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## EXPERIMENTAL INVESTIGATION OF NUTRIENT LIMITATION OF FOREST GROWTH ON WET TROPICAL MOUNTAINS

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**Abstract.** This article reviews literature and summarizes experiments to investigate the extent to which productivity of tropical montane rain forests is constrained by low nutrient supply. On any one mountain, with increase in altitude foliar N decreases, and P and K usually decrease, but Ca and Mg show no consistent trend. However for a wide range of sites N, P, K, Mg, and Ca show no trends. Litterfall contents of N and P and often K, Ca, and Mg are lower in montane forests than in lowland forests, mainly because of reduced litterfall mass, but N and P concentrations are also lower in forests above 1500 m. Tropical montane soils usually have more soil organic matter per unit ground area; N mineralization levels are lower at higher altitudes in Costa Rica, and extractable and total soil P are lower in sites with lower litterfall P concentrations. We speculate that many lowland forests are limited by P and many montane forests by N.

Fertilization studies on ash-derived montane soils in Hawai'i showed a trend for a switch from N limitation on young soils to P, or N and P, limitation on soils over older substrates. Jamaican montane trees were limited by N and by P separately. Venezuelan montane trees were limited by N. The sites in Jamaica and Venezuela have soils of indeterminate age. Taken together these results show that nutrient limitation is widespread in montane soils (all sites have responded to at least one nutrient) and that the particular nutrient(s) that limit(s) production may differ for explicable reasons. First results from lowland forests on sandy soils in Kalimantan show N or simultaneous N and P limitation. Many more experiments, especially in lowland forests, are needed to test our speculation that P usually limits productivity in tropical lowland rain forests and that N limits productivity in tropical montane rain forests.

**Key words:** fertilization experiments; forests in Hawai'i, Jamaica, and Venezuela; growth limitation; montane cf. lowland forests; nitrogen; nutrient limitation of forest growth; nutrients; phosphorus; soil age and nutrient limitation; tropical montane rain forest productivity.

### INTRODUCTION

Among the many factors that vary from lowland to montane tropical forests, decreasing air temperature and increasing cloudiness are probably ultimately—and may be primarily—responsible for limiting the growth and distribution of tropical montane forests (Grubb 1977). Nutrient supply and other factors such as soil saturation are also controlled by temperature and precipitation and may be simultaneously and even proximally limiting. This article investigates the extent to which the productivity of montane tropical forest is constrained by low nutrient availability. We briefly review observational evidence and concentrate on recent experimental studies where forests have been fertilized. We attach particular importance to these experimental

studies because of their importance in the determination of causation.

Limitation by a nutrient is shown if the rate of an ecosystem process is increased by addition of that nutrient, and strictly speaking it can only be determined experimentally. Importantly, limitation can be seen in the response of organisms that already occupy a site, or only after colonization by organisms that are better able to make use of the added resource (Chapin et al. 1986, Berendse 1993). Furthermore while overall ecosystem processes may be nutrient limited, not all species in the ecosystem need be limited; indeed even within a species some individuals could be limited and others not, due, for example, to different crown exposure. Finally, the observation that a nutrient is limiting does not mean that only that nutrient limits the ecosystem—simultaneous limitation by multiple resources is the rule (Bloom et al. 1980, Field et al. 1992), especially with different types of resources (e.g.,

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photosynthetically active radiation, water, depletable resources like N or P, and non-depletable resources like CO<sub>2</sub>).

It will always be easier to assess the nutrient status of sites or individual trees by measurements, such as foliar and litter concentrations or soil chemical extracts, rather than by experimentation. In general, nutrient limitation of growth is correlated with low concentrations of the limiting nutrient in leaves and leaf litter (and often wood and roots); the low litter concentrations are a result of low leaf concentrations and sometimes (but not always) higher rates of retranslocation of nutrients from leaves during senescence. There are important exceptions to the generalization that nutrient limitation should result in low concentrations of the limiting nutrient in plant parts. This is especially true for N; extra N can cause extra growth but no change in N concentration (e.g., Healey 1989). Soil chemical extracts are more difficult to interpret than leaf and litter concentrations, but sometimes low levels of nutrients extracted with mild extractants (water, dilute salt solutions) are indicative of nutrient limitation. For soils, comparability between studies is limited by the many different extractants used for the same nutrient. Despite these limitations it is important to look for correlations between leaf, litter, and soil nutrients on the one hand and fertilizer responses on the other. Where good correlations exist they are useful for predicting which nutrients limit and to what extent, in areas where fertilizer experiments have not been carried out.

#### CHANGES IN FOREST STRUCTURE ON ASCENDING WET TROPICAL MOUNTAINS

The average trend in the wet tropics is for forests to decrease in stature, growth, and productivity with increase in altitude, but there is much variation at any given altitude due to differences in nutrient availability, water availability, and species composition. In the lowlands the forests range in canopy height (excluding emergents) from a few meters (Bana forest in southern Venezuela) to 40 m tall (in many parts of lowland Southeast Asia). In the mountains, up to 2500 m in altitude, forests can be up to 30–35 m tall. Only above 3000 m are forests with canopy heights >30 m absent; even at 3370 m there is a forest with a canopy height of 22 m (in Colombia; Veneklaas 1991).

#### FOLIAR NUTRIENTS

On any one mountain system with increase in altitude there is usually a decrease in concentrations (on a mass basis) of foliar N (5 of 5 transects in Fig. 1); P and K often fall (3 of 5 transects); but there are no consistent trends for Ca and Mg. However when data from a wide range of sites are combined, foliar nutrient concentrations show no relationship with altitude for N (as found for evergreen woody plants by Körner [1989]), P, K,

Mg, and Ca (Fig. 2). The differences between specific transects and the general pattern shows that one has to be especially careful to make relevant comparisons for N and P (usually specific transects). At any altitude it is possible to find forests with low, intermediate, and high concentrations of nutrients, but at any altitude low-stature forests, especially those where canopy height is <10 m, have low concentrations of N and P (Fig. 3); they also have low concentrations of K, Ca, and Mg (but for these three nutrients there are some tall forests that have low concentrations of these nutrients).

