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Soil characteristics and *Chusquea* bamboos in the *Quercus* forests of the Cordillera de Talamanca, Costa Rica

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Summary

1 Soils supporting different species of *Chusquea* bamboos (*C. talamancensis* Widmer & L.G. Clark, *C. tomentosa* Widmer & L.G. Clark, *C. foliosa* Clark) in the Costa Rican montane oak forests were mainly acidic (pH 3.3–6.0). The pH was negatively correlated with organic matter (OM), total nitrogen (N), exchangeable acidity and clay content, but positively correlated with cation exchange capacity (CEC) and exchangeable calcium (exch. Ca). There was a positive correlation of CEC with clay. The maximum base contents (Ca, K, Mg) were found at 20–30% clay.
2 The concentrations of N, P, exch. K, exch. Ca and exch. Mg were significantly higher in the main rooting zone (0–10 cm) than in the rhizome zone (20–30 cm). Acidity was lower in the main rooting zone than in the rhizome zone, where pH in NaF was significantly higher than in the main rooting zone, suggesting a higher phosphate retention.
3 The effect of canopy cover on the soil characteristics was not very conspicuous. The Ca:Mg ratio was significantly higher in open conditions than under closed canopy while the opposite was the case for the C:N ratio.
4 Individual bamboo species had distinct requirements in terms of soil conditions and could, therefore, serve as fairly reliable plant indicators of soil site quality. The soils carrying *C. talamancensis* were significantly richer in organic matter, and had a higher C:N ratio than soils with *C. tomentosa* or *C. foliosa*. Further, they were more acidic, and had the highest content of exchangeable acidity and the highest acid saturation. *Chusquea tomentosa* grew on soils of higher pH and higher concentrations of exch. K, exch. Ca and exch. Mg, and hence had a higher base saturation. *Chusquea foliosa* usually occurred on soils whose pH and concentration values were intermediate between those of the other two species. However, in order to define its requirements more specifically, further physical analyses are necessary, i.e. water retention and bulk density.

Keywords: soil–plant relationships, soil nutrients, volcanic soils, indicator species

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Introduction

The relationships between plants and soil conditions have been studied for a long time in central Europe. Depending on the ecological range of a species, edaphic factors may restrict its occurrence to a greater or lesser extent. Ellenberg (1979) and Landolt (1977) have assigned indicator values (*Zeigerwerte*) to the plant species of central Europe and Switzerland respectively for a range of climatic factors (light, temperature and continentality) and edaphic factors like soil moisture, soil reaction and nutrient supply. These values are of practical use in vegetation analysis and in the ecological evaluation of sites.

Soil–plant relationships have not been studied as thoroughly in the tropics though it is certain that subtle differences in soil conditions play an equally important role in determining plant species occurrence as in temperate regions. For example, Harcombe (1980) presented several examples of soil-vegetation relationships in the tropics, concluding that soils with different inherent fertility characteristics will support different vegetation. With reference to tropical bamboos, most of the literature is from India, where these plants are economically important. It has long been recognised (Yadav 1963; Qureshi *et al.* 1969) that the distribution of bamboo species differ depending on edaphic factors including moisture regime, fertility status and morphological features of the soils. The need for more detailed and systematic studies has been suggested, but little has been published on the subject since. Recent research is concerned mainly with the role of bamboos in nutrient conservation (Rao & Ramakrishnan 1990; Tripathi & Singh 1994), and shows that bamboos may be an important factor for the stability of some tropical ecosystems.

Uchimura (1978) has recognised the value of bamboos as indicators of soil conditions in SE-Asia. For example, the presence of *Bambusa polymorpha* indicates moist, fertile and well-drained soils while *Dendrocalamus strictus* is associated with dry soils; *Bambusa tulda* occurs on stream bed alluvial flats, *Oxytenanthera albociliata* on low plateaus or hills on sandy lateritic soil, *Dendrocalamus longispathus* on the edges of damp ravines, *Teinostachyum helferi* in very damp valleys in evergreen forests, and *Bambusa arundinacea* on rich and moist sites such as alluvial stretches along streams. Although it is evident from this list that bamboos grow on many different types of soil, most of them appear to prefer well-drained sandy loam to loamy-clayey soils derived from river alluvium or from underlying rocks, and with pH 5–6.5 (Liese 1985).

A conspicuous component of the understory of the oak forests of the Cordillera de Talamanca are several species of bamboo in the genus *Chusquea* (Blaser 1987; Kappelle *et al.* 1991). *Chusquea* is a neotropical genus generally associated with montane forests. Recent taxonomic studies have led to the description of many new species, among them *Chusquea talamancensis* and *C. tomentosa* which are studied in this investigation (Clark 1989; Widmer & Clark 1991). There are some more recent ecological studies on *Chusquea* (Young 1991; Pearson *et al.* 1994; Widmer 1998) but none have treated plant–soil relationships.

