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Aspect and Species Influences on Nitrogen and Phosphorus Availability in Arizona Chaparral Soils

James O. Klemmedson and Brian J. Wienhold*

ABSTRACT

Biota and topography are among the most important factors affecting nutrient status of wildland soils. Knowledge of these relations has a fundamental bearing on management of chaparral ecosystems. This study was conducted to determine the effect of shrub species and topographic aspect on availability of soil N and P in Arizona chaparral soils. Soil was collected under the canopy of 32 randomly selected shrubs, eight each of birchleaf mountain mahogany (*Cercocarpus betuloides* Nutt.) and shrub live oak (*Quercus turbinella* Greene) from both north and south aspects. A pot culture technique, using barley (*Hordeum vulgare* L. var. *gustoe*) and mountain mahogany (*C. montanus* Torr.) as test plants, was used to estimate availability of soil N and P. Both test plants showed that shrub species and aspect influenced nutrient availability. Availability of P was very low, while that of N was quite high. Lower availability of P in soils from southerly aspects was associated with low amounts of total soil P, probably the result of long-standing differential erosion between north and south aspects, aggravated by fire. High N availability was probably associated with inputs of N via symbiosis between actinomycetes and mountain mahogany. Higher fertility of soils from oak systems is associated with lower lignin content of litter from these shrubs.

CHAPARRAL ecosystems cover extensive areas of the U.S. Southwest including 1.3 million ha in Arizona (Bolander, 1982). Resource values are not high, but these ecosystems are important because of watershed and wildlife values, and their susceptibility to damage from disturbance. Knowledge of soil-plant-nutrient relations for chaparral is fragmented and sketchy. Research has been directed chiefly at the California chaparral, much of it focused on N status of the soil-plant system, including mechanisms of loss and replenishment (DeBano and Conrad, 1978; DeBano et al., 1979; Dunn and Poth, 1979; Dunn et al., 1979; Schlesinger and Hasey, 1981; Marion and Black, 1988). However, P also merits attention based on its occasional deficiency (Hellmers et al., 1955; McMaster et al., 1982), susceptibility to loss in chaparral soils (DeBano and Conrad, 1978), and because of the important role P plays in accumulation of N and organic C in soil-plant systems (Stevenson, 1986).

Although we have some insight into how nutrient supply of chaparral soils is influenced by shrub species (Hellmers et al., 1955; Vlamis et al., 1971; Delwiche et al., 1965) and fire (Christensen and Muller, 1975; Marion and Black, 1988), and can speculate about the effects of other state factors such as parent material and topography based on information from other systems (Aandahl, 1949; Klemmedson, 1964; Klemmed-

son and Jenny, 1966), specific information on factors that influenced nutrient availability would improve our ability to make management decisions concerning productivity of chaparral ecosystems.

In a companion study (Klemmedson and Wienhold, 1985, unpublished data), we observed a significant influence of biota (shrub species) and topography (aspect) on accumulation of N and P in a small watershed of the Arizona chaparral. The purpose of the present study was to go one step further and test the null hypothesis that shrub species and topographic aspect have no effect on availability of N and P in Arizona chaparral soils.

STUDY AREA

The study area was a 55-ha drainage of the Battle Flat Watershed in the Bradshaw Mountains of central Arizona (34°19'N, 112°22'W). The topography is rough and highly dissected. The prevailing aspect of the watershed is southeast; slope gradient ranges from 15 to 60%. Elevation is about 1700 to 1770 m above sea level and the geologic parent material is massive bedded crystalline tuff with recent gravels along stream beds (Anderson and Blacet, 1972). The Moano very rocky loam soils are classified as loamy, mixed, nonacid, mesic Lithic Torriorthents (Humbert et al., 1981).

The dense shrubby vegetation averages about 75 to 80% crown cover. Canopy height varies from 1 to 3 m; shrub height and cover are greatest on northerly aspects. Dominant shrubs are: manzanita (*Arctostaphylos pungens* H.B.K.), shrub live oak, and birchleaf mountain mahogany. Subdominant shrubs include: emory oak (*Quercus emoryi* Torr.), alligator juniper (*Juniperus deppeana* Steud.), desert ceanothus (*Ceanothus greggii* Gray), apache plume (*Fallugia paradoxa* D. Don), and yerba santa (*Eriodictyon angustifolium* Nutt.). The herbaceous understory is sparse.

