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Acid and alkaline phosphatase dynamics and their relationship to soil microclimate in a semiarid woodland

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Abstract

The seasonal dynamics of acid and alkaline phosphatase activity (μg *p*-nitrophenol released g^{-1} soil h^{-1}), soil water potential and temperature, and the relationship of phosphatase activity to plant and soil microbial processes underneath *Juniperus monosperma* canopies and *Hilaria jamesii*-dominated intercanopy areas were studied in a northern Arizona pinyon–juniper ecosystem. Alkaline phosphatase activity was significantly higher in soils under junipers (126.5 ± 3.9 μg *p*-nitrophenol g^{-1} soil h^{-1}) than in intercanopy soils (106.6 ± 4.0 μg *p*-nitrophenol g^{-1} soil h^{-1}), and significantly exceeded acid phosphatase activity by a factor of 6. Seasonal high phosphatase activities were up to 2.4 times greater than seasonal lows. Activities were maximal in summer and winter. Juniper soils were cooler than intercanopy soils except during the coldest months of the year, when they were up to 2.7°C warmer. Intercanopy soils were up to 6.2°C warmer than juniper soils, and had the highest (30.0 ± 0.3°C) and the lowest average temperatures (2.3 ± 0.2°C). Soil microclimate explained as much as 20% of the variation in acid and alkaline phosphatase. Temperature and water potential together were better predictors of phosphatase activity than either one alone. The soil water potential class -0.1 MPa $\geq \psi > -0.5$ MPa was the most frequent best predictor of phosphatase activity, especially alkaline phosphatase. The winter peak in alkaline phosphatase activity is attributed to a buildup of phosphatase released into the soil from dying soil organisms, and the desorption and reactivation of previously accumulated phosphatase.

Keywords: Alkaline phosphatase; Acid phosphatase; Soil moisture; Soil temperature; *Juniperus monosperma*; Pinyon–juniper; Semiarid soils

1. Introduction

Phosphorus availability may be the most limiting factor to plant growth in many terrestrial ecosystems (Attiwill and Adams, 1993; Chapin et al., 1994). It is at marginal or limiting amounts in pinyon–juniper ecosystems dominated by Utah juniper (*Juniperus osteosperma* (Torr.) Little) (Tiedemann, 1987). Much of the plant demand for phosphorus is met by cycling of phosphorus in organic matter (Attiwill, 1980; Attiwill and Adams, 1993). Since plants utilize only inorganic phosphorus (Stevenson, 1986), organic phosphorus compounds must first be hydrolyzed by phosphatases which mostly originate from plant roots, fungi and soil microorganisms.

Phosphatases measured in soils reflect the activity of enzymes bound to soil colloids and humic substances, free phosphatases in the soil solution, and phosphatases associated with living and dead plant or microbial cells (Skujins, 1976; Nannipieri et al., 1990). Phosphatase enzymes can be a good indicator of the organic phosphorus mineralization potential and biological activity of soils (Speir and Ross, 1978; Dick and Tabatabei, 1993). Phosphatase activity is related to soil and vegetation conditions (Ho, 1979; Herbien and Neal, 1990), responds to changes in management

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Table 1
Chemical and physical characteristics of soils (5–15 cm depth) at research sites. Lower case letters indicate significant differences (*t*-test, $P \leq 0.05$) between intercanopy and juniper soils within research sites. Upper case letters indicate significant differences (*t*-test, $P \leq 0.05$) in intercanopy or juniper soils between research sites

Soil characteristic	Site 1: Winona gravelly loam		Site 2: Epikom complex	
	Juniper	Intercanopy	Juniper	Intercanopy
pH[a]	7.9 *aA*	7.4 *bA*	8.0 *aB*	7.9 *bB*
Organic carbon (%)[b]	1.1	0.7	1.0 *a*	0.7 *b*
Total phosphorus ($\mu g\ g^{-1}$)[c]	858.9 *A*	925.4 *A*	668.2 *B*	685.2 *B*
Available phosphorus ($\mu g\ g^{-1}$)[d]	41.3 *A*	50.0 *A*	23.7 *B*	29.2 *B*
Textural class	sandy loam	sandy loam	loam	loam
% Sand[e]	63.6 *aA*	54.3 *b*	50.7 *B*	48.2
% Clay[e]	14.2	20.1	20.3	21.4
Field capacity ($\mu g\ g^{-1}$)[f]	0.29	0.28	0.32	0.30
Cinder/litter depth (cm)[g]	8.6 *aA*	3.2 *bA*	4.3 *aB*	1.6 *bB*

[a] 1:1 soil/$CaCl_2$ (Page et al., 1982).
[b] Walkley–Black wet oxidation (Page et al., 1982).
[c] H_2SO_4/H_2O_2 digestion (Rowland and Grimshaw, 1985) and Murphy and Riley (1962) P determination.
[d] Sum of resin P, microbial P and NaOH P (Hedley et al., 1982).
[e] Bouyoucos hydrometer (Klute, 1986).
[f] Sand tension table 10 cm deep (Reeve and Carter, 1991).
[g] Measured at three random locations in each plot used for phosphatase analyses.

