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Both nitrogen and phosphorus limit plant production on young Hawaiian lava flows

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Abstract. We applied fertilizers in a 2^3 complete factorial design to determine the effects of nutrient amendments on plant growth in Hawaiian montane forests growing on two different volcanic substrates: ‘a‘ā and pāhoehoe lava. Both sites were about 140 years old and their overstories were nearly monospecific stands of *Metrosideros polymorpha*. Fertilizer applications included N, P, a mixture of essential macro- and micronutrients excepting P and N, and all combinations thereof in each of four blocks. Additions of nutrients other than N or P had no significant effects on measured plant-growth variables. In contrast, additions of either N or P significantly increased tree height growth, diameter increments, biomass growth, and height growth of the understory fern *Dicranopteris linearis* in both sites. The effect of N was greater than that of P. Greatest growth rates occurred in plots receiving both N and P, and signficant N*P interactions occurred in several cases, suggesting a synergistic effect between these two elements. Plant growth on these young, poorly weathered, basaltic lavas is colimited by N and P availability. Growth in a similar-aged stand growing on a mixture of volcanic ash and cinders is N but not P limited, indicating that the texture of the parent material influences nutrient-availability patterns during early primary succession.

Introduction

Walker & Syers (1976) proposed a theory of pedogenesis that can be used to predict patterns of nutrient limitation to plant growth during long-term soil development. Early in soil development nitrogen is predicted to be the most important macronutrient limiting plant growth on primary geological substrates that lack significant populations of symbiotic N fixers, because N is not present in most rocks and must be obtained from atmospheric sources (Vitousek & Walker 1987). Later in soil development rock-derived elements such as P are lost or occluded and therefore become relatively more limiting to plant growth (Walker & Syers 1976).

This general theory of which nutrients limit growth, and why, during long-term pedogenesis has been tested and supported in Hawaii (Herbert & Fownes 1995; Vitousek et al. 1993). These studies suggest that N alone limits tree growth on young sites with volcanic-tephra substrates, but that P is limiting on old, highly weathered soils. However, lava flows are common substrates for early primary succession in Hawaii, and they have much less surface area subject to weathering than do the tephra substrates that were investigated previously. This suggests that rock-derived mineral nutrients such as P may also be limiting to plants on young lava flows, a possibility that was supported by analysis of ecosystem development during primary succession in Hawaii with the CENTURY model (Parton et al. 1989). Parton et al. suggested that P availability appeared to limit plant growth over the first few hundred years on young lava substrates. Even Walker & Syers' (1976) model suggests that both N and P are unavailable at the initiation of primary succession, but that P becomes more quickly available to plants (Vitousek & Walker 1987).

We tested the effects of added N, P, and other essential nutrient elements on plant growth in two young sites on contrasting lava types on windward Mauna Loa, Hawaii. The sites differed in the texture of their lava substrates, but were of similar ages, developed under similar climatic conditions, had similar vegetation communities, and were free of any significant human disturbance. Our objective was to determine whether N, P, or some other essential plant nutrient was primarily responsible for limiting plant growth at this very early stage of soil development on poorly weathered basaltic lavas.

Study sites

Our study sites were located at 1130 m elevation on the windward slope of Mauna Loa Volcano on the Island of Hawaii. Annual rainfall averages 430 cm, and the mean annual temperature is 15.5 °C (Juvik & Nullet 1994). Average monthly rainfall exceeds the evaporative demand during all months of the year. We do not have on-site rainfall data for the duration of our study, but during the first year rainfall in Hilo, Hawaii (10 m elevation) exceeded the annual average (331.5 cm) by 57 cm. During the second year rainfall in Hilo was 27 cm below average.

One of our study sites was located at 19°39′20″ N and 155°16′15″ W on an ‘a‘ā lava flow that originated in 1852. The second site, at 19°41′20″ N and 155°16′40″ W, was on a pāhoehoe flow that originated in 1855. ‘A‘ā lava is composed of loosely piled, very rough lava rocks overlying an uneven bed of solid lava. Pāhoehoe lava forms a solid substrate with an undulating, often ropy-textured surface interspersed with occasional large cracks, and has much less weatherable surface area than does ‘a‘ā. These two lava types are very similar mineralogically, differing principally in their texture (Lockwood & Lipman 1987). However, for Mauna Loa lavas the 1852 flow has a higher-than-usual proportion of olivines [$(Mg,Fe)_2SiO_4$] (Tilling et al. 1987).