The mean annual precipitation of 480 mm is about equally distributed between cyclonic winter and convective summer storms. About 15 to 20% of total precipitation is snow. Mean daily temperature is 15 °C; the annual maximum range is from -29 to 39 °C.

METHODS

Conceptual Model

The conceptual model was based on a formalistic approach to ecological research developed by Jenny (1961) and Major (1951). The model

$$N_{av}, P_{av} = f(o_s, r_a)_{cl,o,r,p,t} \quad [1]$$

states that available N (N_{av}) and available P (P_{av}) of the soil are a function of species of shrub (o_s) occupying the site and topographic aspect (r_a) when climate (cl), biotic factors other than species (o), topography other than aspect (r), parent material (p), and age of the soil-plant system (t) are held constant or nearly so. Using this model, we carried out an observational study (Cochran, 1983) of field sampling with rigid control of extraneous variation, and subsequent greenhouse experimentation to facilitate a test of the hypothesis.

Implementation of Model

Two shrub species, birchleaf mountain mahogany and shrub live oak, were chosen for sampling to express o_s and

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two aspects, north and south, were chosen for sampling to express r_a in the test of the hypothesis. We randomly selected 32 shrubs, eight of each species on each aspect, from a pool of 80 mature shrubs that were widely distributed among lateral drainage channels feeding the main drainage. Each of the 80 shrubs were selected to control, within narrow limits, variation associated with the invariant factors in Eq. [1]. This was done to assure that variation in those factors could be expected to have a negligible effect on the dependent variable.

Climate was invariant within the small study area. Because the 32 soil profiles displayed no differences in maturity and because only mature shrubs were considered, differences in time of soil-plant-system development also were negligible. Only one geologic parent material is described for the study area (Anderson and Blacet, 1972) and field inspection disclosed no discernible parent-material differences. No evidence was found that the human aspect of the biotic factor, including grazing, use of fire, or other human activities leading to differential impact, including erosion, within the drainage, had been other than random within the study area. Differences in plant density, understory vegetation, and microflora were assumed to be associated primarily with aspect and cover differences; hence, these potential differences were expected to show up as effects of aspect or shrub species.

Soil Collection and Greenhouse Experiments

Ten kilograms of the upper 10 cm of mineral soil was collected from within a 40 by 50 cm plot located midway between the main stem and the canopy edge on the upslope side of each shrub. The size of this sample plot was restricted to the smallest size possible to minimize variation among shrubs caused by the steep spatial gradient commonly observed in nutrient concentration under shrubs from the shrub center outward to open intershrub areas (Zinke, 1962; Charley and West, 1975; Barth and Klemmedson, 1978). Soil samples were air dried, passed through a 6.4-mm sieve to remove rocks, and then mixed thoroughly.

The supply of available N and P was evaluated by a pot culture technique (Jenny et al., 1950) using barley and mountain mahogany seedlings as test plants in sequential $2 \times 2 \times 4$ factorial experiments with shrub species, aspect, and nutrient treatments as fixed effects. There were two reasons for use of two test plants. As a standard test plant, barley was the first choice; it provides quick reliable results with low variation among plants (Jenny et al., 1950; Klemmedson and Jenny, 1966). Use of mountain mahogany was time consuming, but permitted confirming results and the possibility of additional information for a species native to chaparral. The risk of no information was high, however, because of the potential for high variation among plants of native species.

In principle, the pot culture method used here (Jenny et al., 1950) is based on the law of limiting factors (Stalfelt, 1960) and estimates nutrient availability in a soil by comparing yield of a test plant grown in soil fertilized to an optimum level to that of the soil fertilized in identical fashion but with the nutrient in question omitted.

For the barley pot test, nutrients required for each pot were added as solutions to 500 g of soil (oven-dry basis), mixed by hand, and then placed in plastic pots. Four nutrient treatments with four replicates each were used: (i) check treatment (no nutrients); (ii) full treatment (N-P-K-S) consisting of 134 mg N, 89 mg P, 45 mg K, and 22 mg S kg^{-1} ; (iii) N_0 (P-K-S); and (iv) P_0 (N-K-S). Nitrogen was added as NH_4NO_3 , P as $\text{Ca}(\text{H}_2\text{PO}_4)_2 \cdot \text{H}_2\text{O}$, K as KCl, and S as MgSO_4 . Four barley plants were grown from seed in each pot and given tap water as required.