In some ways it makes more sense to express nutrient concentrations per leaf area, because the primary function of leaves is to absorb light, which is mostly a result of area and only slightly increased by increasing leaf thickness. Unfortunately the necessary measurement of leaf mass per area is only occasionally made. Furthermore leaf mass per area varies so much through the canopy from sun to shade leaves that it is essential to measure leaf mass per area on the sample being analyzed for nutrients, and to collect fully sunlit leaves. Nutrient concentrations per mass show little difference between sun and shade leaves for N, P, S, Fe, and Cu, while shade leaves have higher concentrations of K, Mg, and Mo (Grubb 1977).

At least two papers present nutrient concentrations from tropical montane systems by leaf area and mass. In Hawai'i on a mass basis N and P concentrations decreased with altitude, but on an area basis concentrations increased with altitude particularly above 1600 m (Vitousek et al. 1992). In Puerto Rico, on a mass basis N decreased, and P, K, Ca, and Mg did not change with increase in altitude, but on an area basis all five elements increased with altitude (Medina et al. 1981). In both places leaf mass per area increased with increase in altitude. The higher leaf mass per area is in turn correlated with longer-lived leaves in tropical montane forests; for example in 'Mor Ridge forest' (at 1550 m in Jamaica) leaves last for 18 mo on the average (Tanner 1980)—much longer than the average leaf life in tropical lowland rain forests. It seems likely from these results that the instantaneous nutrient-use efficiency (the rate of CO<sub>2</sub> fixation per unit nutrient) decreases with increase in altitude; this is partly due to lower temperatures and partly due to the short-term inefficiency of sclerophyllous leaves.

#### PRODUCTIVITY, NUTRIENT CYCLING, AND NUTRIENT RETRANSLOCATION

Tropical montane forests generally have reduced productivity compared to lowland forests (Tanner 1980). The major components of net primary production (NPP) in tropical montane forests are, in order, above-ground litterfall, root production, and, to a much lesser extent, wood increment; wood increment is particularly low in montane forests compared to lowland forests.

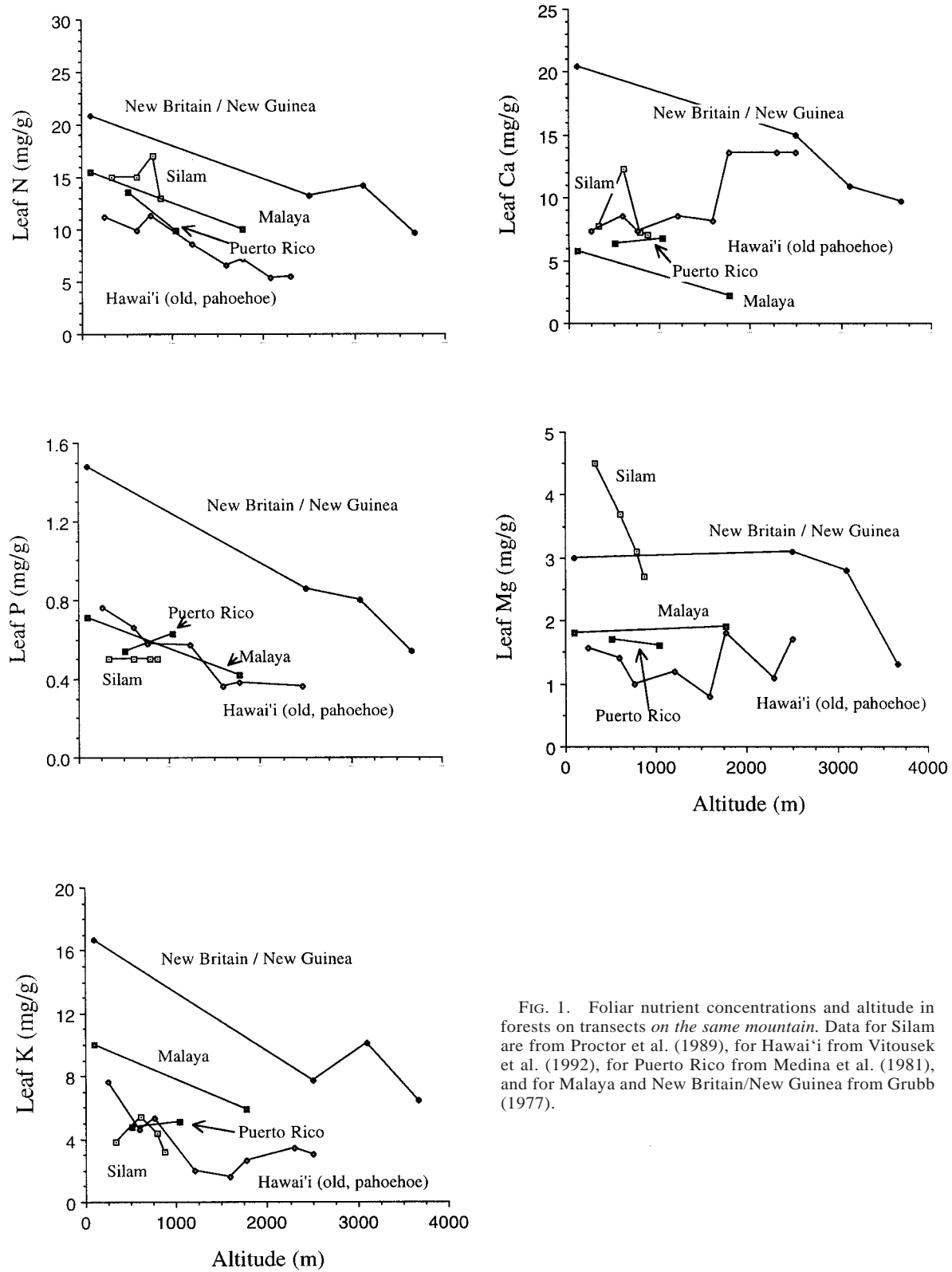


FIG. 1. Foliar nutrient concentrations and altitude in forests on transects on the same mountain. Data for Silam are from Proctor et al. (1989), for Hawai'i from Vitousek et al. (1992), for Puerto Rico from Medina et al. (1981), and for Malaya and New Britain/New Guinea from Grubb (1977).

