MORTALITY AND RECRUITMENT OF TREES IN A SECONDARY MONTANE RAIN FOREST IN SOUTHEASTERN BRAZIL

GOMES, E. P. C.,[1] MANTOVANI, W.[2] and KAGEYAMA, P. Y.[3]

[1]Departamento de Biologia, Universidade de Taubaté, Praça Marcelino Monteiro, 63, CEP 12030-010,
Taubaté, SP, Brazil

[2]Departamento de Ecologia Geral, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, 326,
C.P. 11461, CEP 05422-970, São Paulo, SP, Brazil

[3]Departamento de Ciências Florestais, ESALQ, Universidade de São Paulo, Av. Pádua Dias, 11,
C.P. 09, CEP 13418-900, Piracicaba, SP, Brazil

Correspondence to: Eduardo Pereira Cabral Gomes, Departamento de Biologia, Universidade de Taubaté, Praça
Marcelino Monteiro, 63, CEP 12030-010, Taubaté, SP, Brazil, e-mail: epcgomes@ig.com.br

Received November 21, 2001 – Accepted May 13, 2002 – Distributed February 28, 2003

(With 5 figures)

ABSTRACT

Mortality and recruitment rates were obtained for tree species over a 5.6 year period in a 1-ha fragment of secondary montane rain forest in Southeastern Brazil. All plants with a diameter at breast height (dbh) $\geq$ 8 cm were sampled in 1989-1990 and 1995. There was an increase from 90 to 96 species, and 669 ind./ha to 749 ind./ha over the period. The mortality rate of 1.67%/yr was similar to findings for other forests, while recruitment of 3.46%/yr was the highest rate reported. Both mortality and recruitment were significantly higher in the smaller dbh classes. Recruitment was higher among rare species, and the relatively slow-growing species had significantly higher mortality rates. Differences between species dynamics were marked. Species with high values of λ were mainly early successional and understorey trees but some understorey species also suffered a marked population decline. The classification system of species in response to light which divides understorey species into "partial shade-bearers" and "shade-bearers" groups showed to be the most suitable to the obtained results. The results suggest that this forest is undergoing a process of recovery from past disturbance.

Key words: forest dynamics, mortality, recruitment, rain forest, ecological groups.

RESUMO

Mortalidade e recrutamento de espécies arbóreas em floresta montana secundária no Sudeste do Brasil

Taxas de mortalidade (M) e recrutamento (R) foram obtidas para espécies arbóreas em um fragmento de 1 ha de floresta secundária montana no Sudeste do Brasil. Amostraram-se as árvores com dap $\geq$ 8 cm em 1989-1990 e em 1995. Houve aumento de 90 para 96 espécies e de 669 arvs/ha para 749 arvs/ha durante os 5,6 anos. O valor de M obtido foi de 1,67%/ano e o de R, 3,46%. O primeiro situou-se em torno dos valores médios registrados em outras florestas tropicais, o último, porém, apresentou-se como o mais elevado. Ambas as taxas foram significativamente maiores nas menores classes de dap. As espécies raras apresentaram maiores taxas de recrutamento e as espécies com baixo crescimento relativo tiveram mortalidade significativamente maior. As diferenças entre a dinâmica de espécies foram altas. Altos valores de λ foram registrados nas espécies secundárias iniciais e de sub-bosque, mas espécies de sub-bosque também apresentaram acentuado declínio populacional. O sistema de classificação de grupos ecológicos em função da luminosidade, que separa as espécies de sub-bosque em "parcialmente tolerantes à sombra" e "tolerantes à sombra", foi o que melhor se ajustou aos resultados encontrados. Os dados sugerem que o trecho de floresta estudado encontra-se em processo de recuperação de algum evento de distúrbio.

Palavras-chave: dinâmica florestal, mortalidade, recrutamento, floresta pluvial, grupos ecológicos.

