When the shifting agriculture is gone: functionality of Atlantic Coastal Forest in abandoned farming sites

Depois que as roças foram embora: funcionalidade da Mata Atlântica em locais de roças abandonadas

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Abstract: Slash-and-burn agriculture has been practiced for a very long time by the traditional populations (caiçaras) on Ilha Grande, Rio de Janeiro State, Brazil. After a few years of use the plots are abandoned to fallow. We examined the processes of litter production and decomposition and the relationships between forest lands used by caiçara populations and landscape functionality. Five and 25-year-old forests growing on areas once used for subsistence agriculture were compared to a near-climax forest site. No significant differences between the three areas were noted in terms of litter production over a 2-yr period; the average litter productions were 9,927, 8,707 and 10,031 kg/ha/yr for the 5-year, 25-year and climax forests respectively. N and K nutrient input through litter was greatest in the climax forest; P and Mg input was greatest in the 5-yr forest; and Na greatest in the 25-yr forest. Ground litter accumulation (3,040-3,730 kg/ha/yr) was not significantly different in the three areas. Litter turnover times (1/K) were 0.33, 0.42 and 0.38 for the 5-yr, 25-yr and climax forests respectively. These secondary forests cover almost all of Ilha Grande and demonstrate low species diversity, but they have production and decomposition systems similar to those of mature forests.

Keywords: Slash-and-burn agriculture. Caiçaras. Turn over of nutrients. Litter layer. Secondary forest.

Resumo: A agricultura de coivara é praticada há longo tempo por populações de caiçaras na Ilha Grande, Rio de Janeiro, Brasil. Depois de alguns anos de uso as roças são abandonadas. Foi examinado o processo de produção e de decomposição de serapilheira e as relações entre o uso da floresta pelos caiçaras e a funcionalidade da paisagem. Foram utilizadas duas áreas abandonadas, uma com cinco e outra com 25 anos, e comparadas com uma floresta climácica. Não foram encontradas diferenças significativas entre as três áreas em dois anos de coleta; a produção média foi de 9.927, 8.707 e 10.031 kg/ha para as áreas de cinco anos, 25 anos e climácica, respectivamente. As entradas de N e K através da produção de serapilheira foram maiores na floresta climácica; as de P e Mg, na área de cinco anos; e a entrada de Na foi maior na área de 25 anos. A serapilheira estocada sobre o solo (3.040-3.730 kg/ha) não foi significativamente diferente nas três áreas. O tempo de ciclagem (1/K) foi de 0,33; 0,42 e 0,38 para as áreas de cinco anos, 25 anos e climácica, respectivamente. Estas florestas secundárias recobrem quase toda a Ilha Grande e apresentam baixa diversidade de espécies, mas têm os sistemas de produção e de decomposição similares aos de florestas maduras.

Palavras-chave: Agricultura de coivara. Caiçaras. Ciclagem de nutrientes. Serrapilheira. Florestas secundárias.

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INTRODUCTION

The Brazilian Atlantic Coastal Forest is one of the most threatened biomes in the world. With the arrival of European colonization the devastation of this biome accelerated beyond any thing that could result from the cultural practices of the indigenous populations that inhabited the region. As a result, remnants of the Atlantic Forest demonstrate the history of human presence at many levels, and not man's absence. This is particularly notable in the case of the *caiçara* populations, who have caused significant alterations in the structure, composition and functionality of the forest biome through subsistence agricultural practices.

The caiçara culture is typical of the indigenous populations that inhabit the coastline of the states of Rio de Janeiro, São Paulo and Paraná, and is based on fishing and subsistence agriculture. The original indigenous populations along these shores first experienced a cultural and genetic miscegenation with the Portuguese colonizers, which was later compounded by the influence of African slaves (Adams, 2000a,b). Mussolini (1980) saw this culture as defined by (among other factors) the distinct lifestyle that developed along the coastline, which was relatively isolated from the rest of the continent in terms of trade and cultural influences. Of course this relative isolation was in a complementary way from the regional economy. This isolation and this people's close link to the local natural resources separated these communities from any wider economy (Hanazaki et al., 2007).

The planting system used by the *caiçaras*, called locally as *roça de toco* or *roça de coivara*, is well known in the interior of the country and represents an authentic heritage of the Amerindians themselves. However, the *caiçara* agricultural system is somewhat different from other indigenous populations as, for example, they cultivate plants that yield natural dyes for their fish-nets in the fallow plots and utilize beach sand to help combat leaf-cutter ants. The slash-and-burn agricultural method is based on the felling and burning of the forest followed by planting, and then rotation into fallow to restore the soil fertility over rest periods that

can vary from a minimum of four years up to 50 (Schmidt, 1958). The restoration of soil conditions is linked to the nutrient inputs and the inexistence of severe processes of erosion, and is influenced by the proximity from the source of native species and the soils' seed bank.

The energy balance of this system is largely favorable when compared to techniques that depend on industrialized agricultural products (Bayliss-Smith, 1982; Altieri, 1987; Adams, 2000b) as these are generally unavailable to poor rural populations. However, this indigenous system is totally dependent on the maintenance of soil fertility by alternating between a cultivation period and a period in which the land is left fallow (Boserup, 1972). In terms of the impact of shifting cultivation on the ecosystem, Ewel (1976) pointed out that the restoration of fertility that occurs during fallowing is due in large part to the recycling of organic material and nutrients into the upper layers of the soil through the production and subsequent decomposition of leaf litter. If the fallow period is too short, local soil degradation will occur and productivity will decline sharply. If land is left fallow for too long, on the other hand, the system again becomes impractical due to difficulties related to manually clearing the relatively large areas of land necessary for subsistence agriculture. In the lands held by the caiçaras in the states of São Paulo and Rio de Janeiro the average agricultural period is 3.1 years, while the average fallow time is 7.8 years; the average size of the cultivation plot is 0.42 ha (Adams, 2000b). Inherent in these practices is a permanent control over the levels of biodiversity and biomass in the system as they are adjusted to the needs of each cycle (Silva, 1998). However, as subsistence agricultural practices have been declining on Ilha Grande due to the rise of tourism and urbanization (Wunder, 2000), what was previously fallow land can often now be considered abandoned agricultural areas. According to Peroni (2004), the low numbers and advanced ages of the farmers involved in rotating agricultural activities in the Atlantic Forest demonstrate that this activity is experiencing a steep falling off.