Table 1. Structural characteristics of vegetation in the 'a'ā and pāhoehoe sites prior to fertilization (means + SE).

	'A'Ā site	**Pāhoehoe site**
Age (yr)	138	135
Tree density (stems/ha)	1780±179	1130±116
Mean tree diameter (cm)[a]	5.2±0.5	4.9±0.8
Basal area (m^2/ha)	4.1±0.4	2.4±0.3
Mean tree height (m)	4.1±0.4	3.7±0.4
Dicranopteris height (m)	0.8±0.4	1.1±0.5

[a] The diameter of a tree with an average basal area.

Soils of both study sites are poorly developed isothermic, Lithic Tropofolists consisting of shallow, very dark brown muck overlying lava bedrock.

Both sites were primary successional stands that had never been burned, cut, cleared or otherwise substantially disturbed since their origin. They were both dominated by *Metrosideros polymorpha* Gaud. (Myrtaceae), which forms an essentially monospecific overstory on young sites in this area. Stand structural data are provided in Table 1. Understories of both sites contained a variety of ferns, shrubs, and herbaceous plants, the most abundant of which were *Dicranopteris linearis* (Burm.) Underw. (Gleicheniaceae), *Machaerina angustifolia* (Gaud.) T. Koyama (Cyperaceae), *Palhinhaea cernua* (L.) Franco & Crav. Vasc. (Lycopodiaceae), *Vaccinium* spp. (Ericaceae), *Styphelia tameiameiae* (Cham. & Schlechtend.) F.v. Muell. (Epacridaceae), *Cibotium* spp. (Dicksoniaceae), and *Sadleria* spp. (Blechnaceae). There was no sign of any significant human disturbance in any of our study plots, and the prevailing low levels of feral pig (*Sus scrofa*) activity did not impact the vegetation substantially.

Methods

In each site thirty-six 10 m by 10 m plots were established in a 6 by 6 square design, with 5 m borders left between plots. This large block was divided into four blocks of 9 plots each, and 8 of these 9 plots were selected for fertilizer treatments. Generally, the single plot per block that was excluded contained either the lowest or highest density of trees. The eight study plots per block were then randomly assigned to one of eight fertilization treatments: no fertilizer (C), fertilization with N alone (N), fertilization with P alone (P), fertilization with a combination of other essential plant nutrients and micronutrients excluding N and P (T), and all possible combinations of these treatments (N+P, N+T, N+P+T, P+T).

Fertilization was initiated in January 1991. Nitrogen, P, Ca, K, and a micronutrient mix were each applied initially at a level of 100 kg/ha; and Mg was applied at an initial level of 50 kg/ha. Nitrogen was added one-half as ammonium nitrate and one-half as urea. Phosphorus was applied as triple super phosphate [monocalcium phosphate, $Ca(H_2PO_4)_2$], potassium was applied as muriated potash, Mg was supplied in dolomite and the micronutrient mixture, and Ca in the no-P treatments was supplied in dolomite and gypsum. The micronutrient mixture (Granusol #2gb5) contained 5.61% Mn, 5.12% Zn, 5.36% Cu, 5.38% Mg, and 0.54% Bo. Both sulfur and iron are abundant in these soils, but sulfur was added in gypsum and Fe was included in the micronutrient mixture. Fertilizer was reapplied at one-half of the initial rate to each plot twice annually over the next two years, generally in January and July. However, due to an error, K was applied at 5 kg/ha following the initial 100 kg/ha dose.

Prior to fertilizer application, all trees within each plot were measured. Individual trees in these sites frequently had multiple stems arising from a common base, and often branched below breast height. Individual upright stems are hereafter referred to as trees. The circumference of each tree and branch $\geq$ 10 cm in circumference at breast height (1.4 m) was measured to the nearest 0.5 mm with a metal tape, and the height of each tree was measured to the nearest 0.1 m with a fiberglass extension pole. The place on the bole where the circumference was measured was marked with a blue dot of paint, and a numbered aluminum tag was nailed onto each tree 20 cm below breast height so that each tree could be individually relocated. At the same time that we measured tree heights, we also measured the height to which the climbing fern *Dicranopteris linearis* grew up each tree.

