# Effect of water, temperature and fertilizers on soil nitrogen net transformations and tree growth in an elfin cloud forest of Colombia

JAIME CAVELIER*[1], EDMUND TANNER* *and* JOHANNA SANTAMARÍA†

*Botany School, University of Cambridge, Downing St., Cambridge CB2 3EA, UK*
*†Departamento de Ciencias Biológicas, Universidad de los Andes, Santafé de Bogotá, Colombia*

ABSTRACT. In the 'elfin' cloud forest of Serrania de Macuira, exchangeable ammonium and nitrate, and the rates of soil nitrogen mineralization and nitrification were measured in soil samples under different water, temperature and mineral nutrient additions. The effects of nitrogen, phosphorus and nitrogen plus phosphorus fertilization on radial trunk growth were measured in three tree species. In the cloud forest soils, concentrations of ammonium were much higher than those of nitrate. Nitrate was higher in samples collected during the afternoon than during the morning, probably as a result of leaching during the night or nitrification during the day. When samples were incubated under different water and temperature treatments, rates of nitrogen mineralization and nitrification increased more with changes in soil water content than with changes in temperature. Nitrification was significantly increased in soils amended with ammonium or with ammonium plus phosphorus, suggesting that nitrification is substrate-limited. Fertilization with nitrogen and phosphorus resulted in significantly increased girth increments in *Guapira fragrans* (Dum. -Cours.) Little and *Rapanea guianensis* Aublet. *Myrcianthes fragrans* (Sw.) D.C. did not respond to the fertilization. The results of this study support the hypothesis that the characteristics of montane rain forest in small and large tropical mountains (the 'Massenerhebung' effect) are greatly controlled by soil water conditions and related soil nitrogen availability.

KEY WORDS: Colombia, elfin cloud forest, exchangeable ammonium, Macuira, mineralization, nitrification, fertilization, trunk growth

## INTRODUCTION

Tropical montane rain forests are characterized by small trees and low rates of wood production. The most stunted forests also have low above-ground

---

[1] To whom corresponce should be addressed, at 2828 Connecticut Avenue, Apartment 608, Washington DC 20008, USA.

biomass and low production of leaf litter (Grubb 1977, Proctor 1984). These forests are usually associated with high elevations, and consequently with low air and soil temperatures (Cuatrecasas 1934, 1958; Troll 1968, van der Hammen 1984). Nevertheless, montane rain forests also occur at lower altitudes (<1000 m) for instance in the Caribbean (Beard 1946, 1949; Howard 1968, 1970) and along the north coast of South America (Sugden 1982a, 1986) where they are known as 'elfin cloud forests', and in Southeast Asia (Bruijnzeel *et al.* 1993, Flenley 1979). The occurrence of montane forests at different altitudes on small and large tropical mountains, and the compression of the vegetation zones along the altitudinal gradients, is known as the 'Massenerhebung' effect (Grubb 1977, Grubb & Whitmore 1966, Richards 1952; van Steenis 1961, 1972).

Grubb & Whitmore (1966) first suggested that the most important factor determining the distribution of montane rain forest in tropical mountains is the frequency of fog. Grubb (1971, 1977) suggested that the zonation of the montane forest could be explained in terms of availability of certain nutrients with the rate of mineralization of humus decreasing with either lower mean temperature (high altitudes) or increase in soil water content. High soil water content, and sometimes waterlogged soil conditions, would result from frequent cloud cover (Grubb 1977, Whitmore 1984). Because clouds tend to form at a particular altitude, increased water availability would start rather abruptly at this elevation, as has been reported in Borneo (Kitayama 1992) and Colombia (Cavelier & Goldstein 1989). Until now, there has been only one study to measure the effect of temperature and water on nutrient availability in tropical montane forest (Marrs *et al.* 1988), and few fertilization experiments in tropical montane rain forest in Hawaii (i.e. Gerrish *et al.* 1988), Jamaica (Tanner *et al.* 1990) and Venezuela (Tanner *et al.* 1992) to investigate whether the growth of trees is limited by natural supplies of mineral nutrients. These studies suggest that growth of trees in tropical montane rain forests is indeed limited by nitrogen and phosphorus and that nitrogen mineralization may be limited under field conditions by the high soil water content and substrate availability. Other limiting factors in these ecosystems include low radiation levels and thus low temperature (Grubb 1977) and high and constant wind speed (Howard 1970, Lawton 1982, Lawton & Dryer 1980).

In this paper we address the following questions: (1) Is the tree growth limited by nitrogen and phosphorus in the low altitude cloud forest of Serrania de Macuira, (865 m) as in high altitude cloud forest? (2) What are the effects of soil water content, temperature and nutrient supply on the soil N-mineralization and nitrification rates? (3) Can the 'Massenerhebung' effect be explained in terms of low nitrogen availability induced by high soil water content?

## MATERIALS AND METHODS

*Study site*

This study was carried out in the 'elfin' cloud forest of Serranía de Macuira (865 m), Guajira Peninsula, Colombia (*c.* 12° N, 71° W). This small mountain

is located within the south Caribbean Dry Zone (Lahey 1958, Snow 1976). In this forest, low values of rainfall (853 mm y$^{-1}$) are complemented by water supplied in the form of mist and fog (796 mm y$^{-1}$) by clouds constantly moving from the ocean toward the mountain (Cavelier & Goldstein 1989). This extra water is supplied only during the night when clouds are intercepted by the vegetation (Cavelier & Mejia 1990, Sugden 1982a). There is an 'elfin' cloud forest located on the upper slopes above 500–550 m on the windward side, and above 600–650 m on the leeward side. The forest is composed of stunted trees 5 to 8 m tall with abundant epiphytes and shallow root systems (Rieger 1976; Sugden 1982a, b; Sugden & Robins 1979). The cloud forest is surrounded by a dry deciduous forest and a thorn woodland on the slopes and lowlands respectively. The transition between the dry deciduous and the cloud forest is very sharp (50 m in altitude) and is correlated with the cloud base at night, and the altitude at which there is fog interception (Cavelier & Goldstein 1989). The soils in the elfin cloud forest are characterized by a thin A horizon (15–20 cm) on top of a 2C gravel horizon (10–15 cm) and a 3C saprolite horizon (30–50 cm). The organic-mineral soils of the A horizon, tend to be thinner on slopes and ridge tops, have a sandy clay loam texture (57% sand, 19% silt and 24% clay), pH of 5.3, 1.6% carbon, 0.26% nitrogen, 8.4 meq/100g total bases (Ca = 3.4 meq/100 g, Mg = 2.8 meq/100g, K = 0.7 meq/100g, Na = 0.8 meq/100g, Al = 0.7 meq/100g ), and 13.5 meq/100 g CEC. The predominant clay type is kaolinite (50%). Soil bulk density is 1.0 Mg m$^{-3}$ (SE = 0.07; n = 5) and holding retention capacity is 24% at −0.1 MPa, 20% at −0.3 MPa and 14% at −1.5 MPa.