The aim of this paper is to answer the following questions: (1) What are the general characteristics of the soils in the study area in Costa Rica? (2) Is there a difference in soil nutrient status between the main rooting zone (0–10 cm) and the rhizome zone (20–30 cm)? (3) Are there differences in nutrient status of the soil associated with different degrees of canopy closure? (4) Are the various bamboo species associated with contrasting soil conditions, i.e. can particular bamboo species be used as indicators of particular soil conditions?

Study site

The study site lies in the northwestern part of the Cordillera de Talamanca, in an area of

5 km^2 on Cerro Abarca and Cerros Cuericí, Province of Cartago (83°39'25"–83°44'22" W and 9°33'7"–9°35'16" N). The selection of the study site was based on criteria such as good accessibility, no significant recent human impact, and a position below tree limit (3200 m a.s.l.). The altitudinal range considered was 2800–3100 m a.s.l.

The Cordillera de Talamanca is primarily built up of Tertiary marine sediments with intercalated volcanic and plutonic rocks. During orogenesis intense andesitic-basaltic volcanism and the intrusion of plutonic rocks occurred (Weyl 1980). The Río Macho intrusion is composed of granodiorite which grades to diorite at the margins and covers an area of 50 km^2. Quaternary volcanic activity in the adjacent Cordillera Volcánica Central also deposited ash (from the Turrialba and Irazú volcanoes) on the Cordillera de Talamanca (Castillo Muñoz 1993). The morphology of the Cordillera de Talamanca is generally characterised by a flattish Pliocene crest with steeply incised valleys, surrounded by intermediate and steep slopes (Weyl 1980).

The soils reflect the volcanic origin of both the intrusions (Talamancan Comagmatic Series) and the ash deposits. Two main soil types have been differentiated in the study area. Soil Type I has been characterised as an Andic Humitropept (Order Inceptisol) according to the US soil classification system; according to the FAO classification this soil type may be a Dystric-umbric Regosol. *Chusquea talamancensis* is generally found on this soil. *Chusquea tomentosa* occurs mainly on Soil Type II; this is a Typic Hapludand (Order Andisol) in the US system or a Mollic Andosol in the FAO system (Edwards-Widmer, in prep.).

The climate is characterized by two seasons: the rainy season from May to November, and the dry season from January to the beginning of April. During the rainy season mean monthly rainfall ranges from 250 to 470 mm. In the middle of this period (i.e. July or August) there is a period of reduced rainfall (Coen 1983). In the dry season the mean monthly rainfall ranges from 20 to 35 mm. Daily temperature oscillations are larger than the range of mean monthly temperatures. For example, from 1987 to 1989 the daily temperature range was 9.4–10.3 °C in the dry season and 7.5–8.5 °C in the rainy season. Temperatures below 0 °C occur in the dry season when skies are clear. Temperature decreases with altitude by 0.52–0.57 °C per 100 m (Herrera 1985; Blaser 1987).

The pristine old-growth forests studied here are part of the Upper Montane Forest (*sensu* Kappelle *et al.* 1991). The dominant species, *Quercus costaricensis* Liebmann and *Q. copeyensis* C.H. Müller, form tall stands (>30 m). The understory is characterized by bamboos of the genus *Chusquea* which grow in monospecific stands with distribution patterns reflecting altitudinal gradients and aspect (Widmer 1994). Three *Chusquea* species are present in the study area: *C. talamancensis* and *C. tomentosa,* which are more abundant, and *C. foliosa,* which is confined to humid patches within areas dominated by one of the other species (Widmer 1994). Forest dynamics in these old-growth forests is strongly affected by tree- and branch-fall, leading to a mosaic of closed canopies, canopies with apertures, and forest gaps in various stages of regeneration. Large old gaps (>500 m^2, >10 years old) in the primary forest typically have a two-layered vertical structure: a bamboo layer and a herb layer (Widmer 1993; Widmer 1998). The roots reach a depth between 30 (due to underlying rock) and 130 cm. The top soil contains a dense root mat, and the rhizomes of *Chusquea* are found between 10–40 cm.

Materials and methods

SELECTION OF PLOTS AND SAMPLING

Forty-one 500 m^2 (20 m x 25 m) plots established for vegetation analysis were selected for this study. The plots differed in altitude, aspect and slope angle. They were selected to include different species of bamboo (*Chusquea talamancensis, C. tomentosa* or *C. foliosa*) and to represent different degrees of canopy closure. The canopy closure was classified into three categories: (1) "Gap", corresponds to a plot in a large gap of over 500 m^2 area with an overstory tree cover of less than 10%. (2) "Closed canopy" refers to sites with an old-growth oak canopy cover of more than 60%. (3) "Intermediate canopy" sites refers to sites with an overstory represented by a few scattered mature trees (> 50 cm dbh) and a cover of 10–50% of the overstory canopy, or to medium sized trees (20 < dbh < 50 cm). *C. foliosa* was not found under closed canopy in the study area.

