



# Effect of selective logging on forest structure and nutrient cycling in a seasonally dry Brazilian Atlantic forest

Dora Maria Villela\*, Marcelo T. Nascimento, Luiz Eduardo O. C. de Aragão and Deborah M. da Gama

Laboratório de Ciências Ambientais, CBB, Universidade Estadual do Norte Fluminense (UENF), Campos dos Goytacazes, Rio de Janeiro, Brazil

## ABSTRACT

**Aim** The Brazilian Atlantic forest covers c. 10% of its original extent, and some areas are still being logged. Although several ecological studies in Atlantic forest have been published over the past two to three decades, there has been little research on forest dynamics and there is a particular lack of information on the effects of disturbance. The aim of the present study was to assess the impact of selective logging on forest structure, floristic composition soil nutrients, litterfall and litter layer in a seasonally dry Atlantic forest.

**Location** The Mata do Carvão is located in the Guaxindiba Ecological Reserve in São Francisco do Itabapoana district (21°24' S, 41°04' W), Rio de Janeiro, Brazil.

**Methods** Four plots (50 × 50 m) were set up in 1995 in each of two stands: unlogged and logged. In each plot, all trees ≥ 10 cm d.b.h. were enumerated, identified and measured. Vouchers were lodged at UENF Herbarium. Five surface soil samples were collected in each plot in the dry season (in October 1995). Litterfall was collected in eight traps (0.50 m<sup>2</sup>) in each plot over a year from 14 November 1995 to 11 November 1996. The litter layer was sampled in eight quadrats (0.25 m<sup>2</sup>) in each plot in the dry and wet seasons. Soils were air-dried, sieved, and chemically analysed. The litter was dried (80 °C), sorted into six fractions, weighed and bulked samples analysed for nutrients.

**Results** Forest stands did not differ in stem density and total basal area, with a total of 1137 individuals sampled in 1996 (564 unlogged and 573 logged), and a total basal area of 15 m<sup>2</sup> (unlogged) and 13.0 m<sup>2</sup> (logged). However, unlogged stands had more large trees (≥ 30 cm in d.b.h.) and greater mean canopy height. Among the families, Rutaceae and Leguminosae were the most abundant families in both sites, although the Rutaceae had a higher density in unlogged and Leguminosae in the logged stand. The species diversity index was similar between stands. Late-successional species, such as *Metrodorea nigra* var. *brevifolia* and *Paratecoma peroba*, were less abundant in the logged stand. Selective logging did not affect nutrient concentrations in the soil or in the litter. However, quantities of the nutrients in the total litterfall and in the leaf litterfall and litter layer were higher in unlogged than in logged stands, mainly as a result of fallen *M. nigra* leaves. *Metrodorea nigra* was considered a key species in the nutrients dynamics in Carvão forest.

**Main conclusions** Despite the fact that effects on tree diversity and soil nutrients were not clear, selective logging in this Atlantic forest altered canopy structure, increased the relative abundance of some early-secondary species and decreased the litter input and stock of nutrients. Detailed information on the influence of logging on the distribution and structure of plant populations and in nutrient processes is fundamental for a sustainable logging system to be developed.

\*Correspondence: Dora Villela, Laboratório de Ciências Ambientais, CBB, Universidade Estadual do Norte Fluminense (UENF), Av. Alberto Lamego 2000, Campos dos Goytacazes, Rio de Janeiro 28013-600, Brazil.  
E-mail: dora@uenf.br

## Keywords

Atlantic forest, Brazil, disturbance, floristic composition, litterfall, nutrient cycling, selective logging, tabuleiro forest.

## INTRODUCTION

The major land-use problem in tropical forests has been the clear-felling of entire stands leading to excessive forest fragmentation (Johns, 1992). The Brazilian Atlantic forest, represented mainly by two forest types called *mata ombrófila densa* (evergreen forest) and *mata estacional de terras baixas* (lowland seasonal forest) (Veloso *et al.*, 1991), has been reduced to *c.* 10% of its original area (Fundação SOS Mata Atlântica, 1998; Morellato & Haddad, 2000) for timber, pasture, agricultural monocultures or for reforestation with exotic tree plantations. This has left the remaining natural vegetation strongly fragmented (Fonseca, 1985). Since the last decade of the twentieth century, the amount of deforestation in Atlantic forests in Brazil caused by commercial logging using clear-felling operations has been greatly reduced. However, selective timber harvesting is common.

The intensity of the disturbance caused by selective logging is, in general, related to the number of trees harvested and the logging equipment used. This disturbance has been considered by some to produce little effect on forest structure, composition and dynamics (Deckker & de Graaf, 2003). However, others have reported changes in species composition (Silva *et al.*, 1995; Luna *et al.*, 1999; Magnusson *et al.*, 1999), forest structure (Silva *et al.*, 1995; Hall *et al.*, 2003; Okuda *et al.*, 2003), nutrient cycling (Herbohn & Congdon, 1993) and genetic diversity (Jennings *et al.*, 2001).

As emphasized by Congdon & Herbohn (1993), an understanding of nutrient cycling processes is fundamental to the management of natural and disturbed vegetation growing on tropical soils of low fertility. The deleterious effects of deforestation on litterfall production and nutrient dynamics were shown for some Amazonian forests (Uhl & Jordan, 1984) and tropical forests elsewhere (Ewel, 1976). The nutrient cycling and allocation patterns may also influence the successional processes (Ewel, 1976; Brown, 1982).

Several ecological studies have been published on Atlantic forest recently (notably Morellato & Haddad, 2000). However, there are few studies on forest dynamics (Gomes *et al.*, 2003) and there is a marked lack of information on the effects of disturbance on forest structure and nutrient cycling. A few investigators have studied the structural and compositional aspects of *tabuleiro*, which is a lowland type of Atlantic forest (Peixoto & Gentry, 1990; Jesus *et al.*, 1992; Rizzini *et al.*, 1997; Thomas *et al.*, 1998; Silva & Nascimento, 2001; Garay & Rizzini, 2003) and there have been a handful of studies on nutrient cycling and dynamics (Gama-Rodrigues, 1997; Louzada *et al.*, 1997; Villela *et al.*, 1998; Kindel *et al.*, 1999; Kindel & Garay, 2001). Published data on changes in forest structure and nutrients dynamics in

response to logging are very rare (Villela *et al.*, 1998; Kindel *et al.*, 1999).

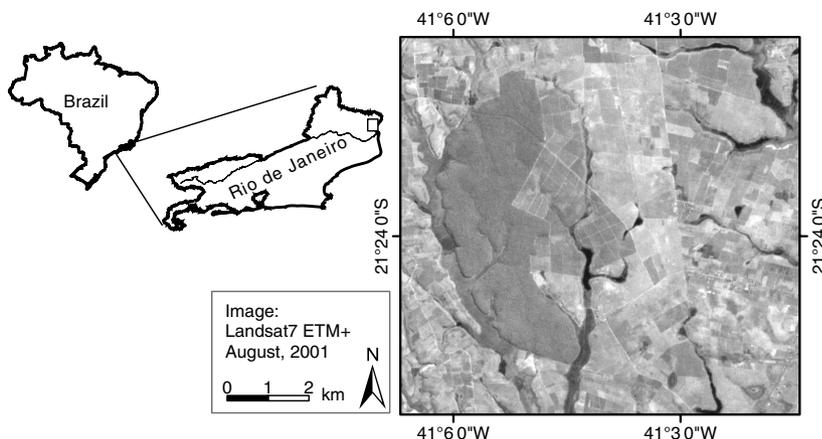
This paper presents the results of an investigation into the effects of selective logging on forest structure, floristic composition and nutrient cycling in a lowland seasonal Atlantic forest. It was hypothesized that as logging alters canopy structure, stem density and floristic composition, it would therefore also affect other functional aspects of the forest, such as soil chemistry, litter production and nutrient dynamics.