All trees were remeasured in January-February of 1992 and 1993, one and two years after the initial fertilizer applications, and the heights of *Dicranopteris* were also remeasured. Both tree heights and the height of the numbered aluminum tag were recorded during the second and third inventories, because we found discrepancies in the location of ground level. New trees and branches that grew to a circumference at breast height of $\geq$ 10 cm were also measured. These new trees were measured in the same way as were trees originally present during the first inventory. Total tree mass per plot was determined from the inventory data of tree diameters and heights, and the allometric relationships described by Raich et al. (submitted). Results from analyses of individual-years growth did not differ in any substantial way. Here we report the results following the first two full years of fertilization, from January 1991 through February 1993. Tree height and biomass growth could only be analyzed for year 2 because of the uncertainties in initial tree heights mentioned above.

During early 1993 the leaves of several *Metrosideros* trees in each plot were collected for nutrient analyses. Only trees with pubescent leaves were sampled as these were most common. Following the methodology of Vitousek et al. (1993), the youngest flush of mature, fully expanded leaves was selected for analysis. The total leaf area of these leaves was measured with a Delta-T leaf area meter, and dry weights were measured after oven drying to constant mass at 70 °C. The leaves were then ground in a Wiley mill. Subsamples were digested using a persulfate-peroxide procedure in a block digestor using mercuric oxide as a catalyst. Concentrations of N and P were determined colorimetrically with an autoanalyzer. Another subsample was dry-ashed at 500 °C for 4 h, dissolved in hot nitric acid, and analyzed for Ca, Mg, and K by atomic absorption spectrophotometry.

Results of our plant growth and leaf property measurements were analyzed using a factorial ANOVA design with four blocks and three treatments: N, P, and T, where T refers to the total nutrient addition excluding N and P. Residuals plotted as a function of both fitted and actual values, and normal probability plots, were used to assess the assumptions of constant variance and normality of error terms. According to these analyses, the data did not depart from these assumptions. Variables tested included mean tree diameter increments (mm/yr), mean tree height growth (cm/yr), plot-level tree growth ($g{\cdot}m^{-2}{\cdot}yr^{-1}$), and height growth of the fern *Dicranopteris linearis* (cm/yr). These variables may be influenced by the size or density of trees within the study plots. Hence, we used the initial plot basal area (m^2/ha) and the initial tree density per plot (stems/ha) as covariates in our ANOVA. Leaf nutrient data were also analyzed using a factorial ANOVA design, but without covariates.

Results

Fertilization with essential nutrients other than N and P (i.e., the T treatment) had no significant effects on plant growth rates (Table 2) or on *Metrosideros* leaf characteristics when added either alone or in combination with N or P (Tables 3 & 4). The only exceptions to this were a significant increase in leaf Mg concentrations on the pāhoehoe site (Table 3), and a significant N*P*T interactive effect on leaf K concentrations in the ‘a‘ā site (Table 4). In contrast, virtually all measured foliar characteristics were significantly influenced by additions of N or P (Tables 3 & 4). Overall, there was very little evidence that any nutrients other than N and P had any affect on plant growth rates or leaf characteristics in either of our study sites.

Table 2. Statistically significant effects of nutrient amendments on plant-growth parameters as determined by ANOVA. Shown are the significance levels for all *P* values <0.10, to a minimum of 0.001.

Effect	Variable			
	Diameter Increment (mm/yr)	Height Growth (cm/yr)	*Dicranopteris* Growth (cm/yr)	Tree Growth (g·m^{-2}·yr^{-1})
Pāhoehoe site				
T	ns	ns	ns	ns
P	0.001	0.020	0.035	0.073
P*T	ns	ns	ns	ns
N	0.001	0.001	0.001	0.019
N*T	ns	ns	ns	ns
N*P	0.006	0.033	0.002	ns
N*P*T	ns	ns	ns	ns
Basal Area[a]	ns	0.035	ns	0.048
Stem Density[a]	ns	ns	ns	0.044
‘A‘Ā site				
T	ns	ns	ns	ns
P	0.010	0.002	0.048	0.014
P*T	ns	ns	ns	ns
N	0.001	0.001	0.001	0.001
N*T	ns	ns	ns	ns
N*P	ns	0.097	0.013	0.073
N*P*T	ns	ns	ns	ns
Basal Area[a]	0.072	ns	0.048	ns
Stem Density[a]	0.088	ns	0.066	ns

[a] Covariates in the ANOVA.

