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INFLUENCE OF SOILS AND TOPOGRAPHIC GRADIENTS ON TREE SPECIES DISTRIBUTION IN A BRAZILIAN ATLANTIC TROPICAL SEMIDECIDUOUS FOREST

W. G. Ferreira-Júnior[1], A. F. Silva†, C. E. G. R. Schaefer[2], J. A. A. Meira Neto[1], A. S. Dias[1], M. Ignácio[1] & M. C. M. P. Medeiros[1]

This study investigated the effect of environmental variables such as soil class, soil water availability, topography and slope on spatial distribution patterns of tree species in a Brazilian Seasonal Semideciduous Forest area. Floristic and structural data for a tree community were obtained by sampling 100 plots 10 × 10 m in which every tree with trunk diameter (dbh) $\geq$ 4.77 cm at 130 cm above ground level was sampled. The area under study showed a marked soil gradient, directly associated with the topography: flat hilltops with Al^{3+}-rich Dystric Latosols give way to steep colluvial slopes with shallower and more Dystric Cambic Latosols without Al^{3+}, changing over, at the bottom of the hollows, to Epieutrophic Cambisols richer in nutrients. The floristic-sociological parameters analysed for the soil habitats did not differ statistically from each other. The diversity and equability indices were 3.6 and 0.84, 3.48 and 0.85, 3.49 and 0.84 for the Dystric Latosol, Dystric Cambic Latosol and Epieutrophic Cambisol, respectively. The soil variables (related to the fertility and texture) and the soil water regime (drainage) were probably the principal factors determining the spatial distribution patterns of tree species in the forest.

Keywords. Conservation science, environmental gradients, spatial distribution, tropical soils.

INTRODUCTION

Edaphic and hydrologic characteristics are not only related to the distribution of the vegetation complexes of a particular region but are also correlated with the spatial distribution of species within them. This fact was demonstrated by studies carried out in remnants of Montane Tropical Rain Forest in the state of Minas Gerais (Carvalho *et al.*, 2005a) and in Seasonal Semideciduous Forest in areas of the Cerrado biome in the southeastern and central west regions of Brazil. The environmental heterogeneity was principally determined by the water regime in the soil (drainage classes) and landscape topography, followed by the effect of

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[1] Departamento de Biologia Vegetal – Setor de Ecologia Vegetal, Universidade Federal de Viçosa, s/n. Viçosa, Minas Gerais, Brazil, CEP 36570-000. E-mail: wjr@vicosa.ufv.br

[2] Departamento de Solos, Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brazil.

†Deceased 22 September 2006.

different fertility classes (Oliveira-Filho *et al.*, 1989, 1994a, 1997b, 2001; Oliveira-Filho & Ratter, 1995; Botrel *et al.*, 2002; Espírito-Santo *et al.*, 2002; Martins *et al.*, 2003; Souza *et al.*, 2003; Carvalho *et al.*, 2005b; Meira-Neto *et al.*, 2005). Regarding the spatial species distribution, Oliveira-Filho *et al.* (1997a) and Dalanesi *et al.* (2004) emphasized the influence of the border effect together with the drainage class. Border (edge) effects are the result of the interactions between two adjacent ecosystems when the two are separated by an abrupt transition. The border effect may affect the organisms in a forest fragment by causing changes in the biotic and abiotic conditions (Murcia, 1995).

In-depth studies on the relationship between forest formation and environmental variables are rare (Martins *et al.*, 2003; Oliveira-Filho *et al.*, 2004) and complement studies on floristics, structure and ecological succession in remnant forests in Brazil.

Kageyama & Gandara (2003) claim that, given the devastation of the Brazilian Atlantic Forest biome, the development of techniques and processes leading to its restoration, as well as the conservation of little-affected remnant areas, are crucial. Studies of the dynamics of plant communities and the influence on them of environmental factors can contribute information vital for the development of such techniques.

The objective of the present study was to determine how soil and topographic variables, such as soil class, soil water regime and slope, influence the spatial distribution patterns of tree species within an area of Seasonal Semideciduous Forest. The study site was in the Biological Reserve on the campus of the Federal University of Viçosa, an area which has been undisturbed and undergoing natural regeneration for the last 80 years.

Materials and Methods

The study area

The municipal district of Viçosa (20°45′14″S, 42°45′53″W) is in the Brazilian highlands in a geopolitical division called the Zona da Mata of Minas Gerais State (Fig. 1) (IBGE, 1977). According to Veloso *et al.* (1991) the regional prevailing forest type is Seasonal Semideciduous Forest in an ecosystem called Tropical Atlantic Forest or Brazilian Atlantic Forest (IBGE, 1988). The altitude range is from 620 to 820 m and the relief varies from strongly undulating to mountainous (Valverde, 1958). There are two predominant soil classes: a Dystric Red-Yellow Latosol covers hilltops and mountainsides, while a Cambic Red-Yellow Podzol dominates the upper fluvial terraces (Resende *et al.*, 1988). The regional climate has been classified in the Köppen system as Cw_b, i.e. tropical high-altitude with rainy summers and cold and dry winters (Golfari, 1975). The precipitation pattern, according to Golfari (1975), consists of a rainy season from September to April and a dry season for the rest of the year. From November to April there is a water surplus. According to Castro *et al.*

(1973) the mean annual values are around 80% for relative air humidity, 19°C for air temperature and 1340 mm for annual precipitation.

The area where this study was undertaken is a remnant forest on the campus of the Federal University of Viçosa, known as the Biological Reserve (Fig. 1). It comprises approximately 75 ha, presently in an undisturbed process of natural regeneration that began in 1926 upon purchase of the area. Before 1926 it supported a plantation of coffee. Since then the area has been permanently protected against interference.

Structure of the vegetation on the soil habitats

The method of contiguous plots was used (Mueller-Dombois & Ellenberg, 1974), with 100 plots of 10 × 10 m. Living trees with a trunk diameter (dbh) $\geqslant$ 4.77 cm at 130 cm above ground level were sampled and identified. Standing dead trees were also included. The phytosociological parameters proposed by Mueller-Dombois & Ellenberg (1974) and Pielou (1975) were used to analyse the structure of the community. Shannon's Diversity Index (H') (Brower & Zar, 1984) and the Coefficient of Equability (J') (Pielou, 1975) were also calculated. The software package FITOPAC 1 (Shepherd, 1996) was used to calculate these parameters.