Soil samples were taken at random points within the plots from two depths: 0–10 cm, the main rooting zone, and 20–30 cm, the average depth at which bamboo rhizomes are found (the rhizome zone). In June 1989, 15 plots were sampled. The three random samples from each plot were combined and the material was analysed in the soil laboratory at CATIE (Costa Rica) following the methods described by Díaz-Romeu & Hunter (1978). Due to the high variability of the results a second sampling of 26 additional plots was performed in July 1990; these samples were analysed at the Geobotanical Institute ETHZ (Switzerland) following the same methods.

SOIL ANALYSES

Soil samples were air-dried for several days in Turrialba (625 m a.s.l., mean annual temperature 22 °C). Before analysis the samples were ground and passed through a 2-mm mesh sieve. Soil organic matter, total N, organic C, P and the exchangeable bases K, Ca, Mg and Na were determined on a subsample that had been finely ground and passed through a 0.25-mm mesh sieve.

Soil pH was determined electrometrically in a soil:water volume ratio of 1:2.5. Phosphate retention was predicted from the pH in NaF according to the method of Alvarado (1982) and Mazzarino *et al.* (1985). It was measured electrometrically with a soil: solution ratio of 1:50 and a reaction time of 2 min.

Organic matter was determined by the Walkley-Black wet digestion method using a correction factor of 2.76 for unrecovered organic C and a ratio of organic matter to organic C of 1.72 (Saiz del Río & Bornemisza 1961). Total N was determined by the semi-micro Kjeldahl technique (BÜCHI 320). Total carbon and nitrogen for C:N ratio were determined using a CHN-1000 gas analyzer (LECO) at the Institut für Pflanzenwissenschaften ETHZ. The measurement of total carbon corresponds to organic carbon since it is the predominant form present in humid regions, where extensive leaching of the soil has occurred (Nelson & Sommers 1982).

Cation exchange capacity (CEC) and exchangeable bases were determined with the ammonium acetate method described by Díaz-Romeu (1982). As a first step the exchangeable bases K, Ca, Mg and Na were extracted with 1:20 NH_4OAc 1N (pH 4.8); they were subsequently determined by atomic absorption analysis (SPECTRA AA-400, Varian). After washing with ethanol, CEC was determined by titration. Exchangeable acidity (a measure for exchangeable H^+ and Al^{3+} cations) was extracted with 1 mol l^{-1} KCl, and determined by titration; extractable P was measured colorimetrically (SP6-550 UV-VIS

Spectro) after extracting at 1:10 with Olsen reagent (as modified by Díaz-Romeu & Hunter 1978). Effective cation exchange capacity (ECEC) was calculated as the sum of exchangeable acidity plus the sum of bases (K, Ca, Mg, Na). Base saturation was calculated as the sum of bases expressed as a percentage of ECEC. Acid saturation is the percentage of ECEC accounted for by exchangeable acidity.

Particle-size analysis was performed with the Bouyoucos method (Bazán 1975); hydrometer readings were taken at 40 s and 2 h, and the proportion of sand, silt and clay calculated.

DATA ANALYSES

All data analyses were performed with the statistical software package Statview 4.0 (1992). Correlation coefficients were calculated to identify the interrelationships between soil parameters. The significance of the coefficients was determined with a Fisher's r to z transformation ($P < 0.001$). Regression

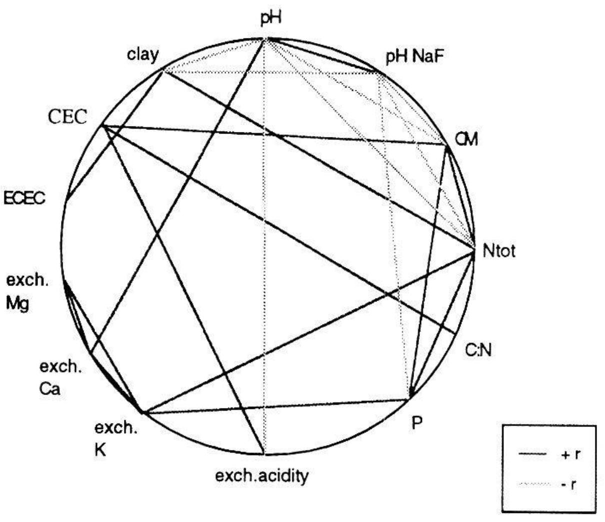

Fig. 1. Significant positive (+ r) and negative (- r) correlations (r ≥ 0.50, P < 0.001) of parameters from soil sampled at 0–10 and 20–30 cm depth (total of 36 observations) in oak forests with Chusquea *understory. Significance tested with Fisher's* r *to* z *transformation. See abbreviations in the text.*

models were calculated using forward stepwise regression with 13 to 16 independent variables (F-to-remove = 4, α = 0.05). One-factor ANOVA was calculated to determine whether variation in any soil parameters could be explained statistically by any of the following factors: *Chusquea* (*C. talamancensis, C. tomentosa, C. foliosa*), canopy closure (gap, intermediate canopy, closed canopy) or soil depth (0–10 cm, 20–30 cm). In addition, two-factor ANOVA's (*Chusquea,* canopy closure) were calculated for each soil depth separately (0–10 cm and 20–30 cm). A Bonferroni/Dunn multiple comparison test for main effects was applied; this sets an upper overall significance level of α when testing multiple hypotheses (Scheiner & Gurevitch 1993).

