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Nutrient limitations to plant growth during primary succession in Hawaii Volcanoes National Park

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Abstract. We determined the effects of nutrient amendments on plant growth in three tropical montane rainforest sites representing a sequence of soil ages (< 30, 200, and ~ 2000 y). Factorial fertilization with nitrogen, phosphorus, and all other essential nutrients (combined) was applied to the two younger sites; only nitrogen was applied to the oldest one. Nitrogen supply represented the most important limitation to plant growth in the two younger sites; additions of nitrogen caused significant increases in tree diameter increment, height growth, litterfall, and most other growth-related parameters. In contrast, nitrogen additions had no significant effect on plant growth in the oldest site. Phosphorus additions increased extractable soil phosphorus and plant tissue phosphorus, but did not increase plant growth at the young sites. The results are consistent with Walker & Syers' (1976) model for the control of nutrient limitation during soil development.

Introduction

The importance of nutrient limitation to plant growth in tropical forests has been discussed more often than it has been determined. Nutrient limitation can be defined unambiguously — it occurs wherever the addition of a nutrient causes increased plant growth — but it can be difficult to analyze in practice. For example, plants adapted to infertile sites may be relatively unresponsive to nutrient additions, the short- and long-term responses to added nutrients may differ, and other processes (adsorption of added nutrients by soil colloids, microbial immobilization) may compete with plants for added nutrients (Chapin et al. 1986; Rastetter & Shaver 1992). Nevertheless, identification of nutrient limitation to plant growth, and of the mechanisms that cause it, is crucial to understanding the regulation of production and nutrient cycling in tropical forest ecosystems and their potential responsiveness to local, regional, and global change (Vitousek & Sanford 1986; Field et al. 1992).

There have been numerous studies of primary production and nutrient cycling in tropical forests (many summarized in Jordan 1985; Vitousek & Sanford 1986; and Proctor 1987) that have yielded substantial information on the quantities of carbon and nutrients taken up and cycled by forests annually. Such studies can be used to calculate element ratios in plant tissue and litterfall (i.e. C:N, C:P, N:P); these in turn can indicate which nutrients are in relatively short supply, and hence potentially limiting (Vitousek 1982, 1984). Comparisons between tropical and higher-latitude forests, and comparisons among tropical forests, have suggested that: (1) many tropical forests are rich in N and impoverished in P and Ca (especially on oxisols and ultisols) relative to most temperate forests; and (2) montane tropical forests often are impoverished in both N and P relative to lowland tropical forests (Grubb 1977; Tanner 1985; Cuevas & Medina 1986; Vitousek & Sanford 1986; Vitousek et al. 1988; Heaney & Proctor 1989; Medina & Cuevas 1989; Veneklaas 1991).

The patterns derived from these studies lead to useful and testable hypotheses, but the indirect nature of the relationship between element ratios in plants and nutrient limitation makes any conclusion based solely upon element ratios uncertain. Fertilization experiments can yield much stronger conclusions, but as discussed above there are impediments to determining nutrient limitation directly through whole-system fertilization experiments, and these are particularly strong in tropical forests. The generally high level of tree species diversity in the tropics can make across-treatment but within-species comparisons difficult, and the widespread occurrence of variable-charge clays with substantial capacity for phosphorus sorption can complicate the delivery of fertilizer to plants (Uehara & Gillman 1981; Sollins et al. 1988). Nevertheless, useful fertilization studies have been carried out in the tropics. Most importantly, Tanner et al. (1992) demonstrated that addition of N and P to a Venezuelan montane forest led to significantly greater diameter growth and annual litterfall in fertilized than in control plots. They further suggested that N represents a more important limitation to growth than does P in this site.

In other studies, Tanner et al. (1990) demonstrated that N and P additions increased tree growth in unreplicated Jamaican montane forest plots, and Gerrish et al. (1988) reported that a complete fertilizer increased tree growth in two Hawaiian montane forests. Within stands, Cuevas & Medina (1988) demonstrated that tree roots in an Amazonian forest on an oxisol responded to spot additions of P and Ca (but not N) with increased growth, while those in a forest on a spodosol responded to added N; these results were consistent with the observed C:nutrient ratios in tissue and concentrations in soils in those sites (Cuevas & Medina 1986; Medina & Cuevas 1989). These few studies demonstrate that certain nutrients can limit tree growth in certain tropical forest sites; they do not provide sufficient information to determine the patterns of nutrient limitation or its controls across a range of tropical forest sites.

Walker & Syers (1976) proposed a theory that can be used to address why particular nutrients are limiting to plant growth in particular classes of sites. They pointed out that early in the development of a new soil (and hence at the initiation of primary succession), most soils contain all of the P (and Ca, Mg, K, etc.) that they will ever have. In warm, moist climates, weathering rapidly releases these elements into biologically available forms, and their availability to plants increases at least as fast as plants demand for these elements. In contrast, new soils generally contain little or no nitrogen. The early stages of primary succession therefore are marked by the accumulation of nitrogen from the atmosphere, rapidly where symbiotic nitrogen fixers are abundant, and otherwise most slowly. Primary production in early successional systems would be expected to be limited by N (Cole & Heil 1981; Vitousek et al. 1989a).

Later in soil development, P and other rock-derived elements gradually are lost and/or bound in insoluble or physically protected forms, while nitrogen can continue to enter systems through biological nitrogen fixation (Walker & Syers 1976). Precipitation and dry deposition continue to bring all elements into sites throughout the course of soil development, but the quantities involved generally are relatively small, and nitrogen inputs by this pathway are greater (in both relative and absolute terms) than are inputs of most rock-derived elements. The potential for biological nitrogen fixation means that overall nitrogen inputs can respond (at least ultimately) to sustained nitrogen limitation (Vitousek & Howarth 1991). Plant growth on the oldest soils therefore should be P, cation, or micronutrient limited, a pattern consistent with the observation of very wide C:P and C:Ca ratios in forests on highly weathered tropical oxisols and ultisols (Vitousek & Sanford 1986).