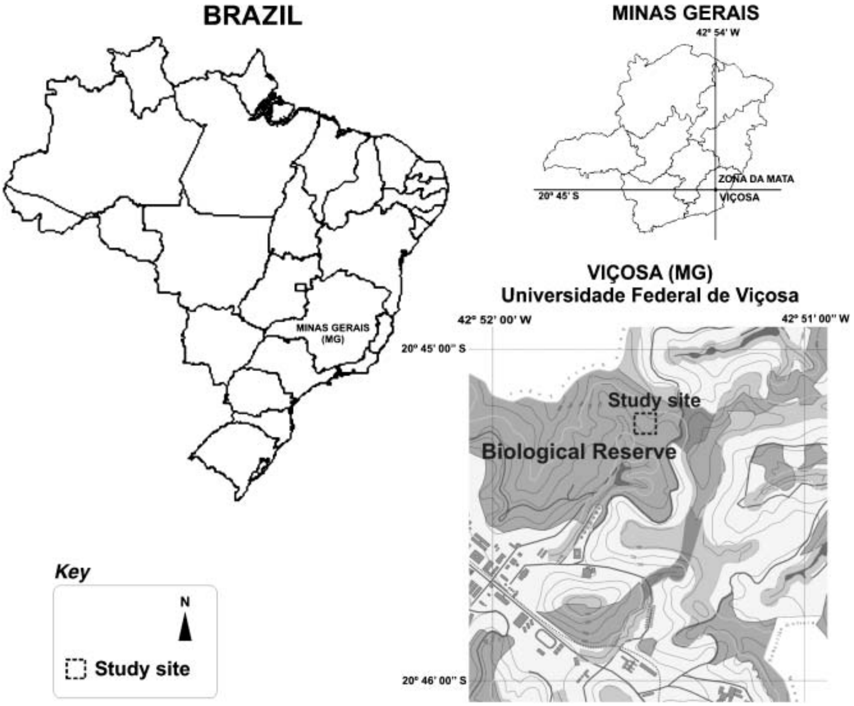

FIG. 1. The location of the study area.

All statistical analyses were carried out using the STATISTICA program (Statsoft, 1998). The tree and species density values, the basal area per hectare and the mean diameter of the soil habitats were submitted to normality tests (Shapiro–Wilks test) and error homogeneity (Levene test). The results obtained were submitted to an analysis of variance and a *t* test at 5% probability (Tukey).

The tree densities were distributed in diameter classes and organized for the soil habitats. With reference to diameter classes, the intervals had increasing amplitudes to compensate the lower densities for greater diameter classes (Oliveira-Filho *et al.*, 2001; Botrel *et al.*, 2002).

In order to equalize the number of samples used for the diversity index and equability (Espírito-Santo *et al.*, 2002), we randomly selected 23 plots in the Dystric Cambic Latosol and Epieutrophic Cambisol soil classes, thereby equalling the number in the Dystric Latosol soil class (see below for comments on soil classes).

Soil and topographic gradients

A detailed soil survey was made, with the excavation of profiles followed by the chemical and granulometric characterization of each horizon. The soils were classified according to the new Brazilian soil classification system (EMBRAPA, 1999) up to the third and fourth category level. These soil classes were used in comparative analyses of tree phytocoenosis in subunits represented by the so-called soil habitats (Dalanesi *et al.*, 2004).

The drainage of each soil class was evaluated by allocating ranking numbers to the drainage classes defined by Resende (1986) and EMBRAPA (1999). To determine the chemical soil values five samples of about 0.5 litres were taken from the surface layer (0–10 cm) in 15 of the 100 plots of the floristic-sociological survey, thus totalling 75 samples. Five samples were taken per plot and the means and standard deviation of the chemical variables were computed. Statistical analyses were carried out using the STATISTICA program (Statsoft, 1998). Soil data were submitted to normality (Shapiro–Wilks) and homogeneity (Levene) tests, both before and after $\log_e x$ and $\sqrt{x}$ transformations. Results were then submitted to an analysis of variance and a *t* test at 5% probability (Tukey).

Distribution of species and soil and topographic variables

The correlations between the soil and topographic variables and the vegetation gradients were analysed by canonical correspondence analysis (CCA) (ter Braak, 1987) using the software PC-ORD for Windows version 4.14 (McCune & Mefford, 1999). The matrix of vegetation consisted of the absolute density of 28 species (Table 4) with more than 10 trees in the total sample. The concept of pedoenvironment (Resende *et al.*, 2002a) refers to areas within a given soil class but with a certain distinctive feature, such as landform, slope, exposure and altitude.

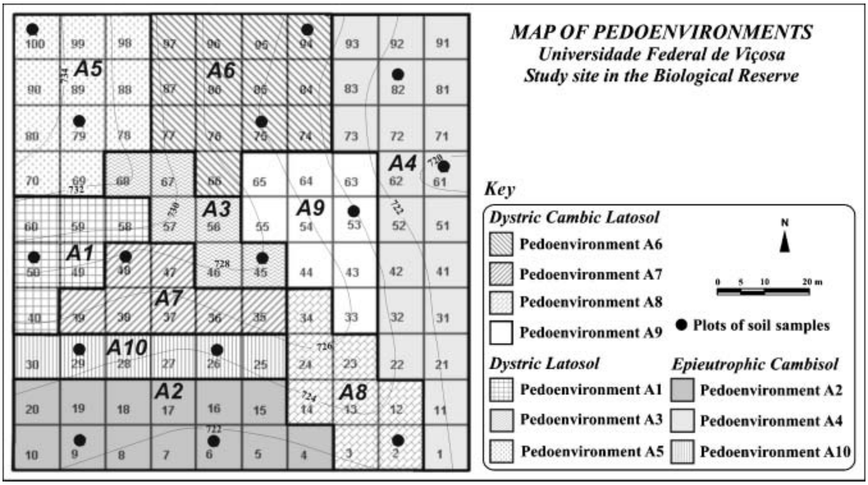

FIG. 2. Map of the spatial distribution of the 10 pedoenvironments and the plots where soil samples were collected.