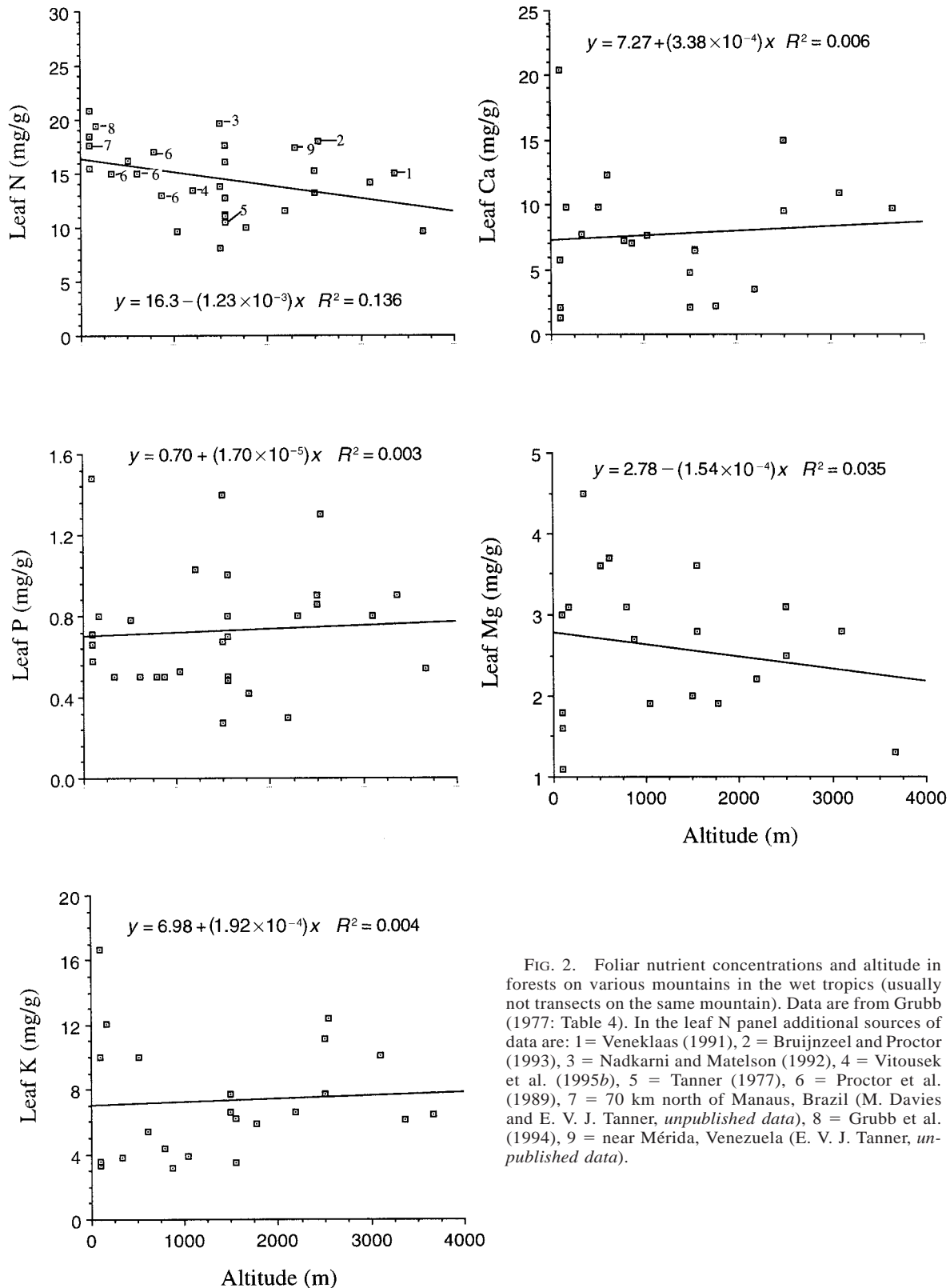


FIG. 2. Foliar nutrient concentrations and altitude in forests on various mountains in the wet tropics (usually not transects on the same mountain). Data are from Grubb (1977: Table 4). In the leaf N panel additional sources of data are: 1 = Veneklaas (1991), 2 = Bruijnzeel and Proctor (1993), 3 = Nadkarni and Matelson (1992), 4 = Vitousek et al. (1995b), 5 = Tanner (1977), 6 = Proctor et al. (1989), 7 = 70 km north of Manaus, Brazil (M. Davies and E. V. J. Tanner, *unpublished data*), 8 = Grubb et al. (1994), 9 = near Mérida, Venezuela (E. V. J. Tanner, *unpublished data*).