The prediction that N supply limits plant growth early in primary succession can be evaluated using fertilization studies in temperate and boreal ecosystems. Factorial experiments in young sites on two types of mine spoils in England demonstrated that only N increased growth when nutrients were added singly; other nutrients had positive effects only when applied in combination with N (Bradshaw & Chadwick 1980; Marrs et al. 1983). Leisman et al. (1957) demonstrated that adding either N or P plus

K increased the growth of cottonwood saplings on mine spoils in Minnesota; the combination of all three nutrients increased growth still further. Lawrence et al. (1967) reported that nitrogen (added alone) increased plant growth in a young site at Glacier Bay, Alaska, and that the application of other nutrients along with nitrogen enhanced or extended the response. Added nitrogen also enhanced production on young river-terrace soils in Alaskan tundra (Giblin et al. 1991). Other studies (cf. Walker & Chapin 1986) have added nutrients only in combined form; these studies often demonstrate that nutrients are limiting early in primary succession, but not which nutrients are limiting.

In this paper, we use factorial fertilization experiments to determine nutrient limitation to plant growth in three tropical montane forests on volcanic ash soils on the Island of Hawaii. The three sites differed in soil age (< 30, 200, and ~ 2000 y), and all lacked vascular plants with symbiotic nitrogen-fixing associations. Our purpose was to test the prediction that N alone should limit plant growth early in soil development, but that the degree of N limitation should decrease with increasing soil age.

Study sites

Nutrient limitation to plant growth was evaluated at three sites differing in soil age on Kilauea Volcano (19° 25′N 155° 15′W) in Hawaii Volcanoes National Park (Fig. 1). The youngest site (Puu Puai or PP) was established on coarse tephra from a 1959 eruption of Kilauea Iki crater; it was 26 years old at the beginning of our experiment. The site is adjacent to the Lower Byron site of Vitousek & Walker (1989) and Walker & Vitousek (1991), although the PP site studied here received more ash in 1959 than did their site, which killed most of the previous forest at PP. The site, described as part of habitat zone 4 (deep cinder) by Smathers & Mueller-Dombois (1974), is at 1120 m elevation and has a mean annual precipitation of approximately 2200 mm (interpolated from Giambelluca et al. 1986). Vegetation in 1985 was sparse, with a large fraction of the ground covered by open cinder, and the soil has not been classified. The dominant species in the site were *Metrosideros polymorpha, Rubus argutus, Buddeleja asiatica, Vaccinium reticulatum,* and *Dubautia scabra* (Wright & Mueller-Dombois 1988; Mueller-Dombois & Whiteaker 1990; Matson 1990).

At the intermediate-aged site (Thurston lava tube or TH), an explosive eruption of Kilauea Iki in 1790 deposited coarse tephra in a 30—40 cm layer overlying a several hundred yr old pahoehoe lava flow. The site is at 1190 m elevation with 2500 mm annual precipitation (Giambelluca et al. 1986); it now supports 14—16 m tall forest dominated by *Metrosideros*