The matrix of soils and topographic variables included the values obtained for the 15 plots sampled, grouped for similarity and used in the classification and definition of the 10 pedoenvironments (Fig. 2). In the final CCA procedure the following five most representative variables with the strongest correlation to the ordination axes were included: active acidity (pH), effective cation exchange capacity (t), organic matter (OM), aluminium saturation (m) and drainage classes.

The Monte Carlo permutation test was applied to verify the significance of the correlations between the emergent species patterns and soil and topographic variables in the final CCA.

RESULTS AND INTERPRETATION

Soil and topographic gradients

The first soil class comprised the Dystric Epieutrophic Cambisol (Fig. 3), renamed Epieutrophic Cambisol, being moderately drained and with a sandy loam soil texture. Landforms with this soil type have a flat to slightly undulating topography and occur near drainage lines and at the bottom of hollows. These are eutrophic habitats with a large soil water reserve, since they are accumulating environments. Observation of the chemical characteristics along the diagnostic profile of this soil class showed that the base saturation (V) attained a value of over 50% only in the 30 cm surface layer, indicating that a eutrophic environment occurred only in the most superficial layers. The environment was therefore designated as epieutrophic, meaning that eutrophic conditions occurred only in the surface layer.

The second class consisted of Cambic Dystrophic Red-Yellow Latosols (Fig. 3), henceforth designated Dystric Cambic Latosol. This is a well-drained soil of clayey

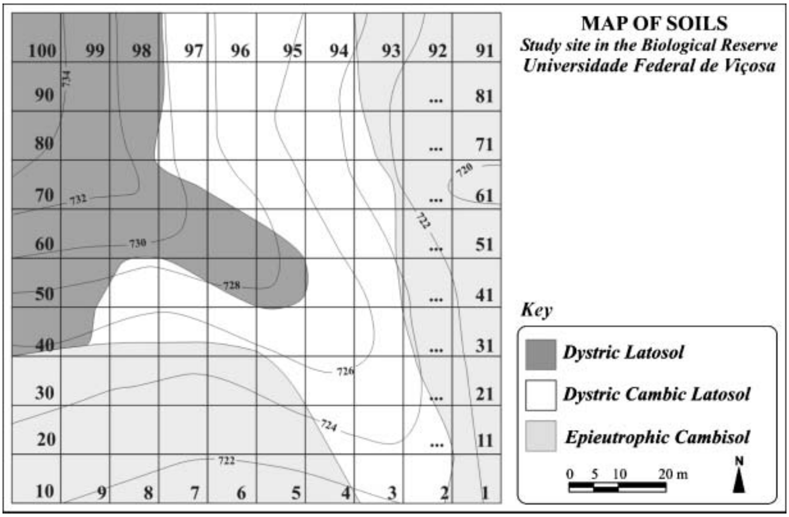

FIG. 3. Map of the spatial distribution of the three soil classes in the study area.

texture, situated on steep mountainsides occurring right beneath the Dystric Red-Yellow Latosol at the top and above the Epieutrophic Cambisol of the lowland. These areas of Dystric Cambic Latosol represent an intermediate environment in chemical fertility and soil water content between the Dystric Red-Yellow Latosol at the top and the Epieutrophic Cambisol of the lowland in these areas of intense mass movement where thick colluvial mantles are common.

The third class was represented by Dystric Red-Yellow Latosols (Fig. 3), henceforth called Dystric Latosol, with markedly drained soils of clayey texture. Such soils were found at the highest altitude on flat hilltops with gentle topography, characterizing a dystrophic environment with high exchangeable Al^{3+}.

It is noteworthy that the Dystric Cambic Latosol and the Epieutrophic Cambisol were influenced by mixed colluvial sediments, derived from the uplands. This is demonstrated by the observed soil layering down to 80 cm depth. In the past the local landscape was quite different from the present and drainage channels were not as well carved as they are now. In the lowland areas and the lower parts of the mountainsides there was a vast area with hydromorphic soils while Latosols prevailed in the well-drained uplands. This hypothesis was reinforced by the fact that on the lower part of the slopes where the Dystric Cambic Latosol was predominant, dark buried horizons of approximately 20 cm (80–100 cm deep) were observed, with an underlying mottled gley horizon of about 20 cm (100–120 cm deep). This fact demonstrates the influence of the groundwater on the development of these soils by the formation of an environment of redox oscillation that favoured the reduction of Fe^{3+} to Fe^{2+}, and the consequent drift of the latter from the system, giving the soil a greyish colour, later covered up with colluvial sediments.

The Epieutrophic Cambisol had the significantly highest Ca^{2+} and Mg^{2+} contents (Table 1) and did not differ statistically for K content from the Dystric Cambic Latosol. It therefore had the highest values of sum of bases (BS) and base saturation (V), besides presenting the highest pH, no exchangeable Al^{3+} and high organic matter content, similar to the Dystric Cambic Latosol. It also had the highest Zn and Mn contents. The Dystric Cambic Latosol had a high pH, though lower than the Epieutrophic Cambisol, and intermediate contents of Ca^{2+} and Mg^{2+}, resulting in a V lower than 50%, which made it dystrophic, with low Al^{3+} saturation (Table 1).

The Al^{3+} contents did not differ statistically between the Dystric Latosol and the Cambic Latosol. The Dystric Latosol of the hilltops was characterized by the higher acidity and low P, K and Ca^{2+} contents, resulting in the lowest BS and V values (Table 1). It also had the highest Cu and Fe contents, as well as the highest Al^{3+} saturation value, in consequence of the highest Al^{3+} contents.

In summary, if the sum of bases (BS) and base saturation (V) values are assumed to be indicators of the soil nutrient status one would obtain a gradient of increasing fertility beginning with the Dystric Latosol → Dystric Cambic Latosol → up to the Epieutrophic Cambisol. This trend in fertility was similar to the trend in soil drainage, since the deepest and most permeable was the Dystric Latosol (markedly drained) followed by the Dystric Cambic Latosol (well-drained) and down to the Epieutrophic Cambisol (moderately drained).