## STUDY SITE

The Mata do Carvão is located in the Guaxindiba Ecological Reserve in São Francisco do Itabapoana district (21°24' S, 41°04' W), Rio de Janeiro, Brazil (Fig. 1). The area of this forest has diminished over time owing to deforestation for charcoal production, plantation crops (sugar cane and pineapple), pasture and logging of commercial timber species such as *Aspidosperma* spp., *Machaerium* spp., *Paratecoma peroba* and *Talisia coriacea*. The Mata do Carvão, with an area of *c.* 1200 ha, is the largest remnant in north-eastern Rio de Janeiro State of a type of lowland Atlantic forest known as *tabuleiro* forest. The *tabuleiro* forest (also called *floresta estacional semidecidual de terras baixas*, Veloso *et al.*, 1991) is a lowland formation that, together with the other types of Atlantic forest and with the *restinga* (sand dune) forest, makes up a characteristic ecosystem of the Brazilian coast (Rizzini, 1979). The term '*tabuleiro* Atlantic forest' is associated with its distribution over large, flat areas on Tertiary deposits of crystalline rock – the Barreiras Group (RadamBrasil, 1983; Bôas *et al.*, 2001).

According to the Brazilian classification (EMBRAPA, 1999), the soils are *Argissolos amarelo textura arenosa* (Ultisols in the USDA classification). The climate is markedly seasonal, with an intense dry season from May to August. Mean annual rainfall is *c.* 1000 mm, with the wettest month being December and the driest being August. Mean annual temperature is 23 °C (RadamBrasil, 1983). The dry season is very windy, with winds blowing mainly from the north-east. The mean annual precipitation in Campos dos Goytacazes town (60 km from Carvão forest) from 1984 to 1995 was 851 mm, with a very marked dry season (May to August) and a mean monthly precipitation of < 100 mm. The mean annual temperature was 24 °C, ranging from 21 to 29 °C. The peak of leaf fall occurs in the dry season, with an annual litterfall production of 7.6 t ha<sup>-1</sup> (Villela *et al.*, 1998).

The Carvão forest consists mainly of secondary semi-deciduous forest, with small patches of flooded ground. The



**Figure 1** Map of location of Mata do Carvão (Guaxindiba Ecological Reserve), São Francisco de Itabapoana, Rio de Janeiro, Brazil.

most species-rich families are Leguminosae, Myrtaceae and Euphorbiaceae; the most important species being *Metrodorea nigra* (Rutaceae), *Paratecoma peroba* (Bignoniaceae) and *Pseudopiptadenia contorta* (Leguminosae) (Silva & Nascimento, 2001).

The forest has not been managed and all ongoing logging can be considered illegal. The logging regime comprised a single cycle of harvesting of selected trees from c. 20 species, mainly for local trade.

## METHODS

### Plot selection and floristic samples

Two forest stands of 25 ha each were selected: one with no signs of logging and the other in a recently logged area (c. 5 years since logging). The distance between the two stands is c. 600 m. The selected forest stands are believed to have been similar before logging. In October 1995, four replicate plots of 50 × 50 m were randomly located in each of the two stands.

From October 1995 to May 1996, all trees and lianas (≥ 10 cm d.b.h.) in the four 50 × 50 m replicate plots in each stand (unlogged and logged) were recorded, measured for the diameter at breast height (d.b.h., 1.3 m), and marked, with a permanent aluminium tag. For trees with large buttresses, or prop roots reaching more than 1.3 m high, the diameters were measured 20 cm above these protrusions. In the few cases of trees with multiple stems, each stem was measured separately and the sum of the basal areas was taken as the tree basal area. Felled trees were measured for the diameter at a height of c. 40 cm above the soil surface. During the enumeration, each tree was identified as far as possible in the field and confirmed from collected specimens. Voucher specimens were lodged at the Herbarium of the Universidade Estadual do Norte Fluminense and Instituto de Pesquisa Jardim Botânico in Rio de Janeiro.

Following Tabarelli & Mantovani (1999), species were classed into three functional groups, pioneers, early-secondary species and late-secondary species, to verify whether

there is a relationship between functional groups and logging.

### Soils, litterfall and small litter layer sampling

Five surface (0–10 cm) soil samples, each of c. 200 g fresh weight, were collected at five random stratified points within each of the four plots in each forest stand in the late dry season (October 1995). The soil samples were air-dried, sieved (< 2 mm mesh), and stored for chemical analyses.

Litterfall was collected in 50 × 100 cm (0.50 m<sup>2</sup>), 10-cm deep traps made of 2-mm nylon mesh and placed c. 1 m above the forest floor. Eight traps were positioned in a randomly stratified way in each of the four plots in each forest stand. The traps were set up at the beginning of the rainy season on 14 November 1995. Litterfall was collected from 28 November 1995 to 11 November 1996 at 14- to 18-day intervals, with the exception of the period from 12 December 1995 to 11 January 1996 (30 days). The total sampling period of the litterfall data was 363 days. The contents of the litter traps were placed in paper bags and dried in a circulation oven at 80 °C after each collection. The litterfall from each trap was sorted into: (1) *Metrodorea nigra* (Rutaceae) leaves, (2) *Paratecoma peroba* (Bignoniaceae) leaves, (3) other leaves, (4) small wood fragments (≤ 2 cm in diameter), (5) flowers and fruits, (6) trash (small < 2 mm, miscellaneous plant and animal debris and frass). The fractions were re-dried and their weights recorded. The leaf species selection was based on the species abundance in the forest.

The small litter lying on the forest floor, as defined by Proctor (1987), was removed from the forest floor within a 50 × 50 cm (0.25 m<sup>2</sup>) quadrat, at one random point in each of the eight litter-trap subplots in each plot in the two forest areas. Two samples were then collected, the first in the mid dry-season (August 1996) and the second at the end of the wet-season (February 1997). The location of the first collection was avoided at the second. The contents of the quadrats were sorted and processed in a similar way to the litterfall mass.

## Chemical analysis

Soil sub-samples from each soil sample were sieved to  $\leq 63 \mu\text{m}$  for C and N analysis. Total C and N were determined using a CHN/SO (PerkinElmer 2400, Series II, Shelton, CT, USA) auto-analyser. Sub-samples of soil (10 g) were leached by ten successive additions of 10 mL 1 M ammonium acetate solution adjusted to soil pH with acetic acid for the analysis of Ca, K and Mg by ICP–AES (Varian Liberty Series II, Axial, Varian, Melbourne, Australia) (Allen, 1989).

The litterfall samples were bulked for each two consecutive months from the eight traps in each plot for all fractions. The small litter layer samples were bulked from the eight quadrats in each plot for all fractions in each of the two sampling seasons. The litter samples were ground in an electric mill for chemical analysis. Sub-samples were homogenized and sieved to  $\leq 63 \mu\text{m}$  for total C and N determination using a CHN/S auto-analyser. For cations, sub-samples (c. 0.20 g dry weight) of each ground sample were digested in 4.4 mL of concentrated sulphuric acid (350 mL), 100 volume hydrogen peroxide (420 mL), selenium (0.42 g) and lithium sulphate (14 g) (Allen, 1989). Ca, K and Mg were determined by ICP–AES (Varian Liberty Series II). All chemical analyses were carried out at the Environmental Sciences Laboratory (LCA) at UENF University, Brazil.

## Data analysis

The floristic data were analysed using the FITOPAC package designed by George Shepherd (Department of Botany, University of Campinas, São Paulo, Brazil). Relative density (RD), relative dominance (Rdo) and cover value (CV) of each family or species were calculated according to Cottam & Curtis (1956). Family and species similarity between each stand was calculated using the Sørensen index; species diversity was measured using the Shannon index (Brower & Zar, 1977). A *t*-test was used to compare the mean values of species diversity, total basal area, density, number of standing dead trees and species richness between stands (Zar, 1984). Between-area comparisons of the soil properties, annual litterfall and small litter layer concentrations and quantities for each bulked sample were tested using one-way analysis of variance (ANOVA) (Zar, 1984). To test differences in litterfall nutrient concentration and quantities pattern between areas with time, an ANOVA with repeated measurement design was applied. For this analysis, time was considered the within-subject factor, and area and plot were taken as the between-subject factors. The multiple comparisons of the forest means were made using a Tukey test (Zar, 1984).