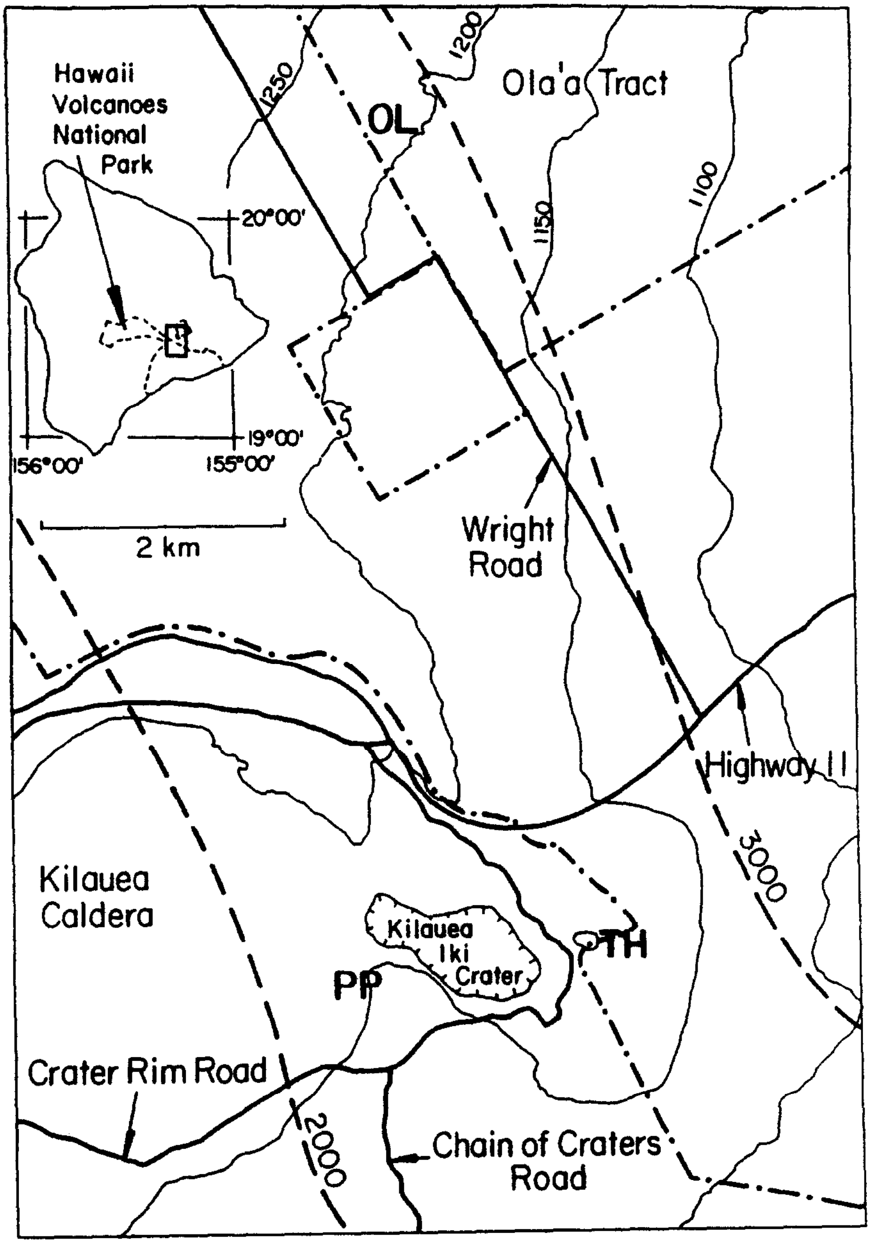

Fig. 1. Locations of the study sites in Hawaii Volcanoes National Park. Roads are represented by coarse solid lines, elevation contours (in m) by fine solid lines, precipitation isohyets (in mm/y, from Giambelluca et al. 1986) in coarse dashed lines, and the Park boundary by an alternating dash-dot line. PP represents the young (26—28 y old) Puu Puai site, TH the intermediate-aged (< 200 y) Thurston site, and OL the old (~ 2000 y) Ola'a site.

polymorpha, with a subcanopy dominated by the tree fern *Cibotium glaucum* (Gerrish et al. 1988). The soil is a hydric lithic dystrandept of the Puhimau series.

The oldest site (Ola'a or OL) was established in deep ash resulting from several eruptions of Kilauea over thousands of years. The 1790 eruption and an earlier one several hundred years ago deposited thin layers of tephra on the site, but these were insufficient to initiate primary succession. We consider a thicker deposit ca. 2000 years ago as the event that probably initiated succession (Vitousek et al. 1989b). The elevation of this site is 1220 m and mean annual precipitation is ~ 2900 mm (Giambelluca et al. 1986). The vegetation at OL consists of an open canopy of large (20—25 m tall) *Metrosideros polymorpha*, diverse subcanopy trees, and a well-developed layer of tree ferns (*Cibotium glaucum, C. chammissois,* and *C. hawaiiense*); the soil is a typic hydrandept of the Puaulu series. *Metrosideros* canopy dieback (Mueller-Dombois 1987) is widespread in the area, although not in the particular site we sampled. The intermediate and old sites (TH and OL) correspond to sites T2 and T3 of Vitousek et al. (1983).

These three sites do not make a perfect chronosequence; precipitation varies from 2200—2900 mm across the sites, and the tephra probably was finer-textured (initially) at OL because of its greater distance from the eruptive vents. Nevertheless, we believe that substrate age is the most important difference among these sites. Results of earlier research demonstrated that rates of N mineralization in soils increase in parallel with the increase in soil age across these sites (Vitousek et al. 1983; Vitousek & Matson 1988).

Methods

We established complete factorial fertilization experiments in Puu Puai (PP) and Thurston (TH), the two younger sites. The treatments were N (initial application 10.0 g/m^2 as N, half as urea and half as $(NH_4)_2SO_4$ – S inputs are substantial in these young volcanic sites and its supply should not be limiting), P (initially 5.0 g/m^2 P as triple superphosphate), and a combination of all other plant macro- and micro-nutrients (abbreviated T; initially, these plots received 5.0 g/m^2 of K as K_2SO_4, 5.0 g/m^2 Ca and 3.0 g/m^2 of Mg as dolomite [calcium-magnesium carbonate], and a commercial micronutrient formulation that added all other essential micronutrients [Granusol #2gb5; 5.61% Mn, 5.12% Zn, 5.36% Cu, 5.38% Mg, 0.54% Bo, and 0.46% Mo]). In the older Olaa site (OL), we applied only the N treatment; little intact forest remains in that area, and it was necessary to minimize our impact on it. The initial fertilizer treatments were applied late in 1985; treatments consisting of 25% of the initial applications were repeated in all of the sites at 6 month intervals thereafter.

Because of the difference in forest structure along the soil age gradient, we implemented the fertilization experiment differently in each site. In PP we selected 40 individual *Metrosideros* from 50 to 100 cm in height, and applied each treatment to a randomly selected set of five individuals. Fertilizer was applied to a 2 m radius around the base of each plant. The height and basal diameter of each plant were measured every two months. Two twigs on each tree were marked, and leaf production and mortality were recorded bimonthly. Finally, photosynthetic rates were determined in July 1987 using a LICOR 6000 portable photosynthesis system.

In the 200 yr old TH site, we established a grid of forty 20 × 20 m plots, then selected 32 plots that were similar in canopy cover and in their near-absence of introduced woody plants. Each fertilizer treatment was applied to the 15 × 15 m interior of four plots. Nickel alloy steel dendrometer bands that had been protected against corrison from volcanic gases (Walker & Whiteaker 1988) were installed on four individual *Metrosideros* trees within each plot, and diameter increments were recorded bimonthly. Two 0.5 m^2 litter traps were placed randomly in each plot, and litterfall was collected monthly.

Twelve individual *Metrosideros* were chosen in the OL site; six of these were selected at random to receive N fertilizer in a circular plot (8 m radius) centered on a tree, and six served as controls. *Metrosideros* diameter increment and litter production were measured as in the TH site. For all of the sites, we report results for the second year of measurements of *Metrosideros* diameter increment and annual litterfall, thereby minimizing any lags or transient effects that occurred immediately after the initial fertilizer application.