Fertilization with N, in contrast, significantly stimulated diameter growth, tree height growth, plot-level tree growth (g·m^{-2}·yr^{-1}, including ingrowth), and *Dicranopteris* height growth on both the pāhoehoe and ‘a‘ā substrates (Table 2). Nitrogen additions also resulted in a lower leaf mass per unit area in the ‘a‘ā site; higher foliar N and Mg concentrations in both sites; and lower foliar P, Ca and K concentrations (Tables 3 & 4). Reduced foliar concentrations of Ca, K, and P in the N-fertilized plots were probably due to a dilution effect; N apparently stimulated leaf production and leaf Ca, K, and P were therefore spread among more leaves. We have no direct measurements of leaf production in our sites, but an abundance of new leaf production was clearly observable in the N-fertilized plots and a rapid production of epicormic

Table 3. Effects of nutrient amendments on *Metrosideros* leaf properties in the ‘a‘ā site. Values are means + S.E. All leaves were from pubescent-leaved varieties.

Treatment	LMA[a] (g/m^2)	Foliar N (mg/g)	Foliar N (g/m^2)	Foliar P (mg/g)	Foliar P (g/m^2)
C	281 ± 5	6.2 ± 0.4	1.7 ± 0.1	0.68 ± 0.03	0.19 ± 0.01
T	272 ± 5	6.5 ± 0.2	1.8 ± 0.1	0.65 ± 0.06	0.18 ± 0.02
P	269 ± 6	6.7 ± 0.3	1.8 ± 0.1	1.62 ± 0.20	0.43 ± 0.05
PT	264 ± 7	6.8 ± 0.4	1.8 ± 0.1	1.62 ± 0.22	0.43 ± 0.06
N	265 ± 10	7.3 ± 0.2	1.9 ± 0.1	0.57 ± 0.06	0.15 ± 0.02
NT	259 ± 6	7.5 ± 0.3	1.9 ± 0.1	0.65 ± 0.01	0.17 ± 0.01
NP	249 ± 7	7.7 ± 0.2	1.9 ± 0.1	0.97 ± 0.05	0.24 ± 0.02
NPT	251 ± 5	7.5 ± 0.3	1.9 ± 0.1	1.00 ± 0.05	0.25 ± 0.01
Significance	N ** P *	N ***	N *	N *** P *** N*P ***	N *** P *** N*P ***

	Foliar N/P	Foliar Ca (mg/g)	Foliar K (mg/g)	Foliar Mg (mg/g)
C	9.1 ± 0.2	9.4 ± 0.6	2.4 ± 0.6	1.2 ± 0.1
T	10.2 ± 1.0	8.7 ± 0.2	4.3 ± 0.4	1.3 ± 0.1
P	4.3 ± 0.5	10.5 ± 0.9	4.0 ± 0.5	1.2 ± 0.1
PT	4.4 ± 0.6	10.8 ± 0.7	2.6 ± 0.8	1.5 ± 0.1
N	13.2 ± 1.5	6.4 ± 0.4	2.8 ± 0.2	1.4 ± 0.1
NT	11.5 ± 0.5	7.1 ± 0.2	2.9 ± 0.5	1.3 ± 0.1
NP	8.0 ± 0.3	10.8 ± 0.7	1.3 ± 0.3	1.9 ± 0.2
NPT	7.6 ± 0.3	10.2 ± 0.6	2.5 ± 0.2	2.1 ± 0.2
Significance	N *** P ***	N ** P *** N*P *	N ** N*P*T **	N *** P *** N*P **

[a] Leaf mass per unit leaf area.

branches following fertilization was documented previously on similar sites (Kliejunas & Ko 1974).

Phosphorus fertilization also stimulated plant growth significantly, as suggested by earlier analysis with the CENTURY model (Parton et al. 1989). Additions of P increased diameter increments, tree height growth, *Dicranopteris* height growth, and tree growth in both sites (Table 2). Fertilization with P also decreased leaf mass per unit area in both sites; increased foliar N, P, Ca, and Mg concentrations in the pāhoehoe site; and increased foliar Ca,

Table 4. Effects of nutrient amendments on *Metrosideros* leaf properties in the pāhoehoe site. Values are means + S.E. All leaves were from pubescent-leaved varieties.