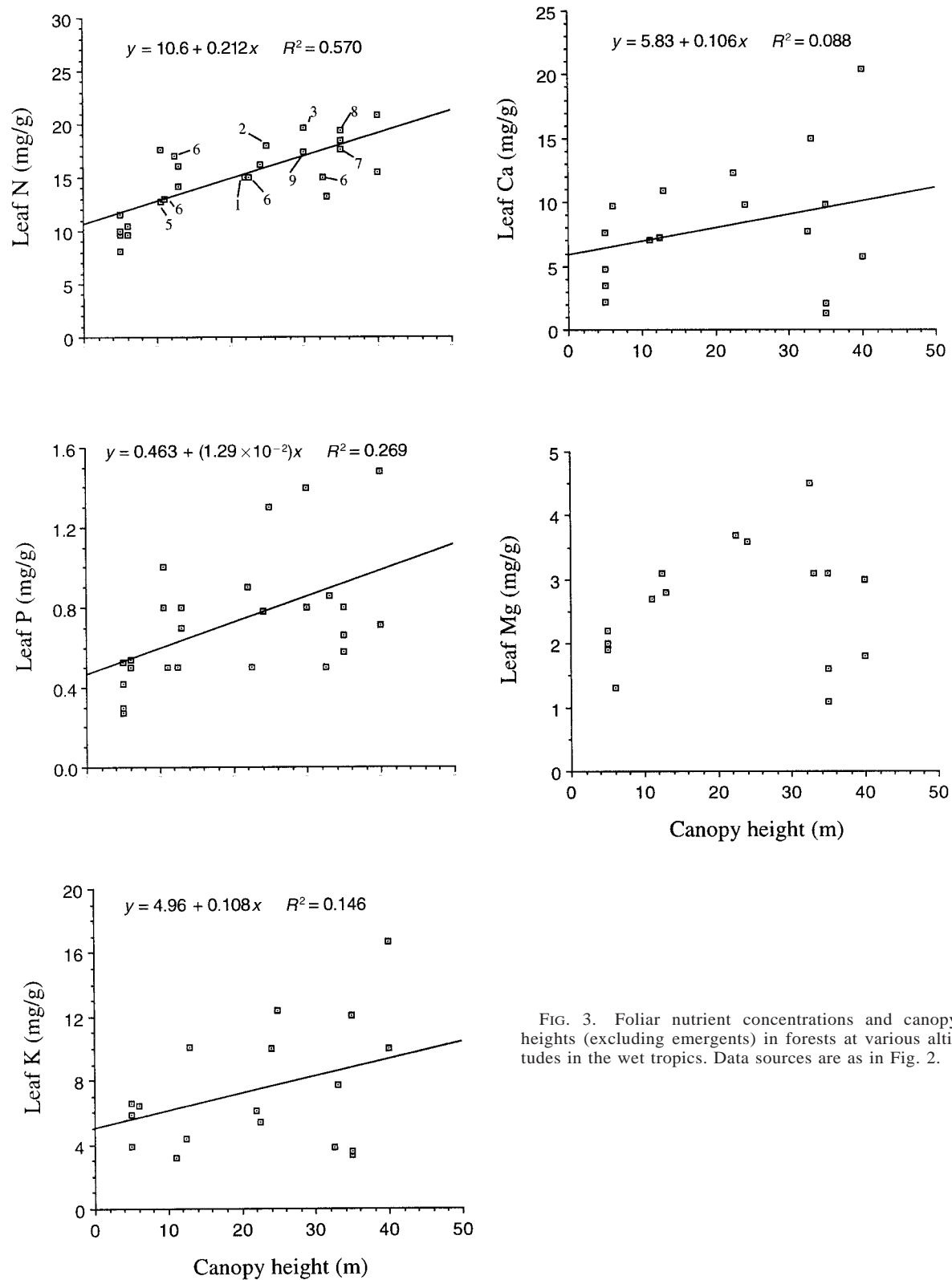


FIG. 3. Foliar nutrient concentrations and canopy heights (excluding emergents) in forests at various altitudes in the wet tropics. Data sources are as in Fig. 2.

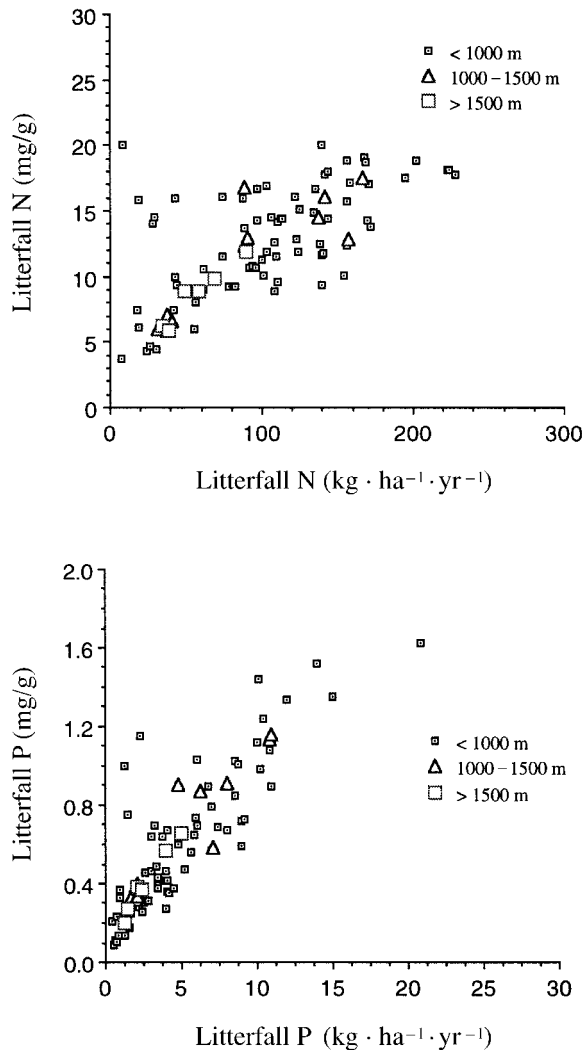


FIG. 4. Litterfall nutrient contents and concentrations in a large number of wet tropical forests, showing that for both N and P higher contents are correlated with higher concentrations, and that forests from the highest altitudes (>1500 m) have low contents and concentrations for both N and P. Data are from Vitousek (1984: Table 2; the present graph has most of the same data as Vitousek's Fig. 1; the present graph plots mg/g on the y axis whereas Vitousek's graph plots the reciprocal of mg/g [=dry mass per unit nutrient]).

Our information on the components of NPP is best for litterfall, which has been widely measured using reasonably comparable techniques. Caution is required when generalizing from only one of the major components of NPP, but the patterns are striking. Montane forests generally have reduced cycling of N and P and often of K, Ca, and Mg, in comparison with lowland forests (Grubb 1977, Vitousek 1984). The main reason for this is reduced rates of litterfall, but N and P concentrations in litter are lower in forests from the highest (>1500 m) altitudes (though concentrations are not systematically lower at intermediate [1000–1500 m]

altitudes; Fig. 4). Transects on the same mountain show lower concentrations of N, but usually not of P, in litter at higher altitudes (Fig. 5). Note that the patterns for P concentrations in litter, lower at the highest altitudes (wide range of sites) or no change with altitude (on the same mountain) contrast with those for foliar P concentrations, which show no change with altitude (wide range of sites) or fall with altitude (on the same mountain). These results conflict because the data for single mountains suggest less retranslocation of P prior to abscission at higher altitude, whereas the pattern from a wide range of sites suggest more retranslocation of P at high altitude. Clearly more data are needed especially from transects on the same mountain (note that for P only one site, Silam, is in both Figs. 1 and 5).