## RESULTS

### Forest structure and floristic composition

Profile diagrams of unlogged and logged stands (Fig. 2) showed the unlogged stand having the tallest trees (reaching

35 m). It also had the highest canopy (20–25 m) and a better developed understorey (10–18 m), while the logged stand had an open canopy and a poor understorey.

No significant difference in stem density was found between unlogged and logged forest stands; however, the unlogged stand had a significantly higher density of large trees ( $> 30 \text{ cm d.b.h.}$ ) (Table 1). The diameter distribution patterns of plants were similar between stands, showing a reversed-J shape curve. Both stands had a high density of stems of a d.b.h. of 10–30 cm and a paucity of trees  $> 50 \text{ cm d.b.h.}$  (Fig. 3). The mean number of standing dead trees per plot was similar between stands (18 unlogged and 22 logged). No significant difference in basal area was found between the unlogged and logged stands (Table 1).

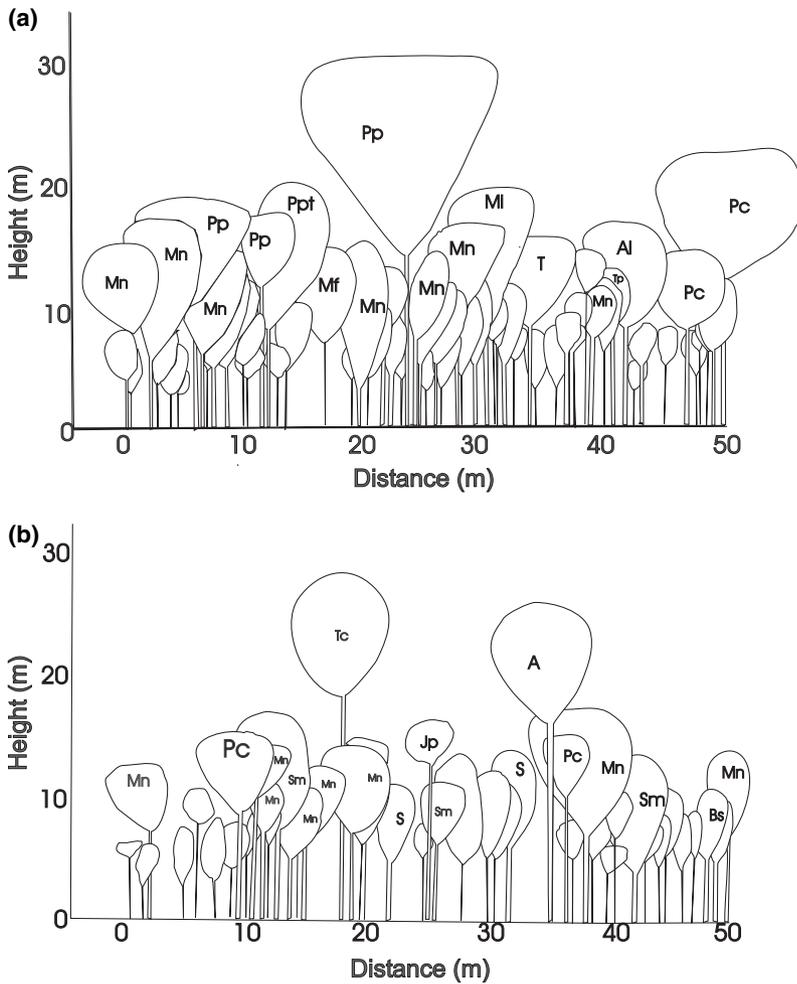
A total of 74 tree species was recorded in the unlogged stand. In the logged stand, a total of 78 species were distinguished. The mean species richness for the trees ( $\geq 10 \text{ cm d.b.h.}$ ) and the Shannon diversity indices (unlogged,  $H' = 3.16$ ; logged,  $H' = 3.25$ ) were similar between the two stands (Table 1).

Altogether, 36 families were recorded in the unlogged stand and 35 in the logged one. Rutaceae, Euphorbiaceae and Leguminosae were the most abundant families in both stands, followed by Bignoniaceae, Meliaceae and Myrtaceae in unlogged stand, and Burseraceae, Chrysobalanaceae and Sapotaceae in logged stand. Families well-known for their high numbers of pioneer and early-secondary species such as Bombacaceae, Moraceae and Leguminosae were more abundant in the logged stand.

*Metrodorea nigra* was the most abundant tree species in all diameter classes in both stands, comprising 32% of trees in the unlogged stand and 23% in the logged stand (Table 2). Species such as *Machaerium* spp, *Paratecoma peroba* and *Trichilia pseudostipularis* were less well represented in the logged stand. *Paratecoma peroba* was the second most dominant species in the unlogged stand and it ranked fifteenth in the logged stand.

About 17% (unlogged) and 11% (logged) of trees were not classified into any of the three functional groups. In both stands, pioneer trees were less than 1% of all recorded individuals. Early-secondary species represented 24% (unlogged) and 38% (logged) of the sampled individuals in each stand. For late-secondary species the corresponding values were 57% and 50%. A statistically significant difference was found only for the number of individuals of early-secondary species (*t*-test =  $-4.02$ , d.f. 6,  $P = 0.007$ ), with the highest value found for a logged plot. Early-secondary species such as *Acacia polycephala*, *Pachystroma longifolium* and *Pseudopiptadenia contorta* had at least three times more trees in the logged than in the unlogged stand.

The average number of trees harvested per plot (0.25 ha) in the logged stand was  $9 \pm 4.9$  (SD) or 37 trees  $\text{ha}^{-1}$ , with mean values of 28 cm for d.b.h. and 0.07  $\text{m}^2$  for basal area. From the total of 37 individual trees harvested in the logged plots, 41% were unidentified, 27% were *Neoraputia alba*, 11% *Copaifera lucens* and *Talisia coriacea*, and 21% were of



**Figure 2** Profile diagrams (50 × 7.5 m) of unlogged (a) and logged (b) stands in Carvão forest, Rio de Janeiro, Brazil. Trees less than 6 m tall excluded. Symbols for trees ≥ 10 cm d.b.h.: A, *Actinostemon verticillatus*; Al, *Acosmium lentiscifolium*; Ap, *Alseis pickelli*; Bs, *Bombacopsis stenopetala*; Jp, *Joannesia principis*; Mi, *Machaerium incorruptibile*; M, *Maytenus brasiliensis*; Me, *Metternichia principis*; Mn, *Metrodorea nigra*; Mf, *Myrocarpus frondosus*; Pl, *Pachystroma longifolium*; Ppt, *Parapiptadenia pterosperma*; Pp, *Paratecoma peroba*; Pc, *Pseudopiptadenia contorta*; Sm, *Senefeldera multiflora*; T, *Tabebuia serratifolia*; Tc, *Talisia coriacea*; Tp, *Trichilia pseudostipulares*; and Z, *Zanthoxylum rhoifolium*.

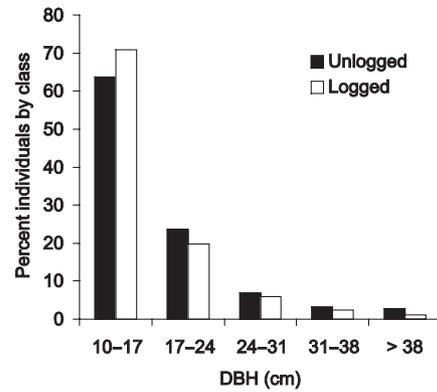
**Table 1** Mean values of total basal area (m<sup>2</sup>) per 0.25 ha, density of trees per 0.25 ha, standing dead trees, harvested trees and early successional trees in 0.25 ha plots in unlogged and logged stands (5 years post-logging) in the Guaxindiba Ecological Reserve (Mata do Carvão), Rio de Janeiro, Brazil. Means within a row followed by different letters are significantly different (*t*-test, *n* = 8 samples, i.e. four plots from each stand; *P* < 0.05)

	Unlogged	Logged
Basal area	3.74 ± 0.51	3.25 ± 0.65
Density of early-secondary species	34 ± 8.1 <sup>a</sup>	54 ± 6.1 <sup>b</sup>
Density of harvested trees	0 ± 0.0 <sup>a</sup>	9 ± 4.9 <sup>b</sup>
Species richness	40 ± 6.2	45 ± 4.5
Standing dead trees	18 ± 7.8	22 ± 5.2
Stem density	141 ± 10.9	143 ± 19.1
Trees > 30 cm d.b.h.	9 ± 2.6 <sup>a</sup>	5 ± 1.4 <sup>b</sup>

another eight species (such as *Paratecoma peroba* and *Tabebuia* spp.).