(Adams, 1992; Clarholm, 1993), and can be related to seasonal changes in soil temperature and moisture (Harrison, 1983; Dormaar et al., 1984; Speir and Cowling, 1991). However, much of the phosphatase research is based on a single sampling date and ignores the dynamics of phosphatase relative to other soil factors over time.

Distinct horizontal gradients of soil nutrient distribution, biological activity, and microclimate are common in shrub- and tree-dominated arid and semiarid ecosystems (Barth and Klemmedson, 1978; West, 1989; Schlesinger et al., 1996), and are recognized as an important structural and functional feature in nutrient cycling dynamics (Garner and Steinberger, 1989; Schlesinger et al., 1990). Pinyon–juniper woodlands share these horizontal gradients (Fresquez, 1990; Padien and Lajtha, 1992; Evans and Ehleringer, 1994); however, reports on the functioning of distinct microsites over time are lacking.

Our primary objectives were to (1) examine seasonal dynamics of soil phosphatase activity, soil moisture and soil temperature under trees and in intercanopy areas and (2) analyze the relationship of phosphatase activity to soil microclimate.

2. Methods

2.1. Study sites and area

We established two study sites in a one-seed juniper–galleta (*Juniperus monosperma* (Engelm.) Sarg.–*Hilaria jamesii* (Torr.) Benth.) dominated woodland of the Colorado Plateau in northern Arizona, USA (35°33′ N, 111°28′ W). The sites were located 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 July, August and September (NOAA, 1994). The closest weather station is about 9.5 km from the research area at 1492 m elevation. Long-term average precipitation is 218 mm, and long-term average temperature is 14.3°C (NOAA, 1994). During the study period, annual temperature was 1.4°C above the long-term average and annual precipitation was 39 mm below the long-term average (NOAA, 1993, 1994).

Soil characteristics varied considerably between study sites (Table 1) although they were within 500 m of each other. Site 1 soil was a Winona gravelly loam, a loamy-skeletal, mixed, mesic Lithic Ustollic Calciorthids, site 2 soil an Epikom complex, a loamy, mixed, mesic Lithic Camborthids (Soil Conservation Service, 1983). Both sites had an open stand of widely spaced, mature one-seed juniper, and distinct tree and intercanopy microsites. Areas under tree canopies lacked vegetation and were covered with a thick layer of juniper litter and dark cinders (Table 1). Intercanopy areas were dominated by galleta (Krämer, 1997) and had a cinder layer less than half the thickness of the cinder-litter mixture under trees (Table 1). Intercanopy soils (5–15 cm depth) had a lower pH and less organic carbon, and slightly more total and available phosphorus than soils under juniper

Table 2
Soil moisture classes and soil microbiological processes[a]

Soil moisture class	Microbiological processes
-0.02 MPa $\geq \psi > -0.05$ MPa	optimum range for decomposition
-0.05 MPa $\geq \psi > -0.1$ MPa	bacteria grow well in soil pores, fungi are generally excluded
-0.1 Mpa $\geq \psi > -0.5$ MPa	fungi enter and grow in soil aggregates and pores, bacterial growth and activity decreases
-0.5 Mpa $\geq \psi > -1.5$ MPa	movement and growth of bacteria and protozoa stops
$\psi \leq -1.5$ MPa	microbial activity mostly limited to fungi and actinomycetes

[a] Based on Cook and Papendick (1970), Wildung et al. (1975), Wilson and Griffin (1975), Griffin (1980), Sommers et al. (1980) and Killham (1994).

canopies (Table 1). Microsites had the same soil texture and water holding capacity. However, on site 1 juniper soils had a larger sand fraction than intercanopy soils.

2.2. Phosphatase analyses

Within each study site, we randomly selected four mature juniper trees and four intercanopy plots for the study of soil phosphatase. Soil was collected from 0 to 20 cm depth at monthly intervals from September 1993 to September 1994. From each tree and intercanopy plot, we obtained three randomly located subsamples using a core sampler lined with a 2.5 cm dia 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, core sections from the 5–15 cm depth were sieved (2 mm) and composited within sample plots. Phosphatase analysis was performed on soils from 5 to 15 cm depth since a preliminary survey indicated that this soil layer contained a large fraction of grass and fine juniper roots. Since phosphatase activity remains stable over 28 d in moist soils stored at 4°C (Pettit et al., 1977), we kept soils refrigerated in polyethylene bottles and processed and analyzed them within 4 weeks of sampling.

