

Substrate conditions, foliar nutrients and the distributions of two canopy tree species in a Costa Rican secondary rain forest

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Abstract

A 28 yr old secondary lowland rain forest in Costa Rica was dominated by two tree species of contrasting ecologies, *Vochysia ferruginea* - a species typical of well-drained but infertile soils of high Al saturation, and *Cordia alliodora*, a species requiring soils of at least moderate fertility. The two species exhibited markedly different spatial distributions in the forest and we sought to determine whether or not these different distributions were related to variation in substrate conditions and the nutrient requirements of the two species. Two soil types were present: ultisols (Typic Haplohumults) and inceptisols (Typic Dystropepts) and topography was of low hills. The study formed part of an analysis of site quality for timber production in the two species and therefore used standard forestry methods for such analyses. 36 plots of 20 m×20 m were established using predetermined criteria of site uniformity, presence of at least four dominant trees of at least one of the study species, and absence of disturbance. The abundance (number of individuals ≥ 10 cm dbh) of each species was determined in each plot. Soil samples were taken in 27 of the 36 plots, 9 plots being considered to replicate conditions already sampled, and 14 soil chemical and physical variables were measured using standard methods. Foliar nutrient analyses were carried out for trees of both species with crowns fully exposed to sunlight, distributed across the gradient of soil conditions. Variations in species abundances were not related to soil type, but plots in which *Vochysia ferruginea* was more abundant tended to be on steeper slopes with soils of higher exchangeable acidity and lower concentrations of Mn; *Cordia alliodora* was more abundant on gentler topography where soils had much lower exchangeable acidity but higher Mn. Differences between the two species in foliar nutrient concentrations were marked and supported previous interpretations of their nutrient requirements; foliar nutrients of *Vochysia ferruginea* were typical of tree species of moist tropical forest on infertile soils, and those of *Cordia alliodora* typical of a species requiring more fertile soils. Factors such as the distributions of seed trees at site abandonment may affect the spatial distributions of tree species in secondary forests such as that studied. The relationships of the distributions of the two species to substrate variation, however, and their evidently different nutrient requirements, support the hypothesis that variation in the composition and structure of the forest studied is at least partially related to exchangeable acidity and its dominant cation, Al.

Introduction

The enormous plant species richness of tropical moist forests, and the consequent local scarcity of many of those species, made relationships between substrate conditions and vegetation difficult to detect for ear-

ly students of tropical vegetation. Though marked and often predictable compositional variation in old-growth tropical moist forests has now been demonstrated and linked to variation in substrate conditions in many studies (e.g. Basnet, 1993; Clark et al., 1995; Hartshorn and Hammel, 1994; Lescure and Boulet, 1985; Lieberman et al., 1985; Richards, 1976; Steege

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et al., 1993; Whitmore, 1984), understanding of the causes of this variation and the different spatial scales at which it may be evident is still very incomplete (Clark et al., 1995).

The information base concerning the effects of substrate on the composition of secondary forests growing on abandoned agricultural land is, in many ways, still more incomplete. Most studies of the effect of site conditions on community characteristics of secondary forests concern young vegetation (< 10 yr after land abandonment) and emphasise between-site comparisons, often in relation to different types and intensity of site use (e.g. Uhl, 1987; Uhl et al., 1981, 1988). As far as within-site vegetational heterogeneity is concerned, attention has been focused to some extent on the fates of seeds and seedlings. Species rich vegetation patches may be generated around remnant trees in pastures, as these serve as perches and food sources for fruit-eating birds and bats which drop or defecate seeds (Guevara et al., 1986; Guevara and Laborde, 1993; see also Janzen, 1988). On recently abandoned subsistence farms, microsites in which seeds are hidden from their predators or seedlings protected from insolation may show denser regeneration, of different species, than those which are more exposed (Hammond, 1995; Uhl, 1987). There is no reason why substrate conditions within secondary vegetation should not be as variable as those within old-growth forests and have similarly important effects on vegetation characteristics. Little information is available on this aspect of the ecology of secondary forests, however. In an isolated study, Lacoste (1991) found that variation in soil drainage conditions in young secondary vegetation in French Guyana did not affect the structure and dynamics of populations of two canopy tree species, even though the distributions of tree species in the old-growth forests of the same area vary significantly in relation to the same soil gradient (Lescure and Boulet, 1985).

