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Phosphorus limitation of forest leaf area and net primary production on a highly weathered soil

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Abstract. We tested the hypothesis that P was the nutrient limiting net primary production of a native *Metrosideros polymorpha* forest on a highly weathered montane tropical soil in Hawaii. A factorial experiment used all combinations of three fertilizer treatments: nitrogen (N), phosphorus (P) and a mix of other essential nutrients (OE), consisting primarily of mineral derived cations and excluding N and P. P addition, but not N or OE, increased leaf area index within 12 months, foliar P concentration measured at 18 months, and stem diameter increment within 18 months. Stem growth at 18 months was even greater when trees fertilized with P also received the OE treatment. N and P additions increased leaf litterfall and N and P in combination further increased litterfall. The sequence of responses suggests that increased available P promoted an increase in photosynthetic area which led to increased wood production. P was the essential element most limiting to primary production on old volcanic soil in contrast to the N limitation found on young volcanic soils.

Key words: chronosequence, montane tropical forest, nitrogen, nutrient limitation, phosphorus, productivity

Introduction

Phosphorus and other rock-derived nutrients are present as primary minerals at the beginning of soil development. P weathers into biologically available forms early, but in the long term becomes less available because of its conversion to recalcitrant organic and adsorbed forms (Walker & Syers 1976; Crews et al. 1995). In contrast, nitrogen is absent from parent material, gradually accumulating with time as soils and vegetation develop (Vitousek et al. 1983; Bormann & Sidle 1990). Consequently, during pedogenesis, biologically available nutrients increase over time to some maximum, after which availability declines (Walker & Syers 1976; Fox et al. 1991).

It has been suggested that N availability could limit biological activity early in soil development, but P availability should limit it late (Walker & Syers 1976; Vitousek & Walker 1987). Net primary production in relatively undisturbed ecosystems may, therefore, follow a pattern similar to that of nutrient availability; low productivity early in ecosystem development increasing to some maximum and then declining as these systems age (Mueller-Dombois 1986; Bormann & Sidle 1990). In line with these predictions of nutrient availability and ecosystem response, it was demonstrated that N is the element most limiting to net primary productivity (NPP) in *Metrosideros polymorpha* Gaud. forests on young volcanic soil in Hawaii (Vitousek et al. 1987, 1993; Walker & Aplet 1994).

Experimental fertilizations have shown that tropical forest trees respond to applications of N and P with increases in NPP and that the response to N or P may be affected by the relative age of the soil. On a young volcanic Dystrandept in Hawaii, tree stem diameter, litterfall and treefern growth increased after fertilization with N, but there was no response to P or a mix of other essential elements (Vitousek et al. 1993; Walker & Aplet 1994). On a montane Humitropept in western Venezuela, Tanner et al. (1992) measured increased tree growth in response to fertilization with N and P and reported evidence of N limitation. Evidence for which element(s) limit production of the naturally occurring vegetation later in soil development is generally lacking, but in a highly weathered Amazonian oxisol near San Carlos Venezuela, fine roots proliferated in P-fertilized ingrowth cores (Cuevas & Medina 1988).

The Hawaiian Islands are well suited to the study of ecosystems in relation to their development and function across a soil chronosequence. The basaltic parent material is, for the most part, uniform in chemical composition (Wright & Helz 1987) and geologic age of the islands increases from southeast to northwest. In this study we examine nutrient limitation of an *M. polymorpha* dominated forest on one of the oldest montane soils in the Hawaiian Islands. The study was designed to determine whether the predicted decrease in P availability on this highly weathered soil is realized to the point where forest productivity is limited by P to a greater extent than by other essential nutrients. The site was selected to match the young site fertilized by Vitousek et al. (1993) in elevation, annual precipitation, slope position, and dominant vegetation, and a similar experimental design was used. The site is the oldest in a well-defined chronosequence of soils derived from similar substrates beginning with an age of approximately 300 years at the youngest site on the island of Hawaii (Crews et al. 1995).