Structure of the vegetation on the soil habitats

Overall, the forest structure showed the valley bottoms with a closed forest, changing to an open forest on the slopes and hilltops. Three canopy layers are observed above the understorey. The lower layer reaches heights up to 5 m; the middle extends from 5 to 12 m high, and the upper reaches up to 25 m. The taller, emergent, species include *Cariniana estrelensis* Kuntze, *Cariniana legalis* Kuntze, *Allophylus edulis* Radlk. ex Warm. and *Senna multijuga* (L.C.Rich.) Irwin & Barneby. On the other hand, *Anadenanthera peregrina* (L.) Speg., *Cedrela fissilis* Vell., *Ceiba speciosa* (A.St.-Hil.) Gibbs & Semir, *Pseudobombax grandiflorum* (Cav.) A.Robyns and *Sapium glandulatum* Pax are the most common deciduous trees. Altogether 1460 trees were sampled with a total basal area of 29.68 m^2. In absolute values the tree and species density was higher on the Epieutrophic Cambisol, while the Dystric Cambic Latosol presented the highest values of basal area and mean dbh. However, no significant differences for these parameters were observed in the three sampled habitats (Table 2).

On the other hand, when balanced data consisting of the same number of plots per soil habitat (see Materials and Methods) were used (Table 2), the highest number of species was observed on the Dystric Latosol and the number of trees was highest on the Epieutrophic Cambisol. The basal area was larger in the Dystric Cambic Latosol and the tree density on the Epieutrophic Cambisol. The Dystric Latosol attained the highest diversity index (H') and a high equability value (J').

TABLE 1. Chemical properties of the soil classes in soil surface samples (0–10 cm depth) collected from 15 plots (Dystric Latosol = 3; Dystric Cambic Latosol = 6; Epieutrophic Cambisol = 6), amongst a total of 100 used in the floristic-sociological survey. The values are means with standard deviations (±) of the *N* samples of each soil class. Where the analyses of variance indicated significant differences between the soils, the means followed by the same letter did not differ from each other at 5% significance by the Tukey test

Property	Dystric Latosol (N = 3)	Dystric Cambic Latosol (N = 6)	Epieutrophic Cambisol (N = 6)	ANOVA	
				F	P
pH (H_2O)	4.6 ± 0.3 *c*	5.6 ± 0.5 *b*	6.5 ± 0.5 *a*	85.75	$<10^{-3}$
P (mg dm^{-3})*	1.1 ± 0.3	1.3 ± 0.6	1.2 ± 0.5	NS	
K ($cmol_c$ dm^{-3})*	34 ± 12 *b*	66 ± 25 *a*	84 ± 45 *a*	11.69	$<10^{-3}$
Ca^{2+} ($cmol_c$ dm^{-3})	0.94 ± 0.56 *c*	3.65 ± 1.58 *b*	6.1 ± 1.71 *a*	61.23	$<10^{-3}$
Mg^{2+} ($cmol_c$ dm^{-3})	0.41 ± 0.25 *c*	1.23 ± 0.37 *b*	2.04 ± 0.52 *a*	78.65	$<10^{-3}$
Al^{3+} ($cmol_c$ dm^{-3})	1 ± 0.5 *b*	0.1 ± 0.2 *b*	0.0 *a*	71.41	$<10^{-3}$
H + Al ($cmol_c$ dm^{-3})	8.1 ± 0.8 *c*	5.4 ± 1.5 *b*	2.7 ± 1.3 *a*	88.84	$<10^{-3}$
BS ($cmol_c$ dm^{-3})	1.44 ± 0.79 *c*	5.05 ± 1.85 *b*	8.35 ± 2 *a*	79.34	$<10^{-3}$
t ($cmol_c$ dm^{-3})	2.41 ± 0.56 *c*	5.17 ± 1.73 *b*	8.35 ± 2 *a*	65.58	$<10^{-3}$
T ($cmol_c$ dm^{-3})	9.51 ± 1.07 *b*	10.5 ± 1.37 *a b*	11.03 ± 1.9 *a*	4.75	0.01
V (%)	14.7 ± 6.8 *c*	47.6 ± 15 *b*	75.3 ± 11.3 *a*	124.18	$<10^{-3}$
m (%)	41.5 ± 22 *c*	3.6 ± 6.8 *b*	0.0 *a*	84.57	$<10^{-3}$
OM (dag kg^{-1})	4.62 ± 0.51 *b*	5.57 ± 0.95 *a*	6.17 ± 1.45 *a*	9.65	$<10^{-3}$
P-rem (mg l^{-1})	27 ± 2.4 *c*	33.9 ± 4.4 *b*	40.2 ± 3.6 *a*	64.34	$<10^{-3}$
Zn (mg dm^{-3})†	1 ± 0.38 *c*	3.74 ± 1.72 *b*	7.83 ± 3.84 *a*	36.72	$<10^{-3}$
Fe (mg dm^{-3})*	62.6 ± 14.5 *c*	20.8 ± 10.4 *b*	10.7 ± 10.2 *a*	110.71	$<10^{-3}$
Mn (mg dm^{-3})	7.4 ± 3.5 *b*	16.9 ± 7.1 *b*	65.9 ± 110.5 *a*	5.04	0.01
Cu (mg dm^{-3})	1.77 ± 0.27 *b*	1.45 ± 0.45 *a*	1.03 ± 0.69 *a*	10.6	$<10^{-3}$

BS, sum of bases; *t*, effective cation exchange capacity; *T*, total cation exchange capacity; *V*, base saturation; *m*, aluminium saturation; OM, organic matter; P-rem, remanescent phosphorus.

* $\log_e x$ transformation; † $\sqrt{x}$ transformation.