With regards to the extension of the areas of previous *caiçara* agricultural plots in relation to 'pristine' areas of Atlantic Forest, research undertaken at Ilha Grande (RJ) by Oliveira (1999) demonstrated that agricultural activities had the greatest single influence on the local landscape - confirming surveys conducted by Adams (1994) in other regions of the country. However, in the case of Ilha Grande, precise quantification becomes difficult due to the lack of classified vegetation images that permit an interpretation of the complex mosaic of secondary forests of differing ages and with subtle variations.

There are actually very few montane forest areas without any signs of having been previously cleared. Such remnant areas are only found on steep hillsides, on talus slopes with many boulders, or along ridge lines. A great majority of the other forested areas show vestiges of human occupation such as the foundations of houses, charcoal fragments in the soil, exotic species, or species that have escaped from cultivation - which helps to explain the occurrence of vast areas of secondary forest. This same situation, with little variation, can be seen in many areas of the Serra do Mar Range situated in other *caiçara* reserves.

The environmental effects of this historical land use can be seen in terms of the diversity, structure and functionality of the Atlantic Forest. Many researchers have begun to take into account ecological succession in the Atlantic Coastal Forest region in southeastern Brazil after rotating agriculture, as in the case of the works of Louzada et al. (1995), Tabarelli and Mantovani (1999), and Siminski and Fantini (2007). In the specific case of studies concerning the structure and composition of the Atlantic Forest at Ilha Grande as related to ecological succession in other areas previously cultivated by the *caiçaras*, the works of Delamonica (1997), Delamonica et al. (2002), and Oliveira (2002) must be cited.

Forest regeneration is defined as a process by which a disturbed forest area recovers the characteristics of a mature forest (Saldarriaga and Uhl, 1991). This definition

presumes that the original community characteristics and species composition were altered (Budowski, 1965; Kappelle et al., 1996), together with aspects linked to the functionality of the original forest system (Jordan, 1991; Delitti, 1995). The role of the leaf litter layer stands out within this aspect of functionality, since this layer functions as an accumulator of material where all of the biotic and abiotic elements of the ecosystem are potentially represented - and the chemical composition of this layer is a reflection of the entire system. The dearth of soil nutrients in vast areas of tropical forests led to evolutionary mechanisms that allow the survival of entire plant communities by acting together to minimize nutrient loss through leaching processes. These sustaining mechanisms (referred to as nutrient conservation mechanisms by Herrera et al., 1978 and Jordan, 1988 and 1991) consist of a set of strategies and structures of individual species that together minimize losses and optimize the capture of nutrients introduced into the ecosystem. Various authors (Stark and Jordan, 1978; Clevelario Jr., 1988, and Jordan, 1991) consider this ensemble formed by the web of roots and surface leaf litter to be the most important mechanism for the direct capture and recycling of nutrients originating in the atmosphere.

The recovery of production and decomposition functions in an ecosystem therefore has great importance for ecological succession (Garay and Kindel, 2001). There is evidence that the *caiçaras* managed the initial phases of plant succession with the intention of producing leaf litter and reconstituting soil fertility (Oliveira, 1999). The entrance of atmospheric nutrients (either by deposition through rainfall or interception of the rain by the tree's crown) represents a significant additional input to the system, even during the initial stages of ecological succession (Oliveira and Coelho Netto, 2001). Within this framework, the present work examined the ecology and functionality of the Atlantic forest by examining the production of leaf litter in areas that had previously been cultivated by the *caiçara* populations.

MATERIALS AND METHODS

Study area - the present study was carried out on the island of Ilha Grande, which covers 184.7 km² and represents a very mountainous fragment of the coastal range; the Pico do Papagaio (959m) and the Serra do Retiro (1.031m) are the island's highest points. According to Veloso et al. (1991), Ilha Grande is situated within the Dense Ombrophilous Forest domain. Due to the many scattered subsistence farm plots developed by the local populations of caiçaras, and principally because of the large number of abandoned fields undergoing regeneration, the landscape is composed of a mosaic of secondary forest areas of differing ages. Some remnant stands of climax Atlantic Forest can still be found in a few remote areas of difficult access. The predominant soils in the region are redyellow latosols, cambisols and lithosols (Oliveira, 2002). The regional climate is warm and humid, with an average annual temperature of 24°C and without a well-defined dry season. Local rainfall distribution is very uneven due to the orographic landscape, varying between 2.400 and 4.500 mm in the same year on different parts of the island (Oliveira and Coelho Netto, 2001).

Two areas identified by local residents as having been previously used in slash-and-burn agriculture were selected within the montane forest. One plot was still in the initial stage of regeneration, having been abandoned just five years earlier, while the second plot was in a mid-stage and had already undergone approximately twenty-five years of regeneration. Both of these regenerating forest areas were situated near a locality called Vila do Aventureiro, close to some active farm plots. An area of mature forest without any evidence of anthropogenic alterations and having a similar topographical situation was selected as a control plot. This control plot was located within the Ilha Grande State Park and represents the best preserved forest fragment on the island. All studied areas were in a similar topographic condition. The 5-year, the 25-year and the climax plots were respectively in east, southeast and east-facing slopes. The principal characteristics of the

vegetation within the three study plots are presented in Table 1 (Oliveira, 2002).

Methods: The leaf litter produced in the experimental plots was monitored for two complete years (from 1998 to 1999) by using collectors constructed with a wooden frame holding a polyethylene screen (1 mm mesh) with a

Table 1. Principal characteristics of the vegetation (with dbh \geq 5 cm) within the three study plots on Ilha Grande. Data from Oliveira (2002).

Characteristics	5-yr plots	25-yr plots	climax
Number of species	26	70	134
Density (ind./ha)	1,915	2,784	1,996
Basal area (m²/ha)	5.6	26.3	57.9
Shannon index (nats/ind.)	2.51	3.33	4.28

0.25 m² collecting area. Each collector was mounted 70 cm above soil level in order to avoid contamination by rainsplash material. A total of 20 collectors were distributed randomly throughout each of the three research plots and were not moved during the course of the experiments. Branches more than 2 cm in diameter that fell into the collectors were discarded as at least part of the biomass of a branch that size would probably require more than one year's growth and would therefore not be a true measure of the annual litter production (Clark *et al.*, 2001).