In this paper, we report on a study of the variation of topography and soil, and its relationship to the distributions; and abundances of two dominant tree species, *Vochysia ferruginea* Mart. (Vochysiaceae) and *Cordia alliodora* (Ruiz and Pavón) Oken. (Boraginaceae), in a secondary rain forest in northern Costa Rica. Both *V. ferruginea* and *C. alliodora* are large, long lived pioneer tree species (species which, like classic pioneers such as *Cecropia* and *Ochroma*, may quickly colonize disturbed areas, but which reach much larger sites and live much longer than the classic pioneers; see Finegan 1992, 1996; Finegan and Sabogal, 1988) and have

wind-dispersed seeds. Both species have wide geographical distributions, though their soil preferences and nutrient requirements are clearly different. Thus *V. ferruginea* is distributed from Nicaragua to Peru and Brazil and *C. alliodora* is found throughout the American tropics (Croat, 1978). *V. ferruginea* is an occasional canopy tree in old-growth forests, particularly associated with less fertile soils of slopes and hilltops (Hartshorn and Poveda, 1983; Montagnini and Sancho, 1994; Pérez et al., 1993) and is common in secondary forest (Finegan, 1992). *C. alliodora*, though it may occur (or may have occurred) in old-growth on fertile alluvial terraces (e.g. Hartshorn and Hammel, 1994), is best known as an invasive species of areas heavily disturbed by human activity. It requires soils of at least moderate fertility (Greaves and McCarter, 1990; Johnson and Morales, 1972). Both species are commercially important in Costa Rica.

The forest at our study site is under management for sustainable production of timber and the initial forest inventory of the site showed that the two study species, though coexisting throughout the forest, reached dominance in different sectors of it (Guillén, 1993). The work reported here was carried out in the context of a wider study of site quality and productivity in this forest (Herrera, 1996) and aimed to determine whether or not the different distributions of the two principal species were related to nutrient requirements and substrate variation.

Materials and methods

Study site

The study was carried out in Florencia de San Carlos, Alajuela Province, Costa Rica, in Holdridge's tropical wet forest life zone (Tosi, 1969). Altitudinal range within the secondary forest is 280 - 360 metres above sea level. There is no meteorological station at the site and the nearest in the same life zone, Quebrada Azul (7 km north of Florencia but at only 83 m.a.s.l.) reports a mean annual precipitation of 3,300 mm and a mean annual temperature of 28 °C (Herrera, 1996). The secondary forest was 28 years old at the time of the study, the site having supported pasture for the grazing of horses for a short period (A. Riggioni, personal communications). The forest covers 32.5 ha of hilly terrain with occasional streams and slopes of 15-60%. It is long and narrow, not more than 300 m wide and some 1400 m long, this longest axis running approximately