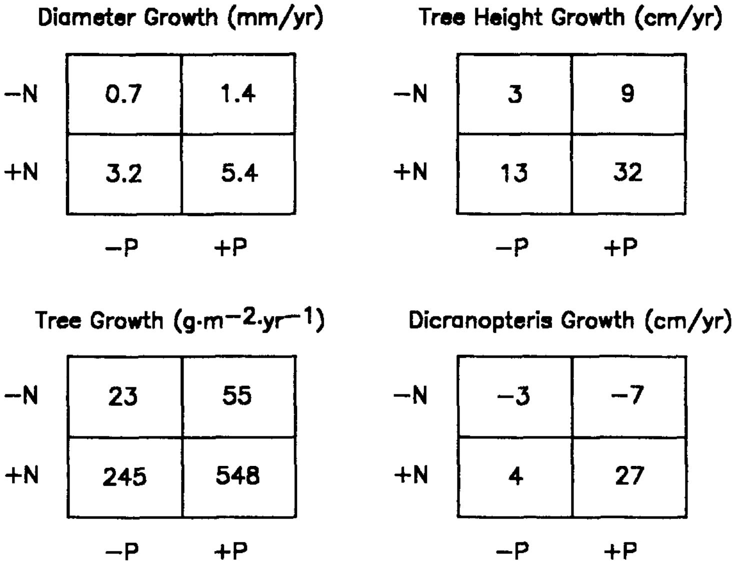
Treatment	LMA[a] (g/m^2)	Foliar N (mg/g)	Foliar N (g/m^2)	Foliar P (mg/g)	Foliar P (g/m^2)
C	265 ± 14	7.1 ± 0.1	1.9 ± 0.1	0.73 ± 0.03	0.19 ± 0.01
T	265 ± 2	6.7 ± 0.1	1.8 ± 0.1	0.72 ± 0.03	0.19 ± 0.01
P	241 ± 8	6.9 ± 0.2	1.7 ± 0.1	1.50 ± 0.18	0.36 ± 0.04
PT	237 ± 6	7.5 ± 0.1	1.8 ± 0.1	1.69 ± 0.22	0.40 ± 0.05
N	263 ± 5	8.0 ± 0.1	2.1 ± 0.1	0.66 ± 0.01	0.17 ± 0.01
NT	261 ± 7	8.1 ± 0.2	2.1 ± 0.1	0.66 ± 0.03	0.17 ± 0.01
NP	215 ± 8	9.0 ± 0.4	1.9 ± 0.1	1.41 ± 0.10	0.30 ± 0.03
NPT	222 ± 12	9.2 ± 0.3	2.0 ± 0.1	1.23 ± 0.07	0.27 ± 0.03
Significance	P ***	N *** P *** N*P *	N *** P *	N * P ***	N ** P ***

	Foliar N/P	Foliar Ca (mg/g)	Foliar K (mg/g)	Foliar Mg (mg/g)
C	9.9 ± 0.3	8.8 ± 0.4	4.4 ± 0.4	1.3 ± 0.1
T	9.4 ± 0.4	8.1 ± 0.7	4.4 ± 0.3	1.4 ± 0.1
P	4.8 ± 0.4	9.6 ± 0.6	4.2 ± 0.7	1.5 ± 0.1
PT	4.7 ± 0.6	11.7 ± 0.8	4.6 ± 0.3	2.2 ± 0.1
N	12.1 ± 0.1	5.8 ± 0.5	3.7 ± 0.2	1.4 ± 0.2
NT	12.2 ± 0.5	6.3 ± 0.4	3.6 ± 0.4	1.5 ± 0.1
NP	6.4 ± 0.2	10.6 ± 1.1	2.4 ± 0.1	2.1 ± 0.1
NPT	7.5 ± 0.5	10.5 ± 0.7	3.2 ± 0.3	2.4 ± 0.3
Significance	N *** P ***	N * P *** N*P *	N ***	N * P *** T **

[a] Leaf mass per unit leaf area.