In a steady state the amount of a nutrient in litterfall (per unit ground area per time) is a reasonable approximation to net nutrient uptake into aboveground parts (per unit ground area per time). Based on litterfall,

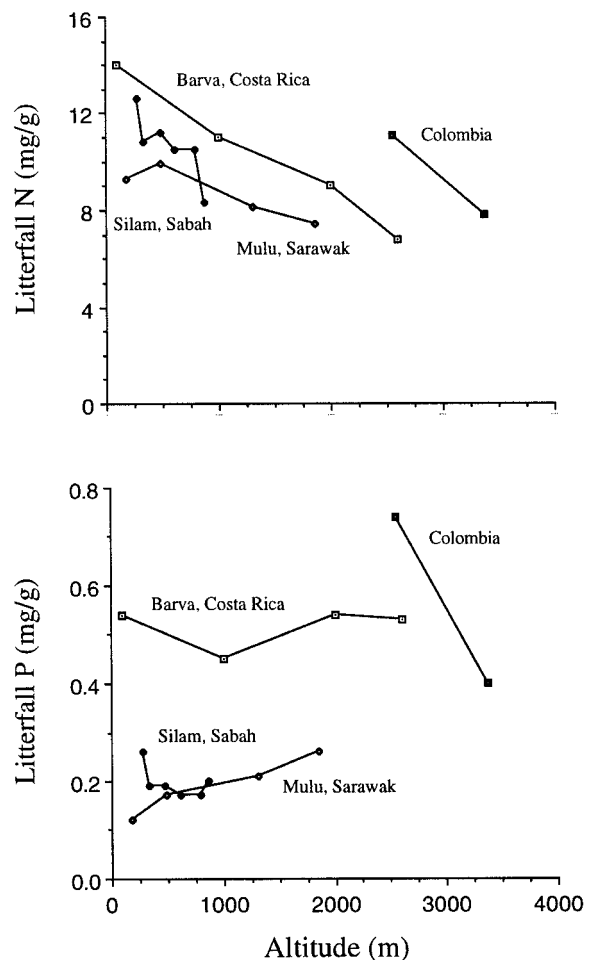


FIG. 5. Litterfall nutrient concentrations and altitude in tropical forests on transects on the same mountain. Redrawn from Bruijnzeel and Proctor (1993); Mulu data are from Proctor et al. (1983).



N and P and sometimes K, Ca, and Mg uptake is lower in montane forests (for transects on individual mountains [Fig. 6]; though for a wide range of sites on many different mountains there is no general trend except for low values of N and P above 1500 m [Fig 4]). For N and P, and sometimes K, Ca, and Mg, these low amounts result in low concentrations in the leaves (but there is a problem of a chicken and egg argument here).

#### A HYPOTHESIS THAT IN GENERAL P LIMITS GROWTH IN LOWLAND FORESTS AND N IN MONTANE FORESTS

A reasonable speculation from the patterns of foliar and litterfall concentrations is that N is in excess supply in most lowland rain forests, a speculation supported by the relatively high rates of N mineralization and N-containing trace gas emissions from the soils (a by-product of high rates of nitrogen transformations) in such sites (Matson and Vitousek 1987). In contrast, many tropical montane forests seem to be likely to suffer from insufficient N. A further speculation is that P is likely to limit growth in a substantial subset of lowland rainforests, and N in many montane forests.

Thus, with regard to N, tropical montane forests appear to function more like many temperate and boreal forests than like most lowland tropical forests. Tropical lowland rain forests produce more litter annually than do most temperate forests—and in most cases they produce litter with much higher concentrations of N (lower C:N ratios) than do temperate or boreal forests. Phosphorus and other major elements (Ca, Mg, K) are more variable—many tropical forests produce litter with much lower concentrations of P than most temperate forests but others produce litter with higher concentrations (Vitousek 1982). This variation among tropical lowland rain forests is associated with soil type and fertility; tropical forests on highly weathered clay soils (oxisols and ultisols) generally produce litter low in P, those on richer soils (i.e., alfisols) produce litter with high P concentrations, and those on sandy soils are often low in N (Vitousek and Sanford 1986).

#### TROPICAL MONTANE SOILS

The decreased nutrient concentrations in leaves and decreased cycling of nutrients in litter that occur as one ascends tropical mountains could be due to immobilization in the soil, which in turn is due to a buildup of soil organic matter resulting from incomplete decomposition. Montane soils usually have more soil organic matter per unit ground area (e.g., in Malaya, Whitmore and Burnham 1969; and in Thailand, Kira and Shidei 1967); their organic matter is also often concentrated near the top of, or above, the mineral layers of the soil. Another reason for supposing that nutrient supplies might be limited in montane soils is that many montane soils are of low pH. (In such soils the low pH is a result of the leaching of bases and/or

the high cation-exchange capacity due to the high organic-matter concentration; low pH is not the cause of nutrient limitation—low pH is caused by the same factors that cause nutrient limitation; pH is easily measured and may indicate nutrient shortage). Often there is a decrease in nutrient status as one moves from sites with higher to lower pH, especially when pHs are below 5. For example in three ridge-top sites in close proximity in Jamaica the surface soil  $\text{pH}_{\text{H}_2\text{O}}$  (i.e., pH measured in water) falls from 4.3 to 3.0 and average foliar N falls from 1.76% to 1.05% and average foliar P from 0.10% to 0.05%; the most stunted forest, Mor Ridge forest, has soil with the lowest pH (Tanner 1977). However, not all low-pH soils have stunted forests; e.g., both the extremely stunted forest on East Peak at 1034 m in Puerto Rico (Lyford 1969) and the much better developed El Verde forest at 510 m on the same mountain (Edmisten 1970) have the same surface soil pH (4.3).