INTRODUCTION

Various studies of tropical forests have reported mortality and recruitment rates of trees. These studies have shed light on the question of maintenance of the great diversity of tree species (Hubbell & Foster, 1983, 1986c, d, 1987, 1990, 1992; Hubbell *et al.,* 1990; Primack & Hall, 1991, 1992; Condit *et al.,* 1993) and increased understanding of the dynamics of these communities (Hartshorn, 1980, 1990; Swaine *et al.,* 1987b; Phillips *et al.,* 1994; Phillips & Gentry, 1994; Sheil, 1995a, b; Phillips, 1996). Most of this research has been carried out in well conserved lowland tropical rain forests, usually in sites located in Central America and the Amazon Basin (Gomes, 1998). These studies classified species into ecological groups according to their response to gaps, and it was expected that species in a particular ecological group share characteristics of importance and facilitates predictions about forest processes (Connell *et al.,* 1984; Lieberman & Lieberman, 1987; Manokaran & Kochummen, 1987; Lieberman *et al.,* 1990; Korning & Balslev, 1994a; Taylor *et al.,* 1996; Oliveira Filho *et al.,* 1997).

Results of similar surveys conducted in other types of tropical forests have demonstrated that it is difficult to use the forest-cycle model prevalent in the current literature on forest stand dynamics, which focuses on one simple mechanism of disturbance: the opening of gaps (Uhl, 1982; Swaine *et al.*, 1990; Pascal & Pelissier, 1996) followed by recolonization by a clear group of pioneer species (Swaine *et al.*, 1990).

In the Atlantic Rain Forest, which has been reduced to less than 10% of its original area, there have been few studies of stand dynamics in montane rain forests (Gomes, 1998), such as the one studied here. The forest type studied here is unlike most others analyzed in the literature, in that it is a secondary, sub-tropical montane forest forming an isolated fragment inside an extensive urban area, exposed to impacts such as air pollutation absent in most forest areas studied to date.

The main questions addressed here are: how stable are the local populations of common and rare species? How are mortality and recruitment rates related to diameter classes and ecological species groups? Predictions made in previous work (Gomes & Mantovani, 2001) regarding population structure of the six most abundant species are also examined. Finally, the results are compared to data from other tropical sites.

MATERIAL AND METHODS

The study was conducted in the "Fontes do Ipiranga" State Park (FISP), located at, 23°38'40"S, 46°36'38"W, and at an altitude of 760 to 830 m in São Paulo city, Brazil (Fig. 1). Established in 1883 outside the then urban limits, the park was partly occupied by small country properties and tea plantations (*Camelia sinensis*). The city has grown from a population of 61,000 in 1883 to more than 10,000,000 today, and this conservation area is now inside the city's urban perimeter. The park had 549.31 ha, and 109.31 ha of the more heavily frequented area were allocated to government agencies and departments (Melhem *et al.,* 1981). The remaining 340 ha became a biological reserve in 1883 (Fig. 2).

This biological reserve is characterized as a montane Atlantic rain forest, in various stages of succession.

The main causes of disturbance result from its urban location, and include acid rain, atmospheric pollution and the "heat island" effect (Lombardo, 1985), as well as isolation. Other sporadic causes of disturbance are the extraction of wood and ornamental plants, hunting, and fires that occur around the edge of the park. The flora has been described in a series of studies by the Instituto de Botânica de São Paulo (Hoehne *et al.,* 1941; Melhem *et al.,* 1981, 1984; Milanez *et al.,* 1990). Studies have been carried out in the park of arboreal vegetation (Struffaldi-de-Vuono, 1985; Costa & Mantovani, 1992; Nastri *et al.,* 1992; Teixeira *et al.,* 1992; Knobel, 1995; Penhalber & Mantovani, 1997; Gomes & Mantovani, 2001).