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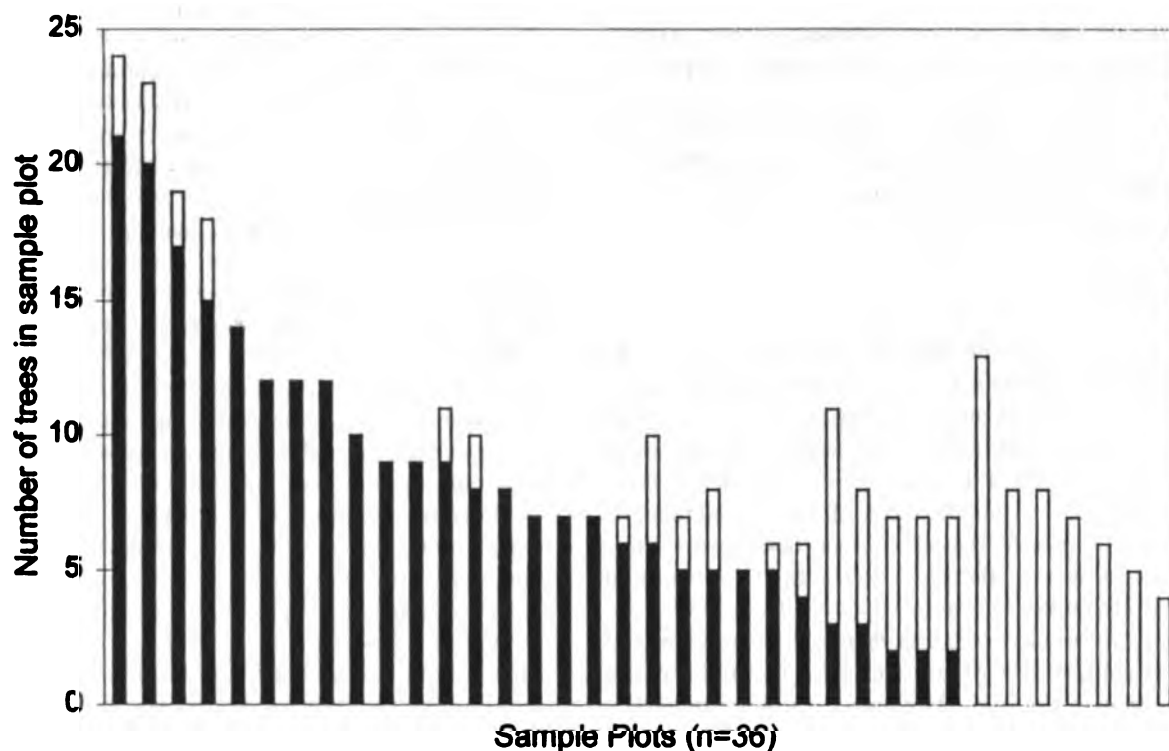


Figure 1. Map of the secondary forest study site, Florencia de San Carlos, Alajuela Province Costa Rica showing distribution of soil types and 20 m x 20 m sample plots. Soils are ultisols (Typic Haplohumult) to the left of the trail which crosses the western part of the forest in a north-south direction (consociation codes Qb-), and inceptisols (Typic Dystropept), mainly to the right of the trail which is indicated by parallel dashed lines (consociation codes Cr-). Lines of alternate dots and dashes indicate streams in narrow, steep-sided valleys. *Vochysia* plots (see Figure 2) open, *Cordia* plots hatched.

Table 1. Characteristics of representative profiles of the two soil types in the secondary lowland rain forest study site, northern Costa Rica, 28 years after abandonment of pasture (Vásquez, 1994)

Horizon (thickness in	Typic Dystropept				Typic Haplohumult			
	A (0-12)	Bw (12-31)	Bt1 (31-59)	Bt2 (59-169)	A (0-12)	Bw (12-26)	Bt1 (26-52)	Bt2 (52-112)
Organic matter (%)	6.92	2.16	1.3	0.43	12.1	3.5	1.7	1.3
pH (H ₂ O)	4.7	4.5	4.5	4.7	5.9	5.3	5.0	5.3
Ca (cmol L ⁻¹)	1.2	1.0	0.8	0.7	4.8	2.4	1.8	2.2
Mg (cmol L ⁻¹)	1.0	0.6	0.4	0.4	2.0	1.2	0.8	0.9
K (cmol L ⁻¹)	0.29	0.10	0.06	0.10	0.18	0.10	0.08	0.09
Al (cmol L ⁻¹)	0.85	1.55	1.60	1.60	0.25	0.35	0.30	0.20
CEC (cmol L ⁻¹)	3.24	3.25	2.66	2.80	7.23	4.05	2.28	3.29
Base saturation (%)	17.6	7.2	8.7	7.6	47.3	20.1	17.7	21.7
Al saturation (%)	26.2	47.7	55.9	57.1	3.45	8.64	13.2	6.07
P (μg mL ⁻¹)	6.0	5.0	5.0	6.0	4.0	5.0	6.0	5.0
% sand	24.4	19.4	23.4	15.4	55.4	25.4	20.0	21.4
% silt	38.6	62.6	56.6	48.6	24.6	46.6	23.8	19.8
% clay	34.0	18.0	20.0	36.0	20.0	28.0	52.8	58.8