TABLE 2. Parameters of structure and tree sample composition in the plots representing the three soil classes in the total sample. The plots for all the soil classes were scored for the number of species, number of trees, Shannon's Diversity Index (H') and Pielou's Coefficient of Equability (J'). The values are means with standard deviation (±) of the number of plot (N) samples of each soil class. Analyses of variance and the F test applied at 5% probability were carried out for density, basal area, mean dbh and species density per plot

Soil	N	Density (ind. ha^{-1})	Basal area (m^2 ha^{-1})	Mean dbh (cm)	No. of trees	No. of species	Species density per plot
Dystric Latosol	23	1404 ± 377.2	21.55 ± 18.6	11.34 ± 2.9	323	72	10.09 ± 2.29
Dystric Cambic Latosol	38	1395 ± 446.6	32.97 ± 38.3	12.56 ± 3.4	530	80	9.53 ± 3.24
Epieutrophic Cambisol	39	1556 ± 535.5	31.27 ± 21.3	12.11 ± 2.3	607	86	10.48 ± 2.69
Total sample	100	1460	29.68	12.1	1460	131	10.03
ANOVA		$F = 1.16$, $P =$ 0.32 NS	$F = 1.8$, $P =$ 0.17 NS	$F = 0.49$, $P =$ 0.61 NS			$F = 1.11$, $P =$ 0.33 NS

Soil	N	No. of species	No. of trees	H'	J'	Basal area (m^2 ha^{-1})	Density (ind. ha^{-1})
Dystric Latosol	23	72	323	3.60	0.84	21.54	1404
Dystric Cambic Latosol	23	58	325	3.48	0.85	33.04	1413
Epieutrophic Cambisol	23	63	358	3.49	0.84	31.49	1556

Soil	N	No. rare spp.	% rare spp.
Dystric Latosol	23	32	44
Dystric Cambic Latosol	23	21	36
Epieutrophic Cambisol	23	22	35

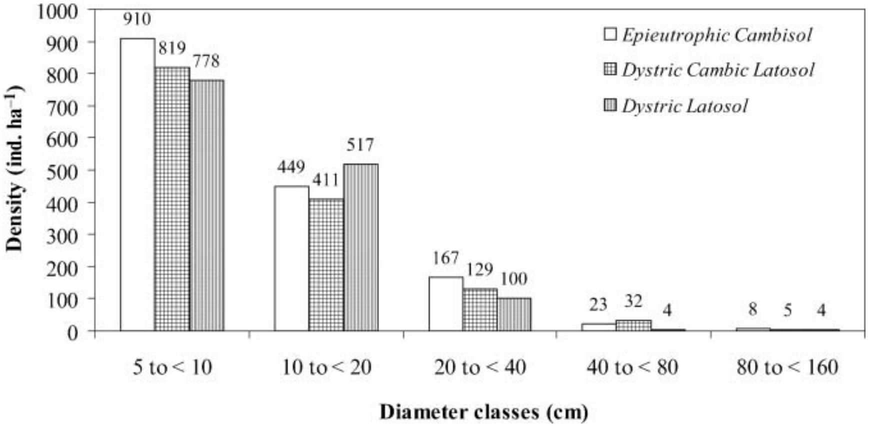

FIG. 4. Distribution of the number of trees with dbh ⩾ 4.77 cm in increasing diameter classes per soil class, in the 100 plots used to sample the tree community.

The tree density in the dbh classes from 5 to 10 cm, 20 to 40 cm and 80 to 160 cm was highest on the Epieutrophic Cambisol, and there was a decreasing density from the Dystric Latosol in these classes (Fig. 4). A marked difference was observed for the Dystric Latosol, where the dbh class between 10 and 20 cm contained the highest number of trees.

According to Martins (1991), rare species are those that have one or fewer individuals per hectare. In a comparison, the high number of rare species of the sample in the oligotrophic environment of the Dystric Latosol is interesting (Table 2). This observation, along with the high diversity and equability indices found in this environment, indicates a great heterogeneity of vegetation. This suggests that the tree populations cannot find favourable conditions for the establishment of a large number of trees, except for those species with specific characteristics that would give them a greater capacity to exploit the environment. This capacity can be observed in the two leguminous species whose distribution is nearly restricted to areas of Dystric Latosol. *Dalbergia nigra** had a population of 45 trees and of these, 42 were found in environments with low levels of nutrients and water availability. Likewise, nine of the 10 *Apuleia leiocarpa* trees were localized in these same environments.

Species distribution and soil and topographic variables

With the aim of investigating vegetation variation correlated with the soil and topographic gradient by means of the CCA, 10 pedoenvironments were marked off in the sample area, of which three represented the Epieutrophic Cambisol, four the Dystric Cambic Latosol, and three the Dystric Latosol areas (Fig. 2).

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[*] Authorities for species mentioned in the text are given in Table 4.

TABLE 3. Intraset correlations in the first two ordination axes, and weighted correlations matrix for the five environmental variables

Environmental variable	Intraset correlations		Environmental variable				
	Axis 1	Axis 2	pH	t	Al^{3+}	OM	Drainage
pH	−0.959	0.206	–				
t	−0.917	0.202	0.967	–			
Al^{3+}	0.917	0.247	−0.826	−0.805	–		
OM	−0.736	−0.183	0.738	0.859	−0.746	–	
Drainage	0.898	−0.215	−0.931	−0.975	0.732	−0.839	–

The eigenvalues presented by the CCA for the first two ordination axes were low, 0.370 (axis 1) and 0.168 (axis 2), indicating the existence of short gradients. This means that most species were distributed along the entire gradient, of which some varied only in density. Canonical correspondence analyses accounted for a low cumulative percentage variance of species abundance data, 38.7% and 56.4% for axes 1 and 2, respectively. According to Borcard *et al.* (1992), this may be due either to some overlooked factors or to a large amount of stochastic variation ('noise'). However, low percentage variances for species data are normal in vegetation data and do not impair the significance of species–environment relations (ter Braak, 1988). In fact, the CCA-generated positive values of species–environment correlations in axis 1 (0.97) and axis 2 (0.97) and the Monte Carlo tests of permutation indicated that the cited densities were also significantly correlated with the soil and topographic variables in use, with $P < 0.03$ for axis 1 and $P < 0.05$ for axis 2.

The first canonical axis is most strongly correlated with pH (negatively), followed by t (negatively) and aluminium saturation (positively), and these soil variables are also highly interrelated (Table 3).