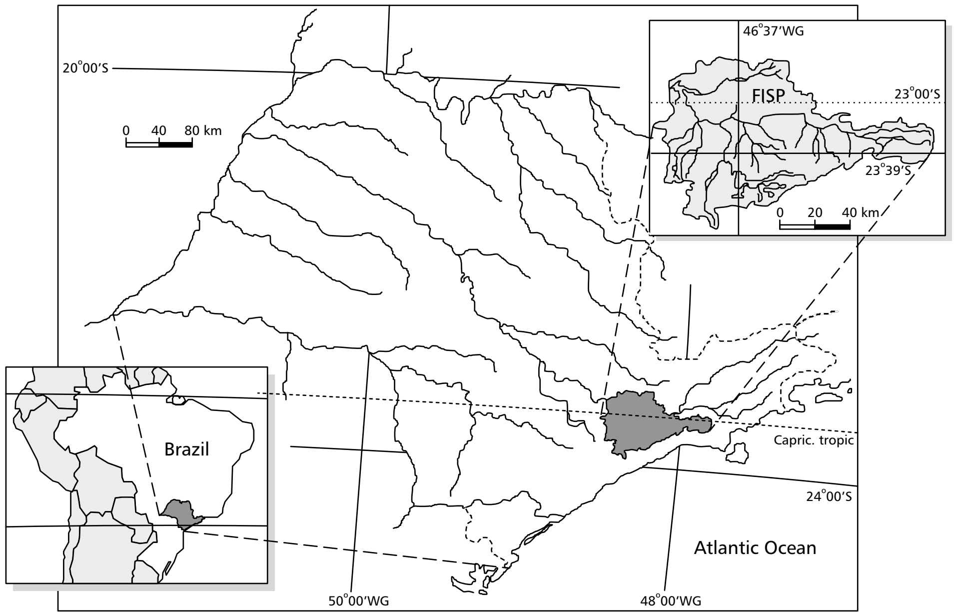

Fig. 1 — Location of Fontes do Ipiranga State Park (FISP) in Southeastern Brazil.

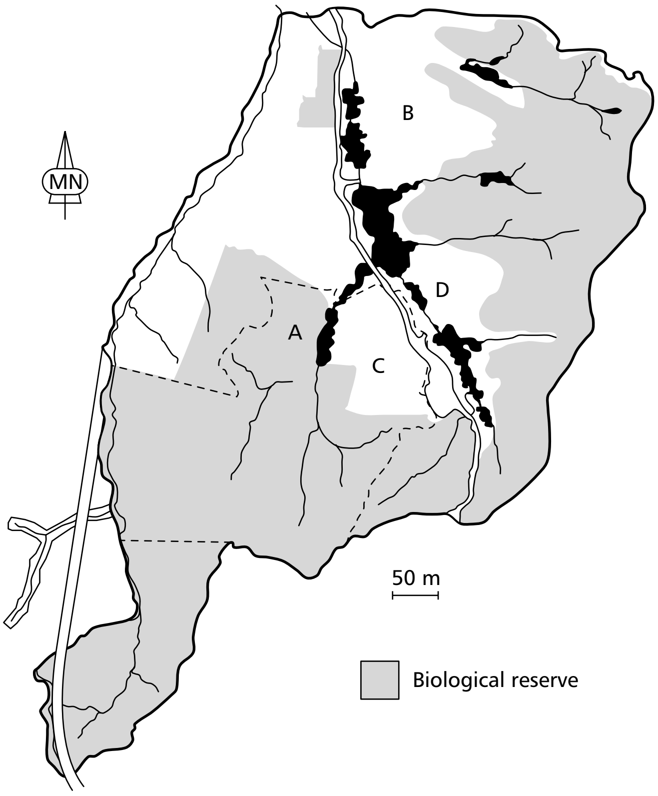

Fig. 2 — Map of FISP (Fontes do Ipiranga State Park) in São Paulo city. A – study area in Instituto Astronômico e Geofísico, Universidade de São Paulo (23º39'S-46º37'WG, 775-790 m); B – Botanical Garden and Instituto de Botânica; C – Meteorological Station; D – Zoological Park (modified from Melhem *et al.*, 1981).

Forest has a discontinuous canopy and tree heights are between 10 and 15 m, with a dense understory, and in the open areas two species of gramineae predominate *(Olyra micrantha* H.B.K. and *Chusquea* sp.). Many of the trees have inclined trunks, and there are numerous lianas. Gomes & Mantovani (2001) reported marked dominance of six tree species in permanent sample plot: *Plinia glomerata* (O. Berg) Amsh. (Myrtaceae), *Ouratea semiserrata* (Mart. & Ness.) Engl. (Ochnaceae), *Coccoloba warmingii* Meiss. (Polygonaceae), *Maytenus robusta* Reissek (Celastraceae) *Pera glabrata* (Schott) Baill. (Euphorbiaceae) and *Syagrus romanzoffiana* (Cham.) Glassm. (Palmae).

Meteorological data were obtained from an observatory of the "Institute of Astronomy and Geophysics" of the University of São Paulo, located 300 m from the forest fragment under study. During the period between the 1989 and 1995 census the average annual temperature was 19.2°C, the monthly average being highest in January (22.3°C) and lowest in July (15.7°C). There was frostσ in July 1988 and July 1989. The average rainfall for the years in question was 1556.1 mm, varying from 1918 mm in 1991 to 1315 mm in 1994 (Fig. 3). Half the rainfall occurred between December and March, the four warmest months of the year, and the lowest rainfall occurred in July (41 mm). The most severe drought was in 1994, with two other severe droughts in 1988 and 1992 (Fig. 3). At the end of the dry season in 1994, fire occurred in the southern area of the reserve affecting 20 ha of forest.