Mg, and P concentrations in the ‘a‘ā site (Table 4). Apparently, additions of P increased nutrient uptake in both sites, but without the same increase in leaf production that was observable in the N-fertilized plots. Triple super phosphate, used to supply P in our study, also contains Ca. However, additions of Ca without P had no significant impacts on plant growth rates in either site.

Significant N*P interactive effects on growth and foliar nutrient concentrations were observed in both sites (Tables 2, 3 & 4). Significant N*P effects on



Diameter Growth (mm/yr)

	−P	+P
−N	0.7	1.4
+N	3.2	5.4

Tree Height Growth (cm/yr)

	−P	+P
−N	3	9
+N	13	32

Tree Growth ($g \cdot m^{-2} \cdot yr^{-1}$)

	−P	+P
−N	23	55
+N	245	548

Dicranopteris Growth (cm/yr)

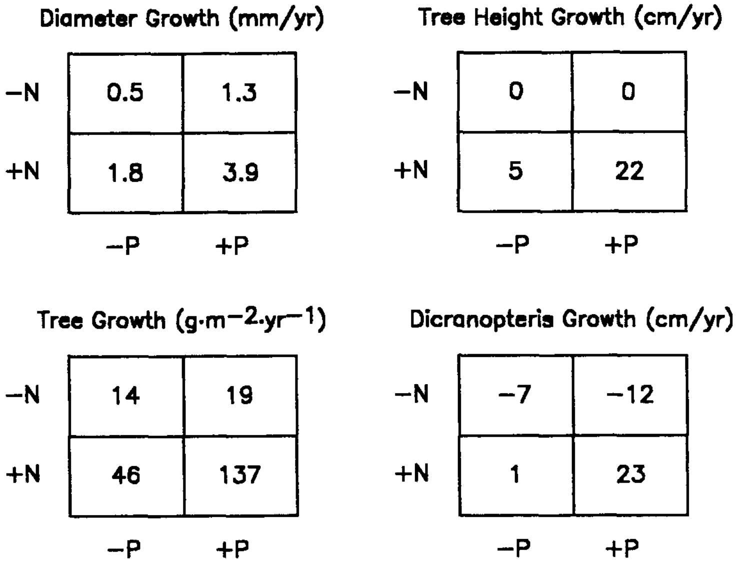
	−P	+P
−N	−3	−7
+N	4	27

Fig. 1. Mean plant growth rates in the ‘a‘ā site. Data from the T (total less N and P) treatment are combined herein because no significant effects of that amendment were observed. Each value therefore represents the mean effect combined across two plots in each of four blocks; significance levels are presented in Table 2.

foliar nutrient concentrations are difficult to interpret, as they varied among sites and nutrients. For instance, foliar N concentrations were highest in plots fertilized with both N and P, but this effect was only significant in the pāhoehoe site. Foliar Ca levels showed significant N*P interaction in both sites, but were similar in plots receiving P alone versus those receiving both N and P. The N*P effect on plant growth, in contrast, suggests a synergistic interaction; the greatest growth occurred in plots that received both N and P (Figs. 1 & 2).

Discussion

Our study was conducted on young basaltic lavas that had a very small surface area subject to weathering, and that develop into Histosols with a minimal admixture of mineral soil. Hence, we investigated nutrient limitations to plant productivity at the very earliest stages of soil development. Virtually any essential nutrient element that is not present in a readily soluble form may be in limited supply to plants at the initiation of primary succession. Our results indicate unambiguously that both N and P limit plant growth during



Diameter Growth (mm/yr)

	−P	+P
−N	0.5	1.3
+N	1.8	3.9

Tree Height Growth (cm/yr)

	−P	+P
−N	0	0
+N	5	22

Tree Growth ($g \cdot m^{-2} \cdot yr^{-1}$)

	−P	+P
−N	14	19
+N	46	137

Dicranopteris Growth (cm/yr)

	−P	+P
−N	−7	−12
+N	1	23

Fig. 2. Mean plant growth rates in the pāhoehoe site. Data from the T (total less N and P) treatment are combined herein because no significant effects of that amendment were observed. Each value therefore represents the mean effect combined across two plots in each of four blocks; significance levels are presented in Table 2.

early soil development on these basaltic substrates. Either N or P, when added alone, stimulated plant growth in both of our sites.