Site description

The study site is located in the Na Pali – Kona Forest Reserve in Kokee State Park, island of Kauai, Hawaii (22°08′ N and 159°38′ W) at 1134 m elevation. The site is on a ridge top remnant with a geologic age estimated to be between 3.9 and 4.3 million years (Clague & Dalrymple 1988). The soil is mapped as a clayey ferritic isomesic Plinthic Acrorthox (Soil Survey Staff 1972) revised to an Acrudox (Soil Survey Staff 1992). Mean annual precipitation is 2500 mm (Giambelluca et al. 1986).

Vegetation is characterized by a closed forest canopy composed predominantly of *Metrosideros polymorpha* Gaud. var. *glaberrima* (H. Lev.) St. John, with *Syzigium sandwichensis* (A. Gray) Nied., *Cheirodendron trigynum* (Gaud.) A. Heller and *Cheirodendron platyphyllum* (Hook. & Arnott) Seem. subspecies *kauaiense* (Kraj.) Lowry and a fern understory.

Total soil P at the site was 0.44 kg P m^{-2} to a depth of 50 cm with a soil bulk density of 0.80 g cm^{-3}. Of this, 25% was organic P, 27% was secondary mineral P and 48% was occluded inorganic P (Crews et al. 1995). Resin-extractable inorganic P was 16.0 μg g^{-1} in the organic layer and 5.0 μg g^{-1} in the mineral A horizon (T. Crews, pers. comm.). By comparison with the low availability of P, N is relatively available. During 30-day laboratory incubations, net N mineralization rate was 26.4 mg N m^{-2} day^{-1} and net nitrification rate was 16.4 mg N m^{-2} day^{-1} (Riley & Vitousek 1995).

Methods

Experimental design

DBH of all tree stems greater than 50 mm were recorded in each of 42 plots measuring 10 × 10 m prior to the application of treatments. In early March 1991 a fertilization experiment was started on the 32 most similar plots. Treatments were applied to the 20 × 20 m area encompassing each plot to provide a 5 m border.

The three main treatments were N and P applied at the annual rate of 100 kg ha^{-1} yr^{-1} each, and a mix of other essential (OE) nutrients (excluding N and P) which consisted of K (100 kg $ha^{-1}yr^{-1}$), Ca (100 kg $ha^{-1}yr^{-1}$), Mg (58 kg $ha^{-1}yr^{-1}$), S (40 kg $ha^{-1}yr^{-1}$), Fe (8 kg $ha^{-1}yr^{-1}$), Mn (8 kg $ha^{-1}yr^{-1}$), Zn (8 kg $ha^{-1}yr^{-1}$), Cu (2.25 kg $ha^{-1}yr^{-1}$) and B (0.75 kg $ha^{-1}yr^{-1}$). P was applied as treble super phosphate and N was applied as a mixture of urea and ammonium nitrate, each fertilizer supplying equal amounts of N. The OE treatment included muriate of potash, dolomite, gypsum and Granusol, an agricultural micronutrient mix.

Treatments were applied at two levels: zero or plus. The initial fertilizer application was equal to the annual rate. Subsequent applications began six months later and were made in semi-annual allotments, each equal to half the annual rate. Eight factorial combinations of N, P and OE treatments were randomly assigned to plots in four blocks.

The experiment was analyzed as a randomized complete block ANOVA. Fixed model F tests were performed on the three main treatments and all interactions (Snedecor & Cochran 1980). An alpha of 0.05 was used for determining significance. All statistical tests were performed on log-transformed data in order to homogenize variance. Tables and figures use arithmetic means and standard errors for simplicity in presentation.

Field measurements

Spring-loaded dendrometer bands were installed on six *M. polymorpha* trees per plot and diameter growth was measured every six months for eighteen months. The first six months of growth were excluded from analysis to allow for settling of the dendrometer bands (Keeland & Sharitz 1993).