Because of limited soil available under each shrub (i.e., small plot area and very stony soils), it was necessary to use the same soil for both pot tests, first barley, then mountain mahogany. The influence of the barley experiment was as-

sumed to be uniform across all treatments, i.e., it would not bias the test of hypothesis for the subsequent mountain mahogany experiment. Following the barley test, soil from all four replicates representing each combination of species, aspect, and nutrient treatment was thoroughly mixed, placed in a plastic bag, and then stored for 120 d prior to the pot test with mountain mahogany seedlings. Three pots each were then filled with 625 g of soil. Since the mountain mahogany pot test was of longer duration than the barley pot test, only three replicates were used to allow more soil per pot. For pots whose soil had previously been treated with the P_0 and full nutrient treatments, 67 mg kg^{-1} equivalent of N was added to soils at the beginning of the test; a second equivalent dose was added midway through the experiment. Mountain mahogany seedlings were taken from a germinator, transplanted three to each pot, and given tap water as required. Shoots were harvested after 7 wk for barley and 28 wk for mountain mahogany, oven dried for 48 h at 70 °C, and weighed.

Both experiments were arranged on a greenhouse bench in randomized block design to control variation that may have been introduced by gradients possibly existing in the greenhouse (i.e., light, temperature). Analysis of variance was performed on raw plant yields for both test plants, with shrub species, aspect, and nutrient treatment as main effects. All phases of field and greenhouse experimentation were conducted to comply with the model. Fisher's least significant difference (LSD) procedure for comparison of means was performed for sources of variation declared significant at $P < 0.05$ by F test.

For chemical analysis, soils were sieved to remove the >2 -mm fraction and then ground to pass a 0.150-mm sieve. Samples were analyzed for organic C by dry combustion (Nelson and Sommers, 1982) in a Leco high-frequency induction furnace (Leco Corp., St. Joseph, MI). Total N was determined by semimicro-Kjeldahl (Bremner and Mulvaney, 1982) and inorganic N by KCl extraction and steam distillation (Keeney and Nelson, 1982). Soil P was determined using the ammonium molybdophosphoric blue color method following Na_2CO_3 fusion (Jackson, 1958) for total P and NaHCO_3 extraction (Olsen and Sommers, 1982) for extractable P. Litter samples were oven dried (70 °C), ground to pass a 0.425-mm sieve, and permanganate lignin content determined using the method of Goering and Van Soest (1970).

RESULTS

Barley Experiment

Dry-mass yields of barley grown in soil from oak systems were greater than yields of plants grown in soil from mountain mahogany systems for the check and P_0 nutrient treatments but were not different for the N_0 and full nutrient treatments (Fig. 1). The significant species \times nutrient treatment interaction ($P < 0.002$; Table 1) can be attributed to this yield response difference among the four nutrient treatments. The pattern of barley yields from plants grown in soil collected under both shrub species, however, was similar across nutrient treatments (Fig. 1). Averaged across nutrient treatments, yields were higher for soils from oak (1.71 ± 0.04 g pot^{-1}) than from mountain mahogany (1.48 ± 0.04 g pot^{-1}). Moreover, the mean square for the species main effect was large relative to that of the species \times nutrient treatment interaction (Table 1). Thus, it appears that nutrient availability was higher in oak soils than in mountain mahogany soils.

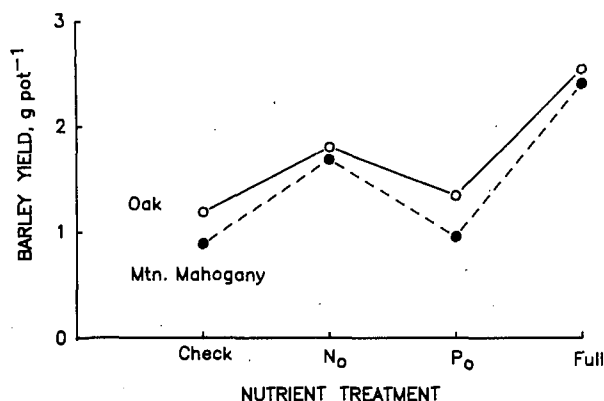


Fig. 1. Dry-mass yield of barley shoots grown in soil of oak and mountain mahogany systems with four nutrient treatments. $LSD_{(0.05)} = 0.13 \text{ g pot}^{-1}$.