*Soil water content and fog interception*

Percentage soil water content [(fresh mass−dry mass/dry mass) × 100] was measured in the top 0–10 cm at an altitude of 750 m between 18 December 1989 and 1 January 1990. Five to ten soil cores (4.6 cm in diameter and 10 cm in length) were taken at 07h00 and 17h00. Fresh mass was measured in the field and dry mass at the laboratory (2 d after the end of the field work), after drying the soils at 105 °C for 48 h. Mass was measured to the nearest 0.1 g.

Fog interception was measured between 18 December 1989 and 9 January 1990. Water inputs to the forest floor were calculated after applying a conversion factor of 318 cm$^3$ in the fog catcher to 1 mm of throughfall (Cavelier & Goldstein 1989). Fog catchers were placed above the canopy in the area where soil samples were collected.

*Nitrogen mineralization and nitrification rates*

Ammonium and nitrate contents, and rates of mineralization and nitrification were measured in the surface soils (0–10 cm) of the 'elfin' cloud forest at 750 m, between 19 December 1989 and 10 January 1990. All samples were taken with a soil corer 4.6 cm in diameter and 10 cm in length. Cores were not maintained intact because roots were taken out of the samples.

Ammonium ($NH_4–N$) and nitrate ($NO_3–N$) concentrations were measured in soil samples collected at 07h00 and 17h00 between December 19 and 22 1989. Samples were collected in the morning and afternoon in order to assess the effect of nocturnal inputs of cloud water and potential diurnal drying of the soils, on soil extractable $NH_4–N$ and $NO_3–N$, as well as on the rates of nitrogen mineralization and nitrification. Fifteen soil cores were collected at the site on every occasion. In a 10-g subsample from each core, $NH_4–N$ and $NO_3–N$ were extracted in the field using 100 ml of 2M KCl. Subsamples were shaken in the extracting solution for 1 min, allowed to come to equilibrium for 6 h and filtered (Whatman No. 44). Percentage soil water content was estimated for each soil core in a 10–20-g subsample.

Net mineralization [final ($NH_4–N$ + $NO_3–N$ + $NO_2–N$) − initial ($NH_4–N$ + $NO_3–N$ + $NO_2–N$)] and net nitrification [final ($NO_3–N$ + $NO_2–N$) − initial ($NO_3–N$ + $NO_2–N$)], were measured following Robertson (1984) and Robertson & Vitousek (1981), using *in situ* incubations under different water, temperature and nutrient amendments, as follows.

*Incubation under field conditions* Fifteen soil cores (10 cm deep) collected at 07h00 and 17h00 on 19 and 20 December 1989, and *c.* 100-g subsamples of each core were put in polyethylene bags (Eno 1960), tightly closed, placed in the hole left by the withdrawal of the soil corer and incubated under field conditions for 20–21 d (collection on 8 and 9 January 1990 respectively). Before and after the incubation, $NH_4–N$ and $NO_3–N$ were extracted from a 10 g subsample from each core as described above. Percentage soil water content was estimated for each soil core in a 10–20-g subsample.

*Incubations under higher temperature and lower soil water content* Sixty soil cores collected on 20 December 1989, were buried at −10 cm and incubated in groups under different water and temperature regimes. Groups of 15 samples were incubated under the following treatments: (A) in the cloud forest (750 m) under field soil temperature (*c.* 23 °C) and soil water content of *c.* 35% (field condition), (B) in the cloud forest (*c.* 23 °C) with partly air-dried soils (*c.* 25%), (C) in the lowlands (200 m) under field soil temperature (*c.* 35 °C) and soil water content (*c.* 35%) and (D) in the lowlands (*c.* 35 °C) with partly air-dried soils (25%). The large difference in soil temperature between the cloud forest and the lowlands is the result of the differences in cloud cover, humidity and soil water content of the soils (Cavelier & Mejía 1990). Ammonium and nitrate were extracted from a subsample before the samples were randomly assigned to the lowlands and cloud forest treatments. Percentage soil water content was estimated for each soil core in a 10–20-g subsample before and after the incubations. Mean soil water content was the same for drier montane forest soils incubated in the lowlands and in the uplands, and soil water content remained constant throughout the experiment. Samples were

recovered on 9 January 1990 (20-d incubation) and final ammonium and nitrate extractions carried out as described above.

*Incubations with added nutrients* In a short-term nutrient addition experiment (18 d) net nitrogen mineralization and nitrification rates were measured in soil samples with added (1) nitrogen (N; 100 mg N as $NH_4Cl$ $kg^{-1}$ wet soil), (2) nitrogen and phosphorus (N+P; 100 mg N as $NH_4Cl$ $kg^{-1}$ wet soil + 5 mg P as $NaH_2PO_4$ $kg^{-1}$ wet soil), (3) phosphorus (P; 5 mg P as $NaH_2PO_4$ $kg^{-1}$ wet soil), (4) calcium (Ca; 20 g Ca as $CaSO_4$ $kg^{-1}$ wet soil) and (5) control (no nutrient addition). Five replicates were used for each treatment. Nutrients were added in 6 ml solution (or in de-ionized water in controls) and incubated *in situ* under cloud forest soil, water and temperature conditions. Ammonium and nitrate were extracted before and after the incubation as described above. The nutrient addition treatments followed those of Marrs *et al.* (1988) and Robertson (1984).

*Chemical analysis*

Ammonium, nitrate and phosphate in soil extracts were preserved in the field with 1 mg $l^{-1}$ of mercuric chloride (Robertson 1984), and flown to Cambridge (UK) for chemical analyses. Concentrations of ammonium-N, nitrite+nitrate–N and phosphorus were determined colorimetrically using a ChemLab Instruments Ltd. continuous flow analyser. For the determination of $NO_3$–N + $NO_2$–N, nitrate was reduced to nitrite, and total nitrite analysed. Extractable $PO_4$–P was measured in dilute acid-fluoride (1N $NH_4F$ and 0.5N HCl) following Olsen & Sommers (1982).

*Field fertilization experiment*

In December 1985, four plots 10-m × 10-m were located on a single slope, exposed to the prevailing trade winds (northeast). One plot was used as a control, one fertilized with N, one with P, one with N+P. Fertilizers were urea (300 kg N $ha^{-1}$) and phosphate rock (100 kg P $ha^{-1}$). Since it was not possible to establish true replicates, special care was taken to locate the plots at the same altitude and in areas with the same topographic characteristics (slope) and soil depth. Trees of *Guapira fragrans* (Dum.-Cours.) Little, *Rapanea guianensis* Aublet, *Myrcianthes fragrans* (Sw.) DC., that account for 78% of the woody stems in this forest (Sugden 1982a), were permanently tagged and the girth of those greater than 10 cm in diameter (at 50 cm above the ground), measured to the nearest millimetre. In December 1989, trees were re-measured.