LAI was estimated optically using a LI-COR LAI 2000 plant canopy analyzer, which uses gap fraction analysis of diffuse radiation transmittance to indirectly estimate LAI (Welles & Norman 1991). The method agreed with direct harvest estimates in red oak (Gower & Norman 1991) and a variety of tropical hardwoods (Harrington & Fownes 1995). However, this method may underestimate LAI where canopy elements are strongly clumped or aggregated in space, such as in conifers. Gower and Norman (1991) found that four conifer species required a correction factor ranging from 1.49 to 1.67 for accurate estimation of LAI by the LI-COR LAI 2000. A correction factor of 2.63 was determined for Douglas-fir by Smith et al. (1993). Preliminary results from tree harvest on the island of Hawaii indicate that a correction factor for the strongly aggregated *M. polymorpha* canopy may be equally high (D. Herbert & J. Fownes, unpublished data). Despite the underestimate in LAI, it is nevertheless directly related to differences among our treatments in light absorption by canopies. Because the study area is in a State Park, native rainforest trees could not be harvested to determine a site-specific calibration factor. Therefore, we used the optical method to detect relative differences among treatments, and no correction factor has been applied to the results presented here.

LAI was estimated from six points within each plot at 6, 8 and 12 months. No LAI estimates were made at 18 months because of extensive canopy damage from Hurricane Iniki (September 11, 1992) which reduced pre-hurricane LAI by as much as 60%.

N and P concentrations and leaf mass per area (LMA) were measured in early September 1992, 18 months after initial fertilizer application. The most recently fully expanded sun leaves were obtained from the uppermost part of the canopy. Area was measured with a LI-COR LI-3100 area meter, after which samples were dried at 70 °C. Leaves were ground and then acid-digested in a block digester using a persulfate procedure with a mercuric oxide catalyst. N and P concentrations were determined using an Alpkem auto-analyzer.

Monthly fine litterfall collections began at the end of September 1991, six months after initial fertilization. Collections were made using four 0.2 m^2

frame traps in each plot. Litterfall collections were taken through September 1, 1992, after which canopy damage from the hurricane eliminated treatment effects.

Allometric equations and biomass estimation

Wood biomass (W), including boles, branches and twigs, was estimated using an allometric equation generated from the destructive sampling of 45 *M. polymorpha* trees ranging in size from 1.0 to 38 cm basal diameter (D), harvested from several different sites on the Island of Hawaii (Gerrish 1988; J. Raich, unpubl. data; G. Aplet, unpubl. data). Regression of ln W versus ln D produced the equation $\ln W = 2.619 + 3.034 * \ln D$ ($r^2 = 0.977$, $P < 0.0001$, $S_{y.x} = 0.548$). Height improved the regression ($r^2 = 0.983$, $P < 0.0001$, $S_{y.x} = 0.345$), but since we did not have heights for all trees we use only D in our allometric equation. The correction factor $\exp(S_{y.x}{}^2/2)$ was applied to counteract bias from logarithmic transformation (Baskerville 1972; Sprugel 1983). The final equation was $W = 15.945 * D^{3.034}$ where D is measured in cm and W is predicted in g.

Estimates of production

Above ground net primary production (ANPP) was estimated as the sum of the change in wood biomass and the fine litterfall on a per area basis. Annual litterfall was estimated from the available pre-hurricane values. The change in wood biomass was estimated by applying the allometric equation for biomass, as described above, to stem diameters at the beginning and end of each measurement interval. There was no evident relation between radial stem growth and initial stem diameter to suggest that differences in diameter increment were dependent on initial stem diameter, so the mean growth increment of measured trees in each treatment plot were applied to all trees within the plot to estimate wood production on a stand basis. As an index of growth efficiency, production per unit leaf area was calculated as ANPP from 6 to 18 months divided by LAI at 12 months.

Results

Canopy response to fertilization

LAI increased with P application by 8 months and increased further by 12 months after initial fertilizer application (Table 1). All plots without P amendments exhibited reductions in LAI during the interval for which data are

Table 1. Treatment effects on LAI (m^2/m^2) at 12 months, foliar P and N (% dry mass) and LMA at 18 months ($g\ m^{-2}$). Values are means with standard errors in parentheses. P, N and other elements, OE (K, Ca, Mg, S, Fe, Mn, Zn, Cu, and B), were applied in factorial combination at rates described in the text. P increased LAI (3.1 vs. 2.4; $p = 0.001$), foliar P (0.060% vs. 0.104%; $p < 0.001$) and decreased LMA (174 vs. 193 $g\ m^{-2}$; $p = 0.046$).