Between 1950-1959 and 1988-1995, the average annual temperature increased by 1.2°C (from 18°C to 19.2°C). The climate during the period under analysis was Cwa, Cwb or Cwf type, according to the Köppen System (1948), due to the variations in the average annual temperature of around 18°C, with the hottest month around 22°C (Aragaki & Mantovani, 1998). The soils are predominantly ferralsols type.

Between November 1989 and March 1990, the time of the first census, 1 ha plot of forest in the center of the reserve was demarcated, with a slope of 10% to 25%. All standing trees with a diameter at breast height (dbh) ≥ 8 cm were measured and mapped into a grid of 400 sub-plots of 5 x 5 m. No antropogenic disturbance events were recorded in the plot and surrounding area. The trees were marked and the species were identified. The area was re-sampled between February and June 1995, in a second census.

Mortality (M) and recruitment (R) rates were calculated (Sheil, 1995b; Sheil *et al.*, 1995) as follows:

$$M = \{1 - [(N_O - m)/N_O]^{1/\Delta t}\} \times 100,$$

where N_O = population count at the beginning of the measurement interval, m = number of deaths among the initial population, following the between-census period (Δt), Δt = measurement interval between census ($t_1 - t_0$) and:

$$R = \{[(N_O + r)/N_O]^{1/\Delta t} - 1\} \times 100,$$

where: r = number of individuals recruited, excluding the dead recruited, between the censuses (Sheil & May, 1996). Stand half-life ($T_{0.5}$, Swaine & Lieberman, 1987) and time necessary to double the number of individuals (T_2, Pinto-Coelho, 2000) were obtained using:

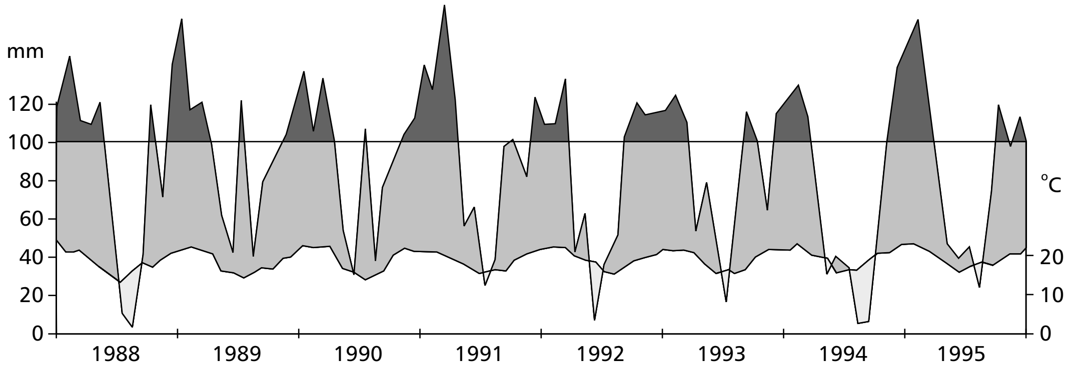

Fig. 3 — Climatic diagram of Walter-Lieth for study area (FISP) from 1988 to 1995 yr. (Data from Instituto Astronômico e Geofísico – Universidade de São Paulo.)

$T_{0.5} = (\ln 0.5)/\ln[(N_O - m)/N_O]^{1/\Delta t}$ and
$T_2 = (\ln 2)/\ln[(N_O + r)/N_O]^{1/\Delta t}$.

Dynamic (D) and stability (S) measures were calculated by (Gomes, 1998, modified from Korning & Balslev, 1994b):

$$S = [(m + r)/N_O] \times 100 \text{ and}$$
$$D = [(r + m + d)/N_O]^{1/\Delta t} \times 100,$$

where d = number of individuals that were recruited and died between the censuses. Generally, recruits that died are not indicated in permanent sample plot studies. Over longer periods between the census, trees can be recruited, die, and not be recorded, thus underestimating dynamics. The above equation makes explicit the dependence of dynamics value D on the number of dead recruits.

