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Response of secondary vegetation in Eastern Amazonia to relaxed nutrient availability constraints

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Abstract. This study evaluated the effect of nutrient application on the regrowth dynamics of secondary fallow vegetation in an intensely exploited shifting cultivation area in the eastern Amazon region of Brazil. The importance of N, P, K, Ca, Mg, S and a mixture of micronutrients was tested in a minus-one-trial by comparison with a full complement of nutrients and unfertilized control plots. Fertilizers were applied three times during the experiment and their effects were monitored over a period of $2^1/_2$ years. Prior to the second fertilization, one third of each experimental plot was cleared of the vegetation cover and planted in maize, prior to the third fertilizer application these subplots were planted in sorghum. Biomass of maize and sorghum were used to indicate nutrient constraints and fertilizing effects due to the different treatments. Both crops were limited by P- and N-availability, with greater responses to P. The initial fertilization did not affect the biomass accumulation of the secondary vegetation during the first 15 months, but two additional applications significantly increased biomass in the complete fertilizer treatment compared to the unfertilized control. Biomass accumulation was primarily P-limited, N-limitation was apparent but not significant. The remaining nutrients did not affect plant growth. Fertilization favored production of nutrient-rich leaves. Application of readily available nutrients gave grasses a competitive edge over slower reacting woody vegetation. Fertilization also caused significant shifts in the contribution of woody species to biomass accumulation, as could be demonstrated for two prominent pioneer tree species. Growth response to fertilization as well as the primary limiting nutrient varied among seven dominant species monitored in the secondary vegetation. We conclude that growth of tropical secondary vegetation can be nutrient limited and it might respond significantly to additional nutrients by increasing biomass production.

Introduction

Increasing human population density and demand for land has caused an increase in agricultural exploitation in traditional shifting cultivation systems of the humid tropics. As fallow periods have been gradually reduced, frequently observed consequences include delayed regeneration of woody regrowth and extended persistence of grasses, eventually culminating in the development of a derived savanna (Kellman 1980; Ramakrishnan 1988).

Secondary fallow vegetation is of crucial importance for shifting cultivation systems. Following a brief cropping period of 2–3 years, fields are abandoned due to failing productivity generally caused by weed pressure and declining soil fertility. During the fallow period secondary vegetation re-establishes rapidly on the depleted soils with land use intensity and soil type being the predominant factors that determine floristic composition and biomass production (Nunez 1995; Baar 1997). The suppression of weeds and the accumulation of nutrients in the biomass are the most important effects of the fallow vegetation and are decisive in low-input agriculture for the success or failure of the subsequent land use (Denich 1989).

Numerous studies have tried to find relations between species richness of primary forests in the humid tropics and soil fertility (e.g., Ashton 1977; Gartlan et al. 1986; Huston 1994; Clinebell et al. 1995; Swaine 1996). Less frequent are studies on the relationship between soil fertility and rain forest biomass, which appears weak at best (Jordan 1985). Growth responses to N- and P-application in the tropics so far have only been reported for primary montane forests (Tanner et al. 1990; Tanner et al. 1992; Herbert & Fownes 1995). Recent fertilizer trials on differently aged lava flows in Hawaii have shown early primary successions to be mainly limited by N-availability and advanced primary successions to be mainly limited by P-availability (Walker & Aplet 1994; Vitousek et al. 1995; Raich et al. 1996), largely confirming pedogenetic theory (Walker & Syers 1976; Cole & Heil 1981). Comparable studies in tropical secondary vegetation are scarce. Observational studies have failed to demonstrate any influence of soil nutrient status on species composition or productivity in secondary regrowth (Kellman 1969; Buschbacher et al. 1988; Vogt 1994; Herold 1994). To date, only two fertilizer experiments have been conducted in tropical secondary vegetation. On a relatively fertile Inceptisol in Costa Rica, Harcombe (1977) found that biomass of spontaneous fallow vegetation did not differ after an initial NPK fertilization compared to the unfertilized control. He concluded that secondary regrowth was not affected by nutrient losses during burning and cultivation (Harcombe 1980). Following a 6-year cultivation period on an Oxisol at a Rio Negro site in Venezuela, Uhl (1987) found a shift in fallow vegetation towards grasses and herbs and a delay in woody succession after NPK-application compared to the unfertilized control treatment, however, his observations were restricted to a six month period.

Table 1. Soil data of the experimental site at the onset of the experiment (means of 16 composite samples consisting of four cores each).

	coarse sand	fine sand	silt	clay	$pH_{[H_2O]}$	N_{tot}	P[1]	K[1]	Ca + Mg[2]	Al[2]
	[% of weight]					[%]	[mg kg^{-1}]		[meq 100 g^{-1}]	
0–10 cm	45	35	11	10	5.5	0.10	3.6	30.8	2.2	0.04
10–20 cm	40	34	10	15	5.1	0.07	2.1	17.4	0.8	0.33
20–30 cm	34	33	12	21	4.9	0.06	1.4	12.7	0.6	0.46
30–50 cm	33	31	11	24	4.9	0.05	1.2	10.5	0.5	0.56

[1] extracted with Mehlich double-acid solution
[2] extracted with KCl

In this study, we investigate the influence of a range of plant nutrients on the regrowth of secondary vegetation in the humid tropics of Eastern Amazonia over a period of $2^1/_2$ years.

