3). It was higher in intercanopy than juniper microsites and higher in Winona than Epikom soils. Residual P accounted for 94 to 97% of total soil P and was higher in Winona than Epikom soil.

Total extractable P_o exceeded total extractable P_i, except in Winona intercanopy soils, which had the highest total extractable P_i. Total extractable P_o was higher in Winona than Epikom soil.

Resin P was the largest extractable P_i fraction. The Winona intercanopy microsite contained more resin P than the Winona juniper microsite and the Epikom intercanopy microsite. Hydroxide extractable P_i was a large P_i pool in Winona soil, where it contributed 23% to total P_i in intercanopy soil and 24% in juniper soils. In the Epikom soil, $NaHCO_3$ P_i was a larger P_i pool than NaOH P_i. Microsites did not differ significantly in NaOH P_i. Bicarbonate P_i was higher in Winona than Epikom intercanopy microsites, but did not differ in juniper microsites. Both microsites contained more NaOH P_i in the Winona than the Epikom soil.

Hydroxide extractable P_o was the largest P_o pool in both soils and microsites and exceeded or equaled the amount of resin P. It was significantly higher in Winona than Epikom soil. Hydroxide-extractable P_o contributed up to 94% to total P_o and was the largest extractable P pool in Winona soil. Bicarbonate-extractable P_o in the Winona intercanopy microsite was significantly lower than in the juniper microsite and lower than in the Epikom intercanopy microsite.

DISCUSSION

Total and extractable P pools reflected large aboveground vegetation differences between microsites only to a limited extent. Absolute values for P_i fractions and $NaHCO_3$ P_o were significantly different between microsites in Winona but not in Epikom soil. Hydroxide-extractable P_o, microbial P, and residual P did not vary significantly between microsites on either soil. We expected to find more labile, microbial, and total P under trees than in intercanopy areas since soil nutrients and microbial activity are usually more concentrated under canopies of shrubs and trees in semiarid and arid ecosystems (Barth, 1980; Schlesinger et al., 1996). However, total soil P in this study was significantly higher in intercanopy than juniper microsites. DeBano et al. (1987) also found higher total P concentrations in intercanopy than tree soils in a stand of Utah juniper [*J. osteosperma* (Torr.) Little] in central Arizona.

Total P in these juniper–grass soils was higher than the mean but below the maximum total P in A horizons of 120 benchmark soils, representing eight soil orders from all regions of the USA (Tiessen et al., 1984). Winona total P exceeded all values reported for 88 natural, unfertilized, and uncultivated soils reported by Cross and Schlesinger (1995). Total P is considered a primary property of a soil (Tiessen et al., 1984) and normally decreases because of the effects of weathering and leaching from weakly weathered Entisols to strongly weathered Oxisols (Smeck, 1985). Differences in total P of the two Aridisols could be due to variations in P content of parent materials, differences in soil development, or most likely, a combination of both.

On average, 96% of the total soil P was in sparingly soluble form (residual P) and therefore available to the biotic components of the juniper–grass ecosystem only through long-term P transformations and weathering.

Of the more rapidly cycling P forms, 18.5 to 36.1% were in readily plant-accessible resin and $NaHCO_3$ P_i pools (Tiessen and Moir, 1993). The sum of resin P and $NaHCO_3$ P_i constituted an average of 13.7 μg P g^{-1} soil. This value is much lower than the average of 43.5 μg P g^{-1} soil for nine Aridisols calculated from data in Cross and Schlesinger (1995) and the mean (42.7 μg P g^{-1} soil) of 120 A horizons from wildland and agricultural soils (Tiessen et al., 1984). This suggests that P availability may be limiting to plant growth in this pinyon–juniper ecosystem.