Rates were obtained for those species which had at least 10 individuals sampled in the first census (Gomes & Mantovani, 2001). Two recorded trees had a smaller dbh than the minimum required for inclusion in the second census. One of these, a specimen of *Alchornea triplinervia* (Spreng.) Muell. Arg. (Euphorbiaceae), presented three trunks in the first census, the largest of which was broken, and the dbh was thus lower than the criterion for inclusion in the second census. The other tree with a negative increment was a specimen of *Pera glabrata*, which fell, but remained alive, and resprouted on the lateral branches. These two individuals were considered false dead (Table 1) and were treated as dead in the calculations.

Based on the differences in diameter, the rates of relative growth were calculated as follows (Welden *et al.,* 1991):

$$RGR = \{[(dbh95 - dbh89]/dbh89]^{1/\Delta t} - 1\} \times 100,$$

where dbh89 is the dbh in the first census and dbh95 is the dbh in the second census. The species were classified into two groups according to their mean annual relative growth rate (RGR) – low RGR (RGR_{low}, < 0.62%/year) and high RGR ($RGR_{high} \geq 0.62$%/year) – for all species with ten or more trees in first census.

The species were distributed into three classes of abundance: rare (1 or 2 ind./ha), occasional (3 to 9 ind./ha) and common (10 or more ind./ha). The diameter classes were: small (8 cm ≤ dbh ≤ 12 cm), medium (12 cm < dbh ≤ 16 cm) and large (dbh > 16 cm). The palm tree *Syagrus romanzoffiana* was not included in calculations because of negative increments for many individuals whose trunks were not free from their leaf sheaths when their dbh was measured at 1.3 m in the first survey.

RESULTS

The second census recorded 749 individuals whose total basal area was 19.55 m^2/ha, whereas the first census recorded 669 indiv./ha with total basal area of 17.031 m^2/ha. The Shannon-Wiener diversity index was also greater in the second census with 3.529 nats, though not significantly differing ($t = 1.019$, $p > 0.10$) from the value obtained in the first census with 3.445 nats. Of trees with dbh ≥ 10 cm in the second census, 571 individuals belong to 87 species with 18.46 m^2/ha total basal area, and H' = 3.362.

Diametric distribution curves (Fig. 4) obtained for total live individuals did not differ from the first to the second census (Kolmogorov-Smirnov Test, $D = 0.026376 < D_{0.05} = 0.072303$). Nor did they differ for rare species between the two surveys (Kolmogorov-Smirnov Test, $D = 0.120565 < D_{0.05} = 0.224415$) or between rare and other species in first census (Kolmogorov-Smirnov, $D = 0.079242 < D_{0.05} = 0.183791$). However, the relative number of higher diameter values were significant lower for rare species than to other ones (Kolmogorov-Smirnov Test, $D = 0.154717 > D_{0.05} = 0.149792$) in the second sampling (Fig. 4).

The mortality rate of 1.67%/yr for all trees (1.59%/yr for dbh ≥ 10 cm) was much lower than recruitment rate, 3.46%/yr (3.67%/yr for dbh ≥ 10 cm), and half-life time ($T_{0.5}$) was 41.23 years and doubling time (T_2) was 20.39 years.

Recruitment rates would have been higher and mortality lower if *Syagrus romanzoffiana* population had been included. Many negative increments were recorded for this palm species because the inclusion criterion for phanerophytes (dbh ≥ 8 cm) was used, and the leaf sheath was measured frequently in the first survey. However, it is certain that none of the marked palms died during the study, and a number were recruited. The R value for *Syagrus romanzoffiana* was estimated to be between 4.0 and 6.6%/yr.

TABLE 1

Mortality and recruitment between 1989 and 1995 for size, relative growth and common species (10 or more individuals) size classes in 1 ha of secondary montane rain forest (Fontes do Ipiranga State Park, IAG-USP, 23°39'S-46°37'WG, 775-790 m), São Paulo, SP. Dt = time interval between census (years); N_O = inicial number of individuals (1st census); m = dead[i]; r = recruits[ii]; M = mortality rate (%); R = recruitment rate (%); RGR_{low} = tree species (ten or more individuals)[iii] with relative growth rate (RGR) below median for all community (0.62%/year); RGR_{high} = tree species (ten or more individuals)[iv] with relative growth rate above median for all community (0.62%/year). The palm species *Syagrus romanzoffiana* (Palmae) is not included.