east to west (Figure 1). It is adjoined on its upper (northern) side by disturbed old-growth forest and cultivated land, and on its lower (southern) side by pasture. Soils are inceptisols (Typic Dystropepts), the predominant soil type at the site, and ultisols (Typic Haplohumults) located in the western sector of the site; both soil types originate from volcanic mudflows (Vásquez, 1994). Details of soil characteristics, as determined by Vásquez (1994), are presented in Table 1.

Sampling

A total of 36 sample plots of 20 m × 20 m were established for this study. In keeping with recommendations for studies of site quality (Carmean, 1975), these plots were established using predetermined criteria, which were: sampling of the complete gradient of soil conditions present within the site; uniform soil and topography within each 20 m × 20 m plot (both the preceding criteria were applied by reference to the soils map of the site (Vásquez, 1994) as well as by field observation); no evidence of disturbance to the plot; at least 4 dominant trees of at least one of the study species present in the plot (dominant trees were defined as individuals whose crowns formed part of the upper canopy of the stand and were fully illuminated from above). As approximately half the total forest area was subjected to an experimental thinning in 1994, this was not available for the study by the "no disturbance" criterion; within the thinned area, however, some plots were located within four 80 m × 100 m unthinned stands established as controls for the thinning experiment. Further limitations to the area to be sampled were imposed by the decision to sample only that part of the forest available for timber production under current Costa Rican forestry law, which meant excluding all areas of slope > 50° or within 20 m of permanent or seasonal water courses.

We analysed the abundances of the two study species in the 36 sample plots in relation to variation in soil conditions. The number of individuals ≥ 10 cm dbh (diameter at breast height, 1.3 m) of each species was determined in each sample plot. Soil samples were taken at two depths, 0-12 cm and 12-30 cm, in 27 of the 36 plots, it being considered that the 9 plots not sampled duplicated soil conditions sampled in other plots. Soil analysis was carried out in the laboratory of the Centre for Agricultural Research (CIA) at the University of Costa Rica in San Jose, Costa Rica, using standard methods (Henriquez et al., 1995). pH was determined in water with a potentiometer. P, K,

Fe, Cu, Zn and Mn were extracted with a modified Olsen solution, Ca and Mg by 1 M KCl and S and B with a calcium phosphate solution. P and B were determined colorimetrically, S by turbidity and other elements by atomic absorption spectrophotometry. Exchangeable acidity was determined using 1 M KCl as a neutral solution and titrating with 0.01 M NaOH, organic matter by the method of Walkley and Black and soil texture by Bouyoucos' method.

Foliar nutrient analyses were also carried out. Living mature foliage, fully exposed to sunlight, undamaged and without apparent symptoms of disease, was collected from the upper part of the crowns of individuals of both species whose crowns were fully exposed to light from above, or emergent from the forest canopy. Trees sampled were distributed across the gradient of soils conditions (*V. ferruginea*, $n = 46$; *C. alliodora*, $n = 13$). Nutrient analysis was carried out in the soils laboratory at CATIE as follows (Henriquez et al., 1995): samples of 100-300 leaves per tree were washed in distilled water and dried in an oven at 70 °C and ground.