Results

GENERAL SOIL PROPERTIES

The analysis of chemical characteristics of the soil samples from the main rooting (0–10 cm) and the rhizome zone (20–30 cm) revealed a high but variable organic content (organic matter 5.8–90.7%, organic C 3.8–46.5%), which is characteristic of soils derived from volcanic ash (Nanzyo *et al.* 1993). Further, effective cation exchange capacity (ECEC) was much lower (2.6–24.0 meq/100 g soil) than CEC (27.4–160 meq/100 g soil), showing the variable charge characteristics. Finally, there was a linear relationship between organic C and cation exchange capacity ($CEC = 18.2 + 2.5\ orgC\%$, $r^2 = 0.85$, $n = 36$), which is common for humus-rich Andisols.

Acidity was generally high (pH = 3.28–6.04). There was a negative correlation between pH and organic matter (OM) content (Fig. 1). Total nitrogen (0.34–2.34%) was also negatively correlated with pH levels. Clay content (3.6–54%) and exchangeable acidity (0.2–23.3 meq/100 g soil) were higher at

Table 1. Regression models to describe pH in H_2O, pH in NaF, total nitrogen (Ntot), C:N ratio and phosphorus from 36 soil samples at 0–10 and 20–30 cm depth in montane oak forests with bamboo understory in the Cordillera de Talamanca (models after forward stepwise regression; Iv = independent variables tested, Sa = serial autocorrelation). Abbreviations see text

Regression models	Iv	r^2	*P*	Sa
pH = 4.72 - 0.03 OM - 0.04 Exch.Ac. + 0.02 CEC + 0.08 Exch.Ca - 0.01 clay + error	14	0.87	0.001	0.03
Ntot = 0.53 + 0.03 OM - 0.01 CEC + error	15	0.84	0.001	0.03
C:N = 3.05 + 0.27 CEC - 0.19 ECEC + error	15	0.73	0.001	0.24
pH in NaF = - 1.82 + 2.33 pH + 0.04 Ac.Sat. - 0.04 clay + error	16	0.90	0.001	0.41
P = 2.67 - 0.23 pH in NaF + 0.03 OM + error	15	0.48	0.001	0.15

lower pH. The regression model for pH (Table 1) explained 87% of the variation and included as positively correlated parameters CEC and exchangeable calcium (exch.Ca).

As expected, the regression between organic matter and organic carbon (both parameters determined independently) was linear ($\%C = 0.77 + 0.51\ OM$, $r^2 = 0.99$, $P < 0.001$). Attributes such as total nitrogen, C:N ratio, phosphorus (P), CEC and indirectly the bases (Ca, Mg, K) were correlated with organic matter (Fig. 1), which is expected from theory (Nelson & Sommers 1982). The regression model for total nitrogen showed a positive dependence on organic matter and a negative relation to CEC ($r^2 = 0.84$, $P < 0.001$). C:N ratios ranged from 7.5–21.7 and were positively correlated with the variable charge attributes of the soil, i.e. with CEC and ECEC ($r^2 = 0.73$).

Like pH, pH in NaF (7.2–11.7) was also negatively correlated with organic matter and total nitrogen (Fig. 1). The calculated regression model for pH in NaF included positively correlated acid saturation (Ac.Sat.) and negatively correlated clay content as explanatory parameters. The negative correlation between pH in NaF and phosphorus (0.22–19.5 $\mu g\ ml^{-1}$) was evident in the regression model for P, which also indicates that P was positively associated with organic matter.

The exchangeable bases K, Ca and Mg (but not Na) were correlated with each other, and there was a positive correlation of ECEC with clay (Fig. 1), which is expected from theory. The bivariate scattergram of K, Ca and Mg with clay content showed that all three bases had bell-shaped curves with maximum base contents at 20–30% of clay. The relationship of KCl-extractable Al with clay was linear and exchangeable acidity also increased with clay content. The potassium contents were low but positively correlated with total nitrogen and phosphorus (Fig. 1).