Categories	Δt	N_o	m	r	M	R	λ	RGR
Abundance Class rares (1 or 2 trees/ha)	5.60	60	7	41[v]	2.17	9.35[vi]	1.083	2.08
ocasionals (from 3 to 9 trees/ha)	5.59	174	20	37	2.16	3.51	1.017	1.43
Commons (10 or more trees/ha)	5.56	435	33	62	1.41	1.42	1.012	1.19
Size Class 8 cm ≤ dbh ≤ 12 cm	5.58	270	36	128	2.53	7.20	1.054	1.71
12 cm < dbh ≤ 16 cm	5.55	175	13	53	1.38	4.88	1.038	1.07
dbh > 16 cm	5.59	224	11	32	0.90	2.40	1.016	1.09
Relative Growth Rate (RGR) Class RGR_{low}	5.55	255	31	17	2.31	1.17	0.989	0.28
RGR_{high}	5.60	180	5	45	0.50	4.07	1.036	1.44
Species *Alchornea sidifolia*	5.60	16	0	15	0.00	12.63	1.125	7.13
Amaioua guianensis	5.59	22	0	4	0.00	3.03	1.030	0.62
Coccoloba warmingii	5.60	56	3	3	0.98	0.94	1.000	1.05
Guatteria australis	5.50	16	0	3	0.00	3.14	1.031	0.30
Guapira opposita	5.54	10	0	8	0.00	11.13	1.112	2.83
Myrcia pubipetala	5.49	17	2	0	2.26	0.00	0.977	0.25
Maytenus robusta	5.52	72	15	4	4.14	0.98	0.970	0.29
Ouratea semiserrata	5.54	76	2	2	0.48	0.47	1.000	1.00
Pera glabrata	5.52	32	5[vii]	4	3.03	2.16	0.994	0.63
Plinia glomerata	5.60	96	6	2	1.15	0.37	0.992	0.69
Psychotria nemorosa	5.65	22	0	17	0.48	10.66	1.107	3.73
only dbh ≤ 10 cm (without palmae)	558	493	42	100	1.59	3.37	1.020	–
All trees (without palmae)	5.59	669	60	140	1.67	3.46	1.020	–

[i] Including false dead (2 trees) in total and not including 3 dead recruits.
[ii] Not including 3 dead recruit.
[iii] *A. guianensis, G. australis, M. pubipetala, M. robusta, P. glabrata, P. glomerata.*
[iv] *A. sidifolia, C. warmingii, G. opposita, O. semiserrata, P. nemorosa* and rares.
[v] In 41 recruits 14 were from 12 new recorded species (2nd census).
[vi] Excluding the 14 individuals pointed out above R = 6.81%/year.
[vii] Including false dead. Without these M = 2.39%/year.