If immobilization in soils per se is the cause of low availability of N, P, K, and Ca, why have trees been unable to accumulate these elements slowly, over the centuries, from weathering rock fragments, which are often seen near the surface in montane forests, and from inputs in rainfall and/or dust, and from N fixation? This question is not specific to montane forests; vegetation throughout the world growing on soils developed from infertile substrates can be shown to be nutrient limited despite millenia of rainfall, dust inputs, and N fixation. The extra nutrients could be insufficiently available to plants because of their form or because they are at concentrations so low as to be unavailable, or because the rooting medium somehow limits root uptake. Infrequent but severe disturbance could also lead to losses of accumulated nutrients. Alternatively Hedin et al. (1995) recently demonstrated that old-growth Chilean forests lose dissolved organic N in streams at about the same rate that they receive (mostly inorganic) N in precipitation; they speculate that losses of dissolved organic nitrogen (and dissolved organic phosphorus) could be sufficient to maintain nutrient limitation in the long term, at least in unpolluted regions.

Data on levels of instantaneously extractable soil nutrients in montane tropical forests are few, and sometimes show inconsistent patterns with altitude (Brujnzeel and Proctor 1993). Measures of N mineralization made in Costa Rica showed much reduced rates at higher altitude (Marrs et al. 1988), which correlated with reduced amounts of N cycling in litterfall at higher altitude on the same transect. Extractable and total soil P were lower in sites with higher P nutrient-use efficiency (litterfall dry mass divided by litterfall P amount) both for all tropical rain forest sites and for tropical montane rain forest sites (Silver 1994), which suggests that P may limit growth in many lowland and some montane sites. Exchangeable basic metals have been found to both increase and decrease with in-

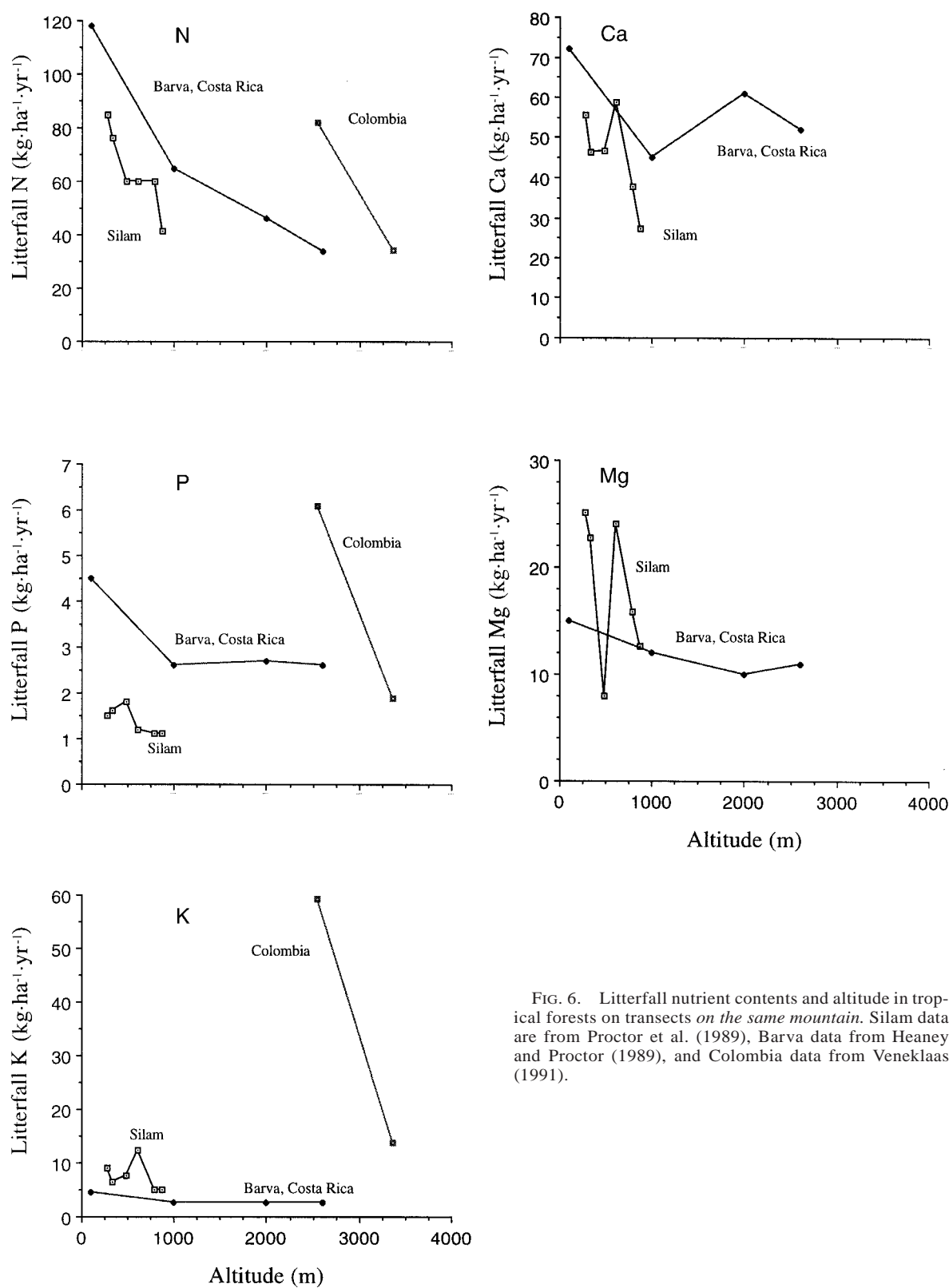


FIG. 6. Litterfall nutrient contents and altitude in tropical forests on transects on the same mountain. Silam data are from Proctor et al. (1989), Barva data from Heaney and Proctor (1989), and Colombia data from Veneklaas (1991).



creased altitude on different mountains (Bruijnzeel and Proctor 1993). However, there is little evidence that K, Ca, or Mg limit growth or affect composition in natural (as opposed to plantation) forests in the tropics—a notable exception being the root-ingrowth experiments of Cuevas and Medina (1988), which showed that roots in Tierra Firme forest in southern Venezuela grew preferentially into cylinders of vermiculite doped with Ca (or potassium dihydrogen phosphate). The interpretation of this experiment was considerably strengthened by results from Hawai'i where root growth into bags doped with an element was correlated with increased growth caused by fertilization with that element (Raich et al. 1994). Thus with a few exceptions the data on extractable soil nutrients do not add much to the interpretation based on foliar and litterfall nutrients. Where they are available, soil nutrient data generally support the suggestion that tropical montane rain-forest soils have less available N than many tropical lowland rain-forest soils though there are some montane sites where P is likely to limit growth as well as N.