In all, 198 trees were used for the fertilization experiment, 51 trees in the control plot, 40 in the N-fertilized plot, 69 in the P-fertilized plot and 38 in the N+P-fertilized plot. For *Guapira fragrans* and *Rapanea guianensis* there were between 13 and 30 trees per plot, while for *Myrcianthes fragrans* there were only three trees in the control plot, five in the N-fertilized plot, 15 in the P-fertilized

plot and 11 in the NP-fertilized plot. Radial trunk growth was calculated on a per tree basis.

*Statistical analysis*

One factor ANOVA was used to test statistical differences between (a) day-to-day and diurnal (AM–PM) variations in soil water content, (b) available ammonium and nitrate and diurnal variation in the concentration of these two nitrogen forms, (c) net mineralization and nitrification rates and their diurnal variations, (d) net mineralization and nitrification in the short-term fertilization experiment with N, P, N+P, Ca and control, and (e), growth rates for each of the three species in the long-term fertilization experiment with N, P, N+P or control. The level of significance was set at 5%.

<div align="center">RESULTS</div>

*Water supply in the 'elfin' cloud forest*

Between 18 December 1989 and 9 January 1990 there were only 2 d with no rain or fog interception (Figure 1). Six out of the 23 d of collection had fog mixed with drizzle and 15 d had fog only. Fog interception occurred only at night, and days were sunny or partly cloudy but not foggy.

Mean soil water content was 33% and there were significant variations in soil water content from day to day ($P < 0.01$; Figure 2). Although soils were wetted only during the night and had the potential to dry during the day, there were no significant diurnal differences in soil water content (0–10 cm). There was diurnal precipitation during 26, 27 and 31 December 1990.

*Extractable ammonium, nitrate and phosphate*

In the cloud forest soils, extractable ammonium (mean value of 12.7 µg $NH_4$–N $g^{-1}$ dry soil) was decidedly higher than extractable nitrate (0.38 µg $NO_3$–N $g^{-1}$ dry soil). There were no differences in exchangeable ammonium in soils collected early in the morning and late in the afternoon (Figure 3). Extractable nitrate was slightly and significantly higher ($P < 0.01$) in samples collected during the afternoon (mean value of 0.47 µg $NO_3$–N $g^{-1}$ dry soil) than those collected during the morning (0.28 µg $NO_3$–N $g^{-1}$ dry soil). Acid-fluoride-extractable phosphorus in the upper soils (0–10 cm) of the elfin cloud forest of Macuira ranged from 2.4–3.0 (µg $PO_4$–P $g^{-1}$).

*Net nitrogen mineralization and nitrification*

Under forest soil temperature and soil water content conditions, net nitrogen mineralization (mean = 0.26 µg N $g^{-1}$ dry soil $d^{-1}$) was significantly higher ($P < 0.01$) than net nitrification (mean = 0.06 µg N $g^{-1}$ dry soil $d^{-1}$), and there were no differences between incubations with soils collected in the morning or afternoon (Figure 4).
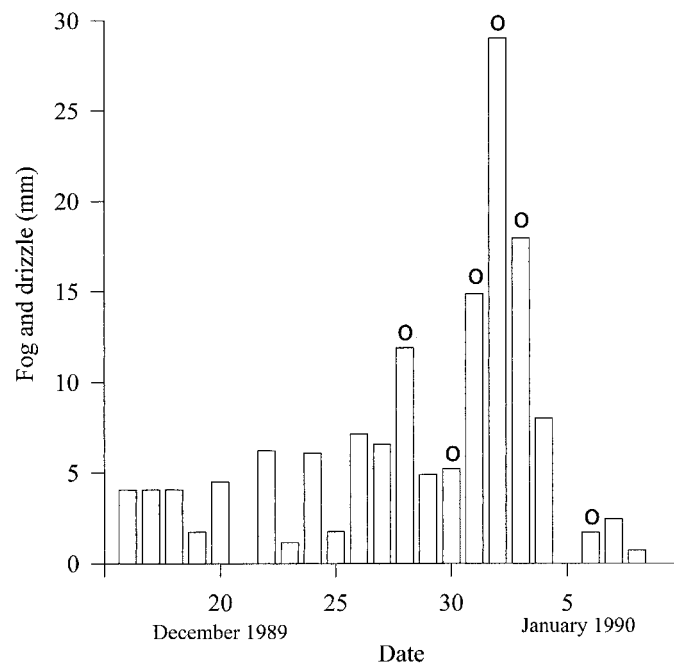
Figure 1. Fog interception (□) at 750 m in the elfin cloud forest of Serranía de Macuira. The circles indicate the days when fog was mixed with drizzle (○)