The deciduous material harvested from the leaf litter racks was removed every two weeks and subsequently dried in a drying oven to a constant weight. The material was then sorted into leaves, branches, reproductive structures and other residues (diverse fragments tree bark etc.). An aliquot with a mixture of material from 20 collectors of each collect and area was ground in a Willey mill and the powder submitted to chemical analysis. Each sample was degraded with a mixture of nitric acid and hydrogen peroxide and maintained overnight at 90 °C in a digester block. The resulting solutions were analyzed using an inductively coupled plasma-mass spectrometer (ICPMS). By multiplying the concentration of each of the elements identified in the fractional samples their total

quantities in the leaf litter could be calculated. The total accumulated leaf litter biomass above the soil was obtained using a harvesting frame 50 cm on each side and processed in a similar way to the litter produced. Twenty frames were distributed randomly over the ground in each successional formation and the residues were collected four times a year. Leaf litter decomposition was calculated using the decomposition coefficient derived from the equation $K = L.X^{-1}$, where L = leaf litter produced, and K = leaf litter accumulated on the ground. The average turn-over time was obtained from the expression 1/K, which can be converted into number of days (Poole, 1974).

RESULTS AND DISCUSSION

LEAF LITTER PRODUCTION

Yearly leaf litter production is presented in Table 2. The averages of total litter production for the two years were 9,230, 8,710 and 10,040 kg/ha/yr in the 5-year, 25-year and climax plots respectively. Neither the different totals nor the averages for the two years differed significantly among any of the three areas according to the Tuckey test at a 5% probability level.

The leaf fraction was always preponderant during the study, attaining values of 7,260, 6,320 and 6,750 kg/ha/year in the 5-year, 25-year and climax areas respectively. These numbers correspond to 78.7%, 72.6% and 67.2% of the total litter production (again respectively). It is interesting to note, however, that the leaf fraction describes a negative tendency in relation to the successional ages of the study areas. The branch fraction demonstrated similar percentages in the 5-yr (14.1%) and 25-yr (14.3%) plots, but was higher in the climax plot (19.0%). The percentage values of the reproductive elements were 3.6%, 9.1% and 8.5%, in the 5-yr, 25-yr and climax areas respectively. The residual material values were 3.7%, 4.0% and 5.2%, in the same order. Of the four fractions considered, the reproductive elements demonstrated the greatest variation during the year in the 25-year-old area, with a variation coefficient (v.c.) of 87%; the least variation was seen among the leaf fraction from the same plot (v.c. = 29.4%).

The previous use of the areas five and 25 years ago apparently modified the expected patterns for a sucessional gradient. The fact that these areas previously served as agricultural plots may be partially responsible for the high leaf litter values observed in Table 3. The

Table 2. Leaf litter production and its distribution among the different fractions (in %) in the three study areas. Values in kg/ha/yr (\pm = standard deviation).

	year	leaves	branches	repr. elem.	residues	total
	First year	7,720 (± 275.9)	1,430 (± 84.0)	400 (± 23.4)	370 (± 20.2)	9,920 (± 338.8)
F .1.4	Second year	6,790 (± 276.5)	1,160 (± 53.5)	260 (± 15.2)	320 (± 14.0)	8,530 (± 301.9)
5-yr plot	Average	7,258.5 (± 230.7)	1,294.2 (± 53.3)	330.0 (± 15.1)	344.5 (± 16.0)	9,227 (± 262.2)
	Average distribution	78.7%	14.1%	3.6%	3.7%	100%
25-yr plot	First year	7,110 (± 266.4)	1,470 (± 81.7)	1,050 (± 82.1)	370 (± 12.9)	10,000 (± 359.6)
	Second year	5,530 (± 136.9)	1,030 (± 68.0)	530 (± 45.7)	320 (± 14.0)	7,410 (± 221.5)
	Average	6,320 (± 262.2)	1,250 (± 154.8)	790 (± 62.7)	350 (± 57.1)	8,710 (± 235.8)
	Average distribution	72.6%	14.3%	9.1%	4.0%	100.0%
	First year	6,950 (± 190.7)	1,840 (± 91.2)	740 (± 44.8)	510 (± 17.0)	10,040 (± 250.8)
climax	Second year	6,540 (± 177.1)	1,970 (± 110.2)	980 (± 78.8)	540 (± 21.2)	10,030 (± 298.2)
	Average	6,750 (± 166.4)	1,910 (± 73.6)	860 (± 46.1)	530 (± 16.0)	10,040 (± 239.0)
	Average distribution	67.2%	19.0%	8.5%	5.2%	100.0%

Table 3. Leaf litter production (Mg/ha/yr) in various forest regions in southeastern Brazil.

Municipality / state	characteristic	deposition Mg/ha/yr	leaves %	source
Rio de Janeiro, RJ	Atlantic Forest	12.9	69	Abreu, 2006
Araras, SP	mesophyllic semideciduous	11.2	66.3	Diniz and Pagano, 1997
Angra dos Reis, RJ	Atlantic Forest, climax	10.0	67.0	Present study
Angra dos Reis, RJ	Atlantic Forest, 5-yr	9.9	79.0	Present study
Anhembi, SP	mesophyllic semideciduous	9.8	64.6	Cesar, 1993
São Paulo, RJ	mesophyllic semideciduous	9.4	62.6	Meguro <i>et al.</i> , 1979
Angra dos Reis, RJ	Atlantic Forest, 25-yr	8.7	73.0	Present study
Guarujá, SP	Atlantic coastal plain	7.9	63.6	Varjabedian & Pagano, 1988
Teod. Sampaio, SP	mesophyllic semideciduous	7.6	62.6	Schlittler et al., 1993
Santo André, SP	montane Atlantic Forest	7.0	72.0	Domingos et al., 1997
Cunha, SP	montane Atlantic Forest	6.4	67.3	Custodio Filho et al., 1997
Cananéia, SP	Atlantic Forest	6.3	71.2	Moraes and Delitti, 1996

total production of the 5-year-old plot (9.2 Mg/ha/yr) was significantly greater than published values for other secondary forests or even climax forests. The production in the 25-year-old plot (8.7 Mg/ha/yr) was also relatively high. The value obtained for the climax area (10.0 Mg/ha/ yr) represents one of the highest litter accumulation rates yet reported. As there was apparently no previous use of the control plot land, other factors besides clearing must have contributed to the high observed accumulation there. According to Mazurec (1998), species composition, basal area, and tree density are important characteristics to be considered in the analysis of tropical forest productivity. The basal area observed in the three areas described a gradient: 5.6, 26.3 and 57.9 m²/ha, in the 5-yr, 25-yr and climax plots respectively (Oliveira, 2002). This parameter does not, however, explain the high productivity of leaf litter observed in the 5-year-old area (which had a basal area 10.3 times smaller than the climax plot). The variations in total productivity only appear somewhat similar to the parameter of arboreal density (1,915 and 1,996 ind./ha in the 5-year and climax plots respectively). It is possible that the high litter production in the 5-year area is due to the combined effects of the former use of the land by the

caiçaras and its species composition. The local farmers leave living tree stumps in their cultivation plots and, when these areas are abandoned, these tree stumps sprout rapidly and vigorously. On the other hand, the pulse of nutrients provided by the burning of the cleared bushes in the agricultural plots may influence the productivity of the regenerating forest. In terms of species composition, 65% of the species in the 5-year plot were pioneer species that have a very important role in litter production (Oliveira, 2002). Pioneer species are characteristically fast growing, have short life spans, invest heavily in the production of biomass (Budowski, 1965; Kageyama and Castro, 1989) and generate a great deal of leaf litter.