Materials and methods

Site

The experiment was conducted in the municipality of Igarapé Açu, 110 km east of Belém, Pará, Brazil, representative of an intensively cultivated slash and burn area (the Zona Bragantina) colonized over 100 years ago. The climate is characterized by an average annual temperature of 26 °C, a yearly precipitation averaging 2400 mm and a dry season from September to December. The landscape is flat to lightly undulating with an altitude of less than 60 m asl. The soils are predominantly Typic Kandiudults (Rego et al. 1993) of poor nutrient status (Table 1).

Fallow periods in the region have been gradually reduced to around 3–7 years, due to a population that increased from 13 inhabitants/km^2 in 1950 (IBGE 1957) to 36 inhabitants/km^2 in 1994 (Diário Oficial, August 30, 1995). The situation has been aggravated by the introduction of cash crops and mechanized land-use practices, thereby reducing the area available for traditional shifting cultivation. The primary forest has largely disappeared, and 73% of the municipality of Igarapé Açu is covered by secondary vegetation, 75% of which is 8 years old or younger (Watrin 1994). Presumably as an adaptation to the repeated land-use cycles, woody fallow vegetation in the region regenerates nearly exclusively by resprouting (Denich 1989; Clausing 1994; Jacobi 1997). The biomass of coarse roots which survived the cropping period is correlated with the initial biomass production of the regenerating secondary vegetation (Wiesenmüller et al. 1996).

Experimental design

At this site, a 4-year-old fallow vegetation was cleared and burned in 1985 and planted with cotton for one year. After an intermittent fallow period of one year, it was again planted with cotton in 1987. Thereafter, secondary vegetation was allowed to regenerate for 4 years before the experiment commenced in November 1992 with slashing and burning. The burn provided an estimated nutrient residue in the ash of 2.2 kg N, 1.4 kg P, 12 kg K, 55 kg Ca, 8 kg Mg and 2.8 kg S per hectare (estimations are based on ash quantification in the field and ash nutrient concentrations published by Hölscher et al. 1997). The high values of Ca in the ashes are due to low rates of Ca-volatilization even at high burning temperatures (Raison et al. 1985) and may be responsible for the Ca-enrichment in the topsoil (Table 1). Plots for the nonburning control treatment were protected against burning by removing the biomass prior to burning.

From May to September 1993 the field was planted in maize (*Zea mays* L.), and no obvious gradients or heterogeneity in the maize performance could be observed across the experimental area. Subsequently, the experiment was installed as a minus-one-trial laid out in a randomized complete block design with 8 replications in order to reduce the influence of the spatial heterogeneity of the growing secondary vegetation. Individual plot size was 60 m^2 (6 m × 10 m), interplot distances 1 m. The minus-one-trial involved 10 treatments, including a burned and an unburned control, a full complement of fertilizers (N, P, K, Ca, Mg, S, micronutrients) and treatments in which one of the plant nutrients or all micronutrients were omitted.

Fertilizers were applied by broadcasting at 1, 17 and 21 months after the harvest of maize and at levels designed to significantly surpass initial nutrient inputs from the ashes and to substantially increase nutrient availability for the fallow vegetation. As the first fertilizer application did not result in a noticeable biomass increase, a second higher one was carried out and split into two doses in order to reduce losses by immobilization or leaching. Fertilizer applications contained NH_4Cl (at rates of 60, 60 and 60 kg N ha^{-1} at 1, 17 and 21 months, respectively), $NaH_2PO_4*H_2O$ (26, 40, 40 kg P ha^{-1}), KCl (33, 25, 25 kg K ha^{-1}), $CaCl_2*2H_2O$ (60, 74, 74 kg Ca ha^{-1}), $MgCl_2*2H_2O$ (20, 60, 60 kg Mg ha^{-1}), S (20, 40, 40 kg S ha^{-1}) and a commercial mixture of micronutrients (10, 20, 20 kg ha^{-1}) of which 53.7% was Zn, 10.8% B, 4.9% Cu, 18% Fe, 12% Mn and 0.6% Mo.

Prior to the second fertilization each plot was subdivided and a 18 m^2 (6 m × 3 m) subplot was planted in maize, subsequently followed by sorghum

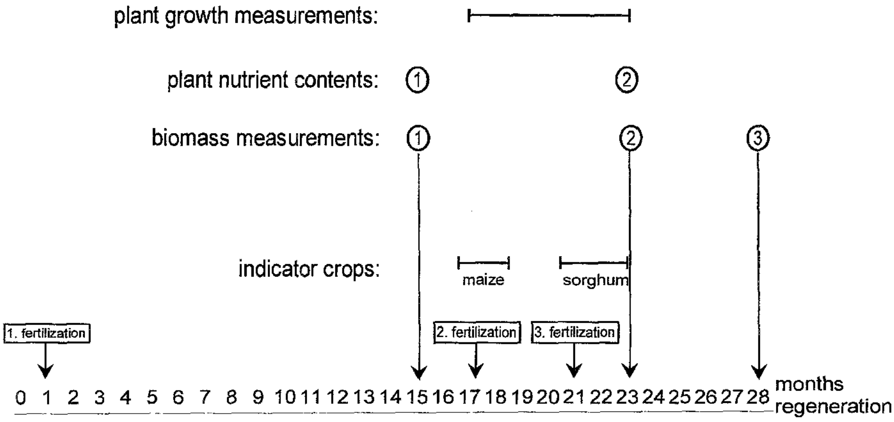

Figure 1. Experimental time line with schedule of cropping, fertilization and measurement events (0 = maize harvest 10 months after burning).