Yield of barley grown in soils from north aspects was significantly greater than the yield of plants grown in soil from south aspects for the check and P₀ nutrient treatments (Fig. 2). For the N₀ and full nutrient treatments, however, barley yields did not differ between north and south aspect soils. This difference in yield response for the two soils among nutrient treatments accounts for the significant aspect \times nutrient treatment interaction (Table 1) and suggests that aspect differentially influences nutrient availability in these soils. Presumably barley seedlings grown in soil from south aspects benefited from the relatively high concentration of inorganic N in these soils (Table 2). Averaged across nutrient treatments, the yield of barley grown in soils from north aspects ($1.68 \pm 0.04 \text{ g pot}^{-1}$) was greater than the yield from soils from south aspects ($1.52 \pm 0.05 \text{ g pot}^{-1}$).

Barley responded more strongly to the nutrient treatments than to either aspect or species main effects. This is shown graphically by the consistent pattern for species (Fig. 1) and aspect (Fig. 2) across all nutrient treatments, as well as by the very large mean square for nutrient treatment (Table 1). Mean squares for the two-way interactions were small by comparison, thus detracting little from the nutrient-treatment main effect. Dry-mass yields of barley were greatest in soils receiving the full nutrient treatment (Fig. 1 and 2). Shrub species and topographic aspect had no influence on the yield of barley grown in soils receiving the full nutrient treatment. These results suggest that the full nutrient treatment supplied sufficient nutrients for an optimum yield, as expected based on the theory of the pot test (Jenny et al., 1950).

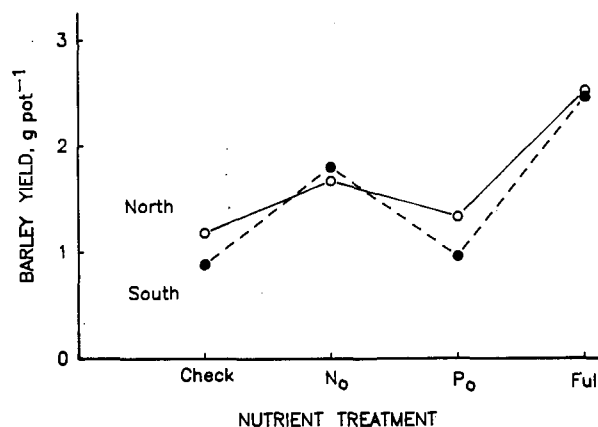


Fig. 2. Dry-mass yield of barley shoots grown in soil from north and south aspects with four nutrient treatments. $LSD_{(0.05)} = 0.13 \text{ g pot}^{-1}$.

The marked response of barley to the full treatment (i.e., averaging 140% > check yield) indicates that either N or P, or both, were limiting yield of the check treatment. Comparison of barley yields for the N₀ and P₀ treatments with those of the check and full treatments suggests that P, rather than N, was the most limiting nutrient. Yields of the check and P₀ treatments ($1.03 \text{ vs. } 1.14 \text{ g pot}^{-1}$) were similar and the P₀ yield was only 46% of the full-treatment yield. By contrast, average yield of barley grown in soil with the N₀ treatment was 70% of the full-treatment yield. This level of N supply would be high for open sites, but it is not unusually high for soil beneath shrub canopies (Tiedemann and Furniss, 1985; Klemmedson and Tiedemann, 1986).

Mountain Mahogany Experiment

Results of the mountain mahogany pot test largely confirmed the barley experiment (Table 1), but with

Table 2. Chemical properties of soils collected as a function of shrub species cover and aspect within an Arizona chaparral watershed.

Nutrient	Aspect	
	North	South
Organic C, g kg ⁻¹	53.7 ± 10.3†	31.6 ± 3.8
Total N, g kg ⁻¹	2.45 ± 0.32†	2.28 ± 0.21
Inorganic N, mg kg ⁻¹	13.8 ± 2.1†	22.3 ± 2.0
Total P, g kg ⁻¹	0.48 ± 0.03‡	0.27 ± 0.04
Extractable P, mg kg ⁻¹	5.7 ± 1.0†	6.6 ± 1.4
pH	6.34†	6.18

† Mean ± SE, $n = 16$.

‡ $n = 8$.

Table 1. Analysis of variance for shoot dry-weight yields of barley and mountain mahogany.