Samples were then digested, moist, in a nitroperchloric mixture from which a concentrate for nutrient analysis was obtained. Ca, Mg, K, Mn, Cu, Fe, Zn and Al were determined from this concentrate by atomic absorption spectrophotometry, while P was determined colorimetrically.

Statistical comparisons of soil conditions between groups of sample plots, and of foliar nutrient concentrations between the two species, were made by the non-parametric Mann-Whitney test on untransformed data.

Results

Soil conditions and species abundances

In 24 of the 36 sample plots, *V. ferruginea* was the more abundant of the two species in terms of the number of individuals ≥ 10 cm dbh; *C. alliodora* was absent from 12 of these 24 plots (Figure 2). In the 12 remaining plots, *C. alliodora* was the most abundant species, *V. ferruginea* being absent from 7 of these 12 plots. From here on, the 24 plots with greater abundance of *V. ferruginea* are referred to as the *Vochysia* plots, while those with greater abundance of *C. alliodora* are referred to as the *Cordia* plots.

Dominance by either species was not related to the distributions of the two soil taxonomic types: four *Cordia* plots and four *Vochysia* plots were located on Hap-

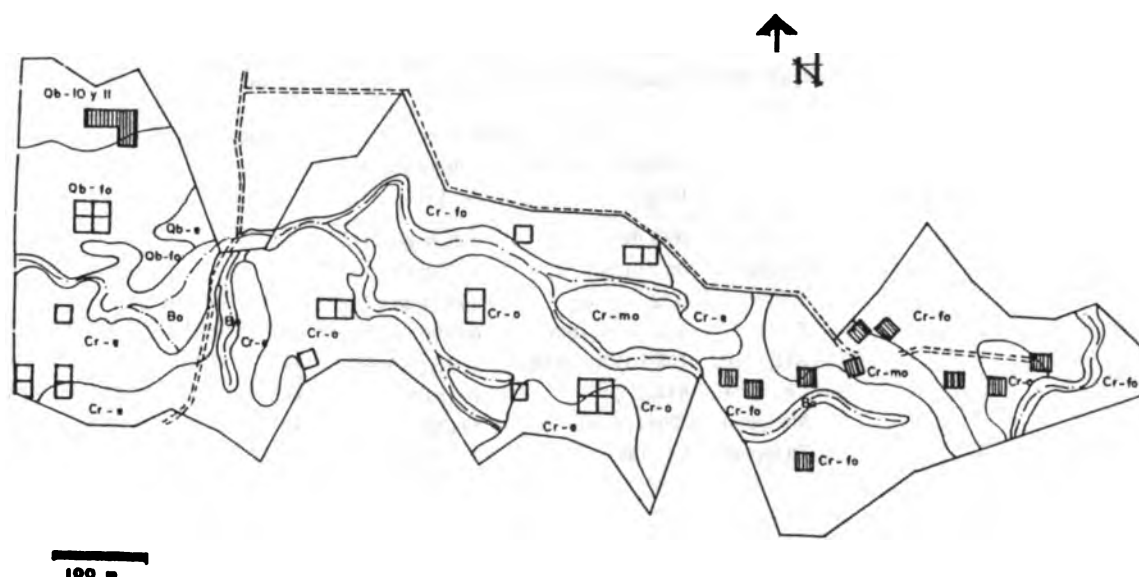


Figure 2. Abundances (all individuals ≥ 10 cm dbh) of two dominant species in 36 sample plots of 20 m \times 20 m in a secondary lowland rain forest of northern Costa Rica, 28 years after abandonment of pasture: filled bars *Vochysia ferruginea*, open bars, *Cordia alliodora*. Plots are arranged from left to right in descending order of abundance of *V. ferruginea*. The first 24 plots, for purposes of this paper, were considered to be dominated by the latter species (*Vochysia* plots) and the remaining 12 to be dominated by *C. alliodora* (*Cordia* plots); see text for further details.