The effects of the fertilization treatments on soil and plant nutrients were assessed by sampling available soil nutrients and *Metrosideros* and *Cibotium* foliar nutrients. Two pairs of soil cores (15 cm deep by 6 cm diameter) were collected from each plot in each site 16—18 mo following the initiation of the treatments. At the TH and OL sites, one core in each pair was enclosed in a polyethylene bag and replaced in the soil for the determination of potential nitrogen mineralization *in situ.* The second (and all of the soil from PP) was returned to the laboratory and divided into: (1) a 10 g subsample that was extracted in 100 ml 2 N KCl for determination of extractable NH_4 and NO_3 concentrations; (2) a 10 g subsample that was extracted in 50 ml of 10% NaCl for determination of extractable Ca, Mg, and K concentrations; (3) except in the Ol site, a 3 g sample that was extracted in 10 ml ammonium fluoride/HCl for PO_4 analyses (Olsen & Sommers 1982); (4) a ca. 100 g sample that was weighed, oven-dried to constant mass at 80 °C, then reweighed to determine soil water content; and (5) in PP, a 10 g subsample that was incubated under constant conditions in the laboratory for 10 days, then extracted in 2 N KCl for NH_4 and NO_3 analyses. The soil cores that had been replaced in the field in TH and OL were retrieved after 10 days and extracted in 2 N KCl for NH_4 and NO_3 determinations. Rates of potential nitrogen mineralization were calculated as final ($NH_4 - N$ plus $NO_3 - N$) minus initial ($NH_4 - N$ plus $NO_3 - N$) (Eno 1960).

Canopy leaves of *Metrosideros* were collected in each plot in July 1987, by hand in PP and by shooting down small branches in the canopy in TH and OL. The youngest flush of mature, fully expanded leaves was selected for analysis. *Cibotium* leaflets also were collected and analyzed in TH and OL. Leaf areas were determined on the day of collection using a Delta-T leaf area meter, and leaves were then oven-dried at 70 °C to constant mass. Leaves were ground in a Wiley mill, digested using a persulfate-peroxide procedure in a block digester using a mercuric oxide catalyst, and analyzed for N and P.

All forms of N and P were determined colorimetrically on a Technicon AutoAnalyzer II at Stanford. Cations were determined by atomic absorption spectrophotometry at NASA-Ames Research Center. The effects of the factorial fertilizer treatments in PP and TH were analyzed statistically using a complete factorial ANOVA design in SYSTAT 5.0; results from OL were analyzed using t-tests. Where means and variances were correlated, values were log-transformed prior to analysis.

Results

Added N caused a very highly significant increase in diameter increment in *Metrosideros* ($p < 0.001$) and a significant increase in height growth ($p < 0.05$) at the young PP site (Table 1). No other nutrient treatment or interaction had a significant effect. The rate of leaf production on marked branches were increased by N addition, and the longevity of the leaves produced by N-amended plants was decreased, yielding a more rapid turnover of leaves following additions of N. Finally, rates of photosynthesis (on a leaf area basis) were increased significantly ($p < 0.01$) by N addition and not by other nutrients or combinations of nutrients. Added P increased concentrations of extractable P in the soil significantly ($p <$ 0.01), and it increased P concentrations in *Metrosideros* leaves (Table 2). The complete (minus N and P) treatment also increased concentrations of

Table 1. Effects of factorial fertilization on plant growth and turnover in the young Puu Puai site, Hawaii Volcanoes National Park. Values are means of 5 plots/treatment, with standard errors in parentheses. The treatments are: O = no addition; N = Nitrogen; P = Phosphorus; T = complete fertilizer, including micronutrients but without N or P. Quantities and timing of fertilizer applications are described in the text. Effects reported as significant are determined from factorial ANOVA main effects and interactions. N.S. = no significant effects, * = $p < 0.05$, ** = $p < 0.01$, and *** = $p < 0.001$.

Treatment	Diameter increment (mm/y)	Height increment (cm/y)	Leaf production (#/yr)	Leaf longevity (% remaining at 18 mo)	Photosynthetic rate (μM m^{-2} s^{-1})
O	4.6 (1.0)	19 (5)	36 (7)	57	10.0 (1.0)
P	6.6 (0.8)	22 (6)	59 (12)	75	9.0 (0.6)
T	7.5 (1.2)	24 (8)	38 (9)	51	9.0 (0.7)
PT	6.0 (1.1)	28 (5)	53 (11)	76	8.8 (0.8)
N	13.3 (2.9)	34 (6)	83 (12)	27	10.2 (1.1)
NP	10.6 (2.0)	47 (3)	70 (15)	46	11.4 (1.5)
NT	10.1 (1.5)	43 (5)	60 (9)	61	11.5 (1.0)
NPT	14.7 (3.4)	48 (8)	56 (13)	59	12.2 (0.9)
Significance	N***	N*	N*	N*	N**

extractable Ca, Mg, and K in the soil ($p < 0.001$, results not shown). Additions of nitrogen caused significant increases in the pool size of available N (NH_4 plus NO_3), and in rates of potential net nitrogen mineralization (Table 2).

Nitrogen additions also increased plant growth at the 200 yr old TH site (Table 3). The rate of diameter growth was slow in all treatments compared to the younger or older sites, but the increase in diameter increment resulting from the addition of N was very highly significant ($p < 0.001$). Further, nitrogen additions increased annual litterfall (and hence turnover of the canopy) (Table 3), and rates of height growth and frond production in the tree fern *Cibotium glaucum* (Walker & Aplet in press).

Phosphorus additions caused a very highly significant increase in extractable P in the soil and in foliar P in *Metrosideros* and *Cibotium* (all $p < 0.001$) (Table 4), but no increase in growth. Nitrogen additions increased foliar N in both species, but had no significant effect on N availability in the soil. Also, the complete (minus N and P) treatment had no significant effect on the concentration of extractable cations in this site (not shown). N additions and/or interactions between N and other treatments (besides P) had significant effects on foliar P concentrations; these

Table 2. Effects of factorial fertilization on plant and soil nutrients in the young Puu Puai site, Hawaii Volcanoes National Park. Values, treatments, and significance levels as in Table 1.