We measured potential acid and alkaline phosphomonoesterase (EC 3.1.3.2., EC 3.1.3.1.) activity in field moist soil samples with a buffered 25 mM disodium *p*-nitrophenylphosphate tetrahydrate solution. We followed the method of Tabatabai (1982) with the following modifications suggested by Schinner et al. (1995): $CaCl_2$ was omitted from the sample and NaOH was added after filtration, just before measuring absorbance with a spectrophotometer. These modifications were necessary as the original method led to flocculation of $Ca(OH)_2$ and occasional release of humic substances, which interfered with absorbance measurements. Analyses were conducted in triplicate with one non-substrate control. Results are expressed as μg *p*-nitrophenol g^{-1} h^{-1} at 37°C.

2.3. Soil temperature and moisture

We installed three type T thermocouples and three soil moisture blocks (Delmhorst GB-1 cylindrical gypsum blocks) in each microsite selected for phosphatase sampling during August 1993. Sensor pairs were pressed into the sides of small soil pits at 10 cm depth in N, ESE and WSW orientations of each tree and intercanopy area. Sensors under trees were located approximately half way between the tree trunk and canopy edge. Soil temperature and water content were measured with dataloggers programmed to summarize hourly recordings into 12 h averages, minimums and maximums at 6.00 and 18.00 h daily. We converted water content measurements in resistance (Ω) to MPa of soil matric potential using the equation: $\text{MPa} = ([4.253 \times 10^{-4} \quad \Omega] + 0.2)/10$ (Roundy et al., 1983). Soil matric potential data was tabulated in five moisture classes that constitute approximate limits for soil microbiological processes (Cook and Papendick, 1970; Wildung et al., 1975; Wilson and Griffin, 1975; Griffin, 1980; Sommers et al., 1980; Killham, 1994) (Table 2) and expressed as the average number of days per soil moisture class during each 22 d period prior to the monthly phosphatase sampling. Temperature measurements were summarized into average daily temperature during the 22-d period prior to phosphatase sampling. The 22-d period was selected because it represented the longest common time interval between sampling for phosphatase with complete soil moisture and temperature data. There were 10 sampling periods with complete data for soil microclimate. Soil temperature and moisture data were incomplete for September 1993, October 1993 and August 1994, due to datalogger programming problems and a lightning strike.

2.4. Statistical analyses

To test the influence of two soils (site 1 and site 2), two microsites (juniper and intercanopy) and their interactions on soil phosphatase activity, temperature and moisture over time, we designed the study as a factorial experiment. Individual trees and intercanopy plots were the experimental units. We used a repeated

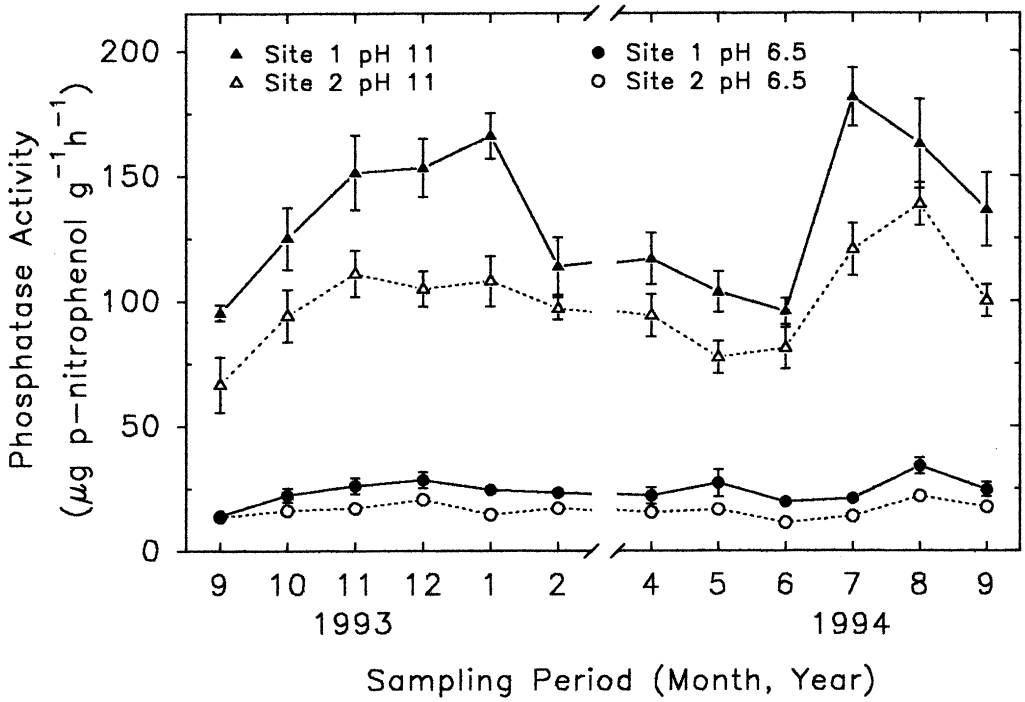

Fig. 1. Seasonal changes in alkaline (pH 11) and acid (pH 6.5) phosphatase activity (μg *p*-nitrophenol g^{-1} h^{-1}) in soils of site 1 and site 2. Numbers are means ± SEM.