**Nutrients in soils and litter**

The concentrations of the soil nutrients analysed were not significantly different between stands (Table 3). For the total



**Figure 3** Diameter distributions of all individuals ≥ 10.0 cm d.b.h. sampled in four unlogged (*n* = 564 trees) and logged (*n* = 573 trees) stands of 50 × 50 m in Carvão forest, Rio de Janeiro, Brazil.

annual litterfall, only the Mg concentration was significantly different between unlogged and logged stands, being higher in the unlogged stand (Table 4). Nevertheless, quantities of most nutrients in the total annual litterfall were significantly

**Table 2** The 12 most important species of trees ( $\geq 10$  cm d.b.h.) occurring in four replicate  $50 \times 50$  m plots in unlogged and logged stands in Mata do Carvão, with number of individuals ( $n$ ), relative density ( $RD = \sum n_i/N$ , where  $n_i$  = number of individuals in the  $i$ th species and  $N$  = total number of individuals), relative dominance ( $Rdo = \sum BA_i/BA_t$ , where  $BA_i$  = value of basal area of  $i$ th species and  $BA_t$  = total basal area of species) and functional group (FG) = PI, pioneer species; ES, early-successional species; LS, late-successional species; NC, not classified

	$n$	RD	Rdo	FG
<b>Unlogged stand</b>				
<i>Metrodorea nigra</i> St. Hill. var <i>brevifolia</i> Engl.	181	32.1	27.6	ST
<i>Paratecoma peroba</i> (Record) Kuhlman	17	3.0	8.5	ST
<i>Pseudopiptadenia contorta</i> (DC.)Lewis & Lima	36	6.4	3.8	SI
<i>Trichilia pseudostipularis</i> (A. Juss.)DC.	31	5.5	3.7	ST
<i>Talisia coriacea</i> Radlk.	8	1.4	5.1	ST
<i>Acacia polyphylla</i> (DC.)Benth.	22	3.9	2.5	SI
<i>Eugenia</i> sp. 1	14	2.5	3.0	NC
<i>Parapiptadenia pterasperma</i> (Benth.)Brenan	9	1.6	3.3	SI
<i>Trigoniodendron spiritusantense</i> Guim. & Miguel	14	2.5	2.4	ST
<i>Opuntia brasiliensis</i> (Willd.)Haw.	11	1.9	2.9	SI
<i>Hieronynia oblonga</i> (Tul.) Muell. Arg.	14	2.5	1.7	NC
<i>Alseis pickelli</i> Pilger et Schmale	12	2.1	1.9	ST
Others ( $n = 62$ )	196	34.6	33.6	
<b>Logged stand</b>				
<i>Metrodorea nigra</i> St. Hill var <i>brevifolia</i> Engl.	139	24.3	23.6	ST
<i>Pseudopiptadenia contorta</i> (DC.)Lewis & Lima	77	13.4	8.9	SI
<i>Trigoniodendron spiritusantense</i> Guim. & Miguel	18	3.1	6.6	ST
<i>Pachystroma longifolium</i> (Nees) I.M.Johnston	28	4.9	4.0	SI
<i>Copaifera lucens</i> Dwyers	14	2.4	4.6	ST
<i>Protium heptaphyllum</i> (Aublet) Marchand	11	1.9	4.9	SI
<i>Acacia polyphylla</i> (DC.) Benth.	22	3.8	2.9	SI
<i>Talisia coriacea</i> Radlk.	5	0.9	4.0	ST
<i>Chrysophyllum lucentifolium</i> Cronq.	17	3.0	1.8	ST
<i>Acosmium lentiscifolium</i> Schott	11	1.9	2.6	SI
<i>Trichilia pseudostipularis</i> C.D.C.	15	2.6	1.5	ST
<i>Parapiptadenia pterasperma</i> (Benth.)Brenan	13	2.3	1.7	SI
Others ( $n = 66$ )	203	35.5	32.9	

higher in unlogged than in logged plots (Table 5). This pattern was observed for most nutrients of the leaf litterfall fraction, especially for *Metrodorea nigra* leaf litterfall (Table 5). The seasonal pattern of the nutrient input through the litterfall was similar between stands, with a peak in the dry season.

**Table 3** Soil surface (0–10 cm) nutrient concentrations and C/N ratio of unlogged and logged stands during the dry season in Carvão forest, Rio de Janeiro, Brazil. Values are means (from five samples in each of the four plots per stand) with standard deviation in parenthesis

Stands	Dry season (October 1995)					
	Percentage			mmol <sub>c</sub> kg <sup>-1</sup>		
	C	N	C/N	Ca	K	Mg
Unlogged	4.64 (0.47)	0.37 (0.04)	12.41 (0.38)	46.0 (27.6)	2.15 (0.41)	10.8 (4.03)
Logged	4.63 (1.08)	0.37 (0.08)	12.68 (0.22)	53.3 (18.9)	2.53 (0.51)	12.7 (2.96)

Leaves were the bulk of the litterfall in relation to the input of C (61–68%), N (69–76%), Ca (55–56%), K (56–60%) and Mg (58–66%), particularly *M. nigra* leaves, which represent from 26% (Mg) to 48% (N) of the total leaf fraction input through the litterfall. Of other abundant tree species, *P. peroba* made a small contribution to the annual input of nutrients (Table 5).

The concentrations of C (unlogged = 45.2%, logged = 44.9%), N (unlogged = 2.06%, logged = 2.00%) and cations (unlogged, Ca =  $15.4 \pm 4.80$ , K =  $4.74 \pm 1.52$ , Mg =  $2.80 \pm 0.94$  mg g<sup>-1</sup>; logged, Ca =  $14.0 \pm 4.14$ , K =  $4.34 \pm 1.34$ , Mg =  $2.53 \pm 0.88$  mg g<sup>-1</sup>), in the annual litter layer did not differ between forest stands, except for Ca concentration in the *M. nigra* leaf fraction, which was significantly higher in unlogged ( $15.3 \pm 0.44$  mg g<sup>-1</sup>) than in logged stands ( $13.9 \pm 2.18$  mg g<sup>-1</sup>). The annual stock of nutrients in the total litter layer was also not significantly different between stands (Table 6). However, the stock of nutrients in all leaf fractions of the small litter layer were significantly higher in unlogged than in logged plots, leading to a reduction of C (26%), N (23%), Ca (38%), K (36%) and Mg (37%) in the small leaf-litter layer.

## DISCUSSION

### Forest structure, florist composition and nutrient cycling in Carvão forest

The values of stem density and basal area found in both stands are within the lower range of values reported for other Atlantic rain forests (Peixoto *et al.*, 1995; Moreno *et al.*, 2003). Tree species typical of the middle or lower stories dominated the canopy, such as *Metrodorea nigra*, *Pseudopiptadenia contorta* and *Trichilia pseudostipularis*. These results confirm that the Carvão forest is secondary, as already indicated by Silva & Nascimento (2001), as it had been disturbed *c.* 30–40 years ago.