Treatment	$NH_4 - N + NO_3 - N$ pool size ($\mu g/g$)	N mineralization ($\mu g \cdot g^{-1} \cdot 10\,d^{-1}$)	Extractable P ($\mu g/g$)	Foliar N (%)	Foliar P (%)
O	0.4 (0.2)	−0.1 (0.1)	1.0 (0.1)	0.83 (0.05)	0.095 (0.010)
P	0.3 (0.2)	−0.1 (0.1)	3.8 (1.4)	0.83 (0.08)	0.142 (0.041)
T	0.7 (0.3)	0 (0.1)	0.8 (0.3)	0.80 (0.05)	0.094 (0.017)
PT	1.1 (0.4)	0 (0.4)	15.9 (7.8)	0.85 (0.02)	0.095 (0.008)
N	1.0 (0.4)	1.0 (0.3)	0.3 (0.1)	0.92 (0.06)	0.072 (0.006)
NP	1.1 (0.4)	0.9 (0.4)	5.3 (2.0)	1.10 (0.06)	0.107 (0.015)
NT	1.8 (0.6)	0.4 (0.4)	0.4 (0.1)	1.04 (0.04)	0.092 (0.010)
NPT	1.8 (0.9)	0.3 (0.6)	4.4 (1.9)	1.02 (0.06)	0.103 (0.007)
Significance	N*	N*	P**	N***	P*

Table 3. Effects of factorial fertilization on plant growth and turnover in the intermediate-aged Thurston site, Hawaii Volcanoes National Park. Values are means of 4 plots/treatments, with standard errors in parentheses. Treatments and significance levels as in Table 1.

Treatment	Diameter increment (mm/y)	Litterfall ($g\ m^{-2}\ y^{-1}$)
O	0.5 (0.1)	537 (33)
P	0.6 (0.2)	446 (27)
T	0.9 (0.2)	531 (60)
PT	0.8 (0.3)	494 (24)
N	1.2 (0.2)	620 (26)
NP	1.4 (0.2)	690 (59)
NT	1.7 (0.5)	540 (19)
NPT	2.1 (0.4)	689 (40)
Significance	N***	N*

effects can be summarized by saying that the addition of N (with P) tended to dilute P concentrations in leaves (Table 4).

In contrast, we observed no significant effect of added N on plant growth at the old OL site (Table 5); Walker & Aplet (in press) reported similar results for tree fern growth. Nitrogen additions in OL had no significant effects on available N pool sizes, N mineralization, or foliar N or P concentrations (Table 6) — all of which were substantially greater in unamended plots at Ol than at the younger PP and TH sites.

Discussion

Overall, these results strongly support Walker & Syers' (1976) model as it applies to early soil development: nitrogen is the primary nutrient limiting plant growth in these young tropical montane sites. The diameter increment of the dominant native tree *Metrosideros polymorpha* was the only measure of plant growth that we determined consistently in all three sites (Fig. 2). Our results demonstrate that nitrogen additions caused increases in growth in the two younger sites, and that the effect was less marked (and not statistically significant) at the oldest site. The lack of a demonstrable response to N in the OL site must be interpreted with some caution; the experimental design at this site (a simple comparison of 6 fertilized and 6 control plots) was not as powerful as the factorial fertilization used in the others. However, the magnitude of the differences

Table 4. Effects of factorial fertilization on plant and soil nutrients in the intermediate-aged Thurston site, Hawaii Volcanoes National Park. Values, treatments, and significance levels as in Table 3.

Treatment	NH_4-N+NO_3-N pool size ($\mu g/g$)	N mineralization ($\mu g \cdot g^{-1} \cdot 10\ d^{-1}$)	Extractable P ($\mu g/g$)	*M. polymorpha*		*Cibotium glaucum*	
				foliar N (%)	P (%)	foliar N (%)	P (%)
O	2.0 (0.6)	0.5 (0.5)	0.2 (0.04)	0.73 (0.03)	0.042 (0.002)	1.23 (0.12)	0.068 (0.008)
P	1.4 (0.8)	1.0 (0.9)	0.7 (0.18)	0.70 (0.02)	0.068 (0.007)	1.41 (0.04)	0.126 (0.021)
T	1.1 (0.3)	2.1 (0.9)	0.1 (0.02)	0.65 (0.03)	0.047 (0.004)	1.15 (0.07)	0.052 (0.002)
PT	3.4 (0.3)	−0.3 (0.3)	1.9 (0.76)	0.67 (0.04)	0.051 (0.004)	1.41 (0.08)	0.100 (0.022)
N	5.3 (2.3)	−0.4 (0.9)	0.1 (0.02)	0.74 (0.03)	0.044 (0.002)	1.37 (0.13)	0.060 (0.011)
NP	3.7 (1.7)	2.7 (0.9)	1.3 (0.84)	0.78 (0.02)	0.050 (0.005)	1.54 (0.13)	0.084 (0.009)
NT	2.2 (0.7)	3.2 (1.8)	0.1 (0.01)	0.74 (0.05)	0.035 (0.002)	1.52 (0.11)	0.064 (0.009)
NPT	2.8 (1.3)	1.0 (1.0)	2.1 (0.95)	0.72 (0.04)	0.050 (0.003)	1.40 (0.08)	0.072 (0.003)
Significance	N.S.	N.S.	P*** PT**	N*	P*** N* NPT**	N*	P*** NP*

Table 5. Effects of fertilization with nitrogen on plant growth and turnover in the old Ola'a site, Hawaii Volcanoes National Park. Values are means of 6 plots/treatment, with standard errors in parentheses. The treatments are 0 = no fertilizer; N = nitrogen addition.