Table 2. Soil properties (values given are medians, ranges are in parentheses) associated with dominance by *Vochysia ferruginea* (*Vochysia* plots) or *Cordia alliodora* (*Cordia* plots) in a secondary lowland rain forest of northern Costa Rica, 28 years after abandonment of pasture. Six other variables which did not show significant differences are not shown (see text). Significant differences (Mann-Whitney test): *, $p < 0.05$, **, $p < 0.01$

Soil variable	<i>Vochysia</i> plots (n=16)	<i>Cordia</i> plots (n=11)	p difference
Slope (%)	32 (20-47)	14 (3-33)	**
Acidity (cmol (+) L ⁻¹ ; 0-12 cm)	0.6 (0.3-1.12)	0.3 (0.14-0.93)	*
Acidity (cmol (+) L ⁻¹ ; 12-30 cm)	1.2 (0.6-1.99)	0.6 (0.14-1.21)	**
Cu (mg L ⁻¹ ; 0-12 cm)	26 (18.1-33.4)	30 (22.7-41.4)	*
Mn (mg L ⁻¹ ; 0-12 cm)	49 (14.4-123)	103 (40.6-197)	*
% sand (0-12 cm)	26 (18-41)	33 (25-36)	*
% clay (0-12 cm)	56 (44-66)	52 (44-60)	*
% clay (12-30 cm)	61 (42-72)	54 (48-71)	*

lohumults, and the 28 remaining plots - 20 *Vochysia* and eight *Cordia* - were all on Dystropepts (Figure 1). We therefore lumped plots from the two soil types for analysis, comparing values of soil and topographic variables between the two groups of plots for which soil samples were taken (16 *Vochysia* plots, 11 *Cordia* plots). Differences between plots were statistically significant for 8 of the 14 variables measured (Mann-Whitney test, $p < 0.05$; Table 2) though in some cases they were small. The principal differences, which in

general conform to expectations derived from knowledge of the ecology of the two species (see Introduction), may be summed up as follows (see Table 2): *Vochysia* plots tended to occur on steeper slopes, median slope at 32% being more than twice that for *Cordia* plots (it may be noted on Figure 1 that most of the *Cordia* plots occurred together in the eastern part of the forest; this is where the topography was gentlest). Soil of the *Vochysia* plots had considerably greater

Table 3. Foliar nutrient concentrations (values given are medians ranges are in parentheses) of two dominant tree species in a secondary lowland rain forest of northern Costa Rica, 28 years after abandonment of pasture. Significant differences (Mann-Whitney test): *, $p < 0.05$, **, $p < 0.01$

	Foliar concentration		<i>p</i> difference
	<i>Vochysia ferruginea</i> (<i>n</i> =46)	<i>Cordia alliodora</i> (<i>n</i> =13)	
Ca(%)	0.52 (0.24-0.88)	1.46 (1.00-2.60)	**
Mg(%)	0.14 (0.06-0.28)	0.57 (0.38-0.86)	**
K (%)	0.32 (0.22-0.50)	2.09 (1.44-2.62)	**
P (%)	0.06 (0.05-0.08)	0.21 (0.11-0.36)	**
Al (ppm)	12800 (7300-16600)	160 (120-320)	**
Cu (ppm)	8 (4-12)	19 (10-36)	**
Mn (ppm)	326 (126-566)	29 (20-52)	**
Zn (ppm)	6 (2-14)	33 (22-64)	**

exchangeable acidity than those of the *Cordia* plots, at both soil depths, and had lower concentrations of Mn.

Foliar nutrients

Although among soil nutrients only Mn and Ca showed significantly different values on comparing *Vochysia* plots and *Cordia* plots, there were very marked differences between the two species in the nutrient concentrations of foliage. Thus Ca, Mg, P, K, S, Cu and Zn were found in significantly greater concentrations in foliage of *C. alliodora* than in that of *V. ferruginea*, while only potentially toxic elements - Al and Mn - were found in greater concentrations in foliage of *Vochysia* than in that of *Cordia* (Table 3). Applying the criterion that foliar Al levels > 1,000 ppm indicate accumulation of that element (Foy et al., 1978), the levels of Al in foliage of *V. ferruginea* are more than sufficient for the species to be classified as an accumulator at the Florencia site; the levels of Mn may indicate that this element is being accumulated as well (Alfredo Alvarado, personal communication). It is notable that foliar Mn was highly significantly lower in *Cordia* than in *Vochysia*, even though Mn levels in soil were significantly higher in *Cordia* plots than in *Vochysia* plots.