The ordination axes clearly distinguished the three soil classes by grouping those of the Dystric Latosol (A1, A3 and A5) on the right of the diagram in the upper and lower quadrants, while those of the Epieutrophic Cambisol (A2, A4 and A10 pedoenvironments) are clustered in the upper left quadrant (Fig. 5A). The position of the pedoenvironments of the Dystric Cambic Latosol indicates the intermediary character of that soil habitat. The pedoenvironments A8 and A9 are close to the pedoenvironments of the Epieutrophic Cambisol in the upper left quadrant, while A7 and A6 are in the centre and lower right, respectively. The existence of a gradient of fertility and soil water content from the top down to the lowland areas, shown by the analysis of the chemical soil properties and physiographic factors, was confirmed by the observation of the same increasing gradient, from the left to the right of the ordination axes diagram (Fig. 5A).

The results obtained from the ordination of species by the CCA (Table 3, Fig. 5B) showed that *Siparuna guianensis*, *Amaioua guianensis*, *Luehea grandiflora*, *Coutarea hexandra*, *Anadenanthera peregrina*, *Apuleia leiocarpa* and *Dalbergia nigra* were

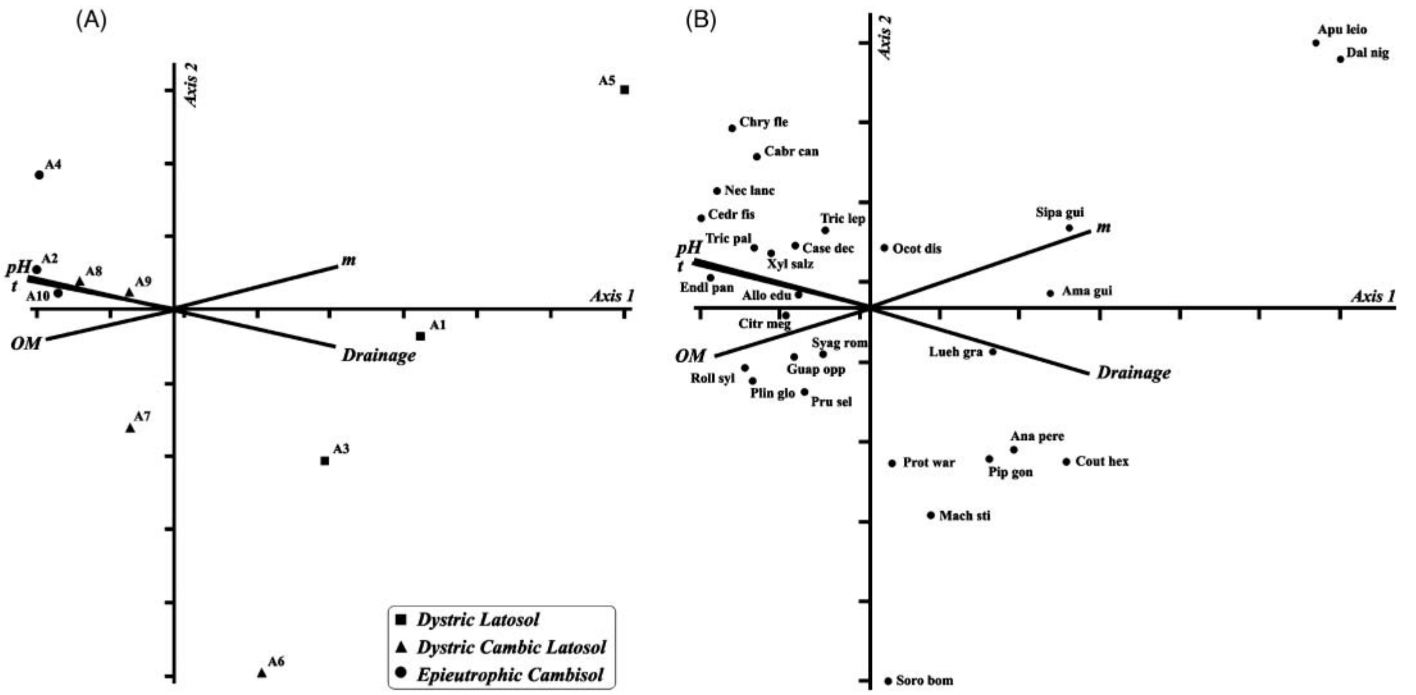

FIG. 5. Ordination diagrams of the pedoenvironments (A), of the species (B) and environmental variables in the first two ordination axes derived from the CCA, of the 28 species (see Table 4) with 10 or more trees sampled.

TABLE 4. Tree species and their abbreviations used in the canonical correspondence analysis (CCA)

Abbreviation	Species
Allo edu	*Allophylus edulis* Radlk. ex Warm.
Ama gui	*Amaioua guianensis* Aubl.
Ana pere	*Anadenanthera peregrina* (L.) Speg.
Apu leio	*Apuleia leiocarpa* (Vogel) J.F.Macbr.
Cabr can	*Cabralea canjerana* (Vell.) Mart.
Case dec	*Casearia decandra* Jacq.
Cedr fis	*Cedrela fissilis* Vell.
Chry fle	*Chrysophyllum flexuosum* Mart.
Citr meg	*Citronella megaphylla* (Miers) R.A.Howard
Cout hex	*Coutarea hexandra* (Jacq.) K.Schum.
Dal nig	*Dalbergia nigra* (Vell.) Allemão ex Benth.
Endl pan	*Endlicheria paniculata* (Spreng.) J.F.Macbr.
Gua opp	*Guapira opposita* (Vell.) Reitz.
Lueh gra	*Luehea grandiflora* Mart.
Mach sti	*Machaerium stipitatum* (DC.) Vogel
Nec lanc	*Nectandra lanceolata* Nees & Mart. ex Nees
Ocot dis	*Ocotea dispersa* Mez
Pip gon	*Piptadenia gonoacantha* (Mart.) J.F.Macbr.
Plin glo	*Plinia glomerata* (Berg) Amshoff
Prot war	*Protium warmingianum* March.
Pru sel	*Prunus sellowii* Koehne
Roll syl	*Rollinia sylvatica* (A.St.-Hil.) Mart.
Sipa gui	*Siparuna guianensis* Aubl.
Soro bom	*Sorocea bonplandii* (Baill.) W.C.Burger, Lanj. & Boer
Syag rom	*Syagrus romanzoffiana* (Cham.) Glassman
Tric lep	*Trichilia lepidota* Sw.
Tric pal	*Trichilia pallida* Sw.
Xyl salz	*Xylosma salzmannii* (Clos) Eichler

strongly correlated with better-drained oligotrophic soils with high Al^{3+} contents, low pH and reduced organic matter content (Fig. 5B). The position of *Apuleia leiocarpa* and *Dalbergia nigra*, which presented the two highest absolute score values for axis 1, is particularly interesting, and indicates that these species have a great capacity for growing in extremely leached and strongly drained environments.