Treatment	Diameter increment (mm/y)	Litterfall (g/m^2)
O	4.0 (1.0)	690 (110)
N	5.2 (1.1)	769 (95)
Significance	N.S.	N.S.

between unamended and N-amended plots was small in this site compared to the younger ones, and the lack of response to added N is consistent with the greater foliar N concentrations and soil N availability at this site.

Nitrogen additions also had the largest, and usually the only, effect on all other plant growth-related measures at the two younger sites (leaf production and photosynthetic rates at PP, litterfall and fern growth at TH). The lack of any growth response to P, in particular, occured because P is not limiting to plant growth at these sites, at least not directly — P additions significantly increased concentrations of extractable P in soils and/or foliar P in *Metrosideros* without increasing plant growth. It is possible that in the longer term, increased P availability would lead to increased biological nitrogen fixation and thereby increase productivity (Walker & Syers 1976; Cole & Heil 1981; Vitousek & Howarth 1991), or that other species could colonize the P-fertilized plots and grow more rapidly — but the growth of natural vegetation of the younger sites is not now limited by P.

Tanner et al. (1990, 1992) clearly demonstrated nutrient limitation in a Jamaican and a Venezuelan montane forest site, and reported evidence that N is the proximate limiting nutrient in both sites. The position of their sites in a soil developmental sequence is unclear, but both are substantially older than the Hawaiian sites discussed here. Tanner et al. (1992) concluded that montane tropical forests may be systematically disposed towards limitation by nitrogen. We are not aware of other published studies of the effects of fertilization on the growth of intact tropical forest (other than cases in which several nutrients were applied together as a single treatment).

It is important to note that all of our measures of plant growth and turnover are for aboveground components only. Gower & Vitousek (1989) measured fine root biomass in a subset of 16 plots (representing the control, N, PT, and NPT treatments) at the intermediate-aged TH site,

Table 6. Effects of fertilization with nitrogen on plant and soil nutrients in the old Olaa site, Hawaii Volcanoes National Park. Values, treatments, and significance as in Table 5.

Treatment	NH_4-N+NO_3-N pool size (μg/g)	N mineralization ($\mu g \cdot g^{-1} \cdot 10\ d^{-1}$)	*Metrosideros polymorpha*		*Cibotium glaucum*	
			foliar N (%)	P (%)	foliar N (%)	P (%)
O	6.8 (1.4)	4.3 (1.3)	1.11 (0.09)	0.088 (0.01)	1.43 (0.13)	0.125 (0.02)
N	11.2 (2.7)	5.4 (3.4)	1.25 (0.03)	0.085 (0.01)	1.74 (0.10)	0.116 (0.03)
Significance	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.

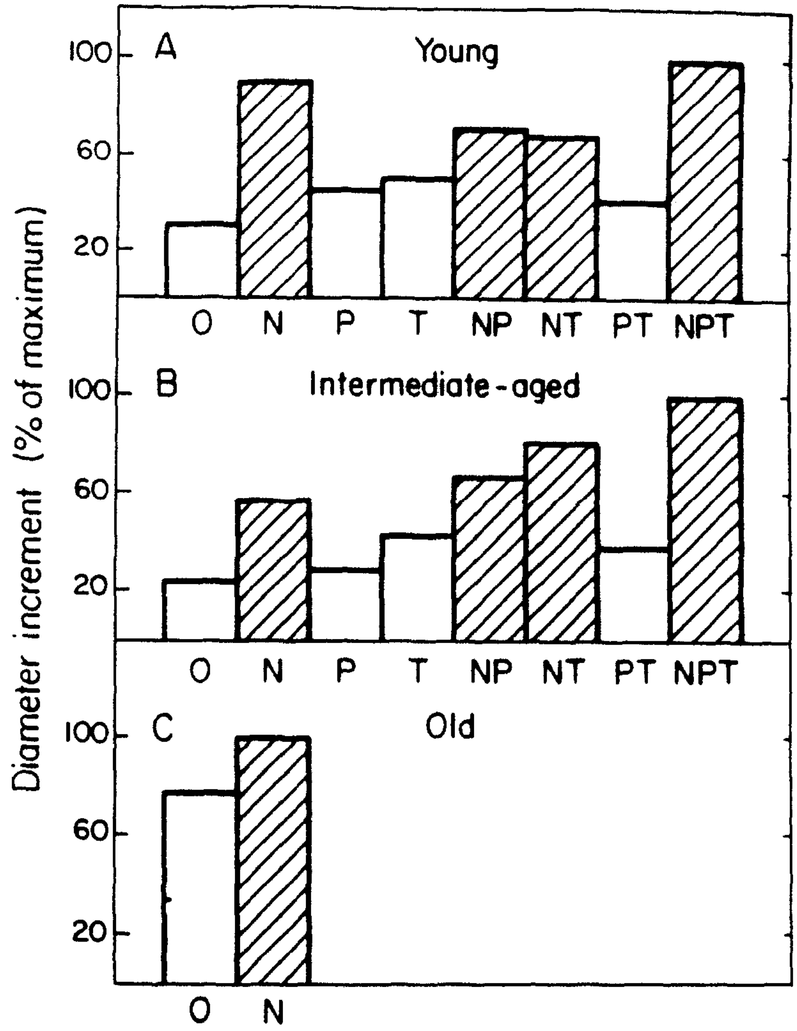

Fig. 2. The effects of nutrient amendments on diameter increments of *Metrosideros polymorpha* trees in 3 sites in Hawaii Volcanoes National Park. All values are reported as percentages of the growth increment in the fastest-growing treatment in that site; growth rates and statistical analyses are reported in Tables 1, 3, and 5. Bars that represent N applications (alone or in combination with other treatments) are hatched. A. Young (26—28 y) PP Puai site. B. Intermediate-aged (< 200 y) TH site. C. Old (ca 2000 y) OL site.

and reported that live root biomass was reduced significantly in all of the fertilized treatments (whether with N or PT) relative to controls. These results are consistent with N limitation to plant growth in this site; plants allocate less energy to roots when nutrient limitation is alleviated (Bloom et al. 1985). The decrease in root biomass in PT treated plots that they found was not reflected in a similar increase in above-ground growth in this study, although T applications were associated with a marginally significant ($0.05 < p < 0.10$) increase in diameter increment at the TH site.