(*Sorghum bicolor* (L.) Moench). Both served as indicator crops to detect possible nutrient deficiencies and prove the availability of the applied nutrients to the plants. Maize and sorghum were planted with a spacing of 70 cm × 40 cm and 60 cm × 20 cm, respectively. Both crops required manual weeding (residues remained on the field) and chemical control with *Mirex* against leaf cutter ants (*Atta spp./Acromyrmex spp.*) and *Malatol* against earth crickets (*Neocurtilla hexadactyla*) during the first two weeks after establishment. To minimize underground transfer of nutrients, plot borders were trenched three times to 40 cm depth and subplots once in the course of the experiment. The chronology of the experiment is provided in Figure 1.

Measurements

Biomass measurements of the secondary vegetation were undertaken in December 1994 (15 months after maize harvest), August 1995 (23 months) and January 1996 (28 months) by destructive sampling from each plot. The biomass was separated in grasses, herbs and woody vegetation, with the latter separated in wood and leaves. Dead vegetation was sampled separately. The first biomass determination was carried out on the 18 m^2 subplot cleared to be planted in maize and sorghum, whereas for the second sampling two representative subplots of 1 m × 2 m within the remaining part of the experimental plots were sacrificed. The final biomass determination involved destructive sampling of the whole remaining part. Measurements of the aboveground biomass of the maize and sorghum crops were taken at maturity without separation into grain and stalk. Dry matter weight was determined in subsamples after oven-drying for one week at 65 °C.

Height and stem diameter were measured on a total of 293 individuals of 7 important species in the secondary vegetation, representing approx. 50% of the total biomass, in 2-week intervals over a period of 24 weeks following the second fertilization. The following species were selected: *Banara guianensis* Aubl. (Flacourtiaceae), *Rollinia exsucca* (Dun.) DC (Annonaceae), *Phenakospermum guyannense* Endl. (Strelitziaceae), *Lacistema pubescens* Mart. (Lacistemataceae), *Vismia guianensis* (Aubl.) Choisy (Guttiferae), *Inga macrophylla* HBK (Mimosaceae) and *Cecropia palmata* Willd. (Cecropiaceae).

Biomass contributions of the two most abundant species present in our study site, *Banara guianensis* and *Lacistema pubescens*, were determined destructively only in the final biomass determination (28 months). Their shares in the biomass of 15-month-old regrowth were estimated as follows: The height and number of all shoots present in the experimental plots were measured at the end of the experiment. The heights of a subsample of differently sized shoots (*Banara*: $n = 22$; *Lacistema*: $n = 22$) were measured at 15 and 28 months The relationships between the two measurements (15 and 28 months) were linear over all shoot sizes and were described by linear regressions for each species and treatment (*Banara* control: $r^2 = 0.62$, complete fertilization: $r^2 = 0.91$; *Lacistema* control: $r^2 = 0.80$, complete fertilization: $r^2 = 0.87$; for all regression coefficients $p < 0.001$). The regression equations were used to calculate the height at 15 months of the remaining majority of shoots, which were measured only after 28 months. The biomass of *Banara guianensis* and *Lacistema pubescens* at 15 months was calculated on the basis of species-specific regressions from shoot height/wood biomass (*Banara*: $n = 52$, $r^2 = 0.68$; *Lacistema* $n = 25$, $r^2 = 0.51$; $p < 0.05$) and wood biomass/leaf biomass (*Banara* $n = 52$, $r^2 = 0.72$; *Lacistema* $n = 25$, $r^2 = 0.81$; $p < 0.01$).

Plant nutrient contents (N, P, K, Ca, Mg and Zn) were determined in maize and sorghum (aboveground plant parts) and in the leaves and wood of the secondary vegetation collected at the first and second biomass measurement. Mixed leaf samples of the secondary vegetation were taken according to the species' abundances and the distribution of leaf ages. Furthermore, the leaves were taken at random heights (Weetman & Wells 1990) and positions in the canopy (Driessche 1974). Wood samples included stem and branch material of representative diameter and bark fraction. P, K, Ca, Mg and Zn were determined after wet ashing with HNO_3-$HClO_4$ – mixture, whereas N was measured directly with a Carlo-Erba autoanalyser. Chemical analyses were carried out in the laboratory of the Faculty of Agricultural Sciences of Pará state (FCAP), Belém, Brazil. Analyses of duplicate samples for quality control, as well as the N analyses were carried out in the laboratory of the Institute of Agriculture in the Tropics, University of Göttingen, Germany.