All of our measurements suggest that N stimulated growth relatively more than did P (e.g., Figs. 1 & 2). However, attempting to tease out the relative importance of N versus P limitations in these sites, based on these results, is probably not warranted. Significant and marginally significant N*P interactive effects on growth parameters (Table 2) suggest that N and P provide simultaneous limitations to growth, and that greatest growth occurred when both nutrients were added together. Kliejunas & Ko (1974) found that *Metrosideros* growth in stands similar to our own was significantly stimulated by fertilizer additions that included both N and P, but not to additions of either element alone. These findings appear contradictory to ours, but the greater statistical power of our experimental design may have allowed us to identify significant results that they could not establish. Our results demonstrate unambiguously that N and P colimit production on these very young, poorly weathered, basaltic lavas.

A number of studies have suggested or demonstrated that N is the principal nutrient limiting plant growth during early primary succession (e.g., Miles & Walton 1993). Complete factorial fertilization studies on coal spoils and china-clay waste deposits in England (Bradshaw & Chadwick 1980; Marrs et al. 1983) and on 30- and 200-year-old tephra substrates in Hawaii (Vitousek et al. 1993) all demonstrated that N and N alone stimulated plant growth rates on these substrates. In contrast, results similar to ours were reported for glacial till and iron-ore spoil banks in Minnesota, where aspen growth was stimulated by additions of either N or P, but the greatest growth stimulation was observed in trees fertilized with both N and P (Leisman 1957). Based on less direct measurements that included fertilization of seedlings in greenhouses, Chapin et al. (1994) concluded that both N and P limited plant growth on pioneer soils from Glacier Bay, Alaska, but that only P limited growth on older substrates. Hence, there is evidence that P as well as N may limit early primary succession, but the importance of P varies among substrate types.

Our results compare well with those of Vitousek et al. (1993), who conducted a similar study in a nearby, somewhat drier site that developed after the 1790 eruption of Kileaua Volcano. Although somewhat older than our study sites, their Thurston site is located at the same elevation and is similarly dominated by pubescent-leaved *Metrosideros polymorpha*. All three sites are on mineralogically similar substrates, but the Thurston site developed on tephra, a mixture of easily weathered cinder and fine ash, whereas the ‘a‘ā site contained rough rocks of various sizes, and the pāhoehoe lava had generally planar surfaces exposed to weathering. Together, these sites represent a gradient of texture of parent material. The finer-textured tephra deposits in the Thurston site should have increased P availability during the early phases of forest development in comparison with the lavas.

Diameter increments in untreated plots on all three substrates averaged about 0.5 mm/yr (Fig. 3), and diameter increments in all three plots were stimulated by N additions. However, diameter increments in the tephra site were not increased by P fertilization (Vitousek et al. 1993), whereas those in both lava sites were. Nitrogen and N alone limited growth in the tephra site, whereas N and P colimited production in the lava sites. There is even a suggestion that the ‘a‘ā site was relatively more N-limited than the pāhoehoe site (Fig. 3). The surface area for mineral weathering is low in both lava sites, but lower in pāhoehoe than in ‘a‘ā. These comparisons suggest that the texture of a mineralogically similar parent material can influence N-P interactions during early primary succession. If weathering is sufficiently slow, initial P limitations to growth may persist along with N limitations for an undetermined period. This initial phase of pedogenesis would presumably be followed by the early N and late P limitations to growth proposed by Walker & Syers (1976).

A surprising result of our study was the dramatic increases in growth rates that were observed in the fertilized plots. It has been suggested that