Concentrations of C and N in soil and litterfall are within the range and Mg and K concentrations and quantities in the upper range of values reported for most Atlantic forest stands (Mazurec, 1998) and other tropical forests (Vitousek & Sanford, 1986; Proctor, 1992; Villela & Proctor, 1999). However, the Ca concentration in the Carvão forest soil is above the range for *tabuleiro* (Gama-Rodrigues, 1997) and sub-montane Atlantic forests (Mazurec, 1998), lowland Amazon forest (Nascimento *et al.*, 1997) and tropical forests elsewhere (Proctor, 1992). The levels are similar or higher than

**Table 4** Mean concentrations ( $\text{mg g}^{-1}$  oven dry weight) of nutrients and C/N ratio (SD) in litterfall collected over a year from four replicate plots in unlogged (U) and logged (L) stands in Carvão forest, Rio de Janeiro, Brazil. Significant differences between stands for each fraction and for the total are represented by different letters within a column (one-way ANOVA,  $P < 0.05$ )

Fractions	Stands	C (%)	N (%)	C/N	Ca ( $\text{mg g}^{-1}$ )	K ( $\text{mg g}^{-1}$ )	Mg ( $\text{mg g}^{-1}$ )
<i>M. nigra</i>	U	45.12 (0.90)	2.04 (0.24)	22.56 (2.58)	18.53 (2.20)	7.75 (0.33)	4.05 (0.37)
	L	45.52 (1.47)	2.10 (0.25)	21.96 (2.47)	17.14 (0.75)	6.59 (0.38)	3.80 (0.23)
<i>P. peroba</i>	U	–	–	–	15.97 (0.90)	7.61 (0.86)	4.51 (0.36)
	L	–	–	–	14.38 (1.44)	7.25 (0.30)	4.02 (0.12)
Other leaves	U	45.99 (1.34)	2.14 (0.26) <sup>a</sup>	21.71 (2.52)	13.64 (1.24)	6.28 (1.36)	4.41 (0.19)
	L	45.57 (0.72)	1.99 (0.18) <sup>b</sup>	23.11 (2.27)	15.18 (0.57)	6.43 (0.29)	3.35 (0.09)
Wood	U	45.29 (0.55)	1.85 (0.32)	25.00 (3.75)	20.30 (1.86)	4.09 (0.11)	2.15 (0.26)
	L	45.59 (1.29)	1.72 (0.16)	26.70 (2.41)	18.22 (2.30)	4.01 (1.08)	1.97 (0.21)
Flower and fruit	U	45.55 (0.78)	2.32 (0.46)	20.24 (3.52)	8.44 (0.15)	9.62 (1.23)	2.57 (0.17)
	L	45.98 (1.42)	2.64 (0.55)	18.34 (5.18)	8.95 (0.75)	8.53 (0.94)	2.42 (0.18)
Trash	U	46.39 (0.67)	2.40 (0.50)	19.95 (3.59)	15.32 (1.00)	5.62 (0.78)	2.57 (0.14)
	L	46.55 (1.10)	2.37 (0.39)	20.05 (3.16)	14.23 (1.21)	4.52 (0.47)	2.46 (0.29)
Total mean	U	45.67 (0.52)	2.15 (0.22)	21.85 (2.02)	15.37 (0.71)	6.83 (0.42)	3.38 (0.10) <sup>a</sup>
	L	45.84 (0.44)	2.16 (0.35)	22.03 (3.18)	14.68 (0.51)	6.22 (0.22)	3.00 (0.08) <sup>b</sup>

**Table 5** Estimated rate of quantities ( $\text{kg ha}^{-1} \text{ year}^{-1}$ ) of nutrients in litterfall collected over a year from four replicate plots in unlogged (U) and logged (L) stands in Carvão forest, Rio de Janeiro, Brazil. Values are means ( $n = 4$ ) with standard deviations in parentheses. Significant differences between stands for each fraction and for the total are represented by different letters within a column (one-way ANOVA,  $P < 0.05$ )

Fractions	Stands	C	N	Ca	K	Mg
<i>M. nigra</i>	U	1373 (203) <sup>a</sup>	68.4 (9.8) <sup>a</sup>	30.44 (4.03) <sup>a</sup>	15.99 (6.42)	9.50 (1.10) <sup>a</sup>
	L	986 (91) <sup>b</sup>	49.9 (7.3) <sup>b</sup>	21.36 (3.72) <sup>b</sup>	12.75 (3.75)	4.69 (0.85) <sup>b</sup>
<i>P. peroba</i>	U	–	–	4.76 (1.03)	2.86 (0.69)	1.77 (0.77)
	L	–	–	5.07 (2.61)	2.88 (1.07)	1.45 (0.56)
Other leaves	U	1722 (634)	74.9 (26.7)	59.37 (21.3)	25.28 (6.74)	14.05 (1.23) <sup>a</sup>
	L	1285 (276)	55.9 (17.6)	52.40 (19.5)	24.91 (7.02)	11.62 (1.46) <sup>b</sup>
Wood	U	668 (73)	18.2 (6.5)	38.05 (20.6)	11.15 (2.30)	3.80 (0.85)
	L	624 (89)	17.4 (7.0)	34.03 (19.9)	8.96 (2.41)	5.19 (0.75)
Flower and fruit	U	273 (47)	12.0 (4.2)	2.45 (0.81)	2.45 (0.56)	1.18 (0.19)
	L	289 (39)	13.1 (5.9)	2.99 (1.46)	2.55 (1.23)	1.05 (0.73)
Trash	U	488 (59)	16.7 (5.3)	36.11 (16.7)	21.33 (4.88)	7.94 (2.37)
	L	521 (101)	17.3 (6.9)	23.44 (16.3)	15.80 (7.26)	6.97 (1.40)
Total	U	4526 (938) <sup>a</sup>	189.3 (62.8)	171.36 (69.7) <sup>a</sup>	79.16 (8.66) <sup>a</sup>	38.49 (3.58) <sup>a</sup>
	L	3708 (875) <sup>b</sup>	154.1 (72.4)	139.56 (71.5) <sup>b</sup>	67.58 (6.30) <sup>b</sup>	30.39 (3.17) <sup>b</sup>

those of *restinga* soils (Silva, 2003) in Brazil. A similar trend was found for Ca concentration in leaf litter and its quantities in the total litterfall.

The seasonal input of all nutrients through litterfall in both areas of the Carvão forest followed the same pattern as litter mass production (Villela *et al.*, 1998), with a peak in the middle of the dry season. Many cases have been reported where the peak of litterfall nutrient input was in the dry season: for example, in *tabuleiro* forest of southeast Brazil (Louzada *et al.*, 1997), in semi-deciduous Atlantic forest (Pagano, 1989), in evergreen and semideciduous forests in Amazonia (Villela & Proctor, 1999), and in other tropical forests elsewhere (Villela & Proctor, 1999). The higher stock of nutrients in the small litter layer in the dry than in the wet season was a consequence

of the high input and low litter decomposition rate during this season (Aragão, 2000).

### Is selective logging affecting the structure, floristic and nutrient cycling in Carvão forest?

The effects of selective logging on forest structure and species abundance were extensive and remained evident 5 years after the termination of the logging operation. The profile diagrams of unlogged and logged stands showed differences in canopy structure, mainly in height and in crown connectivity and this finding has been reported for many other places in the tropics (Gullison & Hardner, 1993; Cannon *et al.*, 1994; Silva *et al.*, 1995; Webb, 1997; Pereira *et al.*, 2002; Okuda *et al.*, 2003).

**Table 6** The mean stock (kg ha<sup>-1</sup>) of nutrients in the small litter layer from four replicate plots in unlogged (U) and logged (L) stands in Carvão forest, Rio de Janeiro, Brazil. Significant differences between stands for each fraction and for the total are represented by different letters within a column (one-way ANOVA,  $P < 0.05$ )