As standard samples for the analyses served acetanylid and an internal standard material calibrated by a standard of the National Institute of Standards (NIST), Gaithersburg, MD (corn bran, Ref. No. 8433).

Soil samples were analyzed for pH (H_2O and KCl), total C and N, and extractable P and K (Mehlich I) and Ca, Mg and Al (KCl). Analyses were conducted at the Soil Laboratory of EMBRAPA Amazônia Oriental, Belém, Brazil, according to the methods described in EMBRAPA (1979).

Statistical analysis

All data were subjected to an ANOVA, in which the level of significance was defined at $p < 0.05$. The Tukey HSD test was used for multiple comparison of means. Data on grass biomass and grass cover, biomass of indicator crops and nutrient concentrations required logarithmic data-transformation before analysis. Treatment effects on the cumulative increase in stem height and diameter of the 7 species over a 24-weeks monitoring period were assessed by comparing the slopes of the linear regressions of repeated measurements (Mead et al. 1993).

Results

Indicator crops

Both maize and sorghum biomass increased markedly due to fertilization and confirmed that plant nutrient availability at the site was indeed limiting to sensitive crops (Figure 2). Crop biomass did not differ between burned and unburned controls. Evidently, nutrients in the residual ashes after burning of the slashed vegetation did not affect biomass production of the indicator crops planted 26 and 30 months after burning.

Crop biomass was increased approximately 6-fold by application of a full complement of nutrients, compared to the unfertilized controls. The minus-P treatment did not differ from the unfertilized controls. Biomass in the minus-N treatment was only 50% of that in the complete fertilizer treatment. No other nutrients were found to be limiting for the indicator crops, as their biomass in all other treatments was at the same level as the complete fertilizer treatment.

Plant nutrient concentrations confirmed the importance of P. Foliar P-levels in the treatments with P-fertilization were two- and fourfold greater than the control and minus-P treatments in maize and sorghum, respectively (Table 2). Tissue concentrations of all other nutrients analyzed (data not shown) were not affected by fertilizer treatments. The marked effects of

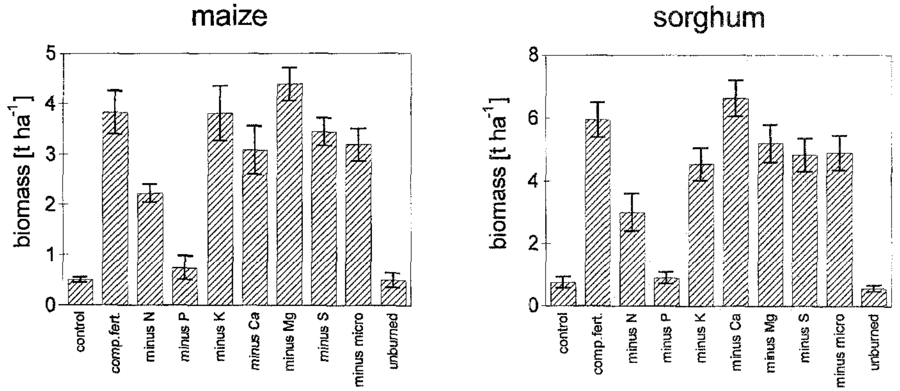

Figure 2. Aboveground biomass of the indicator crops maize and sorghum following fertilization (± SE).

Table 2. P-concentrations (g kg^{-1} ± SE) in the indicator crops and in 23-month-old regrowth after three fertilizer applications.

	maize	sorghum	secondary vegetation	
	(entire aboveground plants)		wood	leaves
control	1.1 (±0.12)	0.9 (±0.02)	0.3 (±0.04)	1.0 (±0.08)
comp. fert.	2.6 (±0.18)	3.1 (±0.38)	1.1 (±0.14)	1.6 (±0.10)
minus N	2.9 (±0.17)	3.3 (±0.45)	1.2 (±0.28)	1.2 (±0.12)
minus P	1.4 (±0.13)	0.8 (±0.02)	0.4 (±0.06)	0.9 (±0.06)

P-application on both tissue P-concentrations and crop growth, combined with no treatment-induced differences of tissue concentration of other nutrients, suggest that P-availability controlled the extent to which the other nutrients are exploited by the crops.

Secondary vegetation

The biomass of the 15-month-old secondary vegetation was not affected by the initial fertilization (Figure 3). On the contrary, the biomass of the woody vegetation was slightly lower in the complete fertilizer treatment, due probably to an increased dominance and persistence of the grassy vegetation. Two additional fertilizer applications enhanced biomass accumulation, particularly of the woody component. Grasses were suppressed and dead biomass – consisting largely of grass – declined substantially. After 28 months, wood, leaf, and total biomass were significantly higher in the complete fertilizer treatment than in the control and the minus-N and minus-P treatments.