Bruijnzeel et al. (1993) have suggested that the high phenolic concentrations in many montane soils might slow decomposition and plant growth, but there is no experimental evidence for this as yet. Much earlier Jordan et al. (1979) showed that nitrification rates in Amazonian rain forest were suppressed, and they hypothesized that this was a result of high tannin concentrations in the root mat; they proposed that this limitation of nitrification was a way of limiting nitrogen losses by limiting the production of highly mobile nitrate ions. The suggestion that low vapor-pressure deficit (the driving force for transpiration) might limit nutrient movement into leaves due to reduced transpiration was shown to be incorrect by Medina et al. (1981) who measured significant transpiration in the exceptionally stunted forests, which are very frequently clouded, on Pico del Este in Puerto Rico. This is the same conclusion as that reached by Grubb (1977) who reported various experiments and observations that showed that transpiration rates were not directly related to the amounts of ions transported, and by Smith (1991) who reviewed the relationship between ion transport and the transpiration stream and concluded that as the rate of flow decreased the concentration in the xylem sap increased, thus maintaining a supply of nutrients to even slowly transpiring leaves. Thus it seems very unlikely that low rates of transpiration might limit nutrient supplies to leaves especially because the highest requirements will be when leaves are developing—when they have very low rates of transpiration because they do not have fully functional stomata and because the air inside buds is near saturation and thus there is almost no driving force for transpiration.

#### FERTILIZATION EXPERIMENTS

Experiments are the only way in which these and other possible causes of decreased productivity and nu-

trient cycling in montane tropical forests can be addressed directly. Nutrients are the major resource most amenable to experimental manipulation, and a number of fertilization experiments have been carried out in montane tropical forests. However, the design and interpretation of forest fertilization experiments is not always straightforward, for several reasons.

1) Trees adapted to infertile soils may respond less to nutrient enrichment than those adapted to more fertile soils. Consequently, fertilization of the most nutrient-deficient sites may yield only a modest response—until the dominant species are replaced by others that are capable of responding to (and may indeed require) higher levels of nutrients (Chapin et al. 1986). The evidence for the importance of this pattern is mixed—for example, *Pinus nigra* will grow on very infertile soils derived from blown sand in Scotland but it responds strongly to fertilization (Miller et al. 1976); how to interpret these results is unclear, however, because the trees may have come from natural populations growing on relatively fertile soils.

In the experiments that we discuss below there was often a lag time in response; this was due to the slow response of the individuals present when the plots were first fertilized, not to the arrival of species or to changes in species relative abundance.

2) Phosphorus-fixing soils are widespread in tropical regions (Uehara and Gillman 1981, Sollins et al. 1988), and even relatively large additions of this element may not increase plant-available P significantly.

3) It is difficult to measure belowground production in forests—particularly in fertilized plots, in which calculations based on CO<sub>2</sub> emissions (cf. Raich and Nadelhoffer 1989) are inappropriate because increased nutrient availability may affect soil carbon pools with long turnover times. Increases in response to fertilization in aboveground production alone may simply reflect reallocation of carbon from belowground.

4) The diversity of tree species in many tropical forests makes it difficult to track species-level responses across treatment plots of any practical size. The possibility that different species in a site might respond to different nutrients further makes it difficult to determine ecosystem-level responses.

Despite the potential problems with the interpretation of fertilization studies, cautious insights can be drawn from several that have been performed in tropical montane forests, mostly in the American tropics or Hawai'i. In Jamaican montane forest with average foliar concentrations of N, P, Ca, and Mg and high concentrations of K (compared to the range of values for tropical forests in Fig. 2), and low litter concentrations for N and especially so for P, trunk growth was 77% more following N fertilization, and increased by 32% following P fertilization (Table 1). In Venezuelan montane forest with average foliar concentrations of N and P, and near-average litterfall concentrations of N

TABLE 1. Responses of various natural tropical rain forests to fertilization. Percentage increases in trunk growth and litterfall were calculated from results from control and fertilized plots (or individuals—some experiments used individuals not plots). Significance levels were often calculated for overall N or P effects (which are more powerful), not simply pairwise comparison; sig. = significant at 0.05, NS = not significant at 0.05. For litterfall in Venezuela, litterfall in year 1 was standardized to that in control plots, and litterfall for year 4 was multiplied by that standardization factor to eliminate differences in litterfall between treatments in year 1 (before fertilization had a significant effect); this procedure was also adopted for litterfall in the Hawaiian data from Vitousek et al. (1995a).

Site	Data source	Soil age (yr)	Substrate	Fertilizer	Increase in trunk-diameter growth (%)	Increase in litterfall (%)	N in leaves (%)	P in leaves (%)
Hawai'i Puu Makaala	Gerrish et al. 1988	1500–3000	Lava	Comp.†	167 (sig.)	...	0.61	0.08
Hawai'i Saddle Road	Gerrish et al. 1988	3400	Lava	Comp.†	25 (NS)	...	0.78	0.07
Hawai'i Thurston lava tube	Gerrish et al. 1988	200	Ash	Comp.†	87 (sig.)	...	0.73	0.042
Hawai'i Thurston lava tube	Vitousek et al. 1993	200	Ash	N	140 (overall N effect sig.)	15 (overall N effect sig.)	...	...
				P	20 (overall P effect NS)	–17 (overall P effect NS)	...	...
				N and P	180 (interaction NS)	29 (interaction NS)	...	...
Hawai'i Mauna Loa	Raich et al. 1996	140	'a'a lava	N	357 (overall N effect sig.)	...	0.62	0.068
				P	100 (overall P effect NS)	...	...	...
				N and P	671 (interaction NS)	...	...	...
		140	Pahoehoe lava	N	260 (overall N effect sig.)	...	0.71	0.073
				P	160 (overall P effect sig.)	...	...	...
				N and P	680 (interaction sig.)	...	...	...
Hawai'i Mauna Kea	Vitousek and Farrington 1997	20 000	Ash	N	75 (overall N effect sig.)	...	1.17	0.09
				P	13 (overall P effect NS)	...	...	...
				N and P	188 (interaction NS)	...	...	...
Hawai'i Olaa	Vitousek et al. 1987, Vitousek et al. 1995a	2000	Ash	N	25 (NS)	24 (NS)	1.1	0.088
Hawai'i Kauai	Herbert and Fownes 1995	4.1 × 10 <sup>6</sup>	...	N	4 (overall N effect sig.)	23 (overall N effect sig.)	0.80	0.058
				P	–32 (overall P effect sig. and positive)	22 (overall P effect sig.)	...	...
				N and P	24	48	...	...
Venezuela	Tanner et al. 1992	...	...	N	...	35 (overall N effect sig.)	1.6	0.081
				P	...	23 (overall P effect NS)	...	...
				N and P	133 (sig.)	42 (interaction NS)	...	...
Jamaica	Tanner et al. 1990	...	...	N	77 (sig.)	...	1.6	0.07
				P	32 (sig.)	...	...	...