measures analysis of variance (ANOVA) for data analyses (Winer, 1971). ANOVAs were performed with the GLM procedure in MINITAB for Windows version 10.1 (MINITAB, 1994). Soil moisture data (number of days/22 d sampling period within each soil moisture class) were arcsine transformed with a modified Freeman and Tukey (1950) transformation (Zar, 1984). Treatment means for significant interactions were separated with linear contrasts (Petersen, 1985). We used a significance level of $P \leq 0.05$ for ANOVAs and means separations. Data are reported as means ± their standard errors (SEM). For ease of interpretation, soil moisture data are presented untransformed.

We tested the functional dependence of soil phosphatase activity on soil temperature and moisture with simple linear and multiple regression procedures (Zar, 1984). Acid and alkaline phosphatase activity in intercanopy and juniper microsites with site 1 and site 2 data separated and combined, were regressed against average daily soil temperature and each soil moisture class (Table 2). Regressions were calculated for each dependent variable with either temperature or soil moisture class, and all possible combinations of temperature and soil moisture class. The best single or combinations of two predictors were selected based on highest coefficients of determination (r^2, R^2) and significance levels of the calculated regressions. Regressions with $P \leq 0.1$ were considered as significant.

3. Results

3.1. Phosphatase activities

Alkaline phosphatase activity was significantly different between microsites averaging 126.5 (±3.9) μg *p*-nitrophenol g^{-1} h^{-1} in juniper soils and 106.6 (±4.0) μg *p*-nitrophenolg^{-1} h^{-1} in intercanopy soils. Average acid phosphatase activity was significantly lower than alkaline phosphatase in both microsites, but it was not different between juniper and intercanopy soils. Juniper microsites averaged 20.5 (±0.8) μg *p*-nitrophenol g^{-1} h^{-1} and intercanopy microsites 20.0 (±0.9) μg *p*-nitrophenol g^{-1} h^{-1} for acid phosphatase activity.

Acid and alkaline phosphatase activities were higher at site 1 than site 2, however only differences in alkaline phosphatase levels were significant (Fig. 1). Phosphatase activities were not different within microsites between sites. On both sites, alkaline phosphatase activity was significantly higher than acid phosphatase throughout all sampling periods.

Within sites, acid and alkaline phosphatase varied more than 2-fold among sampling periods (Fig. 1). Acid phosphatase levels ranged from 11.3 (±1.2) at site 2 to 34.1 (±3.2) μg *p*-nitrophenol g^{-1} h^{-1} at site 1, alkaline phosphatase ranged from 66.6 (±11.1) at site 2 to 181.6 (±11.8) μg *p*-nitrophenol g^{-1} h^{-1} at site 1. Both enzymes followed a similar seasonal pattern at site 1 and 2. Activities increased from fall to winter