Leaf litter production is quite similar among the three different plots in spite of their large age differences, which shows that at least some functional aspects of the forest (such as litter production) recover much more quickly than those linked to species composition and structure. As such, the 5-yr and climax forests are much more similar to each other in terms of their functionality than in terms of their floristic and structural natures.

Table 4 lists the total quantities of nutrients transferred to the soil by leaf litter fall in the three study

areas. In the 5-yr area, the C load was 4,382.6 kg/ha/yr, a value much lower than seen in the other areas. Nitrogen accumulation was intermediate (127.0 kg/ha/yr). Calcium and magnesium accumulations were greater than observed in the other areas (315.2 and 53.8 kg/ha/yr, respectively). Sodium accumulation was greatest in the 25-yr area (17.6 kg/ha/yr) but that of potassium was the lowest (28.6 kg/ ha/yr). The carbon and nitrogen accumulations tended to be higher in the climax area (4,546.3 and 156.2 kg/ha/yr, respectively), as was potassium (37.7 kg/ha/yr), while calcium and magnesium were lowest there (205.1 and 46.4 kg/ha/yr, respectively). As the climax area indicated a tendency to the greatest total annual accumulation of leaf litter and the lowest values for calcium and magnesium accumulation, it had by far the lowest average concentrations for these elements in its litter. The opposite was observed in the 5-yr area (less litter mass but higher Ca and Mg flux, which signifies their higher concentration in the accumulated biomass), so that the litter from the climax area is significantly poorer in Ca and Mg than the 5-yr plot. The annual transfer of phosphorous in the three areas was very similar, and much less than the flux of the other cations examined.

It is important to note the exceptional quantities of nutrients encountered in the 5-yr area in the present study, even though it has an arboreal biomass significantly inferior to the other two study areas. These high concentrations may be attributable to the re-mobilization of nutrients that occurred when the agricultural area was first burned for planting. Table 5 presents the quantities of these nutrients

in the annual litter production of other forest ecosystems. In terms of N, K and Na, the values encountered are within the variation range seen in southeastern Brazil, while phosphorous levels are lower that those observed in almost all of the other areas. Calcium (principally) and magnesium in the study areas were above the usual levels observed. According to Vitousek (1982), nitrogen is usually not a limiting factor in tropical forests due to the relative abundance of the Leguminosae, responsible for atmospheric nitrogen fixation. Furthermore, the species that are colonizing the abandoned area can contribute to changes in litter and the physical and chemical characteristics of the soil, resulting in seemingly discordant values of minerals found in the three areas of study.

DYNAMICS OF LEAF LITTER STOCKED ON THE GROUND

In general, the forest humus in all three forest areas examined was in the form of 'moder' - characterized by the presence of a layer of amorphous organic material just under the leaf litter layer. However, in many places in the same areas (especially in the 5-yr plot) there is humus of the 'mull' type, characterized by a morphological discontinuity between the organic material and the first organic-mineral horizon, with the leaves resting directly on the ground (Garay and Kindel, 2001).

The total mass of litter stocked on the ground in each of the study areas is presented in Figure 1. The annual averages of the three areas do not differ significantly (Tukey test, p < 0.05). The 5-yr area demonstrated a medium level of accumulation with 3,046 kg/ha and

Table 4. Total nutrient flux (kg/ha/yr) in leaf litter produced in the three study areas on Ilha Grande, RJ, Brazil (\pm = standard deviation).

Study area	Total litter	С	Ν	Р	K	Na	Ca	Mg
5-yr plot	9,924.3	4,382.6	127.0	1.6	30.6	14.9	315.2	53.8
	(± 338.8)	(± 115.5)	(± 3.4)	(± 0.1)	(± 1.3)	(± 0.6)	(± 11.3)	(± 2.0)
25-yr plot	9,998.5	4,581.7	110.2	1.5	28.6	17.6	286.9	49.7
	(± 359.6)	(± 122.5)	(± 2.6)	(± 0.1)	(± 0.6)	(± 0.5)	(± 9.4)	(± 1.2)
climax	10,037.5	4,546.3	156.2	1.7	37.7	15.0	205.1	46.4
	(± 239.0)	(± 158.7)	(± 5.3)	(± 0.1)	(± 1.1)	(± 0.4)	(± 6.9)	(± 1.2)

Table 5. N, P, K, Na, Ca and Mg content (in kg/ ha/yr) in the leaf litter produced in Atlantic Forest formations in southeastern Brazil.

Local	Ν	Р	K	Na	Ca	Mg	Source
São Paulo, SP	186	9.4	38	-	104.0	18.2	Meguro <i>et al.</i> , 1979
Rio Claro, SP	198	6.8	48.3	-	149.0	27.3	Pagano, 1989
Campos, RJ	108	5.7	40.8	20.8	38.7	25.5	Mazurec, 1998
Campos, RJ	125	7.6	64.2	18.5	52.1	29.6	Mazurec, 1998
Cubatão, SP	159	7	12	-	90	11	Domingos et al., 1997
Cananéia, SP	102	4	21	-	60	19	Moraes et al., 1993
Anhembi, SP	203	6	43	-	109	24	Cesar, 1993
Cubatão, SP	128	3	14	-	56	13	Leitão Filho et al., 1993
Ilha Grande, RJ (5-yr. area)	127	1.6	30.6	14.9	315	53.8	present study
Ilha Grande, RJ (25-yr. area)	110	1.5	28.6	15.0	205.1	49.7	present study
Ilha Grande, RJ (climax area)	156	1.7	37.7	15.0	205	46.4	present study

variation coefficient of 34.2%. The highest accumulation was registered in November, while May had the lowest value for the whole year. In the 25-yr area, the total mass was 3,729 kg/ha, with a v.c. = 33.6%. As in the 5-yr area, the largest litter accumulation for the 25-yr site was observed in November (5,122 kg/ha), although the least accumulation was seen in February. The climax area had a total accumulation of 3,735 kg/ha and c.v. = 26.8%. Moraes et al. (1993) reported finding a total accumulated litter of 3,207 kg/ha in a montane forest area on the Ilha do Cardoso (SP), which was very similar to the results seen in the present study. Mazurec (1998) encountered values quite larger than those reported here in montane Atlantic Forest areas at different altitudes: 7,410 kg/ha in a forest at 250m, and 6,130 kg/ha at 50m. However, not even considering the peculiarities of each of the areas, methodological differences and differences in the definition of the litter horizons will account for a considerable part of the recorded differences between these studies.