RELATIONSHIP WITH VEGETATION

Organic matter, nitrogen and phosphorus

These components were significantly higher in the main rooting zone than in the rhizome zone (Tables 2, 3). The plots with *Chusquea talamancensis* in the understory had on average the highest content of organic matter followed by *C. tomentosa* and *C. foliosa.* The C:N ratio did not vary with depth, but was significantly different between the soils sustaining these bamboo species. It was highest for *C. talamancensis* and lowest for *C. foliosa* ($P < 0.05$). C:N ratios were smaller under

Table 2. *Content of organic matter, total nitrogen, C:N and phosphorus for* Chusquea talamancensis, C. tomentosa *and* C. foliosa, *under gap, intermediate canopy and closed canopy conditions at 0–10 cm (main rooting zone,* MRZ*) and 20–30 cm (rhizome zone,* RZ*). The number of samples* (n) *refers to both soil depths; for C:N the number of samples is indicated in brackets (means ± SE; –, no data)*

Canopy closure		Gap			Intermediate canopy			Closed canopy	
Chusquea species		*talamancensis*	*tomentosa*	*foliosa*	*talamancensis*	*tomentosa*	*foliosa*	*talamancensis*	*tomentosa*
n		4	4	5	7	2	5	7	7
Organic matter	*MRZ*	45.5 ± 14.1	30.3 ± 9.8	31.1 ± 7.0	65.8 ± 10.3	34.9 ± 7.3	23.6 ± 1.5	52.0 ± 8.8	56.1 ± 9.2
(% dry weigth)	*RZ*	16.2 ± 2.3	16.9 ± 5.0	14.4 ± 3.0	23.6 ± 3.5	23.3 ± 2.8	8.0 ± 1.4	19.6 ± 3.6	16.3 ± 3.0
Total nitrogen	*MRZ*	1.70 ± 0.17	1.01 ± 0.18	1.25 ± 0.21	1.69 ± 0.22	1.24 ± 0.31	0.98 ± 0.07	1.57 ± 0.14	1.64 ± 0.22
(% dry weigth)	*RZ*	0.58 ± 0.05	0.72 ± 0.09	0.82 ± 0.11	0.70 ± 0.11	0.79 ± 0.12	0.47 ± 0.03	0.60 ± 0.10	0.54 ± 0.06
C:N ratio	*MRZ*	17.9 (1)	12.6 ± 2.1 (2)	11.9 ± 2.3 (2)	17.9 ± 0.8 (7)	–	11.3 ± 0.5 (5)	19.1 ± 1.4 (4)	16.8 ± 0.9 (4)
	RZ	14.2 (1)	9.8 ± 0.2 (2)	12.3 ± 2.6 (2)	16.9 ± 0.4 (7)	–	9.7 ± 0.6 (5)	15.8 ± 0.8(4)	16.2 ± 2.1 (5)
Phosphorus	*MRZ*	11.4 ± 3.6	6.99 ± 1.68	10.2 ± 3.3	5.50 ± 2.23	11.4 ± 1.2	1.60 ± 0.20	7.57 ± 1.62	6.63 ± 1.92
($\mu g\ ml^{-1}$)	*RZ*	4.74 ± 1.71	5.44 ± 2.97	5.51 ± 2.10	1.24 ± 0.29	10.9 ± 4.5	0.39 ± 0.04	2.91 ± 1.12	2.47 ± 1.51

Table 3. *Summary statistics of organic matter, total nitrogen, C:N ratio and phosphorus after one-way ANOVA (α = 0.05) for the factors 'canopy closure',* 'Chusquea *species' and 'soil depth' (ns,* $P > 0.05$; *, $P \le 0.05$; **, $P \le 0.01$; ***, $P \le 0.001$*)*

Factor	Canopy closure			*Chusquea* species			Soil depth		
Variable	df	*F*-value	*P*	df	*F*-value	*P*	df	*F*-value	*P*
Organic matter	2	1.41	ns	2	4.62	*	1	47.58	***
Total nitrogen	2	0.2	ns	2	1.46	ns	1	86.99	***
C:N ratio	2	5.54	**	2	24.99	***	1	1.95	ns
Phosphorus	2	4.21	*	2	0.57	ns	1	12.88	***

open conditions; the strongest significant difference in the C:N ratio being between gap and closed canopy ($P < 0.01$). On the other hand, phosphorus was significantly higher under gap conditions than under intermediate canopy ($P < 0.01$).

Soil acidity

As expected, pH was also significantly lower in the main rooting zone than in the rhizome zone (Fig. 2). Tables 4 and 5 show that there were significant differences in the acidity characteristics in the main rooting zone, and that these could be related to *Chusquea* species but not to canopy closure. The plots with *C. talamancensis* had the lowest pH, the highest content of exchangeable acidity, and the highest acid saturation; all these differences could be related to the higher organic content of the *C. talamancensis* soils. The differences in soil pH between sites with *C. talamancensis* and those with the two other species were significant (*C. tomentosa,* $P < 0.001$; *C. foliosa,* $P < 0.01$). The difference in exchangeable acidity in main rooting zones was significant between *C. talamancensis* and *C. tomentosa* ($P < 0.01$). Similarly, acid saturation was significantly higher in the main rooting zone and in the rhizome zone of plots with *C. talamancensis* than those with *C. tomentosa* ($P < 0.05$ and $P < 0.001$, respectively).