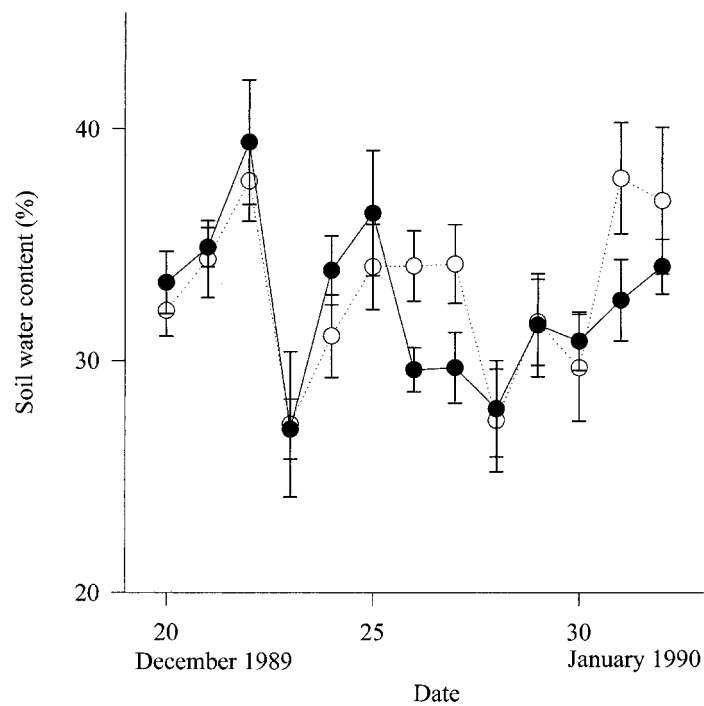Figure 2. Soil water content (% dry weight) in the elfin cloud forest at 750 m in samples collected at 07h00 (–●–) and 17h00. (–○–). The bars represent ± 1 SE (n = 5 to 10).
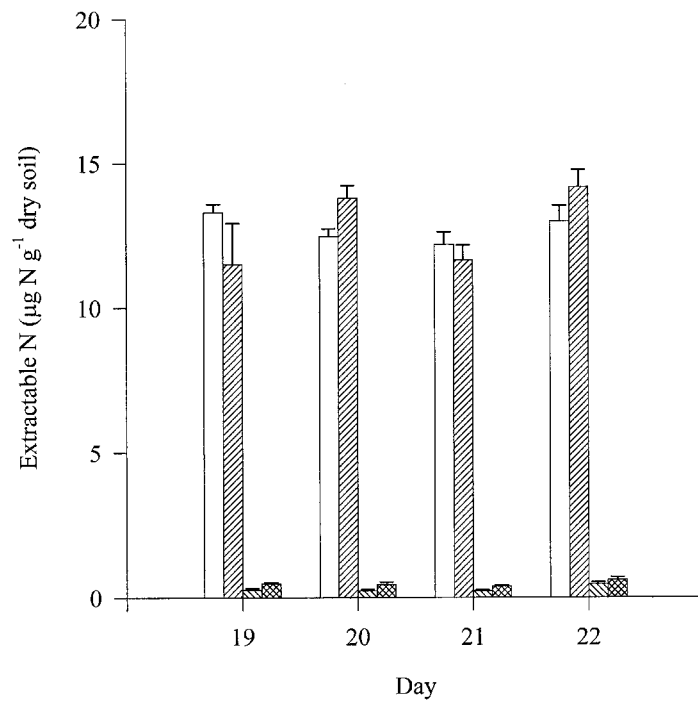
Figure 3. Extractable ammonium and nitrate in soils collected at 07h00. and 17h00. The bars represent ± 1 SE (n = 15). $NH_4$–N collected in the morning (□), $NH_4$–N collected in the afternoon (▨), $NO_3$–N collected in the morning (◩) and $NO_3$–N collected in the afternoon (⊠).
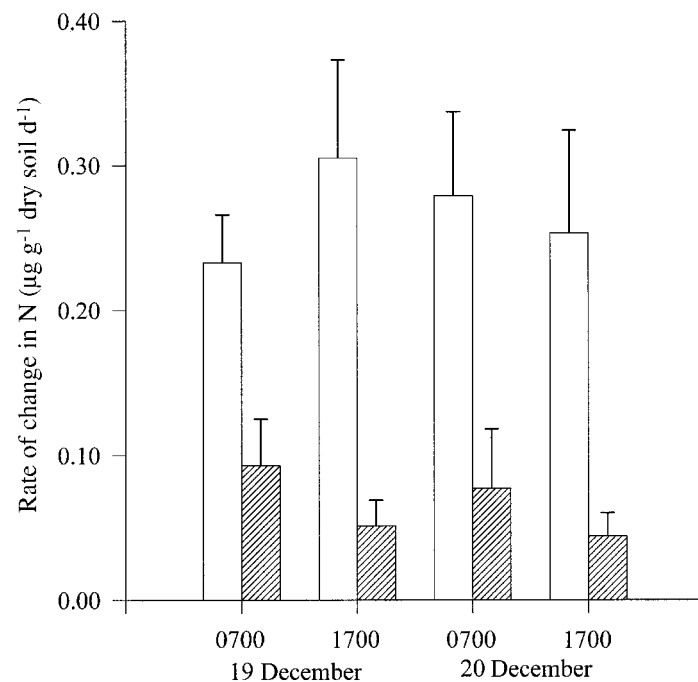


Figure 4. Net nitrogen mineralization (□) and nitrification rates (▨) in soils collected in the morning (07h00) and afternoon (17h00) during 19 and 20 December 1989. Soils were incubated for 20–21 d. The vertical lines represent ± 1 SE (n = 15).

When samples were incubated under different water and temperature treatments, rates of nitrogen mineralization and nitrification increased more with reduction in soil water content than with increases in temperature. For instance, there was a 1.3-fold difference in the rates of nitrogen mineralization between samples incubated in the cloud forest at high and low water content (same low temperature), while there was no difference in this rate between samples incubated in the cloud forest and in the lowlands (different temperatures) at the same high water content (Figure 5). Furthermore, there was a 2.1-fold difference in the rates of nitrogen mineralization between samples incubated in the lowlands at high and low water content (a measure of the effect of changes in water content). In contrast there was a 1.6-fold difference between samples incubated in the cloud forest and the lowlands at the same low water content—a measure of the effect of temperature (Figure 5).

Nitrification was significantly greater in soil samples amended with ammonium, or with nitrogen plus phosphorus, than control or soils amended with only phosphorus (Figure 6). However, the total amount of nitrogen (ammonium + nitrate) produced during the incubations (32.7 µg N $g^{-1}$ dry soil) was drastically lower than the amount of nitrogen added to the soils (100 µg N $g^{-1}$ dry soil), immobilization being a possible sink. Nitrification in soils with added calcium tended to be greater than in the control, but the difference was not statistically significant.

Net nitrogen mineralization was significantly higher for soils amended with N or N + P than control or soils fertilized with only phosphorus or calcium (Figure 6). The results for the controls are inexplicably low, but the patterns described still hold if we use as a control rate the values from 19 and 20 December (Figure 4) or from the experiment on different temperatures and water contents (Figure 5).

### Effects of nitrogen and phosphorus fertilizers on trunk growth

Mean trunk girth increment of *Rapanea guianensis* was significantly greater (P < 0.05) in the N+P fertilized plot than in the control and P-fertilized plot, but not different from the one in N-fertilized plot (Figure 7). Trunk growth was greater for larger (20–30 cm in girth) than for small trees (10–20 cm in girth) especially when fertilized with N + P together.

Mean trunk girth increment of *Guapira fragrans* was significantly greater (P < 0.05) in N+P fertilized plots than in the control, N or P fertilized plots. As in the case of *R. guianensis*, trunk growth tended to be higher for larger than for small individuals. *Myrcianthes fragrans* did not respond significantly to the addition of fertilizers.