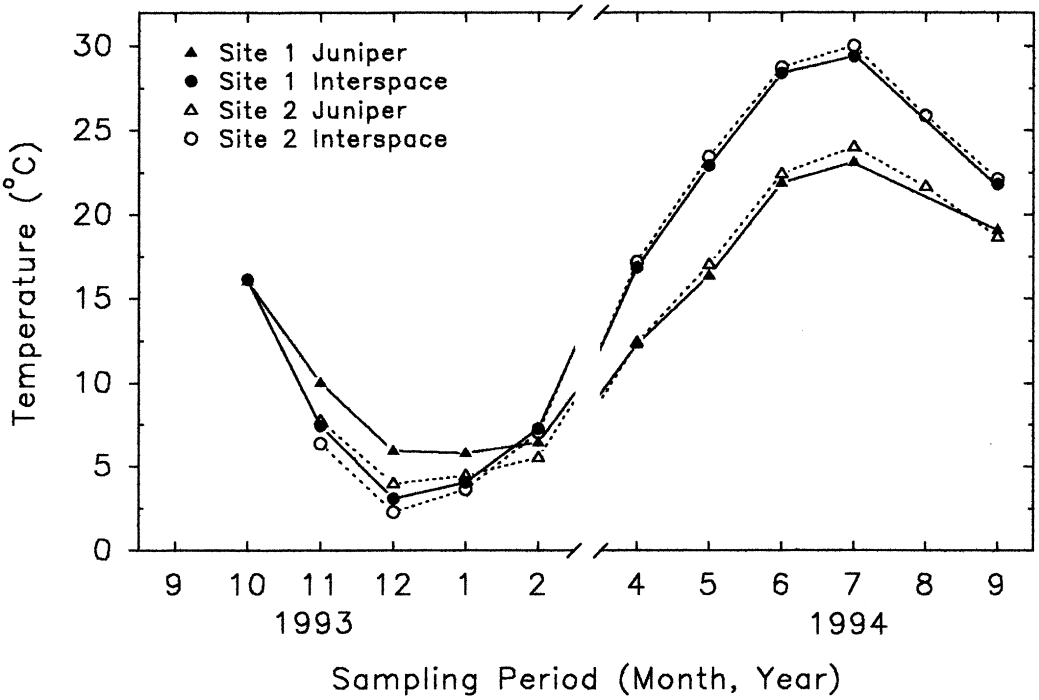

Fig. 2. Average soil temperatures (°C) at 10 cm depth in juniper and intercanopy microsites of site 1 and site 2. Error bars (SEM) are too small to display at the graph scale.

1993 to the first peak in activity, decreased through spring and early summer, reached their maximum in summer 1994, and then dropped again in fall (Fig. 1).

3.2. Soil temperature

Soil temperatures at both sites and microsites followed a sinusoidal pattern with minima in winter and maxima in summer (Fig. 2). Soils at site 1 were warmer than site 2 until February 1994, and cooler or the same as site 2 from April 1994 to September 1994. Juniper microsites were significantly different between sites from November 1993 to January 1994, intercanopy soil temperatures were not significantly different between sites during any sampling period.

At site 1, juniper microsites were significantly warmer than intercanopy microsites from November 1993 to January 1994. Juniper soil temperatures stayed 2.7°C above intercanopy soils during December 1993, when the lowest soil temperatures were recorded. Intercanopy soils were significantly warmer than juniper soils from April 1994 to September 1994. The largest temperature differences between microsites at site 1 occurred during July 1994, when intercanopy areas averaged 29.4 ($\pm$0.2)°C, and exceeded juniper soil temperatures by 6.2°C.

Site 2 juniper soils were significantly warmer than intercanopy soils during November 1993 and December 1993, and significantly cooler from February 1994 to September 1994. The lowest and highest average soil temperature occurred in intercanopy areas at site 2 with 2.3 ($\pm$0.2)°C in December 1993, and 30.0 ($\pm$0.3)°C in July 1994. Site 2 intercanopy soils were up to 1.7°C cooler than juniper soils in winter, and up to 6.0°C warmer in summer.

3.3. Soil moisture

In both microsites, soil matric potential dropped to -1.5 MPa or lower for at least 2 d during all sampling periods with the exception of December 1993 (Fig. 3). From April 1994 to July 1994, soil matric potential was ≤ -1.5 MPa 77–100% of each time period.

In juniper microsites, soils were ≤ -1.5 MPa during 61%, and in intercanopy microsites during 56% of the total sampling time. Juniper soils were at matric potentials of -0.02 MPa $\geq \psi > -0.05$ MPa during November 1993 and August 1994 or 5% of the total sampling time, at matric potentials of -0.05 MPa $\geq \psi > -0.1$ MPa during November 1993, December 1993, and from July 1994 to September 1994 for a total of 2% of the total sampling time, and at matric potentials of -0.1 MPa $\geq \psi > -0.5$ MPa during November 1993, January 1994 to March 1994, August 1994 and September 1994 for a total of 20% of the sampling time.

Intercanopy soils were at $-0.02 \geq \psi > -0.05$ MPa during November 1993, February 1994 and August 1994, a total of 10% of the sampled time. They reached soil matric potentials of $-0.05 \geq \psi > -0.1$