The pH in NaF was significantly higher ($P < 0.001$) in the rhizome zone than in the main rooting zone, with values suggesting a high phosphate retention. Values of pH in NaF in the main rooting zone were significantly

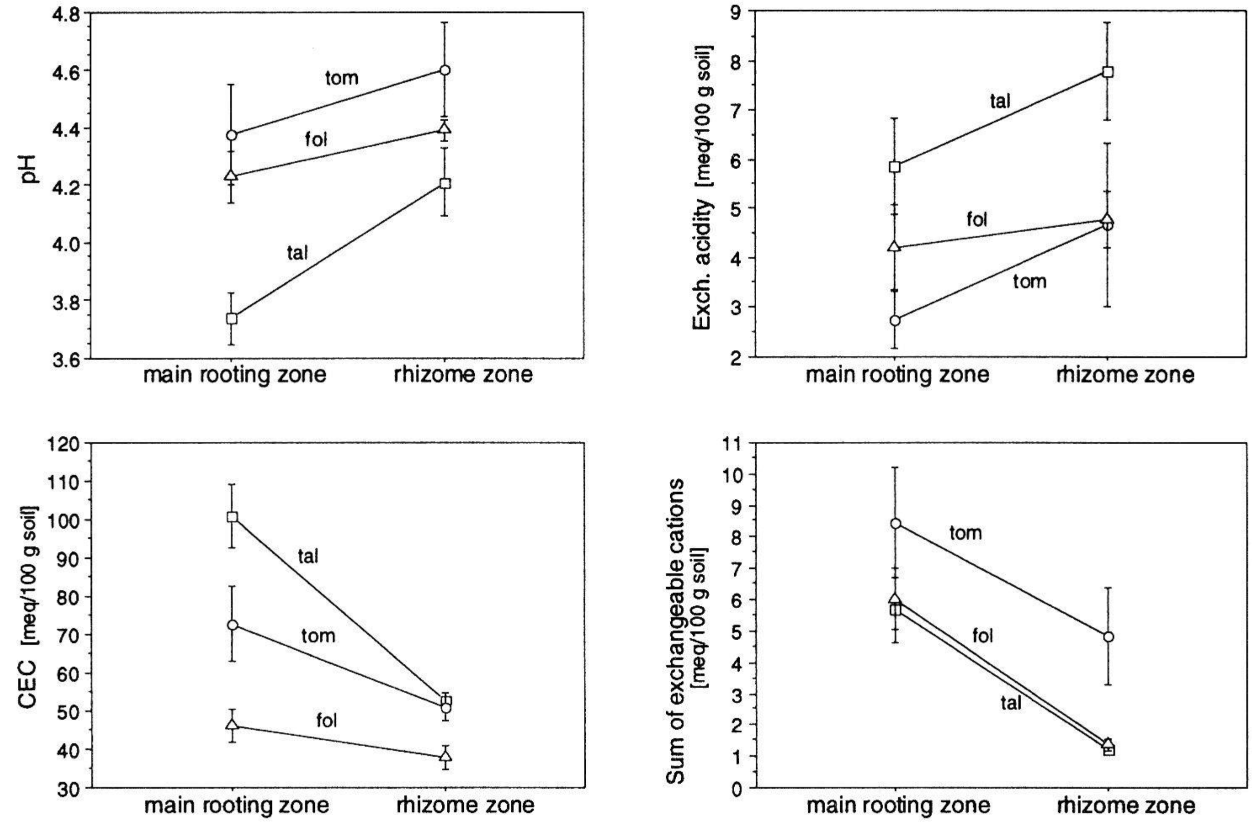

Fig. 2. *Means (± SE) of pH, cation exchange capacity (CEC), exchangeable acidity (Al^{3+}+H^+), sum of exchangeable bases (Ca, Mg, K, Na) of soils in plots with the* Chusquea *species:* C. talamancensis *(tal),* n = *18;* C. tomentosa *(tom),* n = *13, and* C. foliosa *(fol),* n = *10. Data are given for the main rooting (0–10 cm) and rhizome zone (20–30 cm).*

lower at *C. talamancensis* sites than at sites with either *C. tomentosa* ($P < 0.01$) or *C. foliosa* ($P < 0.01$). However, in the rhizome zone there were no significant differences between species in pH in NaF.

Cations and cation exchange

There were highly significant differences in cation exchange capacity and total base content (Ca + Mg + K + Na; $P < 0.001$) between the main rooting and the rhizome zone (Fig. 2). There were also significant differences with soil depth for the bases Ca, Mg, K considered separately ($P < 0.001$) but not for Na. Variation in base content at rhizome zone was more strongly associated with species of bamboo than with degree of canopy closure. Exchangeable bases were far higher at *C. tomentosa* sites, than at those of *C. foliosa* and *C. talamancensis,* which were very similar (Fig. 2, Tables 4, 5); ECEC and also CEC were similar for *C. talamancensis* and *C. tomentosa* sites, and higher than for *C. foliosa,* though this difference was only significant for CEC ($P < 0.001$). Finally, the base saturation data confirmed that sites with *C. tomentosa* had a significantly higher base status in the rhizome zone than sites with *C. talamancensis* ($P < 0.001$) or *C. foliosa* ($P < 0.05$).