Turnover rates for litter stocked on the ground were statistically similar in all three study areas. However, these rates seems to occur under different processes in each area, as will be explained as follows. The decomposition quotient (K_L) calculated for the 5-yr area was 3.26 yr⁻¹; for the 25-yr and climax areas this value was 2.68 yr⁻¹.

The litter stock turnover time $(1/K_1)$ was 0.30 years (109) days) for the 5-yr area, and 0.37 years (135 days) for both the 25-yr and climax areas. Importantly, however, these decomposition quotients occur under very distinct C/N ratios in the three areas. The C/N ratio for ground litter followed an increasing gradient: 10.2 in the 5-yr area; 16.0 in the 25-yr area; and 32.5in the climax plot. In the 5-yr area the humus is a type of 'mull', while in the other two areas it is in the form of 'moder' (Garay and Kindel, 2001). The lower C/N ratios observed in the 5-yr and 25-yr areas (in relation to the climax site) are essentially due to the greater concentrations of N in the litter. This lowering of the C/N ratio may be due to the high frequency, dominance and density of the leguminous angico tree (Anadenanthera colubrina) - a highly efficient nitrogen fixer that is actively disseminated by the caiçaras in the tingüeras (first regrowth areas) with the objective of obtaining raw material to dye their fish-nets. These local residents are also aware that this species can improve soil fertility (Oliveira, 2002). The family Leguminosae is normally associated with the formation of 'mull' humus (Garay, 1989).

Table 6 lists the principal aspects of the organic material decomposition system observed in the present work. Perhaps paradoxically, the smaller quantity of litter

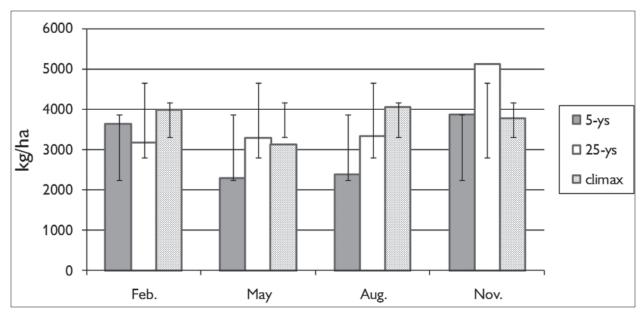


Figure 1. Litter mass stocked on the ground as measured each trimester in the three study areas (vertical bars: standard deviation).

stocked on the ground in the 5-yr area is actually the result of a greater production of litter than observed in the 25-yr area but a more rapid turn-over time, as was in fact observed (0.3 and 0.37 yr⁻¹, respectively). This more rapid decomposition is probably due to its lower C/N ratio (10 in the 5-yr area against 16 for the 25-yr area). Litter accumulation in the 25-yr and climax areas was similar. The fact that the 25-yr area had a lower C/N ratio than the climax area was not sufficient, however, to give it a more rapid decomposition rate - indicating that other factors may be involved. In terms of physical-chemical environment itself, it is important to note that there were 62% less canopy gaps in the climax area than observed in the 25-yr area (Oliveira, 1999) - a situation that will no

doubt create accentuated microclimatic differences on the forest floor. On the other hand, the low 'adherence' encountered among the C/N values in the soil and in the stocked leaf litter may indicate that distinct mineralization processes are occurring in the three areas due to a high heterogeneity in the decomposition subsystems at the observational scale used here (Garay, 1989). The higher number of arboreal and shrub species present in the climax area (more than double those encountered in the 25-yr area) means that a wider variety of substrates is available to the decomposers. As a result, decomposition should be more rapid due to the greater specific and functional complexity of the decomposer subsystem even though the C/N ratio was relatively high. This is in agreement with the

Table 6. Principal variables of the organic material decomposer systems of the three study areas ($\pm =$ standard deviation).

Variable	5-yr plot	25-yr plot	climax
Litter production (kg/ha/yr)	9,924.3 (± 338.8)	9,998 (± 359.6)	10,037 (± 239.0)
Accumulated litter (kg/ha/yr)	3,046.6 (± 1,044.4)	3,729.3 (± 1,254.9)	3,735.8 (± 1,003.1)
Turnover time (1/K _L)	0.30	0.37	0.37
C/N ratio in recently fallen litter	33.2	41.6	30.9
C/N ratio of ground litter (L)	10.2	16.0	32.5

idea that complexity increases as the system approaches its sucessional climax state (Horn, 1976).

It is important to note that phosphorous levels were quite reduced in all three areas (in both the recently fallen litter as well as the litter stocked on the ground) and levels of this nutrient were reduced even more (by a factor of three) between recently fallen litter and that found on the ground. As this element was present in very low concentrations in the soil-plant system in the three study areas, it can be considered a critical factor in the functioning of this system (Silva, 1998).

Another relevant aspect is the recomposition velocity of the leaf litter production and decomposition systems, principally in the 5-yr area. The recomposition time, the nutrient concentrations, litter production and the dynamics of its decomposition allow one to suppose that the functional recuperation of the system is not primarily dependent on the species diversity, but rather on the preservation or development of mechanisms to capture and conserve nutrients. In other words, the functional aspects of the system seems to be more important for the maintenance of nutrient and energy flow than is species richness.

FINAL CONSIDERATIONS

The forests of Ilha Grande grow on poor soils, and phosphorous is the probable main limiting factor for plant growth (Silva, 1998). Sánchez (1981) pointed out that many tropical soils used in shifting agriculture are deficient in phosphorous. Small quantities of this element normally circulate in a nearly closed circuit, at concentrations sufficient only to prevent its deficiency. Fire is therefore fundamental in shifting agricultural as it transfers back to the soil phosphorous accumulated in the plant biomass (Nye and Greenland, 1960; Silva, 1998). McGrath (1987) observed that although these agricultural systems may appear primitive, inefficient and environmentally unsound, under appropriate circumstances they can actually be highly productive, energetically efficient and relatively neutral in their long term ecological effects - even sophisticated in terms of their adaptations and ecological strategies.