		−OE		+OE	
	P Trt.	−N	+N	−N	+N
LAI	−P	2.3 (0.31)	2.3 (0.19)	2.4 (0.27)	2.7 (0.17)
	+P	2.6 (0.15)	3.5 (0.16)	3.1 (0.30)	3.3 (0.40)
Leaf P%	−P	0.058 (0.005)	0.061 (0.005)	0.063 (0.004)	0.057 (0.003)
	+P	0.100 (0.009)	0.117 (0.015)	0.104 (0.008)	0.095 (0.012)
Leaf N%	−P	0.802 (0.061)	0.874 (0.066)	0.856 (0.030)	0.844 (0.056)
	+P	0.850 (0.031)	0.935 (0.104)	0.840 (0.018)	0.935 (0.023)
LMA	−P	211 (19)	197 (12)	175 (4)	191 (10)
	+P	183 (14)	175 (21)	190 (14)	150 (7)

available (Fig. 1). That LAI was maintained or increased when P was applied suggests extended leaf retention or increased leaf initiation in response to increased availability of P.

P addition nearly doubled foliar P and significantly decreased LMA (Table 1). N addition did not increase foliar N and had no effect on LMA.

Annual litterfall increased with both N and P addition (Table 2). Leaf litterfall increased in response to N addition beginning in November, 1991, and in response to P in addition to N beginning in May, 1992. The magnitude of litterfall responses to N and P were approximately equal. A positive interaction of N with P began in July 1992 and continued through the end of the experiment (Fig. 2). Patterns for litterfall including twigs were similar to those for leaf litter, except for winter months when storms increased twig litter.

Stem growth

Stem diameter initially increased in response to the combined P and OE treatments (Table 3). Later (12 to 18 months) there were increases in response to P and N separately, and to the combined P and OE treatment. Cumulative increment for the year (6 to 18 months) was greatest among P treatments with a positive and significant interaction when P and OE were applied

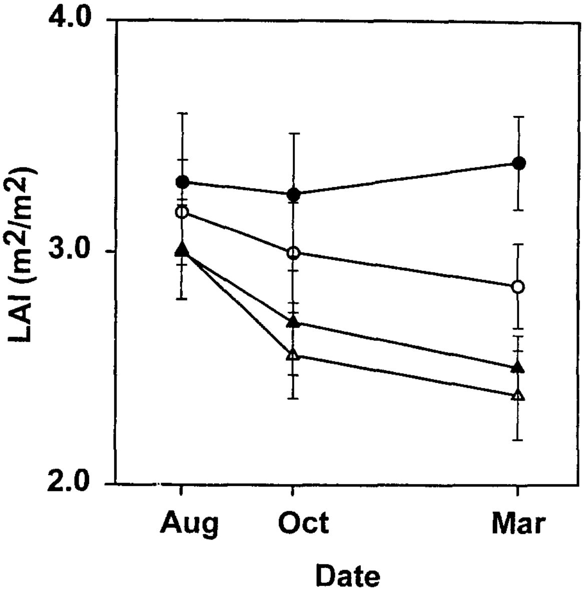

Fig. 1. Leaf area index (m^2/m^2) in −N −P (open triangles), +N −P (filled triangles), −N +P (open circles) and +N +P (filled circles) treatment plots. The values are means +/− standard errors.

Table 2. Treatment effects on annual litterfall leaves and on total litterfall (g dry mass m^{-2} yr^{-1}). Values are means with standard errors in parentheses. Treatments as presented in Table 1. Leaf litter was increased by N (455 vs. 376 g m^{-2}, $p = 0.001$) and P (446 vs. 385 g m^{-2}, $p = 0.007$). Total litterfall was also increased by N (580 vs. 484 g m^{-2}, $p = 0.003$) and P (574 vs. 489 g m^{-2}, $p = 0.006$) treatments.

		−OE		+OE	
	P Trt.	−N	+N	−N	+N
Leaves	−P	340 (17)	414 (33)	372 (16)	416 (41)
	+P	394 (26)	510 (31)	401 (30)	481 (33)
Total	−P	423 (27)	520 (45)	483 (18)	532 (52)
	+P	517 (33)	627 (40)	512 (38)	641 (51)

in combination. Diameter increment never increased when OE was applied without P.