† Comp. = compound; containing N, P, K, Ca, S, Cu, Mg, Zn, and B.

and P, trunk growth was increased by 133% by simultaneous fertilization with N and P (Table 1), and litterfall was increased by 35% by fertilization with N, and by 42% by fertilization with N and P (Table 1).

In Hawai'i there have been several fertilization ex-

periments in forests dominated by one species, *Metrosideros polymorpha*, which were designed to investigate (a) limitation of growth on soils of different ages and (b) limitation of growth on soils derived from physically different (but chemically similar) substrates.

On soils of different ages (and different substrates) Gerrish et al. (1988), using compound fertilizers, showed that tree-diameter growth was limited on both 200-yr-old soil derived from ash, and 1500–3000 yr old soils derived from lava, though it was not on a 3400-yr-old soil (also derived from lava but the trees at that site had higher concentrations of N in their leaves, Table 1). In later experiments with individual nutrients and a larger range of substrate ages (on ash-derived soils) Vitousek and co-workers (Table 1) showed a trend for a switch from N limitation on young soils to P, or N and P, limitation on old soils. On 30- and 200-yr-old ash both trunk growth and litterfall were increased by fertilization with N; on 2000-yr-old ash N fertilization had no effect on either trunk growth or litterfall; on 4.1 million yr old substrate P increased trunk growth and P and N increased litterfall. These responses to fertilization are consistent with N concentrations in leaves being lower in the youngest site, but not with P concentrations in leaves, which were also lowest in the youngest site. The 2000-yr-old site where no responses to N or P were seen had trees with leaves with the highest concentrations of N and P.

On physically different (but chemically similar) substrates different elements limit growth. Raich et al. (1996) showed that trees growing on soils derived from lava 140 yr old (which weathers slowly to produce thin soils) responded to both N and P. In contrast, trees growing in soils developed over 200-yr-old unconsolidated ash (which was chemically similar to the lava) responded to N but not P (Vitousek et al. 1995a).

The tendency to move from N limitation on younger soils, especially those that are derived from unconsolidated substrates, to P and N limitation on older soils, is consistent with the idea that N is accumulated from the atmosphere during soil development, while P is derived from the substrate. Thus N accumulates during soil development but P, which is relatively available in young soils, becomes progressively bound up in insoluble and/or physically protected forms in very old soils (Walker and Syers 1976, Crews et al. 1995). It is not clear whether the results from Venezuela (where N increased litterfall and P had no significant effect) and Jamaica (where both N and P limited growth) are inconsistent with this; it depends on the age of the soils. In general, in both Venezuela and Jamaica the soils are old in that they are not derived from geologically recent volcanic activity; however, both sites are ~500 m below the current tree line, which was much lower in the ice ages, when the sites would have been paramo. Both sites have actively weathering rock fragments <2 m from the surface and these are probably a source of P. Thus if sites are to pass from N limitation to P limitation they probably have to be on deep soils that develop over old, nearly level surfaces; the majority of montane soils are on slopes where erosion rates have probably been sufficient to ensure that there is always

weatherable P accessible to plants. Thus the results from the experiments carried out so far support the general model of Walker and Syers (1976) that plant production should be limited by N on young soils and by P on old soils; N and P supply should more or less equilibrate on intermediate-aged soils.

## CONCLUSIONS

Results from this limited set of experiments suggest that nutrient limitation to aboveground net primary production may be widespread in montane tropical forests—and that the particular nutrient(s) that limit(s) production may vary among sites for explicable reasons. Similar fertilization studies have been started in tropical lowland rain forests in Panama and Kalimantan. In Panama, Cavelier (1989) showed that fertilization with N and P together had no effect on litterfall in 4 mo after first fertilization; with hindsight we can suggest that any effects would have been unlikely to appear in such a short time. In Kalimantan, on sandy soils, N increased girth increment for some trees and N plus P together increased fine litterfall 18–24 mo after first fertilization (Mirmanto 1996; J. Proctor *personal communication*). We await further results from these studies and from fertilization experiments at two altitudes in Puerto Rico with great interest. At present we have insufficient information to say whether in general montane forests differ from lowland forests in the extent of nutrient limitation or even which nutrients generally limit growth, despite indirect evidence that they might differ in both respects.

Comparisons between responses to fertilization and foliar or litterfall nutrient concentrations (or soil nutrients) can only be made for a few sets of data, but obviously such relationships are potentially very valuable because they tell us to what extent simple(r) measures can be used to detect nutrient limitation (determined by fertilizer experiments). The best data come from Hawai'i where *Metrosideros* trees with lowest N concentrations in leaves show the highest increase in trunk growth after fertilization with N; an analogous relationship was not found for P. The other experiments have much less background information because they are in much more species-rich forest, in places that are much less well studied. We still need many more experiments (especially in the lowlands) about the responses to individual nutrients in a range of sites—and clearly negative as well as positive results need to be published—before we can have confidence about the general patterns of nutrient limitation in tropical montane and lowland forests.

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