What then are the principal ecological effects of the fallowing on the functionality of the Atlantic Forest? What influence do the abandoned slash-and-burn plots have on the constitution and functioning of the Atlantic Forest landscape? These are complex questions, but some clear tendencies are beginning to appear. First, it must be stressed that the mechanisms that act to conserve soil nutrients are reconstituted rather quickly, especially the leaf litter producer-decomposer system. The velocity of the recomposition of the 5-yr area, in terms of the development of structures needed to capture nutrients (litter + fine roots) can be attributed to the agricultural techniques adopted by the caicara populations. These populations maintain living trunks of regrowth vegetation from the previous fallow cycle in their newly cleared plots - and these will quickly resprout in the initial stagers of the next fallowing cycle. The selection made by the burning and the agricultural practices used by these populations favor the appearance of a vegetation community that rapidly develops structures capable of capturing nutrients derived from the atmosphere. Thus, when the fallow period ends and the plot is once again burned its ashes will re-incorporate nutrients that originated (in large part) from the atmosphere. The functional presence of these production and recapture mechanisms is supported by the following evidence: a) the rapid decomposition and liberation of nutrients from the leaf litter; b) a large biomass of fine roots is associated with the litter layer and the soil surface; and c) the efficient recovery of nutrients delivered by rainfall to the crowns of the trees.

Oliveira et al. (1995) observed that the fallow period was not a true abandonment of the land, as the farmer took additional steps to manage the area and insure soil recuperation. The recovery of the vegetation and its systems for recycling nutrients are thus an integral part of this agricultural technique. According to the results reported here, abandoned slash-and-burn plots in the Atlantic Forest restore (in decreasing order and decreasing velocity) the mechanisms required for nutrient conservation (especially

the leaf litter producer-decomposer system), biomass, and finally species diversity.

The physiological and morphological adaptations that evolved to overcome the limitations imposed by low soil nutrient levels are part of a complex of strategies that permit successional communities to survive and develop on nutrient-poor tropical soils. However, in addition to the innate evolutionary processes of the species participating in the recovery stages, human actions resulting from the utilization of the land for subsistence cultivation have been superimposed. In that context, it is important to remember that the plants and areas studied here (with the exception of the climax plot) had all no doubt been used innumerable times as agricultural plots over the years by these same caiçara populations within the cultivation/fallow system - and were likewise used in even more remote times by the Tupinambás and Guaianazes Amerindians that preceded them. So, it is important to consider the idea that some environments may be product of coevolutionary processes between a given society and its nature, that is, an interactive overview of the mechanisms of social and natural transformation, as Noorgard (1994) pointed. As such, this form of land use almost certainly extended to most of Ilha Grande, and thus it is also very possible that the chemical and physical characteristics of the soils there reflect this prolonged use - particularly the observed deficiency in phosphorous. Within this perspective, the caiçara agricultural system has resulted in a particular type of forest landscape that maintains: a) a sustainable ecology for long-term agricultural use (Silva, 1998); b) minimal erosive processes in both the planting and fallow stages (Sánchez, 1981; Silva 1998; c) active mechanisms of nutrient capture and conservation in the initial stages of ecological succession (Oliveira, 1999; Oliveira and Coelho Netto, 2001); and d) tracts of forests with differing regeneration ages and low species diversity (Tabarelli and Mantovani, 1999; Delamonica et al., 2002; Oliveira, 2002).

According to Sastre (1982), the very slow evolution of secondary forest formations with their unique structure

and floristic composition gives strength to the concept of anthropogenic climax formations - exactly as we observe in the old caiçara territories. As such, the establishment of an anthropogenic climax (characterized by low diversity but rapid functional recomposition) appears to be a principal result of the agricultural activities of the caiçaras within the forest landscape, and the vegetation should retain these characteristics for a very long time even after the cessation of human intervention. According to Peroni (2004), there is a recent tendency for the natural recuperation of structured forests such as the Dense Ombrophilous Forest on a regional as well as on a local scale independent of population increases seen in the caicara villages. This tendency is becoming quite clear as tourism grows as an alternative source of income for caiçara groups living on Ilha Grande. It is becoming less common now to see the inhabitants of the island disperse throughout the area - in contrast to past generations when population density was strictly regulated by soil fertility and the capacity to maintain the system of nutrient recycling. This traditional occupation strategy led to an increase in the diversity of the landscape, aggregating different functional fragments and generating a landscape mosaic. However, it must be stressed that this areas, with all its cultural contribution and even natural, must remain as patches in the landscape, preferably without connectivity between them and immersed in a matrix of more mature or climax forests. This means a pattern of the landscape which considers the importance of management of the caiçaras in the dynamic of the Brazilian Atlantic Coastal Forest.

The entrance of resources by way of tourism has initiated a complete reformulation of the productive life of the *caiçara* communities on Ilha Grande (and all of this ethnic group's territory in southeastern Brazil). Subsistence agriculture is becoming less important with each passing year because of the increasing ease of receiving goods from the mainland. The great challenge now will be to develop survival strategies that give these indigenous populations access to the benefits of modern society without creating conflicts with their cultural identity.