Fractions	Stands	C	N	C/N	Ca	K	Mg
<i>M. nigra</i>	U	861 (96) <sup>a</sup>	40.3 (6.9) <sup>a</sup>	21	6.4 (1.02) <sup>a</sup>	2.2 (0.21) <sup>a</sup>	1.4 (0.17) <sup>a</sup>
	L	587 (43) <sup>b</sup>	28.6 (3.6) <sup>b</sup>	21	2.1 (0.13) <sup>b</sup>	0.8 (0.07) <sup>b</sup>	0.5 (0.12) <sup>b</sup>
<i>P. peroba</i>	U	–	–	–	0.6 (0.27) <sup>a</sup>	0.2 (0.12) <sup>a</sup>	0.2 (0.08) <sup>a</sup>
	L	–	–	–	0.1 (0.04) <sup>b</sup>	0.1 (0.02) <sup>b</sup>	0.1 (0.02) <sup>b</sup>
Other leaves	U	1107 (294) <sup>a</sup>	47.7 (21.5)	23	20.9 (3.41) <sup>a</sup>	7.3 (0.53) <sup>a</sup>	3.2 (0.41) <sup>a</sup>
	L	877 (86) <sup>b</sup>	39.1 (19.1)	22	15.0 (1.84) <sup>b</sup>	5.3 (0.41) <sup>b</sup>	2.4 (0.13) <sup>b</sup>
Wood	U	1531 (669)	42.6 (16.7)	36	112.6 (3.11)	18.8 (2.68)	6.6 (1.96)
	L	1611 (593)	41.9 (21.2)	38	107.7 (5.67)	17.5 (3.45)	6.0 (2.71)
Flower and fruit	U	–	–	–	0.4 (0.11)	0.1 (0.03)	0.1 (0.04)
	L	–	–	–	0.3 (0.19)	0.1 (0.01)	0.1 (0.03)
Trash	U	1153 (433)	53.6 (19.5)	21	54.8 (2.69)	16.7 (3.41)	9.4 (1.41)
	L	1244 (601)	57.1 (18.7)	22	47.6 (1.99)	15.7 (2.05)	7.7 (1.83)
Total	U	4652 (1567)	184.2 (71.3)	25	195.6 (44.21)	45.4 (8.36)	20.9 (3.77)
	L	4319 (1844)	166.6 (77.1)	26	172.8 (42.71)	39.4 (8.03)	16.7 (3.31)

The floristic composition and tree species diversity of Carvão forest were not altered by selective logging, confirming the results of a number of other studies (Deckker & de Graaf, 2003; Hall *et al.*, 2003). However, a significant shift in canopy dominance was found, with typical late-successional species (such as *Metrodorea nigra* and *Paratecoma peroba*) being replaced by early-successional species (*Acacia polyphylla*, *Pachystroma longifolium* and *Pseudopiptadenia contorta*) in the logged stand. Several studies have shown that disturbance by selective logging reduces the number of shade tolerant species and stimulates light-demanding species (Silva *et al.*, 1995; Péliissier *et al.*, 1998; Deckker & de Graaf, 2003; Okuda *et al.*, 2003).

The fact that selective logging in the Carvão forest did not affect the concentrations of the nutrients in the soil has to be interpreted with caution. Aragão (2000), studying soils in gaps in the logged stand of this forest, found higher concentrations of C and C : N ratios in the gaps compared to adjacent areas. This suggests that selective logging does not alter the soil of the whole area but acts locally. In another *tabuleiro* forest, which was selectively logged 40 years ago, soils showed higher organic C and nutrients than undisturbed forest soil (Kindel *et al.*, 1999). This finding was related to lower decomposition processes which, in general, occur in secondary forests and could also reflect the greater input from organic matter from the logging process.

The reduction of 8–30% in the annual input of nutrients through leaf litterfall in the logged stand was mainly a result of a decrease in leaf production by *M. nigra* (Villela *et al.*, 1998). Many investigators have shown that selective logging does not affect litterfall mass (Herbohn & Congdon, 1993; Louzada *et al.*, 1997; Villela *et al.*, 1998), although they found differences in leaf litter species composition and chemical quality, caused by change in floristic composition as a result of disturbances associated with logging.

Considering that *M. nigra* leaves account for 24% (logged) to 33% (unlogged) of the annual leaf-litter mass in the Carvão

forest (Villela *et al.*, 1998), and that its leaves have a considerable contribution to the input of nutrients to the forest (15–18% Ca and 32–36% N), we may consider *M. nigra* to be a key species in the nutrient dynamics of this forest. A reduction in the nutrient input of 20% (K) to 51% (Mg) via *M. nigra* leaves may be a major determinant in the nutrient dynamics in the logged areas of the Carvão forest and so in the regeneration process. Other studies have shown that key species, which represent dominant trees [for example *Peltogyne gracilipes* in an monodominant Amazon forest (Villela & Proctor, 1999)] and nurse-plants [such as *Clusia hilariana* in *restinga* thickets (Scarano *et al.*, 2004)] have a great influence on nutrient cycling through their litter. Plant species create positive feedbacks to the patterns of nutrient cycling in natural ecosystems, and species effects have been found to be many times more important than abiotic factors in controlling ecosystem fertility (Hobbie, 1992).

*Metrodorea nigra* leaf mass has also influenced the lower stock of nutrients in the leaf litter of the logged area, as it represented between 23% (Ca and K) to 30% (Mg) of the nutrients stored in the total leaf litter layer. In fact, *M. nigra* leaf mass was 64% higher in the litter layer mass of the unlogged stand than it was in the logged stand. This was a response to the higher leaf litter production and lower decomposition ratio in unlogged stands (Villela *et al.*, 1998). Conversely, logging in another *tabuleiro* forest (Kindel *et al.*, 1999) was observed to cause an increase in the small litter layer mass compared with the undisturbed forest. In the first case, this was interpreted as an interruption in the decomposition process in the logged area, related to the harvesting of some tree species. Accumulation of the litter layer was also reported in disturbed forest compared with a primary tropical forest in Singapore (Grubb *et al.*, 1994).

Distinct from *Metrodorea nigra*, *Paratecoma peroba*, an important timber tree that reaches large size (> 50 cm d.b.h.), had little effect on nutrient cycling through its small litter

contribution. Nevertheless, its large individuals can be important in the contribution of carbon sequestration and nutrient stock and cycling through wood and large litterfall. Thus, the removal of these large individuals by logging would affect the nutrient stocks and probably affect the dynamics of the ecosystem. This point was verified in an Amazon forest by Martinelli *et al.* (2000).

Proctor (1995) commented that there is little data on soil nutrient depletion by deforestation in tropical forests and suggested that moderate deforestation will not result in nutrient limitation because the factors contributing to soil erosion, eluviation and leaching are limited. Our data did not show a clear influence of logging on surface soils of the studied forest, but the data for nutrients in litter suggested that nutrient cycling and nutrient stocks were depleted. Kobayashi (1994) stressed that although natural tropical forests have a large stock of nutrients, deforestation processes in general may lead to a decrease. The results from deforestation may vary with factors such as tree species, period and type of logging, rainfall pattern and soil properties (Kobayashi, 1994). Although relatively few trees are cut per hectare in a selective logging operation, the effects on ecosystem structure due to loss of nutrients may be underestimated (Martinelli *et al.*, 2000). Our study is in agreement with Fölster (1994) who considered that managed systems using selective logging promote natural regeneration by altering, but not interrupting, the basic structure and functioning of the forest. However, the impacts of selective logging on nutrients stocks and dynamics must be considered important in tropical forests (Martinelli *et al.*, 2000) and its effects need to be evaluated carefully and with the use of long-term studies.

## CONCLUSIONS

Our findings suggest that selective logging has a minor effect on tree species composition, at least in a single felling cycle. However, more studies are needed, especially on canopy structure, plant regeneration and seed banks, to confirm this and clarify trends over more than one felling cycle. In fact, selective logging can locally – if temporarily – increase species richness. However, our data showed that some species (mainly the late-successional species such as *P. peroba*) may have their populations reduced. Selective logging in the Carvão forest altered some processes of nutrient cycling such as annual leaf litter production and the stock of the main tree species, and also decreased the litter input and its stock of nutrients. The use of key species (such as *Metrodorea nigra* in tabuleiro forests) as indicators of disturbance for processes such as logging and fragmentation is regarded as useful in monitoring and managing some tropical forests.

Detailed information on the influence of logging on the spatial distribution of species and plant population structure, and on other nutrient processes, is fundamental for the development of a sustainable logging system. Therefore, long-term studies of unlogged and logged forest stands from different sites are essential to allow the acquisition of a good ecological data set for the Atlantic forest in Brazil.

## ACKNOWLEDGEMENTS

We thank the National Research Council of Brazil (CNPq) and FAPERJ – Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro for financial support. We also thank Bruno Kurtz, CyI Famey, Dorothy S. Araújo, João Marcelo A. Braga, Haroldo C. Lima and Mário Gomes for help with botanical identifications, Laszlo Nagy for his comments on this manuscript, Guitherme C. da Silva for fieldwork assistance, Alex P. Mazurec for figures, and Arizoli Gobo and Glauce Magalhães for their help in chemical analysis.