### DISCUSSION

### Water supply to the cloud forest

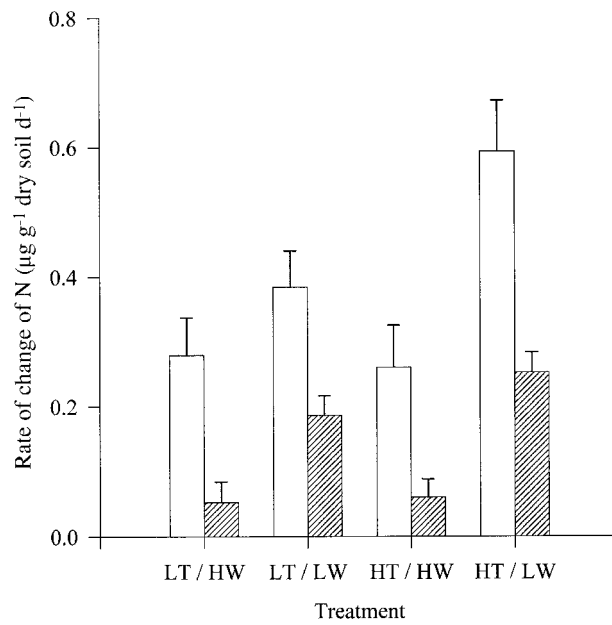During the study period, there was an almost daily supply of water by means

Figure 5.   Net nitrogen mineralization (□) and nitrification rates (▨) in soils incubated under different water and temperature regimes. Low temperature + High water (LT/HW), Low temperature + Low water (LT/LW), High temperature + High water (HT/HW), High temperature + Low water (HT/LW). The vertical lines represent ± 1 SE (n = 7 to 15).
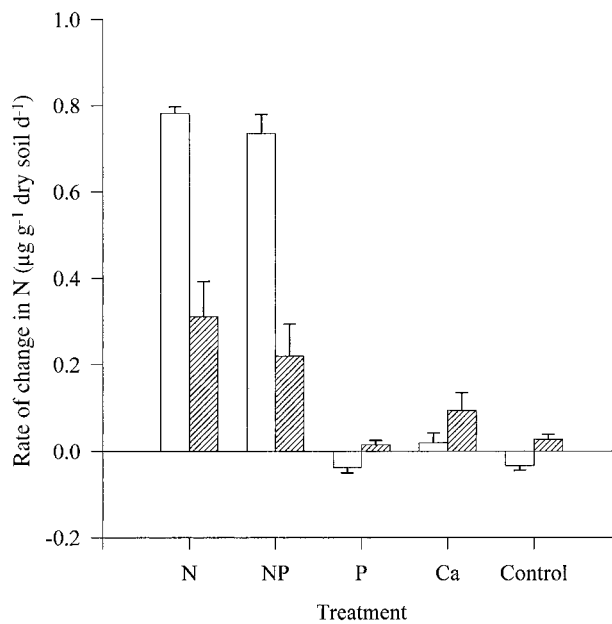


Figure 6.   Net nitrogen mineralization (□) and nitrification rates (▨) in soils fertilized with nitrogen (N; 100 mg N as $NH_4Cl$ $K^{-1}$ wet soil), phosphorus (P; 5 mg P as $NaH_2PO_4$ $K^{-1}$ wet soil), nitrogen and phosphorus (NP; 100 mg N as $NH_4Cl$ $K^{-1}$ wet soil and 5 mg P as $NaH_2PO4$ $Kg^{-1}$ wet soil), calcium (Ca; 20 g Ca as $CaSO_4$) and control (C; no fertilizers). The bars represent ± 1 SE (n = 5).
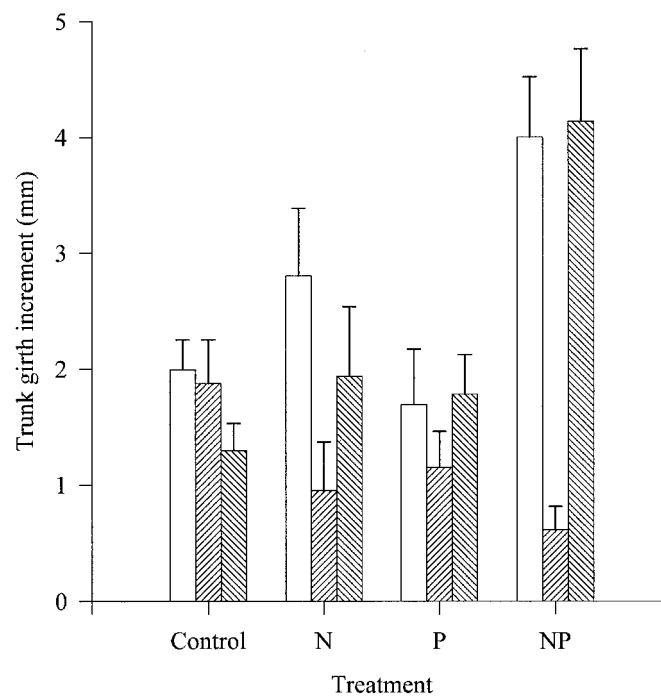
Figure 7. Radial trunk growth in trees of *Guapira fragrans* (▨), *Myrcianthes fragrans* (▨) and *Rapanea guianensis* (□) fertilized in December 1985 with nitrogen (N), phosphorus (P), and nitrogen + phosphorus (N+P). Control plots were not fertilized (C). Trees were remeasured in December 1989.

of fog and drizzle. Cloud water is supplied to the forest only at night when the cloud base is low. During the day, the cloud base rises over the peaks without dissipating, increasing water demands from the cloud forest (Cavelier & Goldstein 1989, Cavelier & Mejía 1990, Sugden 1982a). Although there is a great potential for evaporation (8.0–11.7 mm $H_2O$ $d^{-1}$ measured with Piche evaporimeters; Cavelier & Mejía 1990), soil water content in the first 10 cm of the soil was not significantly different between early morning and late afternoon. It seems that at night, cloud water replaces some of the water in the soil, while during the day there are no measurable changes in soil water content and only the surface layer (0–2 cm) becomes drier.

*Extractable ammonium, nitrate and phosphate*

The KCl-extractable nitrate was five times lower than the pool of KCl-extractable ammonium, indicating a low nitrification rate (0.06 μg N. $g^{-1}$ dry soil $d^{-1}$), leaching during the night by cloud water (nitrate concentrations were lower in the morning after water inputs at night by means of fog interception), rapid immobilization by microbial biomass, or rapid denitrification owing to the very high soil water content (Robertson 1982, 1989).

The pools of ammonium and nitrate in Macuira (12.7 and 0.38 μg N $g^{-1}$ dry soil, respectively) are in the high and low ranges, respectively, of values

reported for tropical lowland rain forests (Vitousek & Matson 1988). The pool of extractable ammonium-N in Macuira was greater than at the same altitude on Volcán Barva, Costa Rica (3.1 µg N $g^{-1}$ dry soil) but similar to values at 2300 m (Marrs *et al.* 1988). In contrast, values of extractable nitrate were lower than those on Volcán Barva, which decreased from 11.6 to 1.5 µg N $g^{-1}$ dry soil between 100 and 2600 m (Marrs *et al.* 1988).