REFERENCES

- ABREU, J. R. S. P. Dinâmica da serapilheira em um trecho de floresta secundária em área urbana do Rio de Janeiro, 2006. 79 f. Dissertação (Mestrado em Ciências Ambientais e Florestais) Universidade Federal Rural do Rio de Janeiro, Seropédica, 2006.
- ADAMS, C. As Florestas Virgens Manejadas. **Boletim do Museu Paraense Emílio Goeldi. Série Antropologia**, v. 10, n. 1, p. 3-20, 1994.
- ADAMS, C. As Populações Caiçaras e o Mito do Bom Selvagem: a necessidade de uma nova abordagem interdisciplinar. **Revista de Antropologia**, v. 43, n. 1, p. 145-182, 2000a.
- ADAMS, C. As Roças e o Manejo da Mata Atlântica pelos Caiçaras: uma revisão. **Interciencia**, v. 25, n. 3, p. 143-150, 2000b.
- ALTIERI, M. A. Agroecology: the scientific basis of alternative agriculture. London: Westview Press, 1987.
- BAYLISS-SMITH, T. P. **The ecology of agricultural systems**. Cambridge: Cambridge University Press, 1982. p. 109.
- BOSERUP, E. **Evolução agrária e pressão demográfica**. São Paulo: Editora Hucitec, 1972.
- BUDOWSKI, G. Distribution of tropical American Rain Forest trees in the light of successional process. **Turrialba**, v. 15, p. 40-45, 1965.
- CESAR, O. Produção de serapilheira na mata mesófila semidecídua da fazenda Barreiro Rico, Município de Anhembi, SP. **Revista Brasileira de Biologia**, v. 53, n. 4, p. 671-681, 1993.
- CLARK, A. D.; BROWN, S.; KICLIGHTER, D. W.; CHAMBERS, J. Q.; THOMLINSON, J. R.; NI, J.; HOLLAND, E. A. Net primary production in tropical forests: an evaluation and synthesis of existing field data. **Ecological Applications**, v. 11, n. 2, p. 371-384, 2001.
- CLEVELARIO JR., J. Quantificação da massa e do reservatório de nutrientes na serrapilheira da bacia do Alto rio da Cachoeira, Parque Nacional da Tijuca, e avaliação da sua participação na ciclagem de nutrientes, 1988. 125 f. Dissertação (Mestrado em Geoquímica) Dept. de Geoquímica, Universidade Federal Fluminense, 1988.
- CUSTODIO FILHO, A.; FRANCO, G. A. D.; DIAS, A. C. Produção de serapilheira em Floresta Pluvial Atlântica Secundária, Parque Estadual da Serra do Mar (Cunha, SP, Brasil). **Revista do Instituto Florestal**, v. 9, n. 2, p. 103-110, 1997.
- DELAMONICA, P. D. Florística e Estrutura de Floresta Atlântica Secundária Reserva Biológica Estadual da Praia do Sul, Ilha Grande RJ, 1997. 178 f. Dissertação (Mestrado em Ecologia) Instituto de Biologia, Universidade de São Paulo, São Paulo, 1997.
- DELAMONICA, P.; LIMA, D. F.; OLIVEIRA, R. R.; MANTOVANI, W. Estrutura e funcionalidade de populações de *Miconia cinnamomifolia* (DC.) Naud. em florestas secundárias estabelecidas sobre antigas roças caiçaras. **Pesquisas Botânicas**, v. 52, p. 125-142, 2002.

- DELITTI, W. B. C. Ciclagem de nutrientes: instrumentos para a análise funcional de ecossistemas terrestres. **Oecologia Brasiliensis**, v. 1, n. 1, p. 469-486, 1995.
- DINIZ, S.; PAGANO, S. N. Dinâmica de folhedo em floresta mesófila semidecídua no Município de Araras, SP Produção, decomposição e acúmulo. **Revista do Instituto Florestal**, v. 9, n. 1, p. 27-36, 1997.
- DOMINGOS, M.; MORAES, M. M.; VUONO, Y. S.; ANSELMO, C. E. Produção de serapilheira e retorno de nutrientes em um trecho de Mata Atlântica secundária, na Reserva Biológica de Paranapiacaba, SP. **Revista Brasileira de Botânica**, v. 20, n. 1, p. 91-96, 1997.
- EWEL, J. J. Litter fall and leaf decomposition in a tropical forest succession in eastern Guatemala. **Journal of Ecology**, v. 64, p. 293-308, 1976.
- GARAY, I. Relations entre l'hétérogénéité des litières et l'órganisation des peuplements d'arthropodes édaphiques. École Normale Supérieure. **Publications du Laboratoire de Zoologie**, n. 35, p. 191, 1989.
- GARAY, I.; KINDEL, A. Diversidade funcional em fragmentos de Floresta Atlântica. Valor indicador das formas de húmus florestais. In: GARAY, I.; DIAS, B. (Orgs.). Conservação da biodiversidade em ecossistemas tropicais: avanços conceituais e revisão de novas metodologias de avaliação e monitoramento. Petrópolis: Vozes, 2001. p. 350-368.
- HANAZAKI, N.; CASTRO, C.; VIVIAN GLADYS OLIVEIRA, V. G.; PERONI, N. Between the sea and the land: the livelihood of estuarine people in southeastern Brazil. **Ambiente e Sociedade**, v. 10, n. 1, p. 121-136, 2007.
- HERRERA, R.; JORDAN, C. F.; KLINGE, H.; MEDINA, E. Amazon ecosystems. Their structure and functioning with particular emphasis on nutrients. **Interciencia**, v. 3, n. 4, p. 223-231, 1978.
- HORN, H. S. Succession. In: MAY, R. M. (Ed.). **Theoretical Ecology: Principles and Applications**. Oxford: Blackwell Scientific, 1976. p. 187-204.
- JORDAN, C. F. Nutrient cycling processes and tropical forest management. In: GÓMES-POMPA, A.; WHITMORE, T. C.; HADLEY, M. (Eds.). Rain forest regeneration and management. Chicago: UNESCO & The Parthenon Publ. Group, 1991. p. 159-180.
- JORDAN, C. F. The tropical rain forest landscape. In: VILES, H. A. (Ed.). **Biogeomorfology**. Blackwelll: London, 1988.
- KAGEYAMA, P. Y.; CASTRO, C. F. A. Secessão secundária, estrutura genética e plantações de espécies arbóreas nativas. **Revista do IPEF**, v. 41/42, p. 83-93, 1989.
- KAPPELLE, M.; GEUZE, T.; LEAL, M.; CLEF, M. Successional age and forest structure in a Costa Rica upper montane Quercus forest. **Journal of Tropical Ecology**, v. 12, p. 681-698, 1996.
- LEITÃO FILHO, H. F.; PAGANO, S. N.; CESAR, O.; TIMONI, J. L.; RUEDA, J. J. (Orgs.). **Ecologia da Mata Atlântica em Cubatão**. Campinas: Ed. UNESP, 1993.