## REFERENCES

- Allen, S.E. (1989) *Chemical analysis of ecological materials*, 2nd edn. Blackwell Scientific Publications, Oxford, UK.
- Aragão, L.E.O.C. (2000) Efeito de clareiras ocasionadas pelo corte seletivo na decomposição foliar e no solo de uma mata de tabuleiros no Norte Fluminense, RJ. Master's Dissertation, Universidade Estadual do Norte Fluminense, Campos dos Goytacazes.
- Bôas, G.S., Sampaio, F.J. & Pereira, A.M. (2001) The Barreiras Group in the northeastern coast of the State of Bahia, Brazil: depositional mechanisms and processes. *Anais da Academia Brasileira Ciências*, **73**, 417–427.
- Brower, J.E. & Zar, J.H. (1977) *Field and laboratory methods for general ecology*. Wm. C. Brown Company Publishers, Dubuque, IA, USA.
- Brown, B. (1982) Productivity and herbivory in high and low diversity tropical successional ecosystems in Costa Rica. PhD Thesis, University of Florida, Gainesville, FL, USA.
- Cannon, C.H., Peart, D.R. & Leighton, M. (1994) Tree species diversity in commercially logged Bornean rainforest. *Science*, **281**, 1366–1368.
- Congdon, R.A. & Herbohn, J.L. (1993) Ecosystem dynamics of disturbed and undisturbed sites in north Queensland wet tropical rain forest. I. Floristic composition, climate and soil chemistry. *Journal of Tropical Ecology*, **9**, 349–363.
- Cottam, G. & Curtis, J.L. (1956) The use of distance measure in phytosociological sampling. *Ecology*, **37**, 451–460.
- Deckker, M. & de Graaf, N.R. (2003) Pioneer and climax tree regeneration following selective logging with silviculture in Suriname. *Forest Ecology and Management*, **172**, 183–190.
- EMBRAPA (Empresa Brasileira de Pesquisa Agropecuária) (1999) *Sistema Brasileiro de Classificação de Solos*. Brasília: Embrapa Produção da Informação. Embrapa, Rio de Janeiro, Brazil.
- Ewel, J.J. (1976) Litterfall and leaf decomposition in a tropical forest succession in eastern Guatemala. *Journal of Ecology*, **64**, 293–308.
- Fölster, H. (1994) Stability of the forest ecosystem in the humid tropics. *Interciência*, **19**, 291–296.
- Fonseca, G.A.B.da. (1985) The vanishing Brazilian Atlantic forest. *Biological Conservation*, **34**, 17–34.
- Fundação SOS Mata Atlântica (1998) *Atlas da evolução dos remanescentes florestais e ecossistemas associados no domínio*

- da Mata Atlântica no período 1990–1995. Fundação SOS Mata Atlântica, São Paulo, Brazil.
- Gama-Rodrigues, A.C. (1997) Ciclagem de nutrientes por espécies florestais em povoamentos puros e mistos, em solos de Tabuleiro da Bahia, Brasil. PhD Thesis. Universidade de Viçosa, MG, Brazil.
- Garay, I. & Rizzini, C.M. (2003) *A Floresta Atlântica de Tabuleiros: diversidade funcional da cobertura arbórea*. Editora Vozes, São Paulo, Brazil.
- Gomes, E.P.C., Mantovani, W. & Kageyama, P.Y. (2003) Mortality and recruitment of trees in a secondary montane rain forest in south eastern Brazil. *Brazilian Journal of Biology*, **63**, 47–60.
- Grubb, P.J., Turner, I.M. & Burslem, D.F.R.P. (1994) Mineral nutrient status of coastal hill dipterocarp forest and *Adinandra* belukar in Singapore: analysis of soil, leaves and litter. *Journal of Tropical Ecology*, **10**, 559–577.
- Gullison, R.E. & Hardner, J.J. (1993) The effects of road design and harvest intensity on forest damage caused by selection logging: empirical results and a simulation model from the Bosque Chimanes Bolivia. *Forest Ecology and Management*, **59**, 1–14.
- Hall, J., Harris, D.J., Medjibe, V. & Asthon, P.M. (2003) The effects of selective logging on forest structure and tree species composition in a Central African forest: implications for management of conservation areas. *Forest Ecology and Management*, **183**, 249–264.
- Herbohn, J.L. & Congdon, R.A. (1993) Ecosystem dynamics of disturbed and undisturbed sites in North Queensland wet tropical rain forest. II. Litterfall. *Journal of Tropical Ecology*, **9**, 365–380.
- Hobbie, S.E. (1992) Effects of plant species on nutrient cycling. *Trends in Ecology and Evolution*, **7**, 336–339.
- Jennings, S.B., Brown, N.D., Boshier, D.H., Whitmore, T.C. & Lopes, J.do.C.A. (2001) Ecology provides a pragmatic solution to the maintenance of genetic diversity in sustainably managed tropical rain forest. *Forest Ecology and Management*, **154**, 1–10.
- Jesus, R.M., Garcia, A. & Rosas, S. (1992) Fitossociologia de uma floresta de tabuleiro na Mata Atlântica. *Resumos do Segundo Simpósio Internacional de Estudos Ambientais em Florestas Tropicais Umidas – Forest 92*. Biosfera, Rio de Janeiro, Brazil, p. 17.
- Johns, A.D. (1992) Vertebrate response to selective logging: implications for the design of logging systems. *Philosophical Transactions of the Royal Society, London*, **335**, 437–442.
- Kindel, A. & Garay, I. (2001) Caracterização de ecossistemas da Mata Atlântica de Tabuleiros por meio das formas de húmus. *Revista Brasileira de Ciência do Solo*, **25**, 551–563.
- Kindel, A., Barbosa, P.M.S., Pérez, D.V. & Garay, I. (1999) Efeito do extrativismo seletivo de espécies arbóreas da floresta Atlântica de Tabuleiros na matéria orgânica e outros atributos do solo. *Revista Brasileira de Ciências do Solo*, **23**, 465–474.
- Kobayashi, S. (1994) Effects of harvesting impacts and rehabilitation of tropical rain forest. *Journal of Plant Research*, **107**, 99–106.
- Louzada, M.A.P., Curvello, A., Barbosa, J.H.C. & Garay, I. (1997) O aporte de matéria orgânica ao solo: quantificação, fenologia e suas relações com a composição específica em área de floresta Atlântica de Tabuleiros. *Leandra*, **12**, 27–32.
- Luna, A.C., Osumi, K., Gascon, A.F., Lasco, R.D., Palijon, A.M. & Castillo, M.L. (1999) The community structure of caged-over tropical rain forest in Mt. Makiling Forest Reserve, Philippines. *Journal of Tropical Forest Science*, **11**, 446–458.
- Magnusson, W.E., de Lima, O.P., Reis, F.Q., Higuchi, N. & Ramos, J.K. (1999) Logging activity and tree regeneration in an Amazonian forest. *Forest Ecology and Management*, **113**, 67–74.
- Martinelli, L.A., Almeida, S., Brown, I.F., Moreira, M.Z., Victoria, R.L., Filoso, S., Ferreira, C.A.C. & Thomas, W.W. (2000) Variation in nutrient distribution and potential nutrient losses by selective logging in a humid tropical forest of Rondônia, Brazil. *Biotropica*, **32**, 597–613.
- Mazurec, A.P. (1998) Ciclagem de nutrientes em uma mata atlântica de encosta na serra do Imbé, Norte Fluminense, em duas altitudes. Master's Dissertation, Universidade Estadual do Norte Fluminense, Campos dos Goytacazes.
- Morellato, L.P.C. & Haddad, C.F.B. (2000) Introduction: the Brazilian Atlantic forest. *Biotropica*, **32**, 786–792.
- Moreno, M.R., Nascimento, M.T. & Kurtz, B. (2003) Estrutura e composição florística do estrato arbóreo em duas zonas altitudinais na Mata Atlântica de encosta da região do Imbé, RJ. *Acta Botanica Brasilica*, **17**, 371–386.
- Nascimento, M.T., Proctor, J. & Villela, D.M. (1997) Forest structure, floristic composition and soils of an Amazonian monodominant forest on Maracá Island, Roraima, Brazil. *Edinburgh Journal of Botany*, **54**, 1–38.
- Okuda, T., Suzuki, M., Adachi, N., Quah, E.S., Hussein, N. & Manokaran, N. (2003) Effect of selective logging on canopy and stand structure and tree species composition in a lowland dipterocarp forest in Peninsular Malaysia. *Forest Ecology and Management*, **175**, 297–320.
- Pagano, S.N. (1989) Produção de folheto em mata mesófila semidecídua no município de Rio Claro, SP. *Revista Brasileira de Biologia*, **49**, 633–639.
- Peixoto, A.L. & Gentry, A. (1990) Diversidade e composição florística da mata de tabuleiro na Reserva Florestal de Linhares (Espírito Santo, Brasil). *Revista Brasileira de Botânica*, **13**, 19–26.
- Peixoto, A.L., da Rosa, M.M.T. & Joels, L.C.M. (1995) Diagramas de perfil e de cobertura de um trecho da Floresta de Tabuleiro na Reserva Florestal de Linhares (Espírito Santo, Brasil). *Acta Botanica Brasilica*, **9**, 177–194.
- Pélissier, R., Pascal, J.P., Houllier, F. & Laborde, H. (1998) Impact of selective logging on the dynamics of a low elevation dense moist evergreen forest in the Western Ghats (South India). *Forest Ecology and Management*, **105**, 107–119.
- Pereira, R., Zweede, J., Asner, G. & Keller, M. (2002) Forest canopy damage and recovery in reduced-impact and conventional selective logging in eastern Para, Brazil. *Forest Ecology and Management*, **168**, 77–89.
- Proctor, J. (1987) Nutrient cycling in primary and old secondary rainforest. *Applied Geography*, **7**, 135–152.