Discussion

The exact mechanisms which underlie the markedly different spatial distributions of *Vochysia* and *Cordia* at the Florencia site would have to be determined by

experiment; studies such as ours may only generate hypotheses (Greig-Smith, 1983). Experiment would have to take into account the individual reactions of each species to substrate variation, their reactions when grown in mixture with interspecific competition (Harper, 1977) and factors other than substrate which may generate the different spatial distributions observed. Differential seed dispersal may be particularly important in this latter respect. This is especially so given that *C. alliodora* and *V. ferruginea* are wind-dispersed, a mechanism which even in the most favourable climatic conditions, tends to generate seed shadows close to, and largely downwind of parent trees (e.g. Harper, 1977, Chapter 2; Janzen, 1988). The dominance of the eastern sector of the forest by *C. alliodora* and the western by *V. ferruginea* could, therefore, be a consequence of the distribution of seed trees at site abandonment, and the relationship of this spatial pattern of dominance to substrate conditions coincidental.

It nevertheless seems clear that the two species have strikingly different nutrient requirements. Work in forest plantations and agroforestry systems shows that *C. alliodora* is highly demanding with respect to macronutrient and intolerant of Al (Bergmann et al., 1994; Greaves and McCarter, 1990). *V. ferruginea*, on the other hand, appears clearly fitted for successful regeneration and fast growth on infertile acid soils of high Al saturation (Montagnini and Sancho, 1994; Pérez et al., 1993). The hypothesis that their spatial distributions are in some way related to substrate variation therefore requires examination.

There was no apparent relationship of species distributions to soil type, but we find this unsurprising.

The diagnostic horizon for differentiation between an ultisol and an inceptisol in tropical soil is usually between 25 and 125 cm soil depth (Baillie, 1989) as was the case in the present study (Table 1). This is below the depth of greatest concentration of roots at the Florencia site (which is why soil samples were taken to a depth of 30 cm) so that it seems unlikely that the factors used in the US Soil Taxonomy to differentiate the two soil types are the same as those to which these two species respond ecologically at the study site. On the other hand, species distributions did show relationships to the values of individual substrate factors. The differences found between plots dominated by *V. ferruginea* and plots dominated by *C. alliodora* were nevertheless small, except in the cases of Mn, slope and acidity. Mn is known to accumulate in level areas within hilly topography (Buol et al., 1989), which may be the reason for its greater presence in the gentler topography of the *Cordia* plots; it does not appear likely that this factor affects the distribution of either species, especially as *C. alliodora* showed lower foliar Mn than *V. ferruginea*, in spite of the greater soil Mn in *Cordia* plots. Slope may have affected species distributions only to the extent that it is correlated with other soil factors which show a more direct relationship to plant nutrition. One of these factors is exchangeable acidity which, it is suggested, may be the key to understanding of the distributions of the two study species at Florencia. The principal cation associated with exchangeable acidity in acid mineral soils like those at Florencia is Al (Sánchez, 1981), an element to which *C. alliodora* is considered intolerant, as we have emphasized in the preceding discussion. This intolerance is probably due to both direct effects of this element—restriction of root growth—and indirect effects such as the inhibition of N and P uptake (Bergmann et al., 1994) (it may be noted here that N was not determined in the present study due to good evidence that it is rarely limiting in forest soils of northern Costa Rica (Martini and Macias, 1974; Parker, 1994)). *V. ferruginea*, on the other hand, may be considered a species adapted to high soil Al.