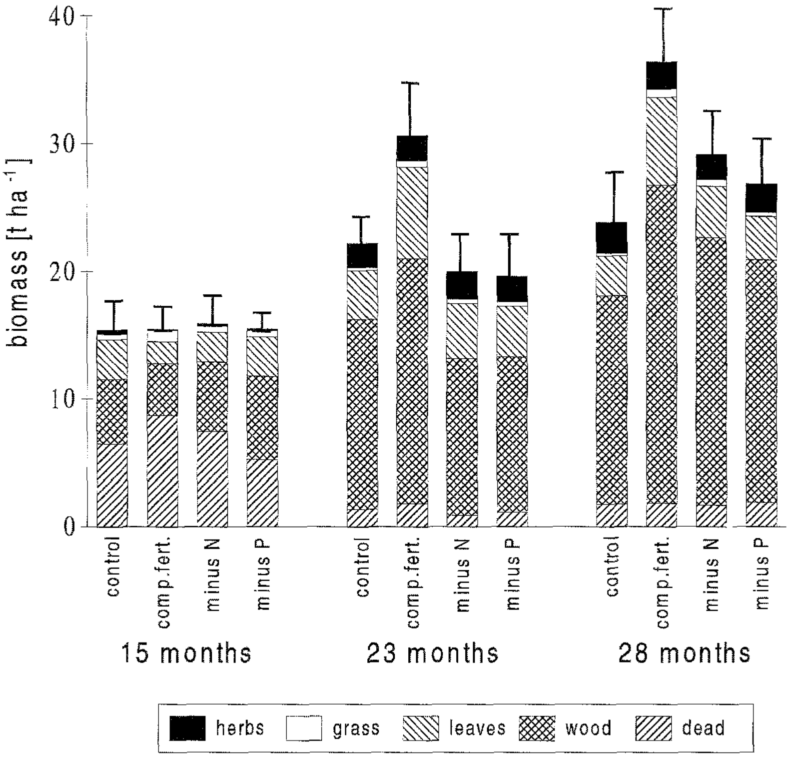

Figure 3. Biomass of the secondary vegetation after 15, 23 and 28 months of regeneration (bars represent one SE of total biomass).

The increase of living biomass following the initial successional stage (i.e., after 15 months) was significantly enhanced by complete fertilization. Living biomass increased 30.0 t ha^{-1} in the complete fertilizer treatment, compared to 13.9 t ha^{-1} in the unfertilized control and 19.7 and 18.3 t ha^{-1} in the minus-N and minus-P treatments, respectively. The proportional increase in living biomass was similar for the minus-P and control treatments (193 and 167%, respectively), compared to a relative increase of 540% for the complete fertilizer treatment. The increase of the minus-N treatment (329%) was not statistically different from the control or the complete fertilizer treatments. Omission of K, Mg, Ca, S and the micronutrients did not lower the production of living biomass of secondary vegetation compared to the complete fertilizer treatment.

Widening wood-leaf ratios with succession are typical for the development of woody vegetation (Schulze & Chapin 1987). A full complement of nutrients retarded this process in favor of leaf biomass, as reflected in the

Table 3. Wood-leaf ratio in the secondary vegetation (± SE).

	15 months	28 months
control	1.6 (±0.15)	5.6 (±0.57)
comp. fert.	2.7 (±0.50)	3.8 (±0.50)
minus N	2.8 (±0.61)	6.9 (±1.76)
minus P	2.4 (±0.34)	6.9 (±1.02)

significantly lower wood-leaf ratios in the plots given a complete fertilization than in the control (Table 3).

Nutrient concentrations in the secondary vegetation reflected those in the indicator crops, responding to P application with threefold higher P in the wood and 50% higher P in the leaves (Table 2). The other nutrient levels were not affected by fertilizer treatments.

Grass

The initial floristic survey in the experiment conducted in 1993 prior to the initial fertilization showed that the burned plots had only half the cover of woody species (31%) than did the nonburned treatment (59%) (Clausing 1994). The reverse was true for the grass cover, dominated by *Imperata brasiliensis* Trin. and *Paspalum melanospermum* Desv. After 28 months of regeneration, *Imperata brasiliensis* accounted for 66% of the grass cover and 52% of the grass biomass. Although grasses had been present in the area before burning, their growth may have responded to the residual nutrients in the ashes. This effect, however, was lost after 15 months of regrowth, when burned and unburned controls did not differ (Table 4). Fertilizer apparently stimulated the growth of grass and prolonged its persistence. The average grass cover was significantly higher in the treatment fertilized with a full complement of nutrients than in the unfertilized controls both at 15 months and at final biomass determination (after 28 months). Grass coverage of the minus-N and minus-P treatments fell in between. The large stocks of dead biomass after 15 months (Figure 3) were largely due to slowly decomposable grass.

Species' responses

Seven second growth species were monitored in this study under conditions of competition with changing neighboring species. They responded differentially to fertilization both in their growth rates and the nutrients limiting

Table 4. Estimated grass cover (% ± SE).