Acid-fluoride-extractable phosphorus in the soils of Macuira (2.4–3.0 µg $PO_4$–P $g^{-1}$) is similar to the values reported by Vitousek & Denslow (1986) at La Selva, Costa Rica (2.3–2.7 µg $g^{-1}$ $PO_4$–P $g^{-1}$ dry soil), and in the range of values reported by Marrs *et al.* (1988) along the altitudinal gradient on Volcán Barva (1.3 µg $g^{-1}$ $PO_4$–P $g^{-1}$ dry soil at 1000 m to 55.0 µg $g^{-1}$ $PO_4$–P $g^{-1}$ dry soil at 2600 m, using Truog's reagent). The absolute values of extractable P in Macuira are low, and thus phosphorus is likely to be a limiting factor for plant growth.

*Nitrogen mineralization and nitrification rates under field conditions*

Absolute values of net nitrogen mineralization (0.26 µg N $g^{-1}$ dry soil $d^{-1}$) and nitrification rates (0.06 N $g^{-1}$ dry soil $d^{-1}$) are low compared to other tropical forest soils (mineralization = 0.1–3.9 µg N $g^{-1}$ dry soil $d^{-1}$; nitrification = 0.0–2.5 µg N $g^{-1}$ dry soil $d^{-1}$) reported by Robertson (1989) and Vitousek & Matson (1988). While values of net nitrogen mineralization in Macuira (750 m) were similar to those at 1500 m on Volcán Barva, net nitrification in Macuira was lower than along the altitudinal gradient in the Central America Volcano, where values decreased from 1.77 to 0.19 µg N $g^{-1}$ dry soil $d^{-1}$, between 100 and 2600 m (Marrs *et al.* 1988). It is interesting to note that nitrification was higher on Volcán Barva than in Macuira, despite the fact that soils at high altitude on Volcán Barva were waterlogged (Marrs *et al.* 1988).

*The effect of water, temperature and nutrient supply on the rates of nitrogen transformations*

Increase in temperature alone had no significant effect on the rates of net nitrogen mineralization and nitrification. This result is similar to those in some temperate (Morecroft *et al.* 1992) and Arctic soils (Nadelhofer *et al.* 1991) where net nitrogen transformation did not change with temperature, in spite of the known effect of temperature on biological and chemical processes (Swift *et al.* 1979). In contrast, a decrease in soil water content from 35 to 25% (with or without increments in soil temperature) had increased mineralization and nitrification. These results support the idea that one of the most important characteristics of the soils and cloud forest studied is a high soil water content (Wadsworth & Bonnet 1951), by reducing nitrification through the decrease of the diffusion of oxygen through water films to individual nitrifiers (Robertson 1989).

The soils of Macuira were only partly dried (35% to 25%) and subsequently placed in plastic bags for field incubation. It is possible that small changes in soil water content caused selective decrease in microbial biomass (Salonius

1983), leaving a population whose nutrient requirements were satisfied by the particular nutrients released during the short drying period (Stevenson 1956). These changes in soil chemistry and microbial biomass, and their effects on the rates of nitrogen transformation may be only temporary. It is possible that under a new soil moisture equilibrium the rates of nitrogen transformation may return to the values measured in the cloud forest under current field temperature and water conditions. The fact that small changes in soil water content caused significant changes in the rates of net nitrogen mineralization and nitrification, supports the idea that these rates are higher in soils that experience changes in soil moisture than in soils with continuous high water content (Birch 1958, 1964). It seems that one of the key effects of the daily water supply by means of fog interception is maintaining soil water content near field capacity, thus not allowing the soils to get drier and to experience fluxes of ammonium and nitrate.

In the nutrient addition experiment, nitrogen was applied as ammonium, and significantly higher nitrification rates were measured in N- and N+P amended soils than in controls, indicating that the nitrification is substrate limited. This is a surprising result because the pool of KCl-extractable ammonium in the soils of Macuira is high when compared to most other tropical forest soils (see Vitousek & Matson 1988). Substrate limitation of nitrification was reported for low- and high-altitude soils on Volcán Barva (Marrs *et al.* 1988) and for successional lowland rainforests in Costa Rica (Robertson 1984).

The addition of calcium and phosphorus had no significant effects on the rates of nitrogen transformation, although some investigators have suggested that ammonium (Chapin *et al.* 1978, Cole & Heil 1981) and nitrate production (Chase *et al.* 1968, Purchase 1974) can be limited by phosphorus availability. Similar results to those reported here, were found in successional forests in Costa Rica (Robertson 1984), while on Volcán Barva, calcium carbonate increased mineralization rates at low and intermediate altitudes, whereas calcium sulphate increased the rates only at the highest altitude (Marrs *et al.* 1988).

*Trunk growth and effect of fertilizers*

Nitrogen plus phosphorus fertilizer significantly increased growth in *Guapira fragrans* and *Rapanea guianensis* while nitrogen or phosphorus alone had no significant effect on trunk growth in these two species. These results accord with those of a well replicated fertilization experiment in the mountains of Venezuela, where trunk growth was significantly higher in N+P-fertilized plots than in control plots (Tanner *et al.* 1992). Significant increases in trunk growth have been reported in fertilization experiments with nitrogen or phosphorus alone in the montane forests of Hawaii (i.e. Vitousek & Farrington 1997, Vitousek *et al.* 1993) or nitrogen alone in Jamaica (Tanner *et al.* 1990). This results show that growth in tropical montane forests is limited by the supply of these nutrients.

The results of the fertilization experiment in Macuira support the idea that N is the primary limiting nutrient of N and P (Tanner *et al.* 1998), and that as soon as N supply increases, P limits growth. Thus, when nitrogen and phosphorus are added together a substantial increase in growth occurs. It is important to notice that the two species that responded to the fertilization had higher foliar N concentration (0.99% in *G. fragrans* and 1.90% *R. guianensis*) than *M. fragrans* (0.78%). Foliar P concentration was higher for *G. fragrans* (0.19%) than for *M. fragrans* (0.07%) and *R. guianensis* (0.06%). This result shows that even in a community of wild plants growing in infertile soils, those species with higher nutrient concentrations are more likely to respond to the addition of nutrients (Chapin 1980, Tanner *et al.* 1998).