The Ca:Mg ratio at 20–30 cm depth showed significant differences associated with bamboo species and with canopy cover (Tables 4, 5). It was highest for *C. tomentosa* and very similar for *C. talamancensis* and *C. foliosa.* The ratio was relatively higher in gaps than under intermediate canopy or closed

Table 4. Values of pH in H_2O, pH in NaF, exchangeable acidity, acid saturation and cation exchange capacity in the main rooting zone (0–10 cm), and exchangeable cations (Ca, Mg, K, Na), base saturation and Ca:Mg ratio in the rhizome zone (20–30 cm) for Chusquea talamancensis *(tal),* C. tomentosa *(tom) and* C. foliosa *(fol) under gap, intermediate canopy and closed canopy conditions (means ±* SE*)*

Canopy closure	Gap			Intermediate canopy			Closed canopy	
Chusquea species	*tal*	*tom*	*fol*	*tal*	*tom*	*fol*	*tal*	*tom*
n	4	4	5	7	2	5	7	7
0–10 cm								
pH in H_2O	3.97 ± 0.28	4.59 ± 0.13	4.21 ± 0.12	3.50 ± 0.07	4.55 ± 0.65	4.25 ± 0.14	3.84 ± 0.11	4.21 ± 0.28
pH in NaF (1N)	7.44 ± 0.20	8.72 ± 0.67	8.12 ± 0.22	6.93 ± 0.28	8.35 ± 0.55	8.31 ± 0.15	7.29 ± 0.20	7.93 ± 0.46
Exch. Ac. (meq/100g)	2.97 ±1.48	2.60 ± 0.55	3.67 ± 1.42	8.52 ± 1.83	1.20 ± 0.95	4.75 ± 1.09	4.86 ± 0.98	3.26 ± 0.98
Acid Sat. (%)	31.0 ±11.0	31.8 ± 8.7	35.5 ± 9.7	61.6 ± 7.9	17.2 ± 15.9	46.1 ± 11.3	50.4 ± 4.4	32.3 ± 9.4
CEC (meq/100 g)	96.6 ± 9.5	44.6 ± 1.6	54.4 ± 6.9	105.2 ± 15.6	72.6 ± 18.6	37.7 ± 1.0	99.5 ± 14.9	89.0 ± 15.2
20–30 cm								
Exch. Ca (meq/100 g)	0.80 ± 0.31	2.97 ± 1.09	0.71 ± 0.21	0.40 ± 0.22	4.41 ± 3.36	0.41 ± 0.11	0.42 ± 0.06	3.18 ± 2.15
Exch. Mg (meq/100 g)	0.25 ± 0.05	0.84 ± 0.34	0.35 ± 0.07	0.30 ± 0.10	1.33 ± 0.77	0.46 ± 0.14	0.37 ± 0.05	0.82 ± 0.41
Exch. K (meq/100 g)	0.13 ± 0.02	0.39 ± 0.08	0.25 ± 0.02	0.23 ± 0.04	0.46 ± 0.15	0.17 ± 0.02	0.22 ± 0.04	0.37 ± 0.15
Exch. Na (meq/ 100g)	0.21 ± 0.02	0.20 ± 0.02	0.20 ± 0.01	0.18 ± 0.01	0.28 ± 0.04	0.18 ± 0.01	0.26 ± 0.03	0.22 ± 0.02
Base Sat. (%)	27.4 ± 9.2	63.3 ± 11.6	31.1 ± 6.7	8.3 ± 1.5	66.5 ± 29.1	17.5 ± 2.9	19.9 ± 4.2	33.1 ± 13.5
Ca:Mg ratio	2.93 ± 0.67	4.09 ± 0.80	2.02 ± 0.41	1.10 ± 0.22	2.79 ± 0.91	0.97 ± 0.16	1.22 ± 0.19	2.02 ± 0.67

*Table 5. Summary statistics of pH, pH in NaF, exchangeable acid, acid saturation and cation exchange capacity (CEC) on the main rooting zone (0–10 cm) and of exchangeable cations (Ca, Mg, K, Na), base saturation and Ca:Mg ratio at the rhizome zone (20–30 cm) using two-way ANOVA ($\alpha = 0.05$) for the factors 'canopy closure' and '*Chusquea *species' (ns, $P > 0.05$; *, $P \le 0.05$; **, $P \le 0.01$; ***, $P \le 0.001$)*