	15 months	28 months
burned control	10.3 (±3.5)	6.9 (±2.3)
unburned control	10.0 (±4.0)	7.5 (±3.1)
comp. fert.	40.3 (±13.0)	28.1 (±9.2)
minus N	24.1 (±9.2)	15.9 (±6.7)
minus P	20.9 (±8.2)	15.0 (±6.8)

their growth. Fertilizer response clearly differed among the control, minus-P, minus-N, and complete fertilizer treatments (Figure 4). In the remaining treatments (not shown in Figure 4) the species behaved similarly to the complete fertilizer treatment. Height growth (data not shown) behaved similarly to the diameter growth. No treatment-induced differences in height/diameter ratios were detected.

Comparing the treatment-specific response patterns (slopes of the linear regressions) in increase in diameter of individual species reveals that the primary limiting nutrient varied among species (Figure 4). *Phenakospermum guyannense* and *Rollinia exsucca* were apparently neither N- nor P-limited and responded to minus-N, minus-P and complete fertilizer treatments by significantly increasing both diameter and height growth. Other nutrients such as K or micronutrients or the combination of different nutrient deficiencies could have been limiting for these species. *Lacistema pubescens* and *Vismia guianensis* were primarily N-limited whereas the leguminous species *Inga macrophylla* was limited by P-availability. The myrmecophytic *Cecropia palmata* showed little response to additional nutrients, while *Banara guianensis* responded significantly to both N and P.

Shifts in species' contribution to total biomass

The share of *Banara guianensis* and *Lacistema pubescens* in total biomass did not differ between treatments after 15 months, but two additional fertilizer applications caused differing growth reactions of the two species resulting in different contributions to total biomass after 28 months (Table 5). Complete fertilization favored the dominance of the vigorously responding *Banara guianensis*, whereas its contribution decreased in the unfertilized control. In contrast, the biomass contribution of *Lacistema pubescens* remained constant in the control but decreased in the complete fertilizer treatment, presumably due to competitive pressure.

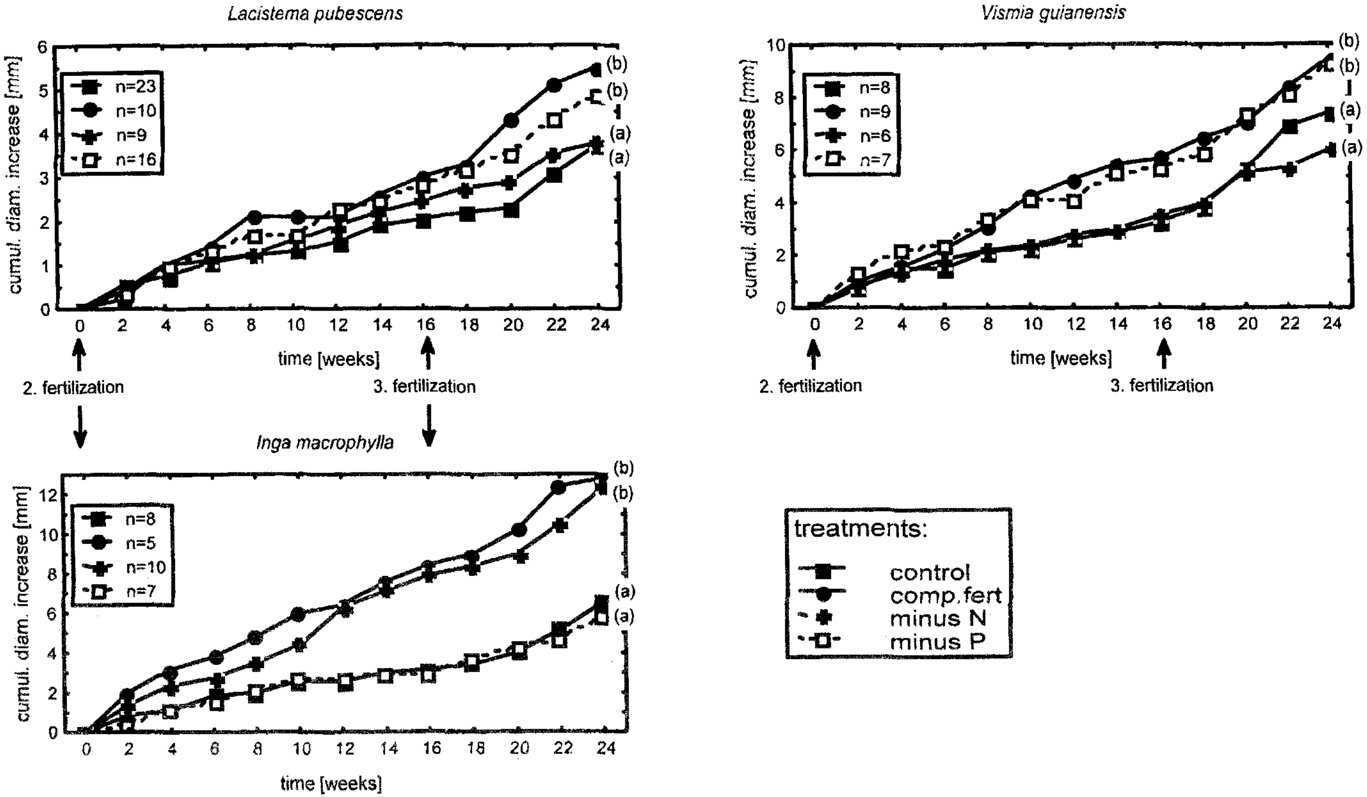

Figure 4. Cumulative diameter increase of selected species in the secondary vegetation following the second and including the third fertilizer application. Letters refer to differences in slopes between treatments (linear regressions of growth), numbers are the quantity of plant individuals measured in each treatment.