- LOUZADA, M. A. P.; QUINTELA, M. F. S.; PENNA, L. P. S. Estudo comparativo da produção de serapilheira em áreas de mata atlântica: a floresta secundária "antiga" e uma floresta secundária (capoeira). **Oecologia Brasiliensis I**: ecologia, funcionamento e manejo de ecossistemas. Rio de Janeiro: Universidade Federal do Rio de Janeiro, 1995. p. 61-74.
- MAZUREC, A. P. Ciclagem de nutrientes em mata atlântica de encosta na Serra do Imbé, Norte Fluminense em duas altitudes, 1998. 88 f. Dissertação (Mestrado em Biocências e Biotecnologia) Centro de Biociências e Biotecnologia, Universidade Estadual do Norte Fluminense, Campos dos Goytacazes, 1998.
- MCGRATH, D. G. The role of biomass in shifting cultivation. **Human Ecology**, v. 15, n. 2, p. 221-242, 1987.
- MEGURO, M.; VENUEZA, G. N.; DELITTI, W. B. C. Ciclagem de nutrientes minerais na mata mesófila secundária São Paulo. I. Produção e conteúdo de nutrientes minerais no folhedo. **Boletim de Botânica da Universidade de São Paulo**, v. 7, p. 61-67, 1979.
- MORAES, R. M.; DELITTI, W. B. C. Produção e retorno de nutrientes via serapilheira foliar de *Euterpe edulis* Mart. em Mata Atlântica de encosta, Ilha do Cardoso, SP. **Naturalia**, v. 21, p. 57-62, 1996.
- MORAES, R. M.; REBELO, C. F.; DELITTI, W. B. C.; STRUFALDIDE VUONO, Y. **Serapilheira acumulada em um trecho de mata atlântica, no Parque Estadual da Ilha do Cardoso**. In: III Simpósio de ecossistemas da costa brasileira, ACIESP, 1993. p. 95-99.
- MUSSOLINI, G. Ensaios de antropologia indígena e caiçara. Rio de Janeiro: Ed. Paz e Terra, 1980.
- MORAES, R. M.; DELITTI, Welington B C; VUONO, Y. S. . Litterfall and litter nutrient content in two Brazilian coastal forests. **Revista Brasileira de Botânica**, v. 22, n. 1, p. 9-16, 1999.
- NOORGARD, R. Progress Betrayed: the demise of development and a coevolutionary revisioning of the future. Londres: Routledge, 1994.
- NYE, P. H.; GREENLAND, D. J. **The soil under shifting cultivation.** London: Commonwalth Bur. Soils Teach. Commun, 1960. v. 5.
- OLIVEIRA, R. R. Ação antrópica e resultantes sobre a estrutura e composição da Mata Atlântica na Ilha Grande, RJ. **Rodriguésia**, v. 53, n. 82, p. 33-58, 2002.
- OLIVEIRA, R. R. **O rastro do homem na floresta: sustentabilidade e funcionamento da Mata Atlântica sob manejo Caiçara**, 1999. 150 f. Tese (Doutorado em Geografía) Programa de Pós Graduação em Geografía, Universidade Federal do Rio de Janeiro, Rio de Janeiro, 1999.
- OLIVEIRA, R. R.; COELHO NETTO, A. L. Captura de nutrientes atmosféricos pela vegetação na Ilha Grande, RJ. **Pesquisa Botânica**, v. 51, p. 31-49, 2001.

- OLIVEIRA, R. R.; LIMA, D. F.; DELAMONICA, P.; SILVA, R. F.; TOFFOLI, D. D. G. Roça Caiçara: Um Sistema "primitivo" autosustentável. **Ciência Hoje**, v. 108, p. 45-51, 1995.
- PAGANO, S. N. Nutrientes minerais do folhedo produzido em mata mesófila semidecídua no município de Rio Claro, SP. **Revista Brasileira de Biologia**, v. 49, n. 3, p. 641-647, 1989.
- PERONI, N. Ecologia e genética da mandioca na agricultura itinerante do litoral sul paulista: uma análise espacial e temporal, 2004. 246 p. Tese (Doutorado em Biologia Vegetal) Instituto de Biologia, Universidade Federal de Campinas, Campinas, 2004.
- POOLE, R. W. **An introduction to quantitative ecology**. Toquio: Mac Graw-Hill, 1974.
- SALDARRIAGA, J. G.; UHL, C. Recovery of forest vegetation following slash-and-burn agriculture in the upper Rio Negro. In: GÓMES-POMPA, A.; WHITMORE, T. C.; HADLEY, M. (Eds.). Rain forest regeneration and management. Chicago: UNESCO & The Parthenon Publ. Group, 1991. p. 303-312.
- SÁNCHEZ, P. Suelos del Trópico: características y manejo. Costa Rica: Inst. Interamericano de Coop. para la Agricultura, 1981.
- SASTRE, C. Notion de climax em régions néotropicales. **Compte rendu des seances de la Societé de Biogeographie**, v. 58, n. 3, p. 117-123, 1982.
- SCHLITTLER, F. H. M.; DE MARINIS, G.; CESAR, O. Produção de serapilheira na floresta do Morro do Diabo, Pontal de Paranapanema, SP. **Naturalia**, v. 8, p. 135-147, 1993.
- SCHMIDT, C. B. **A lavoura caiçara**. Rio de Janeiro: Ministério da Agricultura, Serviço de Informação Agrária, Documento da Vida Rural, n. 14, 1958. 179 p.
- SILVA, R. F. Roça caiçara: dinâmica de nutrientes, propriedades físicas e fauna do solo em um ciclo de cultura, 1998. 164 f. Dissertação (Mestrado em Agronomia) Departamento de Solos, Universidade Federal Rural do Rio de Janeiro, Seropédica, 1998.
- SIMINSKI, A.; FANTINI, A. C. Slash-and-burn agriculture: use of forest resources and dynamics of rural landscape in Santa Catarina State, Brazil. **Ciência Rural**, v. 37, n. 3, p. 31-54, 2007.
- STARK, N.; JORDAN, C. F. Nutrient retention by root mass of an amazonian rain forest. **Ecology**, v. 59, p. 437-439, 1978.
- TABARELLI, M.; MANTOVANI, W. A regeneração de uma floresta tropical montana após corte e queima (São Paulo Brasil). **Revista Brasileira de Biologia**, v. 59, n. 2, p. 239-250, 1999.
- VARJABEDIAN, R.; PAGANO, S. N. Produção e decomposição do folhedo em um trecho de mata atlântica de encosta no município de Guarujá, SP. Acta Botanica Brasilica, v. 1, n. 2, p. 243-256, 1988.

VELOSO, H. P.; RANGEL-FILHO, A. L. R.; LIMA, J. C. A. Classificação da vegetação brasileira, adaptada a um sistema universal. Rio de Janeiro: IBGE, Departamento de Recursos Naturais e Estudos Ambientais, 1991. 124 p.

VITOUSEK, P. Nutrient cycling and nutrient use efficiency. **American Naturalist**, v. 119, n. 4, p. 553-572, 1982.

WUNDER, S. Big Island, Green Forests and Backpackekrs: landuse and development options on Ilha Grande, Rio de Janeiro State, Brazil. Copenhage: Center for Development Research, 2000. Mimeografado.

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