Soils contained higher concentrations of microbial P (12.9 to 17.0 μg g^{-1} soil, 1.4 to 2.0% of total P) than a chronosequence of Haplargids developed on quartz monzonite in southwestern New Mexico (Lajtha and Schlesinger, 1988). Microbial P in quartz monzonite Haplargids was less than 1% of the total P content during most of the growing season except after several rainfall events, when it comprised 2.7%. Although microbial P did not exceed 2% of the total P content in the soils of this study, it may be a significant P pool, as P in microbial biomass is accessible to plants through rapid turnover and seasonal changes of the microbial pool size (Seeling and Zasoski, 1993; Campo et al., 1998).

Hydroxide-extractable P was a large P pool. Inorganic NaOH P is sorbed to Fe and Al compounds of soil surfaces and humic substances (Ryden et al., 1977; Schoenau et al., 1989) and is considered moderately labile or slow turnover P (Hedley et al., 1982; Trasar-Cepeda et al., 1990). It is usually formed at the expense of more labile P_i forms (Tiessen et al., 1984). Inorganic NaOH P made up 2.4 to 25% of total NaOH P in this study. Hydroxide-extractable P_o is generally considered a stable form of organic P involved in long-term P transformations in the soil (Tiessen et al., 1984; Wager et al., 1986). However, Tiessen et al. (1983) reported that NaOH P_o from soil organic matter associated with the coarse silt and fine clay fractions was quite labile and may undergo significant changes during a growing season. Microorganisms can use NaOH P_o in soils of low-labile P_i content (Chauhan et al., 1981) and release at least a fraction of it as more labile P_i and P_o on cell death. The NaOH P_o pool and organic-matter content was found to be increasingly important to P cycling with soil age in a chronosequence of alkaline soils (Carreira et al., 1997). The organic NaOH P pool could constitute a major reservoir for replenishment of more labile P pools, especially in Winona soil, which had significantly more NaOH P_o than Epikom soil. The two soils may vary in NaOH P_o pool sizes because of differences in plant cover. The Winona site had significantly more perennial grass in intercanopy areas and a higher cover of trees than the Epikom site (Table 1), which would result in more plant litter input in Winona than Epikom soil.

Organic $NaHCO_3$ P is a labile P pool that is easily mineralized and contributes to plant- available P (Hedley et al., 1982). It is positively correlated with soil phosphatase activity and microbial biomass during the growing season (Halm et al., 1972). Organic $NaHCO_3$ P in this study was much lower than in five Aridisols, which ranged from 4 to 14 μg P g^{-1} soil (Sharpley et al., 1985). Bicarbonate-extractable P_o is probably of minor importance as a plant-available P pool in this juniper–grass ecosystem because of its small amount.

The ratio of organic $NaHCO_3$ P to the sum of labile P (resin P, $NaHCO_3$ P_i, and $NaHCO_3$ P_o) has been suggested as an index for the amount of P that can be easily mineralized through biological processes (Cross and Schlesinger, 1995). This ratio ranged from 13 to 75% for 61 soils from eight soil orders with Aridisols having the smallest ratio (Cross and Schlesinger, 1995). The average ratio in this study (13.9%) was similar to that reported in Cross and Schlesinger (1995) for Aridisols, indicating that soils in this study do not differ from other Aridisols in their biological mineralization potential.

CONCLUSIONS

Colorado Plateau juniper–grass soils were high in total P, but very low in plant-available P compared with a wide range of soils and several soil orders. The distribution of extractable P pools and total P between tree and intercanopy areas did not reflect the large vegetation differences in juniper–grass ecosystem microsites. This suggests that P pools and cycling processes may not be as tightly linked to microsites as suggested for other nutrients in arid and semiarid ecosystems. The microsite, interacting with soil, was the dominant factor in determining P pool sizes. Resin P, microbial P and NaOH P_o were the largest extractable P pools. However, further research is necessary on microbial P turnover rates and NaOH P_o mineralization to determine the actual contribution of these P pools to plant-available P.

ACKNOWLEDGMENTS

This research was supported in part by a Grant-in-Aid of Research from Sigma Xi, The Scientific Research Society, and the Associated Students of Arizona State University. Thanks to the National Park Service and the staff at Wupatki National Monument for use of the study sites and support of the field work. T. Cory and many others assisted with soil collection and sample analysis.

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