Production

From 6 to 12 months there was an interaction of P with OE where wood production was greatest when both treatments were combined (Table 4). From

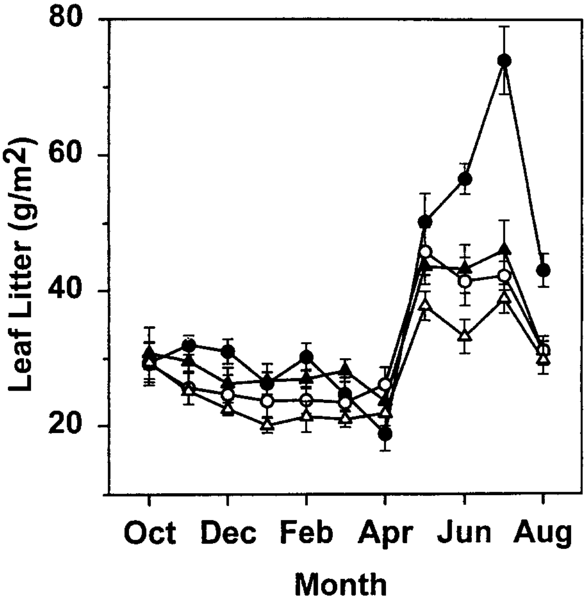

Fig. 2. Monthly leaf litterfall (g dry mass/m^2) for October, 1991 through August, 1992. Values and symbols are the same as in Fig. 1.

Table 3. Treatment effects on stem diameter growth (mm). Diameter increments are separated into semi-annual intervals to illustrate the progression of responses. Values are means with standard errors in parentheses. Treatments as presented in Table 1. In the second interval diameter increment was increased by P (1.6 vs. 1.0 mm, $p = 0.010$) and N (1.5 vs. 1.1 mm, $p = 0.049$). P increased annual increment (2.5 vs. 2.0 mm; $p = 0.046$). P × OE was significant in the first interval ($p = 0.005$), second interval ($p = 0.025$) and annual increment ($p = 0.010$).

		−OE		+OE	
Months	P Trt.	−N	+N	−N	+N
6 to 12	−P	1.2 (0.23)	1.2 (0.11)	0.7 (0.20)	0.5 (0.11)
	+P	0.7 (0.18)	1.1 (0.17)	0.9 (0.09)	1.2 (0.31)
12 to 18	−P	1.3 (0.32)	1.4 (0.17)	0.8 (0.13)	0.8 (0.14)
	+P	1.0 (0.06)	2.0 (0.45)	1.4 (0.28)	1.9 (0.40)
6 to 18	−P	2.5 (0.55)	2.6 (0.27)	1.5 (0.31)	1.3 (0.13)
	+P	1.7 (0.19)	3.1 (0.60)	2.2 (0.35)	3.1 (0.64)

Table 4. Treatment effect on wood production (g dry mass $m^{-2}yr^{-1}$. Production is separated into semi-annual intervals to illustrate the progression of responses. Values are means with standard errors in parentheses. Treatments are as presented in Table 1. Wood production increased in response to P in the second interval (401 vs. 297 g m^{-2}, $p = 0.015$) and for the entire year (662 vs. 442 g m^{-2}, $p = 0.027$). P × OE was significant in the first interval ($p = 0.049$).

		−OE		+OE	
Months	P Trt.	−N	+N	−N	+N
6 to 12	−P	258 (62)	239 (36)	137 (29)	145 (29)
	+ P	218 (42)	239 (52)	289 (35)	298 (128)
12 to 18	−P	282 (79)	291 (54)	176 (45)	240 (58)
	+ P	246 (35)	437 (155)	461 (84)	459 (150)
6 to 18	−P	540 (141)	530 (90)	313 (69)	385 (60)
	+ P	464 (63)	676 (206)	750 (112)	757 (274)

Table 5. Above ground net primary production (g m^{-2} yr^{-1}) and growth efficiency (g m^{-2} leaf area yr^{-1}) in response to fertilizer treatments. Values are means with standard errors in parentheses. Treatments are as presented in Table 1. ANPP was significantly greater when P was applied (1236 vs. 931 g m^{-2}; $p = 0.006$).