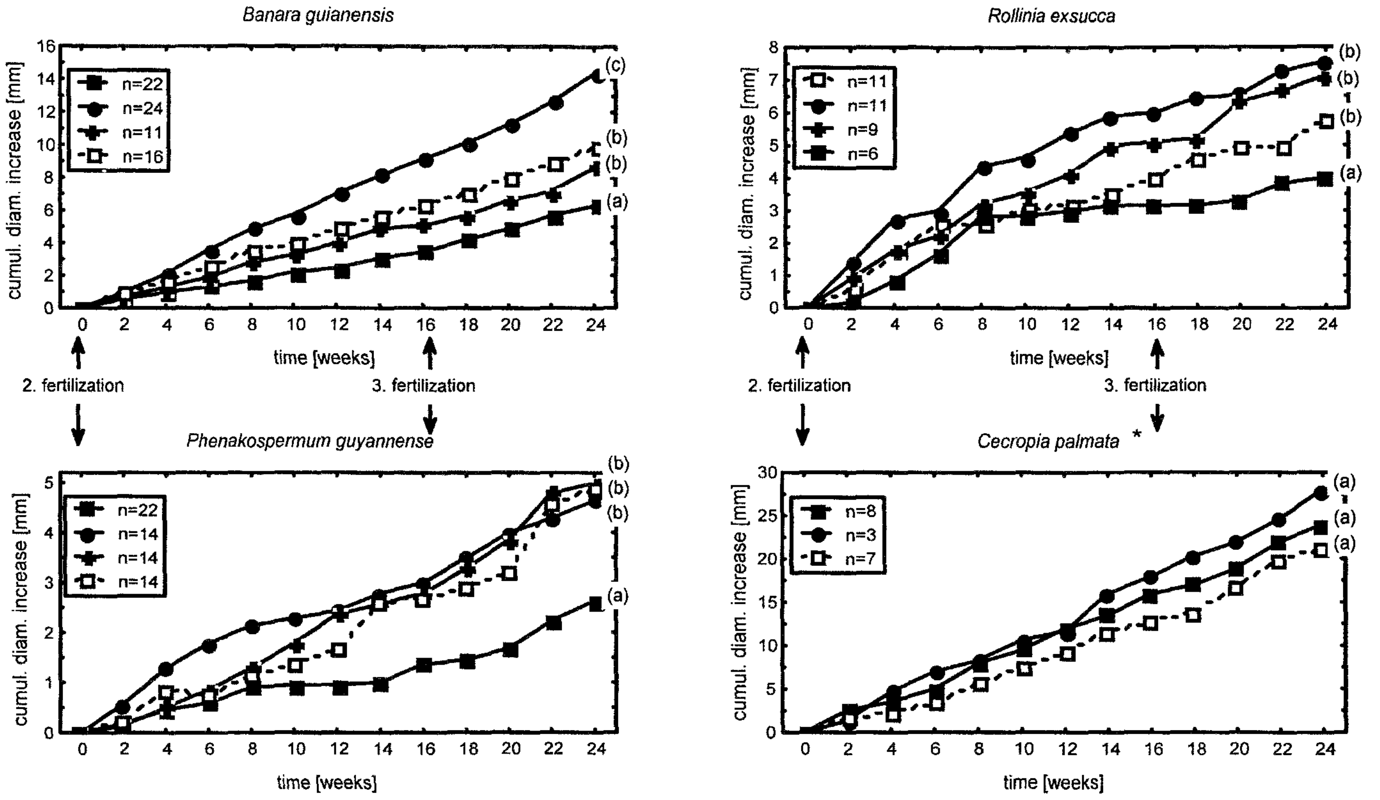

Figure 4. Continued. * minus-N treatment of *Cecropia palmata* omitted because of insufficient number of individuals due to irregular occurrence.

Table 5. Relative biomass contribution of *Banara guianensis* and *Lacistema pubescens* (average of 8 replications; % ± SE of total living biomass) after 15 and 28 months.

	15 months		28 months	
	control	comp. fert.	control	comp. fert.
Banara guianensis	38 ± 11	39 ± 11	19 ± 6	47 ± 6
Lacistema pubescens	11 ± 3	8 ± 4	12 ± 4	4 ± 2

Discussion

The results of this study indicate that the regeneration of secondary vegetation in the humid tropics on nutrient-poor soils may be limited by nutrient availability. Our results contrast with those reported from the fertilizer experiments conducted by Harcombe (1977) on relatively fertile volcanic soils in Costa Rica and by Uhl (1987) on an Oxisol in Venezuela. Inherent differences in soil nutrient status or vegetation composition may explain the absence of biomass increases after fertilization in these studies. Another explanation could be restricted monitoring times (Uhl 1987: 0.5 y and Harcombe 1977: 1 y). In a Venezuelan montane forest, Tanner et al. (1992) found an increased growth in tree diameter, increased litterfall and tissue nutrient concentrations only when N and P fertilizer treatments were compared with a control over 3–4 years, underlining the need of sufficient monitoring times in ecological studies.