Overall, we observed that measures of nutrient cycling and availability that are used as predictors of nutrient limitation in unamended sites (e.g. element ratios) yield results consistent with those of fertilizer experiments on this age gradient. Plant growth at the two younger sites (PP and TH) was strongly N-limited, and foliar nitrogen concentrations were substantially lower at PP and TH than OL (Tables 2, 4, 6). Potential net nitrogen mineralization increases from PP and TH to OL, the C:N ratio in fine litterfall decreases from TH to OL (manuscript in preparation), emissions of nitrous oxide increase from TH to OL (Matson & Vitousek 1987), and the uptake of ^{15}N by soil microorganisms is much more rapid in soils from TH than from OL (Vitousek & Matson 1988). This last observation suggests that microbes could also experience a gretaer degree of N limitation, or at least a greater capacity for N uptake, at the TH than the OL site.

One surprising result is that foliar concentrations of N and especially P in unamended (control) plots decrease from PP to TH before increasing at OL (Tables 2, 4, 6). A possible demand-side explanation for this pattern is that plant plus microbial requirements for nutrients are lower (relative to nutrient supply) at the sparsely-colonized PP site than in the fully-occupied TH site. The few successful colonists in PP sample a larger area and hence experience a beter nutrient environment than the plants at TH (Hirose & Tateno 1984; Grubb 1986). An alternative supply-side explanation is that the plants at PP make use of elements (especially P) released by weathering of particularly labile minerals. At the 200 y old TH site, those elements have been depleted and the pools of soil organic nitrogen and phosphorus are aggrading, with relative little net release. In either case, the increased nutrient concentrations at OL reflect both a relative and an absolute increase in nutrient supply in the oldest site.

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References

Aber JD, Nadelhoffer JK, Steudler PA & Melillo JM (1989) Nitrogen saturation in northern forest ecosystems — hypotheses and implications. BioScience 39: 378—386

Bloom AJ, Chapin FS & Mooney HA (1985) Resource limitation in plants — an economic analogy. Ann. Rev. Ecol. Syst. 16: 363—393

Bradshaw AD & Chadwick MJ (1980) The Restoration of Land. Blackwell Scientific Publications, Oxford

Chapin FS, Vitousek PM & Van Cleve K (1986) The nature of nutrient limitation in plant communities. Amer. Nat. 127: 48—58

Cole CV & Heil RD (1981) Phosphorus effects on terrestrial nitrogen cycling. Ecol. Bull. (Stockholm) 33: 363—374

Cuevas E & Medina E (1986) Nutrient dynamics within Amazonian forests: Nutrient flux in fine litter fall and the efficiency of nutrient utilization. Oecol. 68: 466—472

Cuevas E & Medina E (1988) Nutrient dynamics within Amazonian forests: Fine root growth, nutrient availability, and leaf litter decomposition. Oecol. 76: 222—235

Eno CF (1960) Nitrate production in the field by incubating the soil in polyethylene bags. Soil Sci. Soc. Amer. Proc. 24: 299—279

Field CB, Chapin FS, Matson PA & Mooney HA (1992) Responses of terrestrial ecosystems to the changing atmosphere: A resource-based approach. Ann. Rev. Ecol. Syst. 23: 201—235

Gerrish G, Mueller-Dombois D & Bridges KW (1988) Nutrient limitation and *Metrosideros* forest dieback in Hawaii. Ecology 69: 723—727

Giambelluca TW, Nullet MA & Schroeder TA (1986) Rainfall Atlas of Hawaii. Department of Land and Natural Resources, State of Hawaii, Honolulu

Giblin AE, Nadelhoffer KJ, Shaver GR, Laundre JA & McKerrow AJ (1991) Biogeochemical diversity along a riverside toposequence in arctic Alaska. Ecol. Monogr. 61: 415—435

Gower ST & Vitousek PM (1990) Effects of nutrient amendments on fine root biomass in a primary successional forest in Hawaii. Oecol. 81: 566—568

Grubb PJ (1977) Control of forest growth and distribution on wet tropical mountains, with special reference to mineral nutrition. Ann. Rev. Ecol. Syst. 8: 83—107

Grubb PJ (1986) The ecology of establishment. In: Bradshaw AD, Goode DA & Thorpe E (Eds) Ecology and Landscape Design (pp 83—98). Blackwell Scientific Publishers, Oxford

Heaney A & Proctor J (1989) Chemical elements in litter in forests on Volcán Barva, Costa Rica. In: Proctor J (Ed) Mineral Nutrients in Tropical Forest and Savanna Ecosystems (pp 255—271). Blackwell Scientific Publications, Oxford

Hirose T & Tateno M (1984) Soil nitrogen patterns induced by colonization of *Polygonium cuspidatum* on Mt Fuji. Oecol. 61: 218—223

Jordan CF (1985) Nutrient Cycling in Tropical Forest Ecosystems: Principles and their Application in Conservation and Management. John Wiley and Sons, Chichester, England

Lawrence DB, Schoenike RE, Quispel A & Bonds G (1967) The role of *Dryas drummondii* in vegetation development following ice recession at Glacier Bay, Alaska, with special reference to its nitrogen fixation by root nodules. J. Ecology 55: 793—813

Leisman GA (1957) A vegetation and soil chronosequence on the Mesabi Iron Range spoil banks, Minnesota. Ecol. Monogr. 27: 221—245