Source of Variation	Barley			Mahogany		
	df	Mean Square	P value of F	df	Mean square	P value of F
Species (S)	1	6.311	0.001	1	1.815	0.001
Exposure (A)	1	3.284	0.001	1	0.506	0.001
Nutrient treatment (T)	3	56.359	0.001	3	2.823	0.001
S \times A	1	0.226	0.208	1	0.102	0.084
S \times T	3	0.710	0.002	3	0.092	0.046
A \times T	3	1.689	0.001	3	0.031	0.434
S \times A \times T	3	0.238	0.172	3	0.131	0.010
Blocks	3	2.682	0.001	2	0.486	0.001
Error	493	0.142		366	0.034	

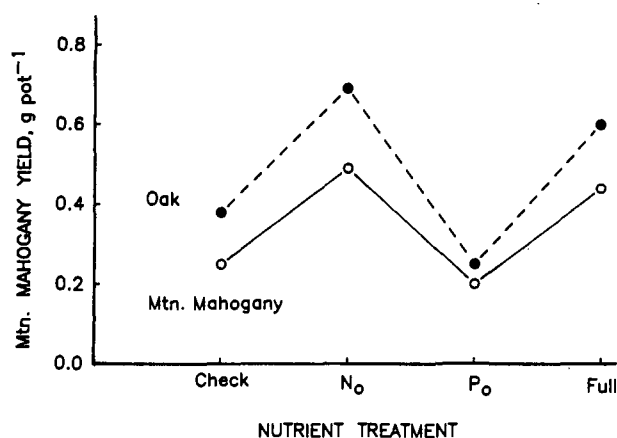


Fig. 3. Dry-mass yield of mountain mahogany shoots grown in soils of oak and mountain mahogany systems with four nutrient treatments. $LSD_{(0.05)} = 0.07 \text{ g pot}^{-1}$.

some marked differences. Dry-mass yields of mountain mahogany grown in soil from oak systems were greater than yields of plants grown in soils from mountain mahogany systems for all but the P_0 nutrient treatments (Fig. 3). This differential response of the test plant to nutrient treatments on the two soils is responsible for the small, but significant, species \times nutrient treatment interaction (Table 1). By comparison, the significant species main effect was large (Table 1). Averaged across nutrient treatments, yields of mountain mahogany seedlings grown in soil from oak systems ($0.48 \pm 0.02 \text{ g pot}^{-1}$) were greater than those from mountain mahogany systems ($0.34 \pm 0.02 \text{ g pot}^{-1}$). This suggests that nutrient availability was greater in oak than in mountain mahogany systems.

The aspect main effect also was significant in this pot test (Table 1). Averaged across nutrient treatments, yields of mountain mahogany seedlings grown in soil from north aspects ($0.45 \pm 0.02 \text{ g pot}^{-1}$) were greater than those from south aspects ($0.37 \pm 0.02 \text{ g pot}^{-1}$).

The effect of nutrient treatments on yield of mountain mahogany seedlings grown on the two soils was significant (Table 1) and similar to that for the barley experiment (compare Fig. 1 and 3). However, differences in the magnitude of separate treatment responses occurred that deserve comment. The full treatment produced a relatively small increase (68%) in the yield of mountain mahogany seedlings over the check treatment, compared with that (140%) for the barley experiment. Considered alone, this is not unusual; one would not expect native shrubs to be as sensitive to nutrient additions as annual cereal species. The yield of the N_0 treatment ($0.59 \pm 0.03 \text{ g pot}^{-1}$), however, exceeded that of the full treatment ($0.52 \pm 0.02 \text{ g pot}^{-1}$) ($P < 0.001$), an unusual result because the full treatment is designed to produce an optimum yield. We attribute this response to mountain mahogany's capacity to support N-fixing actinomycetes (Hoeppel and Wollum, 1971; Vlamis et al., 1971), a symbiosis that is enhanced by favorable P status (Righetti and Munns, 1981; Wienhold and Klemmedson, 1991). Thus, mountain mahogany seedlings grown in N_0 -treated soil collected under oak shrubs