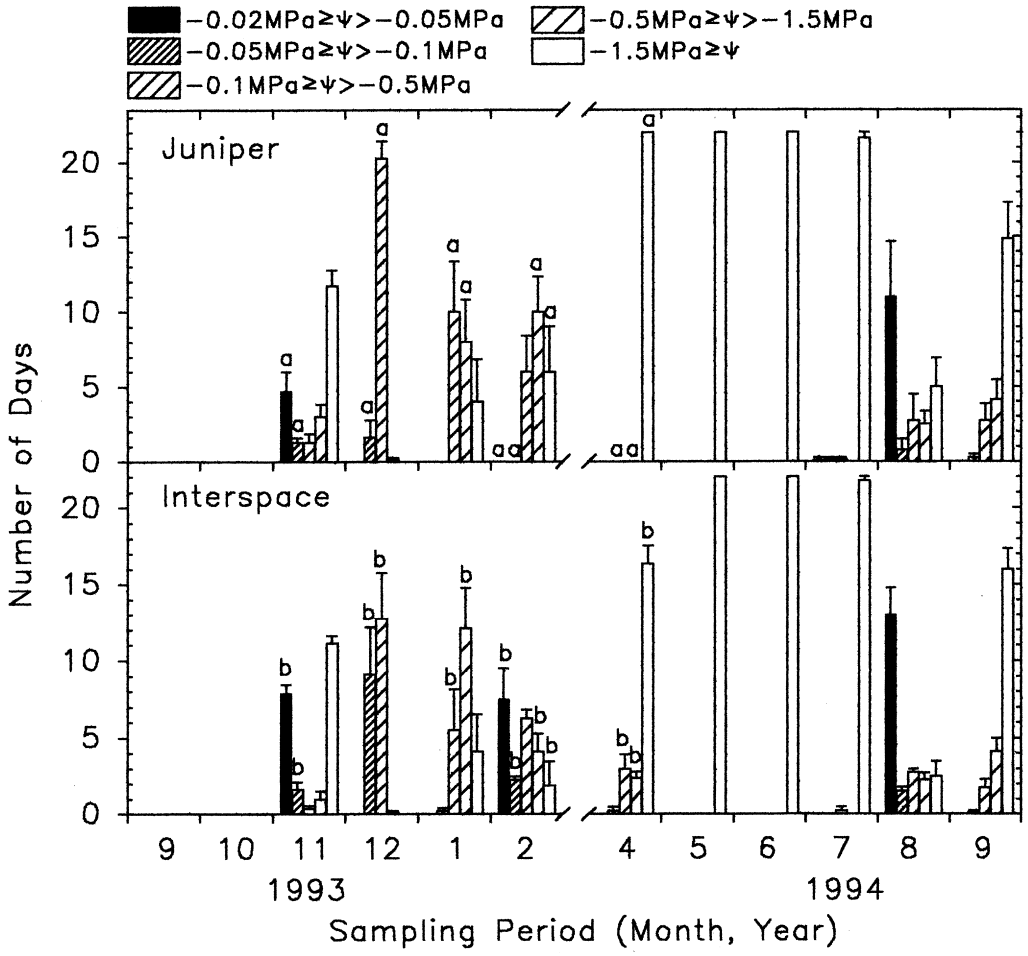

Fig. 3. Seasonal variation in soil moisture (average number of days within each soil matric potential class) in juniper and intercanopy microsites. Numbers are means ± SEM. Lower case letters indicate significant differences ($P \leq 0.05$) in the number of days within matric potential classes between microsites for the sampling period.

MPa during all sampling periods except May 1994 to July 1994, a total of 7% of the sampling time, and were at soil matric potentials of −0.1 MPa $\geq \psi >$ −0.5 MPa from November 1993 to April

Table 3
Best predictors, sample numbers (N), coefficients of determination for simple (r^2) and multiple regression (R^2) and significance levels (P) for regressions of acid and alkaline phosphatase activities in juniper and intercanopy microsites of site 1 and 2 against soil temperature and soil matric potential

Dependent variable	Independent variable(s)	N	r^2, R^2	P
Acid phosphatase activity				
Juniper site 1 + site 2	Temp., −0.5 MPa $\geq \psi >$ −1.5 MPa	76	0.09	0.04
Site 1	Temp., $\psi \leq$ −1.5 MPa	36	0.10	0.18
Site 2	Temp., −0.05 MPa $\geq \psi >$ −0.1 MPa	40	0.15	0.05
Intercanopy site 1 + site 2	Temp., −0.5 MPa $\geq \psi >$ −1.5 MPa	76	0.07	0.08
Site 1	Temp., −0.1 MPa $\geq \psi >$ −0.5 MPa	36	0.06	0.36
Site 2	Temp., $\psi \leq$ −1.5 MPa	40	0.19	0.02
Alkaline phosphatase activity				
Juniper site 1 + site 2	Temp., −0.1 MPa $\geq \psi >$ −0.5 MPa	76	0.04	0.21
Site 1	−0.1 MPa $\geq \psi >$ −0.5 MPa	36	0.09	0.08
Site 2	Temp., $\psi \leq$ −1.5 MPa	40	0.15	0.05
Intercanopy site 1 + site 2	Temp., −0.1 MPa $\geq \psi >$ −0.5 MPa	76	0.04	0.24
Site 1	−0.1 MPa $\geq \psi >$ −0.5 MPa	36	0.05	0.17
Site 2	Temp., $\psi \leq$ −1.5 MPa	40	0.20	0.02