We believe that the foliar nutrient contents of the two species at Florencia back up existing characterizations of their soil preferences and nutrient requirements, as well as supporting the hypothesis that soil Al plays a role in the determination of their distributions. Foliar nutrients in themselves are not reliable indicators of either whole-plant nutrient status, plant nutrient requirements or nutrient use efficiency (Grubb, 1989; Vitousek and Sanford, 1986). There is nevertheless a general tendency, for tropical tree species adapted to

more fertile soils to show greater foliar nutrient contents, while species adapted to less fertile soils show correspondingly low foliar nutrients (Grubb, 1989; Vitousek and Sanford, 1986). In this respect, foliar P, K, Ca and Mg in the more demanding *C. alliodora* at Florencia were well within the general ranges for these elements found in tropical moist forests on moderately fertile soils (Vitousek and Sanford, 1986), while foliar P and K in this species were superior to levels in sun leaves of woody plants on "nutrient-rich" soil in a Mexican tropical moist forest (Bongers and Popma, 1988). Foliar contents of all these nutrients, except Mg, were above the critical levels for "acceptable" growth suggested by Bergmann et al. (1994) on the basis of studies of *C. alliodora* planted in pastures in northern Costa Rica. On the other hand, foliar nutrients of *V. ferruginea* at Florencia were within the general ranges found for tropical moist forests on infertile or very infertile soils (Vitousek and Sanford, 1986) and were comparable with those in species of a secondary forest growing on an ultisol degraded by agriculture in Singapore (Grubb et al., 1994), and mature cerradao vegetation on a dystrophic latosol (pH 4.9) in central Brazil (Haridasan and Monteiro de Araújo, 1988). The Al accumulation and high foliar Mn found at Florencia have also been revealed in plantation trees of *V. ferruginea* in the northeastern lowlands of Costa Rica and appear to be characteristic of both this species (Montagnini and Sancho, 1994; Pérez et al., 1993) and of Vochysiaceae in general (Haridasan and Monteiro de Araújo, 1988). Al accumulation in leaves is considered to be a strategy for tolerating this potentially toxic element, although its absence does not mean lack of tolerance: in evolutionary terms, it is possibly the most primitive strategy for Al tolerance of several, and is shown mainly by woody species of the moist tropics (Chenery and Sporne, 1976).

Given the evident nutritional characteristics of the two species as revealed by the present study and others, and the fact that at Florencia, median exchangeable acidity in *Vochysia* plots was double that in *Cordia* plots at both soil depths sampled, we hypothesize that the contrasting spatial distributions of the two species are related to variation in soil Al, as well as to factors such as seed dispersal. The overlap between the two species distributions evident in Figure 2 is consistent with this hypothesis given: a), the probability that species response curves to soil variation are bell-shaped (Whittaker, 1956) and b), the fact that distributions of tree species in tropical forests tend to vary, at local scales, in terms of relative abundances and

not presence and absence (Lescure and Boulet, 1985; Richards, 1976). This overlap may also represent the influence of seed dispersal or chance. Experimental tests of this hypothesis, as described above, are now necessary.

Increasing knowledge of plant-soil relationships in the humid tropics will contribute to increased efficiency of planning for forest management and conservation. Early studies of neotropical secondary forest placed great emphasis on the presence of the commercially sought-after *Cordia alliodora* in secondary vegetation (e.g. Holdridge, 1957). Inherently infertile soils and soils degraded by agricultural activity are common in zones such as northern Costa Rica, however, and we believe that the relatively high nutrient requirements of this species will limit both its presence in natural secondary vegetation (this study) and its success in plantations (Bergmann et al., 1994). *Vochysia ferruginea*, in contrast, with its evidently low nutrient requirements and tolerance of Al, may be expected to become more abundant as the area of secondary vegetation in northern Costa Rica increases, as well as offering considerable potential for plantation forestry (Pérez et al., 1993).

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