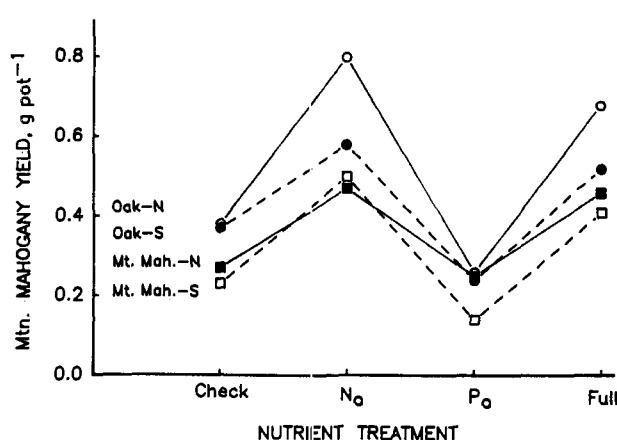


Fig. 4. Dry-mass yield of mountain mahogany shoots grown in soil from oak and mountain mahogany systems from north and south aspects with four nutrient treatments. $LSD_{(0.05)} = 0.10 \text{ g pot}^{-1}$.

on north aspects (note P status in Table 2) produced greater yield than that of seedlings grown on soils with other combinations of species and aspect and the N_0 treatment (Fig. 4). This result is partly responsible for the significant three-way interaction (Table 1).

The yield response of mountain mahogany seedlings to the P_0 treatment was similar to that of the barley experiment; yields for the P_0 ($0.22 \pm 0.01 \text{ g pot}^{-1}$) and check treatment ($0.31 \pm 0.01 \text{ g pot}^{-1}$) did not differ significantly (Fig. 3). This result is consistent with that of the barley experiment, suggesting that P was the most limiting nutrient in these soils. The limited supplying power for P was especially evident in soil from oak systems on south aspects (Fig. 4); this partly explains the significant three-way interaction (Table 1).

There is a question whether N additions in the barley experiment may have influenced the low P_0 yields in this experiment. Thus, N addition may have enhanced P uptake in the barley experiment, thereby lowering P supply in the following mountain mahogany pot experiment (see above). Although this is possible, the argument does not account for the speed of replenishment of inorganic P in the soil solution by mineralization of organic P and chemical equilibria between soluble and insoluble fractions of P (Steven-son, 1986).

DISCUSSION

The higher fertility of soils associated with oak shrubs, compared with those under mountain mahogany, was unexpected. Because mountain mahogany is an actinorhizal plant that associates symbiotically with actinomycetes capable of fixing atmospheric N (Hoeppel and Wollum, 1971; Vlamis et al., 1971), we expected nutrient availability to be greater in soils associated with mountain mahogany. We suspect that the lower lignin content of oak leaf litter (218 vs. 261 g kg^{-1} in mahogany leaf litter) favors more rapid decomposition and release of nutrients. Others (Schlesinger and Hasey, 1981; Melillo et al., 1982; Berg et al., 1984) have noted the effect of litter lignin content on litter decomposition rate. More rapid decay and release of nutrients from oak litter should positively influence nutrient availability (Klemmedson, 1987).

The differential effect of aspect on nutrient availability is consistent with the nutrient status of the soils (Table 2). In general, temperature and moisture conditions of soils from north aspects favor accumulation of nutrients (Aandahl, 1949; Klemmedson, 1964; Jenny, 1980). Based on a strong correlation between nutrient availability and total nutrient content for wildland soils (Klemmedson and Jenny, 1966; Geist, 1977), we expected higher nutrient availability in north-slope soils.

Further insight into N and P fertility of these soils is gained by evaluating graphs of check, N_0 , and full-treatment barley yields as a function of total N, and check, P_0 , and full-treatment barley yields as a function of total P (Fig. 5). These graphs indicate how N and P availability, as expressed by barley yields, varied across the entire range of total N and P observed rather than just at mean levels shown in Fig. 1 and 2. With addition of P (N_0 treatment), availability of N increased linearly across the entire range of total soil N observed. This is manifested by the steeper slope (significant at $P < 0.001$) of the N_0 regression relative to those of the check and full-treatment curves. This was not the case for P. With adequate N (P_0 treatment), the increase in P availability across the range in soil P was much less than that for N (Fig. 5). Moreover, the virtual identity of regressions for check and P_0 treatments indicates that barley yields for the check treatment were controlled by the level of native P rather than N. We arrive at the same conclusion by comparing N_0 and check curves in the upper graph.