Marrs RH, Roberts RD, Skeffington RA & Bradshaw AD (1983) Nitrogen and the development of ecosystems. In: Lee JA, McNeill S & Rorison IH (Eds) Nitrogen as an Ecological Factor (pp 113—136). Blackwell Scientific Publications, Oxford

Matson PA (1990) Plant-soil interactions during primary succession in Hawaii Volcanoes National Park. Oecol. 65: 241—246

Matson PA & Vitousek PM (1987) Cross-system of soil nitrogen transformations and nitrous oxide fluxes in tropical forest ecosystems. Global Biogeochem. Cycles 1: 163—170

Medina E & Cuevas E (1989) Patterns of nutrient accumulation and release in Amazonian forests of the Upper Rio Negro basin. In: Proctor J (Ed) Mineral Nutrients in Tropical Forest and Savanna Ecosystems (pp. 217—240). Blackwell Scientific Publishers, Oxford

Mueller-Dombois D (1987) Forest dynamics in Hawaii. Trends Ecol. Evol. 2: 216—220

Mueller-Dombois D & Whiteaker LD (1990) Plants associated with *Myrica faya* and two other pioneer trees on a recent volcanic surface in Hawaii Volcanoes National Park. Phytocoenologia 19: 29—41

Olsen SR & Sommers LE (1982) Phosphorus. In: Page AL, Miller RH & Kenney DR (Eds) Methods of Soil Analysis, Part II: Chemical and Microbiological Properties (pp 403—430). American Society of Agronomy, Madison, Wisconsin

Proctor J (1987) Nutrient cycling in primary and old secondary rain forests. Appl. Geogr. 7: 135—152

Rastetter EB & Shaver GR (1992) A model of multiple element limitation for acclimating vegetation. Ecology 73: 1157—1174

Schulze E-D (1989) Air pollution and forest decline in a spruce (*Picea abies*) forest. Science 244: 776—783

Smathers GA & Mueller-Dombois D (1974) Invasion and Recovery of Vegetation after a Volcanic Eruption in Hawaii. Washington, DC

Sollins P, Robertson GP & Uehara G (1988) Nutrient mobility in variable- and permanent-charge soils. Biogeochem. 6: 181—199

Tanner EVJ (1985) Jamaican montane forests: Nutrient capital and cost of growth. J. Ecol. 73: 553—568

Tanner EVJ, Kapos V, Freskos S, Healey J & Theobold AM (1990) Nitrogen and phosphorus fertilization of Jamaican montane forest trees. J. Trop. Ecol. 6: 231—238

Tanner EVJ, Kapos V & Franco W (1992) Nitrogen and phosphorus fertilization effects on Venezuelan montane forest trunk growth and litterfall. Ecology 73: 78—86

Uehara G & Gillman G (1981) The Minerology, Chemistry, and Physics of Tropical Soils with Variable Change Clays. Westview Press, Boulder, Colorado

Veneklaas EJ (1991) Litterfall and nutrient fluxes in two montane tropical rain forests, Colombia. J. Trop. Ecol. 7: 319—336

Vitousek PM (1982) Nutrient cycling and nutrient use efficiency. Amer. Nat. 199: 553—572

Vitousek PM (1984) Litterfall, nutrient cycling, and nutrient limitation in tropical forests. Ecology 65: 285—298

Vitousek PM & Howarth RW (1991) Nitrogen limitation on land and in the sea: How can it occur? Biogeochem. 13: 87—115

Vitousek PM & Matson PA (1988) Nitrogen transformations in a range of tropical forest soils. Soil Biol. Biochem. 3: 361—367

Vitousek PM & Sanford Jr RL (1986) Nutrient cycling in moist tropical forest. Ann. Rev. Ecol. Syst. 17: 137—167

Vitousek PM & Walker LR (1989) Biological invasion by *Myrica faya* in Hawai'i: Plant demography, nitrogen fixation, ecosystem effects. Ecoll. Monogr. 59: 247—265

Vitousek Pm, Van Cleve K, Balakrishnan N & Mueller-Dombois D (1983) Soil development and nitrogen turnover on recent volcanic substrates in Hawaii. Biotrop. 15: 268—274

Vitousek PM, Walker LR, Whiteaker LD, Mueller-Dombois D & Matson PA (1987) Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. Science 238: 802—804

Vitousek PM, Fahey T, Johnson DW & Swift MJ (1988) Element interactions in forest ecosystems: succession, allometry, and input-output budgets. Biogeochem. 5: 7—34

Vitousek PM, Matson PA & Van Cleve K (1989a) Nitrogen availability and nitrification during succession: Primary, secondary, and old-field seres. Plant Soil 115: 229—239

Vitousek PM, Shearer G & Kohl DH (1989b) Foliar ^{15}N natural abundance in Hawaiian rainforest: patterns and possible mechanisms. Oecol. 78: 383—388

Walker LR & Aplet GH (in press) Growth and fertilization responses of Hawaiian tree ferns. Biotropica

Walker LR & Chapin III FS (1986) Physiological controls over seedling growth in primary succession on an Alaskan floodplain. Ecology 67: 1508—1523

Walker LR & Vitousek PM (1991) An invader alters germination and growth of a native dominant tree in Hawai'i. Ecology 72: 1449—1455

Walker LR & Whiteaker LD (1988) Rust prevention on dendrometer bands. Biotrop. 20: 336—337

Walker TW & Syers JK (1976) The fate of phosphorus during pedogenesis. Geoderma 15: 1—19

Wright RA & Mueller-Dombois D (1988) Relationships among shrub population structure, species associations, seedling root form and early volcanic succession, Hawaii. In: Werger MJA, vd Aart PJM, During HJ & Verhoeven JTA (Eds) Plant Form and Vegetation Structure (pp 87—104). SPB Publishing, The Hague