After 28 months and three fertilizer applications, biomass of the secondary vegetation was significantly higher than in the control treatments, in spite of the high variability encountered in the naturally heterogeneous vegetation. Following the initial successional stage (i.e., 15–28 months), P was the major limiting nutrient for biomass production. An effect of N-application on increase of living biomass in this period could not be confirmed statistically, as the minus-N treatment took an intermediate position compared to the control and complete fertilizer treatments. A possible explanation for the limited response to N may be atmospheric N_2-fixation.

Aside from site-specific differences, the type and degree of nutrient constraints are likely to undergo changes during secondary succession (Ewel 1986). The rate of root development could initially influence the relative accessibility of N and P, due to the different mobility of nitrate and phosphate (Peace & Grubb 1982). However, high root length densities of the initial grass and weed vegetation as well as of trees and shrubs which survived the slash-and-burn and the cropping period (Wiesenmüller et al. 1996) should ensure sufficient access to soil volume at the time of field abandonment. In the Bragantina region, P appears to be the main limiting nutrient and N appears to be limiting only to a minor extent. Establishing the actual importance of N- and P-limitations in secondary successions and their possible interactions is of considerable practical importance and requires further research.

Fertilization led to nutrient-rich leaf biomass. Similar responses have been observed by Harcombe (1977) and in many other fertilization experiments (Schulze & Chapin 1987). An increased production of nutrient-rich leaf biomass is expected to result in an accelerated rate of nutrient cycling. Herbivores, particularly insects, might respond to the nutrient-rich foliage with its improved food quality. Especially the N content is known for its beneficial effects on herbivore activity. The overall benefits of increased plant-tissue N for herbivores as well as the consequences for the plant community are not yet fully understood (Hartley & Jones 1997).

The observed increase in grass dominance after fertilization agrees with the findings of Harcombe (1977) and Uhl (1987) and is frequently encountered in fertilizer experiments (DiTommaso & Aarsen 1989). The disproportionately strong growth response to nutrient pulses is probably due to the dense network of grass roots in the topsoil. Possibly, physiological advantages of graminoid roots gave grasses a further competitive edge over slower reacting woody species (Mouat 1983). Application of readily soluble nutrients thus may have retarded succession and initially exerted a counterproductive effect on the accumulation of woody biomass. However, along further successional development and with two more fertilizer applications, the completely fertilized vegetation apparently more than compensated for the early suppression caused by grassy competition.

Different growth responses to fertilization among the woody species of the secondary vegetation are caused by different mechanisms and rates of nutrient acquisition. The importance of the key nutrients N and P, for instance, differed markedly among species. Phosphorus did not limit growth of *Lacistema pubescens* and *Vismia guianensis* which might indicate efficient mycorrhizal associations. In contrast, the leguminous *Inga macrophylla* apparently was adequately supplied with N through symbiotic biological nitrogen fixation, which in turn was presumably P-limited.

The extent of growth responses to additional nutrients also varied among the species studied. The limited response to applied nutrients, as observed with *Lacistema pubescens* and *Vismia guianensis*, is a typical feature of plants that are well adapted to nutrient-poor environments (Chapin 1980). Fertilization increased the biomass contribution of *Banara guianensis*, capable of responding to additional nutrients by substantially accelerating growth. On the other hand, a continuing depletion of nutrients in the agro-ecosystem is likely to alter species' composition of fallow vegetation in the long run as well. The prevailing short fallow periods have been shown to be insufficient for complete recovery of nutrient stocks lost by burning and cultivation (Hölscher et al. 1997). This could favor species well adapted to low nutrient availability, such as *Lacistema pubescens*. Little is known about the role species diversity in secondary vegetation plays in nutrient dynamics (Ewel et al. 1991).

It is widely accepted that seed bank, seed dispersal and germination rates (Kellman 1980; Uhl et al. 1981), as well as microclimate (Unruh 1988) and, in vegetatively regenerating systems, the root systems (Wiesenmüller et al. 1996) influence regeneration dynamics of secondary vegetation. Our research suggests that regeneration of a secondary vegetation can also be limited by nutrient availability, and that this should be considered in the management of fallows in rotational cultivation systems.

It is doubtful that farmers would adopt fertilization as a fallow management practice alone, due to fertilizer costs (in our experiment, each additionally produced ton of biomass per hectare over the control cost approximately US$ 46, taking only urea and triple superphosphate into consideration; Denich et al. in press). The most promising option is the development of non-burning land-use systems, thereby drastically reducing nutrient losses. Hölscher et al. (1997) estimated the losses to the atmosphere caused by burning of secondary vegetation at 96% and 47% of the aboveground N- and P-stocks, respectively. The combination of mulching as land preparation and (rock) phosphate application in the cropping period, with possible residual effects for the subsequent secondary vegetation, could be a feasible strategy for optimizing the regeneration of secondary vegetation.

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