The effect of P supplementation was even more pronounced when mountain mahogany was used as a test plant. Yield of mountain mahogany seedlings in the full treatment (Fig. 3), suggesting that seedlings in the N_0 nutrient treatment were utilizing a source of N unavailable to barley. The likely explanation for this result is that some of the mountain mahogany seedlings were supporting N_2 -fixing microbes during the experiment. While high inorganic-N concentrations are known to inhibit symbiotic N_2 fixation (Wheeler and McLaughlin, 1979), P supplementation has been shown to enhance the incidence of nodulation and rate of N_2 fixation in birchleaf mountain mahogany growing in soil from this study site (Wienhold and Klemmedson, 1991). Hence, in the check and P_0 nutrient treatments, P status not only would limit mountain mahogany growth but may also limit symbiosis between the plants and the actinomycete endophyte. In the full treatment, the addition of inorganic N probably inhibited the formation or effectiveness of symbiosis with N_2 -fixing actinomycetes.

Of the two nutrients studied here, P clearly seems to be the key element in productivity and stability of the chaparral ecosystem at Battle Flat. Its status was directly related to topographic aspect. Amount of P (Table 2) and availability of P as expressed by test plant yield (Fig. 2) were both low on south aspects. Low P on the southern aspects, though suspected, was found not to be a function of soil parent material (Klemmedson and Wienhold, 1985, unpublished data). Rather, we believe a long-standing pattern of periodic fire and differential erosion between north

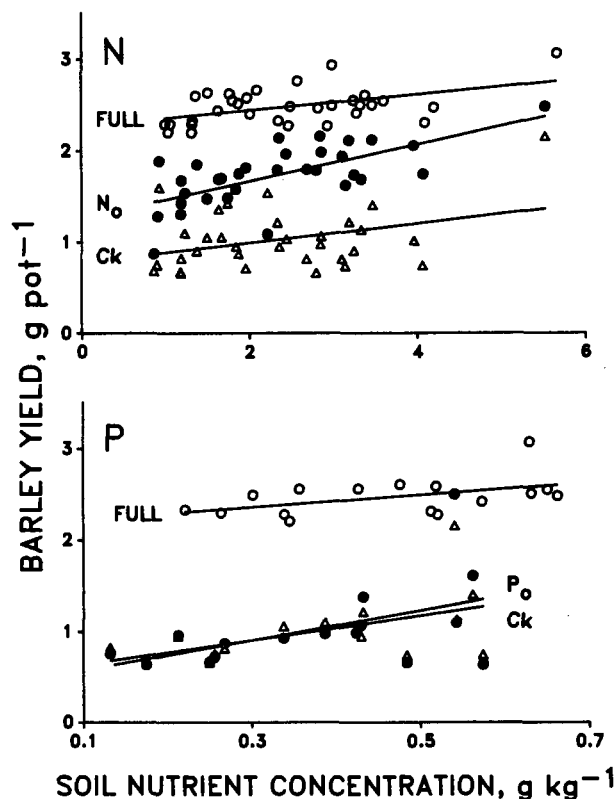


Fig. 5. Functional relation of barley yield and concentration of total N (upper graph) and total P (lower graph) of soils for check, N_0 , or P_0 , and full treatments. The lower graph represents only one-half of the plots because only 16 soils (random) were analyzed for total P.

and south aspects, characteristic of chaparral watersheds (Branson et al., 1981), has resulted in relative depletion of P from southern aspects (Hellmers et al., 1955). Erosion on the typically more open, more sparsely vegetated south aspects selectively removes organic debris and finer soil particles high in P. Fire undoubtedly contributes heavily to P losses, especially from southern aspects that burn more readily, if not more frequently. Although significant amounts of biomass P may be lost by volatilization and particulate transfer (Harwood and Jackson, 1975; Raison et al., 1985), heaviest P losses probably occur when fire-deposited ash is removed by erosion (Pace and Ingebo, 1965; Pace and Lindenmuth, 1971) in the vulnerable post-fire period prior to reestablishment of vegetation.

Although N, because of higher volatility, is subject to greater combined losses from fire and erosion than P in this system, the implications of N losses at Battle Flat are not as serious as P losses in terms of ecosystem function. Whereas N is readily replaced by numerous mechanisms of fixation (Stevenson, 1986), P, once lost, is only slowly replaced by weathering of primary apatites from soil-forming rocks (Smeck, 1985; Stevenson, 1986). Moreover, P plays a key role in accumulation of N and organic C in ecosystems (Walker, 1965; Cole and Heil, 1981). If P already limits accumulation of organic matter and N in Battle Flat soils, the improvement in fertility and stability of these watersheds may be difficult indeed. In this case, the best

course of action may be to place high priority on management practices that maintain P on the site.

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