### *Implications for the Massenerhebung effect on tropical mountains*

Grubb (1971, 1977) suggested that the zonation of montane forests could be explained in terms of the availability of certain nutrients with the rate of mineralization of humus decreasing with either lower mean temperature (high altitudes) or increases in soil water content. In the limit between lowland and montane forests (*c.* 1200–1500 m), the occurrence of a cloud belt correlates with increases in soil water content, organic matter and total nitrogen content in the Andes (van der Hammen 1984), Costa Rica (Marrs *et al.* 1988), Borneo (Kitayama 1992) and Sarawak (Proctor *et al.* 1983). Under these environmental conditions, competitive exclusion is a possible mechanism contributing to the sudden changes in species abundance along altitudinal gradients (Grubb 1977).

Experimental evidence gathered at Volcán Barva (2906 m) in Costa Rica, shows that when the temperature was increased and soil water content decreased simultaneously in laboratory incubations (with a concomitant increase in aeration) net nitrogen mineralization rate increases, and a positive relationship was found with altitude of origin (Marrs *et al.* 1988). The results presented in this paper for the low altitude (*c.* 750 m) and relatively warm cloud forest of Macuira (*c.* 23 °C) suggest that high soil water content, and not low temperatures, reduce nitrogen availability and may be the proximal cause of the 'Massenerhebung' effect in tropical mountains. It is important to emphasize that only high and quasi-constant soil water contents would be required to produce this effect on nitrogen transformations without necessarily having gleying or waterlogging. This would explain why these soil conditions associated with saturated soils, have not been observed consistently with the occurrence of tropical montane forests (Bruijnzeel & Veneklass 1998, Kapos & Tanner 1985).

## LITERATURE CITED

BEARD, J. S. 1946. *The natural vegetation of Trinidad.* Oxford Forestry Memoirs 20. Clarendon Press, Oxford. 152 pp.

BEARD, J. S. 1949. *The natural vegetation of the windward and leeward islands.* Oxford Forestry Memoirs 21. Clarendon Press, Oxford. 192 pp.

BIRCH, H. F. 1958. The effect of soil drying on humus decomposition and nitrogen availability. *Plant and Soil* 10:9–31.

BIRCH, H. F. 1964. Mineralization of plant nitrogen following alternate wet and dry conditions. *Plant and Soil* 20:43–49.

BRUIJNZEEL, L. A. & VENEKLAAS, E. J. 1998. Climatic conditions and tropical montane forest productivity: the fog has not lifted yet. *Ecology* 79:3–9.

BRUIJNZEEL, L. A., WATERLOO, M. J., PROCTOR, J., KUITERS, A. T & KOTTERINK, B. 1993. Hydrological observations in montane rain forest on Gunung Silam, Sabah, Malaysia, with special reference to the 'Massenerhebung' effect. *Journal of Ecology* 81:145–167.

CAVELIER, J. & GOLDSTEIN, G. 1989. Mist and fog interception in elfin cloud forests in Colombia and Venezuela. *Journal of Tropical Ecology* 5:309–322.

CAVELIER, J. & MEJÍA, C. 1990. Climatic factors and tree stature in the elfin cloud forest of Serranía de Macuira, Colombia. *Agricultural and Forest Meteorology* 53:105–123.

CHAPIN, F. S. 1980. The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics* 11:233–260.

CHAPIN, F. S., BARSDATE, R. L. & BAREL, D. 1978. Phosphorus cycling in Alaskan tundra: a hypothesis for the regulation of nutrient cycling. *Oikos* 31:189–199.

CHASE, F. E., CORKE, C. T. & ROBINSON, J. B. 1968. Nitrifying bacteria in soils. Pp. 593–611 in Gray, T. R. C. & Parkinson, D. (eds). *The ecology of soil bacteria.* University of Toronto Press, Toronto, Canada.

COLE, C. V. & HEIL, R. D. 1981. Phosphorus effects on terrestrial nitrogen cycling. Pp. 363–374 in Clark, F. E. & Rosswall, T. H. (eds). *Nitrogen cycling in terrestrial ecosystems; processes, ecosystem strategies and management implications.* Ecological Bulletin 33, Swedish Natural Science Research Council, Stockholm, Sweden.

CUATRECASAS, J. 1934. *Observaciones geobotánicas en Colombia.* Trabajos del Museo Nacional de Ciencias Naturales. Serie Botánica 27. Madrid, 144 pp.

CUATRECASAS, J. 1958. Aspectos de la vegetación natural de Colombia. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales* 10:221–264.

ENO, C. F. 1960. Nitrate production in the field by incubating the soil in polyethylene bags. *Proceedings of the Soil Science Society of America* 24:277–279.

FLENLEY, J. R. (ed). 1979. *The equatorial rain forest: a geological history.* Butterworth, London. 162 pp.

GERRISH, G., MUELLER DOMBOIS, D & BRIDGES, K. W. 1988. Nutrient limitation and *Metrosideros* dieback in Hawaii. *Ecology* 69:723–727.

GRUBB, P. J. 1971. Interpretation of the 'Massenerhebung' effect on tropical mountains. *Nature* 229:44–45.

GRUBB, P. J. 1977. Control of forest growth and distribution on wet tropical mountains: with special reference to mineral nutrition. *Annual Review of Ecology and Systematics* 8:83–107.

GRUBB, P. J. & WHITMORE, T. C. 1966. Comparison of montane and lowland rain forests in Ecuador. II. The climate and its effects on the distribution and physiognomy of the forests. *Journal of Ecology* 54:303–333.

HOWARD, R. A. 1968. The ecology of an elfin forest in Puerto Rico. I. Introduction and composition studies. *Journal of the Arnold Arboretum* 50:381–418.

HOWARD, R. A. 1970. The 'alpine' plants of the Antilles. *Biotropica* 2:24–28.

KAPOS, V. & TANNER, E. V. J. 1985. Water relations of Jamaican upper montane rain forest trees. *Ecology* 66:241–250.

KITAYAMA, K. 1992. An altitudinal transect study of the vegetation on Mount Kinabalu, Borneo. *Vegetatio* 102:149–171.

LAHEY, J. F. 1958. On the origin of the dry climate in northern South America and the southern Caribbean. Department of Meteorology, *University of Wisconsin Scientific Report* 10:1–290.

LAWTON, R. O. 1982. Wind stream and elfin stature in a montane rain forest tree: an adaptive explanation. *American Journal of Botany* 69:1224–1230.

LAWTON, R.O. & DRYER, V. 1980. The vegetation of Monteverde cloud forest reserve. *Brenesia* 18:101–116.

MARRS, R. H., PROCTOR, J., HEANEY, A. & MOUNTFORD, M. D. 1988. Changes in soil nitrogen-mineralization and nitrification along an altitudinal transect in tropical rain forest in Costa Rica. *Journal of Ecology* 76:466–482.

MORECROFT, M. D., MARRS, R. H. & WOODWARD, F. I. 1992. Altitudinal and seasonal trends in soil nitrogen mineralization rate in the Scottish Highlands. *Journal of Ecology* 80:49–56.