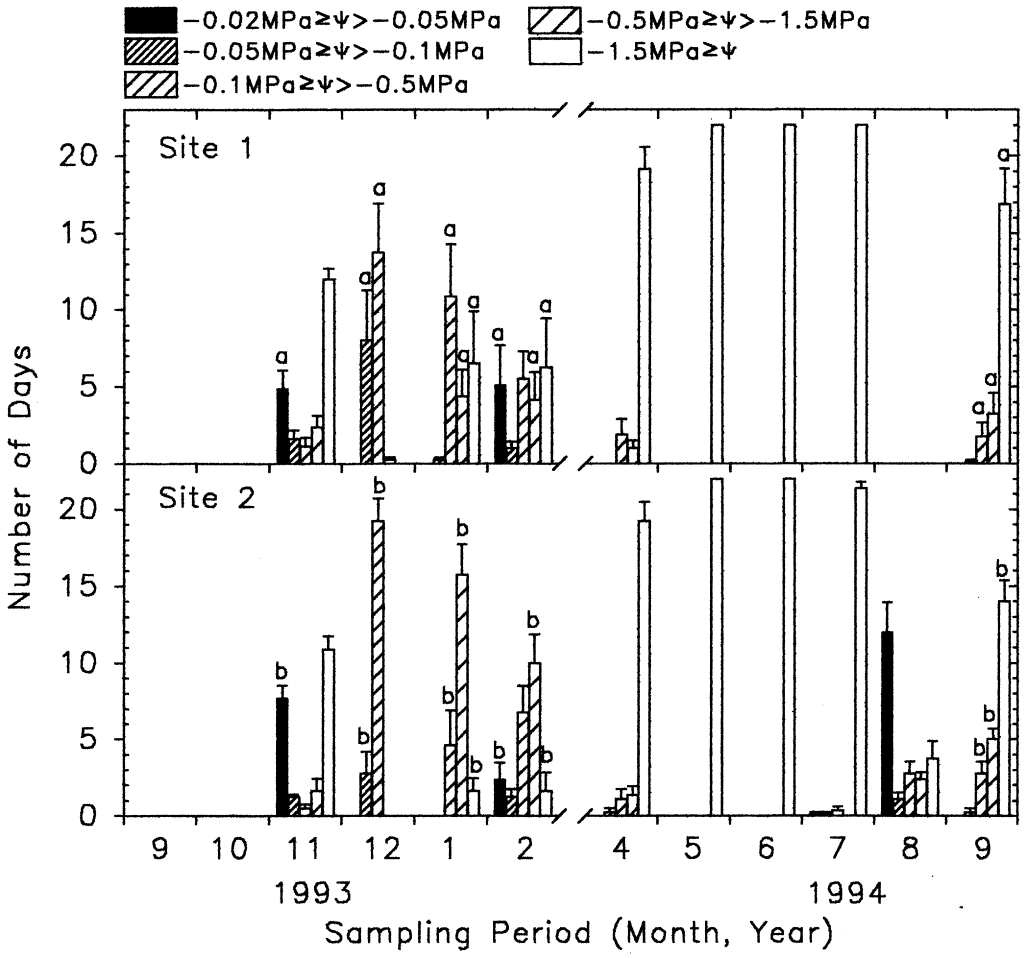

Fig. 4. Seasonal variation in soil moisture (average number of days within each soil matric potential class) at site 1 and site 2. Numbers are means ± SEM. Different lower case letters indicate significant differences ($P \leq 0.05$) in the number of days within matric potential classes between sites.

1994, August 1994 and September 1994 for 15% of the total sampling time. Intercanopy microsites were significantly wetter than juniper microsites during November 1993, December 1993, February 1994 and April 1994, and significantly drier during January 1994. From May 1994 to September 1994, microsites did not differ significantly in their soil matric potentials.

Site 1 soils were generally drier than site 2 (Fig. 4). Soil matric potentials were ≤ -1.5 MPa during 64% of the total sampled time at site 1, and 57% at site 2, excluding August 1994 due to incomplete data. Soils at site 1 were significantly wetter than at site 2 during December 1993 and January 1994 (Fig. 4). Excluding August 1994, site 1 and 2 had the same number of days with matric potentials of -0.02 MPa $\geq \psi > -0.05$ MPa and -0.1 MPa $\geq \psi > -0.5$ MPa. During time periods with soil water potentials above -1.5 MPa, soils at both sites were most frequently at -0.1 MPa $\geq \psi > -0.5$ MPa, a total of 18% of the sampled time.

3.4. Relationships of phosphatase activity and soil microclimate

Soil microclimate explained up to 20% of the observed variation in acid and alkaline phosphatase activities (Table 3). Temperature and moisture together were better predictors for most tested relationships than temperature or moisture separately. The only exceptions were alkaline phosphatase in juniper and intercanopy microsites at site 1 (Table 3). Regressions for the combined site data generally had lower R^2 than regressions for individual sites. Soil temperature and moisture explained the largest percentage of phosphatase variation in site 2 soils with R^2 of 0.15 for acid and alkaline phosphatase in juniper microsites, and 0.19 for acid and 0.20 for alkaline phosphatase in intercanopy microsites.