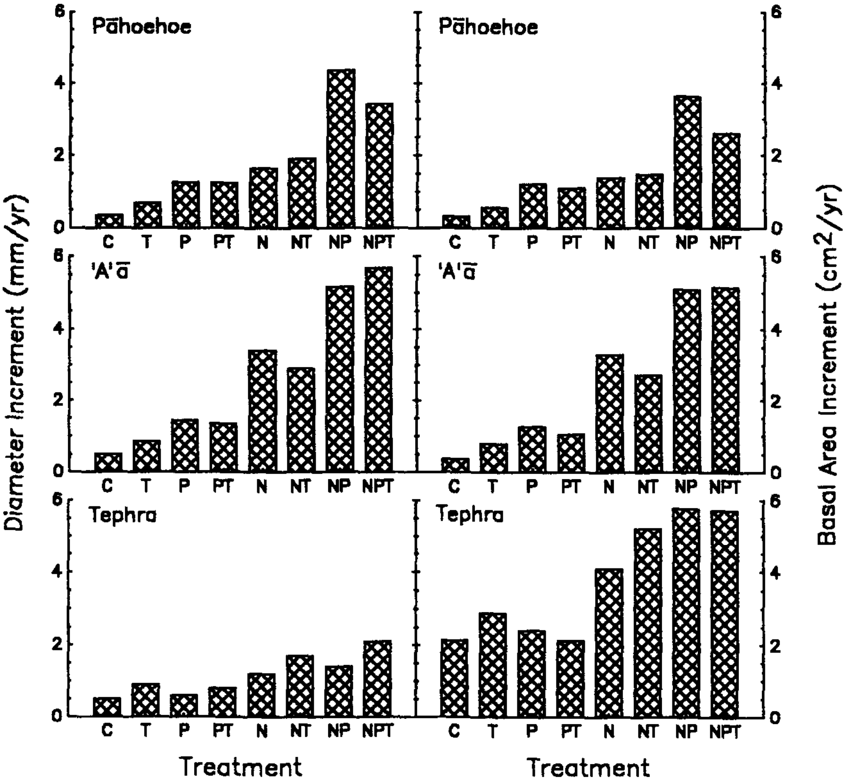


Fig. 3. The effects of nutrient amendments on tree diameter and basal area increments in three sites on different substrates. All three sites were at the same elevation and were nearly monospecific stands of *Metrosideros polymorpha.* Tephra represents the Thurston site of Vitousek et al. (1993).

plants adapted to low-nutrient environments have a limited capacity to adjust their growth or photosynthetic rates in response to increased rates of nutrient supply (e.g., Schulze & Chapin 1987). Foliar N levels in all three sites are extraordinarily low in comparison with other tropical forests (Scatena et al. 1993; Vitousek & Sanford 1986), reflecting the very nutrient-poor condition of our sites. Tree diameter increments in plots fertilized with N or P were higher in our sites than in the comparable tephra site of Vitousek et al. (Fig. 3). Trees were larger in the tephra site, averaging 19.7 cm dbh, so this trend is reversed if growth is expressed on a basal-area basis (Fig. 3). Nevertheless, rates of tree diameter growth in the pāhoehoe and 'a'ā sites were increased by almost an order of magnitude following fertilization with both N and P (Fig. 4), and basal area increments (data not shown) showed a similar trend. The relative response of trees in the tephra-based site was much less (Fig.

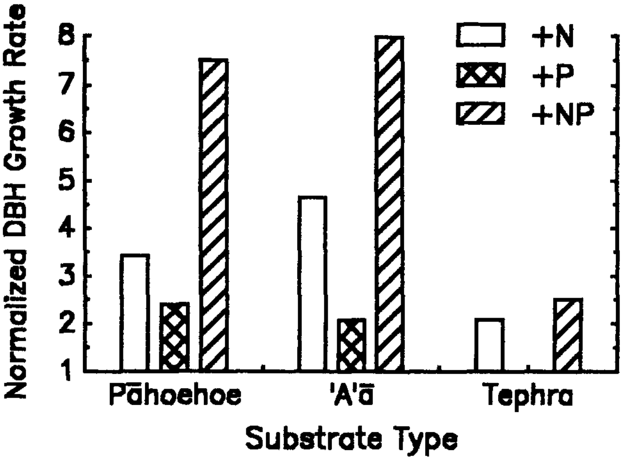


Fig. 4. Relative rates of *Metrosideros polymorpha* diameter growth on three different substrates following additions of N and P. Shown here are the ratios between diameter increments in the treated plots over those in plots receiving no N or P; control plots therefore have a value of one. The P effect was not significant in the tephra (Thurston) site of Vitousek et al. (1993).

4). *Metrosideros*, which clearly is adapted to growth on very nutrient-poor substrates, was able to rapidly and dramatically adjust its growth rate to take advantage of the fertilization, and the relative response was much greater on the pāhoehoe and ‘a‘ā lavas than in the tephra site.

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