At the far end of the ordination diagram, and consequently under quite distinct environmental conditions, the soils with higher pH, moderate drainage, gentle topography and higher t and V values were strongly correlated with the presence of the following species: *Cedrela fissilis*, *Cabralea canjerana*, *Nectandra lanceolata*, *Chrysophyllum flexuosum*, *Endlicheria paniculata*, *Rollinia sylvatica*, *Plinia glomerata* and *Trichilia pallida*. Amongst these, *Nectandra lanceolata*, *Chrysophyllum flexuosum* and *Endlicheria paniculata* were found only in Epieutrophic Cambisol soil habitats in the lowlands and lower third of the mountainsides in wetter areas of higher natural fertility.

DISCUSSION

As the silt content across the profile of the Epieutrophic Cambisol is higher and since this may represent an important nutrient reserve, a higher base saturation (V) would be expected ($V > 50\%$) throughout the profile and not only in the surface layer. This higher silt content is typical of younger Cambisols from the Zona da Mata Region (Nunes *et al.*, 2000). It may be concluded that the greatest amount of nutrients available in the surface layer of this soil is provided by the nutrient cycling process.

The heterogeneity of the environment, reflected in the different soil classes, is related to the topographic gradient of the area. Dystric Latosols are found on the hilltops with least slope, representing more leached and impoverished soils due to their advanced pedogenesis (EMBRAPA, 1999). In addition, drainage is more pronounced, characterizing a very oligotrophic acid environment rich in Al^{3+}. Resende *et al.* (1988, 2002a) observed that in dystrophic soils, the greater the slope, the greater the nutrient drift through erosion and leaching. Erosion is a more marked process than leaching and characterizes a less stable environment, where gains through weathering are limited, owing to the absence of easily decomposable primary minerals. This explains the drift of easily weathered primary minerals from the Dystric Latosol at the higher altitudes and the consequent deposition in the environments of the lowlands. This probably accounts for the existence of a much richer environment with high pH in the lowland areas where these minerals are accumulated in the Epieutrophic Cambisols.

On most of the steep slopes the Dystric Cambic Latosol represents a transitional environment with a tendency to form a eutrophic surface. According to Resende *et al.* (1988) the formation of an increasing nutrient and water content gradient from the top towards the bottom is common in soils of steep-sloping topography in the region.

According to Resende *et al.* (1988, 2002a, 2002b) and Guerra & Cunha (1996), younger soils tend to have a higher natural fertility, greater cation exchange capacity, greater quantity of primary easily weathered minerals, and higher silt content. In contrast, soils on the hilltops are more weathered, deeper, porous, and have lower natural fertility. These more weathered soils function as a great P drain, which becomes adsorbed to iron and aluminium oxides, in unavailable forms (Novais & Smyth, 1999; McGrath *et al.*, 2001; Resende *et al.*, 2002a).

According to Novais & Smyth (1999) soil characteristics gradually change with increasing weathering. The soil becomes positively charged, with very low cation exchange capacity and base saturation, whereas the retention of anions such as phosphate gradually increases.

The above observations explain the low nutrient contents observed (Table 1) in the Dystric Latosol of the hilltops and the high values of potential acidity ($H + Al$) and exchangeable Al^{3+}, aluminium saturation (m), as well as the strongly acid character (EMBRAPA, 1999). They also explain the low P content observed (Table 1) in the three soil classes, supporting the statement of Resende *et al.* (1988) that 65% of tropical soils are strongly P deficient and almost 27% have medium deficiency of this nutrient.

One aspect with ramifications for the conservation and recovery of the forest formations of the Brazilian Atlantic Forest is the presence of environments considered unstable due to erosion and nutrient losses. According to Resende *et al.* (2002b) the sparse nutrient resources present in the poor soils with deep *solum* (A+B horizons) are maintained under natural vegetation by the process of nutrient cycling. When the native vegetation is removed this process is drastically reduced, which significantly increases nutrient loss.

The high H' values and similar J' values of the three soil habitats indicate that the Dystric Latosol had the greatest diversity since dominance by only a few tree species did not occur.

According to Whitmore (1990) the higher species richness and low tree density on the Dystric Latosol is a common feature of tropical forests. The history of the formation of the present landscape with its prevailing oligotrophic soil habitats may help us to understand the greater tree diversity in an environment of great nutrient constraints. The landform stability on the hilltops where Dystric Latosol occurs is greater than in sloping areas on the mountainsides. An older and more stable environment is therefore preserved in the highest areas with gentle slopes on which a larger number of diaspores and survivors of vegetation from the past would be maintained. On the sloping hillsides, however, the situation would be quite different, owing to the greater disturbance and transience of the landscape.

The lowest values found for basal area and tree density in the oligotrophic soil habitat (Dystric Latosol) could be evidence that the lower availability of water and nutrients contributes, in this case, to the relatively lower biomass, reflected in the smaller basal area and the smaller number of trees.

Dalanesi *et al.* (2004) and Botrel *et al.* (2002), in studies conducted in riparian forest fragments in the municipal districts of Lavras and Ingaí (Minas Gerais, Brazil), respectively, detected low biomass values in soils with limited nutrient and water availability. In the second study, a high density of trees with thinner trunks was observed. The oligotrophic soils were, in both cases, localized in areas further away from watercourses, reinforcing the findings of other studies conducted in riparian forests (van den Berg & Oliveira-Filho, 1999; Espírito-Santo *et al.*, 2002; Souza *et al.*, 2003) namely that the soils are richer and have greater water availability when closer to a watercourse and at lower altitude.

The lower density of large trees in the Dystric Latosol, expressed by the low density in the dbh classes from 40 to 80 cm and from 80 to 160 cm, corroborates the hypothesis that restrictions to nutrient and water availability in the soil negatively influence the density and basal area in this soil habitat.