NADELHÖFFER, K. J., GIBLIN, A. E., SHAVER, G. R. & LAUNDRE, J. A. 1991. Effects of temperature and substrate quality on element mineralization in six arctic soils. *Ecology* 72:242–253.

OLSEN, S. R. & SOMMERS, S. R. 1982. Phosphorus. Pp. 403–430 in Page, A. L. (ed.). *Methods of soil analysis, Part 2, chemical and microbiological properties* (Second edition). American Society of Agronomy and Soil Science Society of America. Madison, Wisconsin, USA.

PROCTOR, J. 1984. Tropical forest litterfall. II. The data set. Pp. 83–113 in Chadwick, A. C. & Sutton, S. L. (eds). *Tropical rain forest: the Leeds symposium*. Leeds Philosophical and Literary Society, Leeds.

PROCTOR, J., ANDERSON, J. M. & VALLACK, H. W. 1983. Comparative studies on forest, soils and litterfall at four altitudes on Gunung Mulu, Sarawak. *Malaysian Forester* 46:60–75.

PURCHASE, B. S. 1974. The influence of phosphate deficiency on nitrification. *Plant and Soil* 41:541–547.

RICHARDS, P. W. 1952. *The tropical rain forest*. Cambridge University Press, Cambridge. 450 pp.

RIEGER, W. 1976. Vegetationskundliche Untersuchugen der Guajira- Halbinsel (Nortdost-Kolumbien). *Giessener Geographische Schriften* 40:1–142.

ROBERTSON, G. P. 1982. Nitrification in forested ecosystems. *Philosophical Transactions of the Royal Society of London B* 296:445–457.

ROBERTSON, G. P. 1984. Nitrification and nitrogen mineralization in a lowland rainforest succession in Costa Rica, Central America. *Oecologia* 61:99–104.

ROBERTSON, G. P. 1989. Nitrification and denitrification in humid tropical ecosystems: potential controls on nitrogen retention. Pp. 55–69 in Proctor, J. (ed.). *Mineral nutrients in tropical forest and savanna ecosystems*. Blackwell Scientific Publications, Oxford.

ROBERTSON, G. P. & VITOUSEK, P. M. 1981. Nitrification potentials in primary and secondary succession. *Ecology* 62:376–386.

SALONIUS, P. O. 1983. Effects of air drying on the respiration of forest soil microbial populations. *Soil Biology & Biochemistry* 15:199–203.

SNOW, J. W. 1976. The climate of Northern South America. Pp. 245–379 in Schwerdtfeger, W. (ed.). *World survey of climatology*. Vol. 12. Elsevier, Amsterdam.

STEVENSON, I. L. 1956. Some observations on the microbial activity in remoistened air-dried soils. *Plant and Soil* 8:170–182.

SUGDEN, A. 1982a. The vegetation of the Serranía de Macuira, Guajira, Colombia: A contrast of arid lowlands and an isolated cloud forest. *Journal of the Arnold Arboretum* 63:1–30.

SUGDEN, A. 1982b. The ecological, geographic and taxonomic relationships of the flora of an isolated Colombian cloud forest, with some implications for island biogeography. *Journal of the Arnold Arboretum* 63:31–61.

SUGDEN, A. 1986. The montane vegetation and flora of Margarita Island, Venezuela. *Journal of the Arnold Arboretum* 67:187–232.

SUGDEN, A. M. & ROBINS, R. J. 1979. Aspects of the ecology of vascular epiphytes in two Colombian cloud forests. I. The distribution of the epiphytic flora. *Biotropica* 11:173–188.

SWIFT, M. J., HEAL, O. L. & ANDERSON, J. M. 1979. *Decomposition in terrestrial ecosystems*. Blackwell Scientific Publications, Oxford. 372 pp.

TANNER, E. V. J., KAPOS, V. & FRANCO, W. 1992. Nitrogen and phosphorus fertilization effects on Venezuela montane forest trunk growth and litterfall. *Ecology* 73:78–86.

TANNER, E. V. J., KAPOS, V., FRESKOS, S., HEALEY, J. R. & THEOBALD, A. M. 1990. Nitrogen and phosphorus fertilization of Jamaican montane rain forest trees. *Journal of Tropical Ecology* 6:231–238.

TANNER, E. V. J., VITOUSEK, P. M. & CUEVAS, E. 1998. Experimental investigation of nutrient limitation of forest growth on wet tropical mountains. *Ecology* 79:10–22.

TROLL, C. 1968. The cordilleras of the tropical Americas. Aspects of climatic, phytogeographical and agrarian ecology. Pp. 15–56 in Troll, C. (ed.). *Geoecología de la regiones montañosas de las Americas tropicales*. Proceedings of the UNESCO Mexico Symposium.

VAN DER HAMMEN, T. 1984. Datos eco-climaticos del transecto Buritaca y alrededores (Sierra Nevada de Santa Marta). Pp. 45–66 in van der Hammen, T. & Ruiz, P. M. (eds). *Studies on tropical Andean ecosystems. Vol. 2. La Sierra Nevada de Santa Marta (Colombia), Transecto Buritaca-La Cumbre*. J. Cramer, Berlin.

VAN STEENIS, C. G. G. J. 1961. An attempt toward an explanation of the effect of mountain mass elevation. *Proceedings Koninklike Nederlandse Akademie van Wetenschappen, Series C*. 64:435–442.

VAN STEENIS, C. G. G. J. 1972. The effect of mountain mass elevations. Pp. 19–20 in Van Steenis, C. G. G. J (ed.). *The mountains of Java*. E. J. Brill, Leiden.

VITOUSEK, P. M. & DENSLOW, J. S. 1986. Nitrogen and phosphorus availability in treefall gaps of a lowland tropical rainforest. *Journal of Ecology* 74:1167–1178.

VITOUSEK, P. M. & FARRINGTON, H. 1997. Nutrient limitation and soil development: experimental test of a biogeochemical theory. *Biogeochemistry* 37:63–75.

VITOUSEK, P. M. & MATSON, P. A. 1988. Nitrogen transformations in a range of tropical forest soils. *Soil Biology and Biochemistry* 20:361–367.

VITOUSEK, P. M., WALKER, L. R., WHITEAKER, L. D. & MATSON, P. A. 1993. Nutrient limitation to plant growth during primary succession in Hawaii Volcanoes National Park. *Biogeochemistry* 23:197–215.

WADSWORTH, F. H. & BONNET, J. A. 1951. Soil as a factor in the occurrence of two types of montane forests in Puerto Rico. *Caribbean Forester* 12:67–70.

WHITMORE, T. C. 1984. *Tropical rain forest of the Far East*. Clarendon Press, Oxford. 352 pp.