- Proctor, J. (1992) Soils and mineral nutrients: what do we know, and what do we need to know, for wise rain forest management? *The wise management of tropical forests* (ed. by F.R. Miller and K.L. Adam), pp. 27–35. *Proceedings of the Oxford Conference on Tropical Forests*. Oxford Forestry Institute, Oxford, UK.
- Proctor, J. (1995) Rain forests and their soils. *Ecology, conservation and management of Southeast Asian rainforests* (ed. by R. Primack and T. Lovejoy), pp. 87–104. Yale University Press, New Haven, CT.
- RadamBrasil (1983) *Rio de Janeiro/Vitória. Levantamento de recursos naturais*, Vol. 32, folha SF. 23/24. Ministério das Minas e Energia, Rio de Janeiro, Brazil.
- Rizzini, C.T. (1979) *Aspectos Sociológicos e Florísticos. Tratado de Fitogeografia do Brasil*, Vol. 2. HUCIT & Editora Universidade de São Paulo, São Paulo, Brazil.
- Rizzini, C., Aduan, R.E., Jesus, R. & Garay, I. (1997) Floresta pluvial de tabuleiros, Linhares, ES, Brasil: sistemas primários e secundários. *Leandra*, **12**, 54–76.
- Scarano, F.R., Cirne, P., Nascimento, M.T., Sampaio, M., Vilella, D.M., Zaluar, H.L.T. & Wendt, T. (2004) Ecologia Vegetal: integrando ecossistema, comunidades, populações e organismo. *Pesquisas de Longa Duração na Restinga de Jurubatiba: Ecologia, História* (ed. by C.F. Rocha, F.R. Scarano and F.A. Esteves), pp. 77–97. Editora RIMA, São Carlos, SP, Brazil.
- Silva, A.P. (2003) Solos, produção de serrapilheira e aporte de nutrientes em moitas da área aberta de *Clusia* da restinga de Carapebus, no Parque Nacional da restinga de Jurubatiba, RJ. Master's Dissertation, Universidade Estadual do Norte Fluminense, Campos dos Goytacazes, Brazil.
- Silva, G.C. & Nascimento, M.T. (2001) Fitossociologia de um remanescente de mata sobre tabuleiros no norte do estado do Rio de Janeiro (Mata do Carvão). *Revista Brasileira de Botânica*, **24**, 51–62.
- Silva, J.N.M., Carvalho, J.O.P., Lopes, J.do.C.A., Costa, D.H., Oliveira, L.C., Vanclay, J.K. & Skovsgaard, J.P. (1995) Growth and yield of a tropical rain Forest in the Brazilian Amazon 13 years after logging. *Forest Ecology and Management*, **71**, 267–274.
- Tabarelli, M. & Mantovani, W. (1999) Clareiras naturais e a riqueza de espécies pioneiras em uma floresta atlântica montana. *Revista Brasileira de Biologia*, **59**, 251–261.
- Thomas, W.W., Carvalho, A.M.V., Amorim, A.M.A., Garrison, J. & Arbeláez, A.L. (1998) Plant endemism in two forests in southern Bahia, Brazil. *Biodiversity and Conservation*, **7**, 311–322.
- Uhl, C. & Jordan, C.F. (1984) Succession and nutrient dynamics following forest cutting and burning in Amazonia. *Ecology*, **65**, 1476–1490.
- Veloso, H.P., Rangel-Filho, A.R.L. & Lima, J.C.A. (1991) *Classificação da vegetação brasileira adaptada a um sistema universal*. Instituto Brasileiro de Geografia e Estatística, Rio de Janeiro, Brazil.
- Vilella, D.M. & Proctor, J. (1999) Litterfall mass and chemistry and nutrient retranslocation in a monodominant forest on Maracá Island, Roraima, Brazil. *Biotropica*, **31**, 198–211.
- Vilella, D.M., Buffon, L., Aragão, L.E.O.C., Gama, D.M., Nascimento, M.T. & Rezende, C.E. (1998) *Effect of selective logging on litter production and decomposition in an Atlantic forest, RJ, Brazil. Anais do IV Simpósio de Ecossistemas Brasileiros*, Vol. III, pp. 253–263. Academia de Ciências de São Paulo, Águas de Lindóia, SP, Brazil.
- Vitousek, P.M. & Sanford, R.L. (1986) Nutrient cycling in moist tropical forest. *Annual Review of Ecology and Systematics*, **17**, 137–167.
- Webb, E.L. (1997) Canopy removal and residual stand damage during controlled selective logging in lowland swamp forest of northeast Costa Rica. *Forest Ecology and Management*, **95**, 117–129.
- Zar, J.H. (1984) *Biostatistical analysis*, 2nd edn. Prentice Hall International, Englewood Cliffs, NJ, USA.

## BIOSKETCHES

**Dora M. Vilella** is an associate professor at the Universidade Estadual do Norte Fluminense Darcy Ribeiro (UENF), Rio de Janeiro, Brazil. Her research interests emphasize nutrient cycling of forested systems. She has been working for over two decades on *cerrado* vegetation, flooded forest in Pantanal and monodominant forests in Amazon. More recently, her main interest has been on Atlantic forest ecosystems and the effects of fragmentation on nutrient cycling.

**Marcelo T. Nascimento** is also an associate professor at the Universidade Estadual do Norte Fluminense Darcy Ribeiro (UENF), Rio de Janeiro, Brazil, where he is head of the Terrestrial Ecology Laboratory. For the last 15 years, his research has focused on plant communities, including phyto-sociological studies, herbivory and plant population dynamics.

**Luiz Eduardo O. C. de Aragão** holds a post-doctoral position at the School of Geography and the Environment, Oxford University, UK. He is particularly interested in the application of GIS in analyses of temporal and spatial modelling of patterns of primary productivity in forests.

**Deborah M. da Gama** is a PhD student at the Environmental Sciences Laboratory in the Universidade Estadual do Norte Fluminense Darcy Ribeiro (UENF), Rio de Janeiro, Brazil. She is interested in nutrient cycling of coastal vegetation. Her studies have been developed in Atlantic forest fragments, and aim to investigate the effects of impacts, such as selective logging and fragmentation, on nutrient cycling.

---

Editors: Peter Furley, John Grace and Patrick Meir

This paper is part of the Special Issue, *Tropical savannas and seasonally dry forests: vegetation and environment*, which owes its origins to a meeting held at the Royal Botanic Garden, Edinburgh, in September 2003.