The best predictors for alkaline phosphatase activity in juniper microsites were also the best predictors for intercanopy microsites (Table 3). The soil moisture class -0.1 MPa $\geq \psi > -0.5$ MPa was the most fre-

quent best predictor either by itself or in combination with temperature for alkaline phosphatase. Soil matric potentials ≤ -1.5 MPa in combination with temperature were the best predictors for alkaline phosphatase at site 2. The best alkaline phosphatase regressions for combined sites and site 1 intercanopy soils were not significant.

The best predictors for acid phosphatase were temperature and all soil moisture classes with the exception of -0.02 MPa $\geq \psi > -0.05$ MPa. All regressions on combined sites and site 2 acid phosphatase activity were significant (Table 3).

4. Discussion

Plant roots are major producers of acid phosphatase (Speir and Cowling, 1991; Dinkelaker and Marschner, 1992), but do not produce alkaline phosphatase (Nakas et al., 1987; Tarafdar and Claassen, 1988). Alkaline phosphatase originates from soil bacteria, fungi and fauna (Nakas et al., 1987; Tarafdar and Claassen, 1988). Microbes can produce and release large amounts of extracellular phosphatase due to their large combined biomass, high metabolic activity and short lifecycles (Speir and Ross, 1978). In high pH soils, alkaline phosphatase generally exceeds acid phosphatase activity (Eivazi and Tabatabai, 1977). In this study, alkaline phosphatase was on average 6 times higher than acid phosphatase activity, when sites and sampling periods were combined. Soil microbes therefore appear to be the main producers of phosphatase in these pinyon–juniper soils.

Potential alkaline phosphatase activity was significantly higher in juniper microsites than in intercanopy microsites. This may be due to a larger fungal community under trees. Soil fungi are effective producers of alkaline phosphatase (Tarafdar and Chhonkar, 1979). Fungal propagule counts are significantly higher in soil beneath one-seed junipers as compared to grass-dominated intercanopy areas (Fresquez, 1990). Higher alkaline phosphatase activity and significantly higher fungal communities under trees than under grass have been reported for arid soils in India (Tarafdar et al., 1989). Regressions of soil matric potentials against phosphatase activity from this study also suggest a dominant role of fungi in alkaline phosphatase production. The length of time with soil matric potentials limiting bacterial but not fungal activity (Table 2) were the best predictors for alkaline phosphatase activity (Table 3). Predictors were the same for alkaline phosphatase activity in juniper and intercanopy microsites. (Table 3) This may indicate that functionally similar organisms produce alkaline phosphatase in both microsites.

Alkaline and acid phosphatase activity showed a seasonal pattern with maxima in winter and summer (Fig. 1). Seasonal high phosphatase activities were up to 2.4 times greater than seasonal lows. This observation is inconsistent with Skujins (1976), who noted that seasonal variations in phosphatase activity are generally small. Although significant correlations of phosphatase activity with soil moisture have been reported (Harrison, 1983; Speir and Cowling, 1991), in our study soil moisture and temperature had a limited influence on phosphatase activities (Table 3). Phosphatase activities peaked during periods of high and low soil moisture and temperature. The lack of a discernible relationship between seasonal fluctuations in phosphatase activities and soil microclimate has also been reported by Skujins (1976), Haynes (1987) and Ross et al. (1995).

It is possible that in our study either average soil moisture or temperature were not optimum for microbial growth when we measured maximum alkaline phosphatase activities. During winter, soil temperature may have restricted microbial activity to levels lower than required to obtain the observed winter peak in phosphatase. The highest winter alkaline phosphatase activity occurred when average soil temperatures at 10 cm depth were 4.1 and 5.8°C (Figs. 1 and 2). We propose that the winter peak in alkaline phosphatase was caused by changes in the individual compartments (Skujins, 1976; Nannipieri et al., 1990) that constitute total soil phosphatase activity. The peak may be caused by two processes: a buildup of phosphatase released into the soil from dying soil organisms, and the desorption and reactivation of previously accumulated phosphatase from organic and inorganic soil components. These two processes were suggested to account for winter peaks in phosphatase activity in Canadian mixed prairie and fescue (*Festuca* spp.) grassland soils (Dormaar et al., 1984) and for other hydrolytic soil enzymes in Russian Mollisols (Khaziyev, 1977).

Acid phosphatase is closely tied to root growth activity and plant demand for phosphorus (Tarafdar and Claassen, 1988). We found no difference in potential acid phosphatase activity between juniper and intercanopy microsites. Microsites may not be different, because junipers have an extensive lateral root system, that extends far beyond the tree canopy and can occupy much of the soil in intercanopy areas (Young and Evans, 1987; Krämer et al., 1996), and could therefore produce similar amounts of acid phosphatase in both microsites.

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