Factor	Canopy closure			*Chusquea* species			Interaction		
Variable	df	*F*-value	*P*	df	*F*-value	*P*	df	*F*-value	*P*
pH in H_2O	1	0.68	ns	1	14.23	***	3	1.28	ns
pH in NaF	1	0.45	ns	1	11.96	**	3	0.90	ns
Exch. acidity	1	1.85	ns	1	6.32	*	3	1.96	ns
Acid saturation	1	1.05	ns	1	6.1	*	3	1.39	ns
CEC	1	0.27	ns	1	6.52	*	3	1.48	ns
Exch. Ca	1	0.05	ns	1	7.85	**	3	0.16	ns
Exch. Mg	1	0.86	ns	1	9.22	**	3	0.38	ns
Exch. K	1	0.13	ns	1	7.60	**	3	0.43	ns
Exch. Na	1	0.29	ns	1	1.42	ns	3	3.52	*
Base Saturation	1	1.34	ns	1	19.09	***	3	1.82	ns
Ca:Mg ratio	1	9.16	**	1	7.51	**	3	0.43	ns

canopy, which showed on average a similar ratio.

Discussion

Blaser (1987) measured the physical and chemical characteristics of soils in a plot of 12.4 ha at lower altitudes (2600–2800 m a.s.l.), but on the same side (Atlantic) of the Cordillera de Talamanca as the site of this investigation. From the resulting very low bulk density, the high porosity and the high pH in NaF values, he concluded that the soils were of volcanic origin. The volcanic origin of the soils is confirmed in the present study. Characteristic features of such soils include a high accumulation of organic matter (correlated with a large amount of organic C), variable (or pH-dependent) charge characteristics and a linear relationship between organic C and CEC, as described by Nanzyo *et al.* (1993). In addition, pH in NaF values were also relatively high (7.2–11.7) which suggests high allophane contents in the soil. In humid regions, volcanic ash weathers quickly into allophane, an amorphous Al-silicate mixture that forms complexes with organic matter (Sánchez 1976). Andepts and other soils containing large amounts of allophane and other amorphous minerals have high capacities for binding phosphate (Gebhardt & Coleman 1974). Thus, extractable phosphorus contents were low. However, this may also be associated with the low pH and high concentrations of Al and Fe, that can precipitate P into Al and Fe phosphates, the main mechanism of phosphate fixation in most soils (Bohn *et al.* 1985).

Montane forests are in general low in available P and N. The low temperatures are associated with low rates of decomposition and nutrient release, and favour the accumulation of organic matter in soils of volcanic origin (Vitousek & Sanford 1986). Organic matter, nitrogen and phosphorus decrease with soil depth, but the C:N ratio is less variable, perhaps because C tends to be mineralized faster than N at low pH (Sánchez 1976). The C:N ratios are correlated with CEC, reflecting the fact that N mineralization is inversely proportional to allophane contents (Sánchez 1976).

As in many montane forests, the soils of the study site are acidic to very acidic. In interpreting the exchangeable acidity, acid saturation and cation exchange capacity data one must consider the composition of the soil material. Since soil from 0–10 cm depth consists mainly of humic compounds, there is probably a greater proportion of H than Al ("acid cations") in the main rooting zone than at greater depths. At 20–30 cm there is mineral soil (generally B horizon) and the type of the clay (e.g. allophane) determines the amount of Al present. However, there may be significant translocation of humic substances to such depths, depending on the composition of the vegetation and the soil structure. The concentrations of K, Ca and Mg were also higher in the surface soil compared to the deeper soil, but Na changed little with depth. All concentrations of cations were low if compared with other tropical mountain soils as presented by Edwards & Grubb (1982). The comparison with data of the soils from the Chirripó National Park in Costa Rica (Kappelle *et al.* 1995) is difficult due to different sampling criteria. Only pH and the clay content of soils in the Atlantic side of the Cordillera de Talamanca are in the same range.

The degree of canopy cover proved to be relatively unimportant as a factor affecting soil conditions in this investigation. The strongest relationship was observed with the Ca:Mg ratio, which was consistently higher for all *Chusquea* species in open conditions than under closed canopy. Decomposition is apparently enhanced under open conditions, for the C:N ratios were higher under closed conditions than in gaps, especially for *C. talamancensis* and *C. tomentosa.* Finally, for the same two species, phosphorus seems to be more available in gaps than under closed canopy in the rhizome zone.

There is some evidence for differences in soil conditions associated with the various *Chusquea* species. The soils supporting *C. talamancensis* showed on average the highest organic matter content, C:N ratio, cation exchange capacity and acidity, followed by *C. foliosa.* There were no noticeable differences between the species in the contents of soil nitrogen and extractable phosphorus. Soils carrying *C. tomentosa* had the highest pH, the highest concentration of exchangeable cations and hence the highest base saturation, especially at rhizome zone. Although these findings have to be supported by future research, they confirm what Yadav (1963) first suggested and Qureshi *et al.* (1969) supported with more data: that individual species of bamboos have distinct requirements in terms of soil conditions and can, therefore, serve as fairly reliable plant indicators of soil site quality. This can be of practical importance for the foresters working in the montane oak forests of the Cordillera de Talamanca, in order to develop the most suitable sustainable management.

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