		−OE		+OE	
	P Trt.	−N	+N	−N	+N
ANPP	−P	964 (139)	1050 (107)	795 (83)	916 (84)
	+ P	981 (88)	1303 (224)	1262 (100)	1398 (265)
ANPP/LA	−P	441 (107)	463 (70)	329 (22)	342 (25)
	+ P	374 (29)	370 (54)	424 (61)	433 (68)

12 to 18 months wood production was greatest in P treatments without significant interactions. Cumulative wood production for the year (6 to 18 months) was greatest for P treatments while other nutrients and their interactions were non-significant. ANPP (wood production plus leaf and twig litterfall) increased with P application (Table 5). Production per unit leaf area did not differ significantly among treatments (Table 5).

Discussion

The first measurable responses to P application were increased LAI and litterfall. Although foliar P increased, increased ANPP was apparently caused by increased leaf area and not increased production per unit leaf area. However, the interaction between P and OE ($p = 0.074$), suggested that had the experiment continued longer there may have been increased production per unit leaf area when P plus OE were combined. N also increased canopy production as measured by increased leaf litterfall, a persistent effect first observed six months prior to the litterfall response in P treatments. Both N and P had the effect of increasing canopy production but in different ways. N application increased litterfall while LAI did not change significantly, indicating that leaf production and turnover increased. P application increased litterfall after an increase in LAI, suggesting increased leaf initiation or retention.

A reduction in foliar N:P ratio was the result of increased foliar P concentration in the P treatment plots. This change occurred without a significant increase in foliar N even when fertilizer N was applied. Also, foliar N did not decrease when LAI increased suggesting that N did not become limiting in supply when both P availability and LAI increased. N is known to affect maximum rates of photosynthesis in many plants (Field & Mooney 1986), but foliar P may also limit photosynthesis when P availability is low (Reich & Schoettle 1988).

The decrease in LMA in P treated plots suggests that the increased available P had an effect on leaf structure. Lower LMA in nutrient sufficient leaves is supported in other observations (Chabot & Hicks 1982; Reich et al. 1991; Vitousek et al. 1995). LMA and mass-based net photosynthesis were negatively correlated in 23 Amazonian tree species (Reich et al. 1991). High foliar nutrient concentrations in mature leaves are positively correlated with decomposition rate (Tanner 1981; Cuevas & Medina 1988; Constantinides & Fownes 1994), which in turn, could affect nutrient cycling.

Increased stem diameter increment and wood production generally followed canopy responses in a progression similar to that measured in other forest fertilizations (Miller & Miller 1976). Diameter increment increased in response to P, but was greater when applied in combination with OE. Increases in response to N were also seen late in the experiment. Wood production per plot, which incorporates stem density, also increased in the P treatments, but this did not become readily apparent until late in the experiment. An interaction of P with OE showing increased mean wood biomass increment was not significant after the 6 to 12 month interval, and there was no increased wood production in response to N.

Changes in canopy leaf mass were not included in our estimate of ANPP due to the effects of Hurricane Iniki which brought the study to an early conclusion. Therefore, ANPP was probably underestimated in plots which had a net increase in LAI, that is all P treatments. Despite this potential error there was a strong response to P, supporting the hypothesis that ANPP at the site is limited by the lack of biologically available P.

The persistent effect of increased stem diameter increment when OE was applied with P, the early effect of N on litter production and the late effect of N on stem diameter increment suggests that other nutrients were in short supply at the site and may impose secondary limitations on production. The probability that other nutrients secondarily limit ANPP is not surprising since reductions in the total amounts of Ca, Mg, K and S can occur early during normal soil weathering processes (Walker & Syers 1976; Fox et al. 1991). The availability of N through mineralization processes may be regulated by P availability (Vitousek & Howarth 1991) which could help to explain the early increase in litterfall and the late stem diameter response when N availability was increased by fertilization.

Notwithstanding secondary limitation or the effect of other nutrients on some components of productivity, ANPP increased when P availability was increased. The response clearly demonstrates P limitation on a weathered soil as predicted by Walker & Syers (1976) and Vitousek & Walker (1987).

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