The low eigenvalues for axis 1, as much as for 2, are quite similar to those found by Botrel *et al.* (2002), Espírito-Santo *et al.* (2002), Souza *et al.* (2003) and Dalanesi *et al.* (2004). The accumulated global data variance, 56.4%, indicates that the variables integrated in the environmental matrix explain part of the localized occurrence of some species in certain pedoenvironments. The remaining 43.6% of the global variance that is unexplained may be attributed to environmental variables other than those considered, such as radiation, temperature and history of human disturbance (Oliveira-Filho *et al.*, 2004; Carvalho *et al.*, 2005a; Pinto *et al.*, 2006), or even to biological interactions such as competition (Tilman, 1997) and herbivory (Crawley, 1997).

In addition, considering that autocorrelation (spatial and temporal) is a very general statistical property of ecological variables observed across geographic space (Legendre, 1993), we may suppose that the spatial distribution of species and the associated environmental variables are the result of spatial autocorrelation.

The analysis of the pedoenvironment ordination diagram by CCA confirms the consistency of the use of the soil classification and of the use of the three soil classes as habitat determinators, as observed by Botrel *et al.* (2002), Espírito-Santo *et al.* (2002), Souza *et al.* (2003) and Dalanesi *et al.* (2004), in studies conducted in remnants of Seasonal Semideciduous Forest in the south of the state of Minas Gerais.

Richards (1952) stated that it is common in tropical forests for variations in soil properties to be related to their topographic positions. The reason is that slope and altitudinal variations determine, to a great extent, different water regimes in the soil and this, in turn, affects the soil texture and nutritional status.

The greater affinity of *Dalbergia nigra* for more effectively drained soils, with high Al^{3+} contents, low pH, reduced organic matter content and oligotrophy, may be related to the fact that it is a species of the *Leguminosae* with the capacity to fix nitrogen from the atmosphere by means of a symbiotic association with rhizobacteria (Faria *et al.*, 1984). This probably allows sufficient incorporation of this scarce nutrient into their biomass, despite the great mobility of N in the soil leading to large losses through leaching. Although species–environment studies in the Mata Atlântica (Atlantic Forest) have emphasized the community aspects (Espírito-Santo *et al.*, 2002; Martins *et al.*, 2003) and have not had a population emphasis, the data shown in the present study confirm the patterns observed in similar studies dealing with correlation within communities (e.g. van den Berg & Oliveira-Filho, 1999; Espírito-Santo *et al.*, 2002; Lorenzi, 2002; Martins *et al.*, 2003; Souza *et al.*, 2003).

Lorenzi (2002) and Meira-Neto *et al.* (2005) highlighted *Apuleia leiocarpa* as being indifferent towards edaphic conditions and commented that *Dalbergia nigra* preferred well-drained soils on hillsides. Oliveira-Filho *et al.* (2001) observed a strong correlation between this latter species and soils with high Al^{3+} contents and low pH. Lorenzi (2002) observed the preference of *Anadenanthera peregrina* and *Amaioua guianensis* for drier soils on hillsides. In a recent study carried out in a fragment of Seasonal Semideciduous Forest in Viçosa (Minas Gerais), Martins *et al.* (2003) detected a similar spatial distribution pattern for *Trichilia pallida*, *Endlicheria paniculata* and *Cabralea canjerana*. The findings of Lorenzi (2002) corroborated the preference of these species for wetter habitats, as observed in the present study.

Trichilia pallida has been cited as a species with a preference for more fertile soils. It is positively correlated with Ca^{2+} and Mg^{2+} content and pH, and negatively with Al^{3+} content (Oliveira-Filho *et al.*, 1994b, 1998, 2001).

In studies conducted in the municipal districts of Minas Gerais, Itutinga and Bom Sucesso, Oliveira-Filho *et al.* (1994a) reported the occurrence of *Cedrela fissilis* at a low density with a preference for more fertile soil habitats, while Ratter (1992) and Ratter *et al.* (1973, 1978) describe it as a characteristic forest species of more fertile soils in Central Brazil.

As indicated by Martins *et al.* (2003) and our own CCA data, the species *Siparuna guianensis*, *Amaioua guianensis*, *Luehea grandiflora*, *Coutarea hexandra*, *Anadenanthera peregrina*, *Apuleia leiocarpa* and *Dalbergia nigra* have a great potential for use in the recovery of degraded forest areas, such as hilltops and hillsides with degenerating pastures, which are characteristic of the landscape of the Zona da Mata in Minas Gerais.

In spite of the considerable 'noise' that remained unexplained, the patterns of tree species distribution in this study, verified by the CCA and confirmed by the Monte Carlo test, were related to the observed soil variations (soil fertility and texture) and the soil water regime (drainage), corroborating the observations of Oliveira-Filho *et al.* (1989, 1994a, 1997b, 2001, 2004), Oliveira-Filho & Ratter (1995), Botrel *et al.* (2002), Cardoso & Schiavini (2002), Espírito-Santo *et al.* (2002), Martins *et al.* (2003), Souza *et al.* (2003), Carvalho *et al.* (2005b), Meira-Neto *et al.* (2005) and Pinto *et al.* (2006).

Generalizations regarding the definition of preferential habitats for certain species, based on analyses of correlation between tree species and soil and topographic variables, must be interpreted with caution (Pinto *et al.*, 2006). Botrel *et al.* (2002) argued that the environmental variables responsible, such as light, water conditions and the factors controlling species dispersion, are not always easy to observe and measure.

Conclusions

The patterns of tree species distribution in forest are related to the observed soil variations (fertility and texture) and the soil water regime (drainage).

The area under study evidenced a marked soil gradient, directly associated with the geomorphology: hilltops with Al^{3+}-rich Dystric Latosols giving way to steep colluvial hillsides with shallower Dystric Cambic Latosols without Al^{3+}, and nutrient-rich Epieutrophic Cambisols at the bottom. The P contents in all pedoenvironments were low.

The upland Latosols are poorer, deeper and strongly drained, representing the most stable and oldest environment of the landscape. These showed the greatest species diversity and the lowest biomass.

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