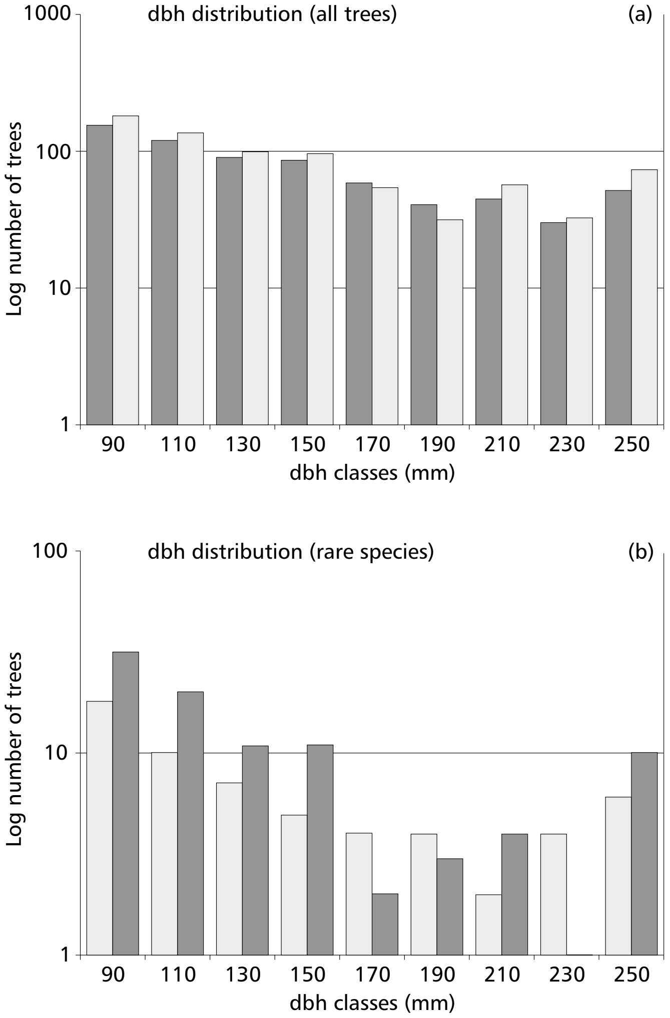

Fig. 4 — Diameter distribution of standing live trees (a) and rares species (b), in the first (1989-1990), light bars, and second (1995) census, dark bars, in Fontes do Ipiranga State Park, São Paulo, Brazil.

Of the eleven species with at least ten individuals sampled in the first census (Table 1), species with a high recruitment rate were *Alchornea sidifolia* Muell. Arg. (Euphorbiaceae), at 12.63%/year, *Guapira opposita* (Vell.) Reitz (Nyctaginaceae) at 11.13%/year, *Psychotria nemorosa* Gardn. (Rubiaceae) at 10.66%/year, and *Guatteria australis* A. St. Hil (Annonaceae) at 3.14%/year. *Alchornea sidifolia* is an early secondary species associated with gaps in sample plots (Gomes, 1998), and the three others are understorey species. Population decline was especially high for *Maytenus robusta* (–3.00%/year), *Plinia glomerata* (–0.80%/year) and *Myrcia pubipetala* Miq. (Myrtaceae) (–2.3%/year). The populations of *Ouratea semiserrata* and *Coccoloba warmingii* remained constant.

Mortality did not differ significantly ($\chi^2 = 2.405$, 2 f.d., $p > 0.10$) among common species, occasional species and rare species. However, rare species had significantly higher recruitment rates ($\chi^2 = 46.38$, 2 f.d., $p < 0.001$).

In regard to dbh classes, there were significant differences for M ($\chi^2 = 10.74$, 2 f.d., $p < 0.001$) and R ($\chi^2 = 42.08$, 2 f.d., $p < 0.001$). The largest difference occurred in dbh ≤ 12 cm class, with more dead and recruited individuals (Table 1).

The number of dead individuals in dbh > 16 cm class (obs = 11) and recruited individuals (obs = 32) were below the expected values of 20 and 71 in contingency tables.

There were significant differences for M (χ^2 = 7.29, 1 f.d., $p < 0.01$) between RGR classes, with more dead trees among the lower RGR class (obs = 28, exp = 22). In the case of low R in the RGR_{low} class (obs = 17, exp = 53), and high R in the RGR_{high} class (obs = 86, exp = 50) the result was highly significant (χ^2 = 50.54, 1 f.d., $p < 0.001$).

The area under study presented higher values for dynamics (D = 0.806) and lower values for stability (S = 0.112) than comparable areas (Fig. 5). Stability is at maximum when S = 0. Comparative studies were carried out in plots of approximately 1-ha, using the same inclusion criteria of dbh ≥ 10 cm, values for the FISP plot in Fig. 5 were only for this criteria, and had similar 5 years intervals between census, thus minimizing effects of comparisons between dissimilar census intervals.

DISCUSSION

The most outstanding aspect of the dynamics in the FISP permanent plot was the clear imbalance between recruitment and mortality, reflecting an increase in density and basal area of 11.96% and 14.79%, respectively. Although density may vary significantly over time (Manokaran & Kochummen, 1987), recruitment and mortality rates recorded at study site were too high to be due to random fluctuations only.

Permanent plots in forests under climatic conditions similar to those of the study area show lower values for R, while M of FISP plot is in the intermediate range (Table 2).

The most likely explanation for the observed changes is that the sampled forest is recovering from the effects of disturbances prior to establishment of the plot. In the first census the percentage of individuals in the area that died standing (14% of the total of trees) was greater than the 4.6% to 7.6% recorded in other forests in São Paulo State, in four studies (Gomes & Mantovani, 2001). There is no removal of trees for fuelwood or record of extreme disturbances, such as fires, logging, epidemics or any other possible cause of catastrophic mortality (M > 5%/ yr, *sensu* Lugo & Scatena, 1996). There are two remaining hypotheses to explain the community's loss of steady state.

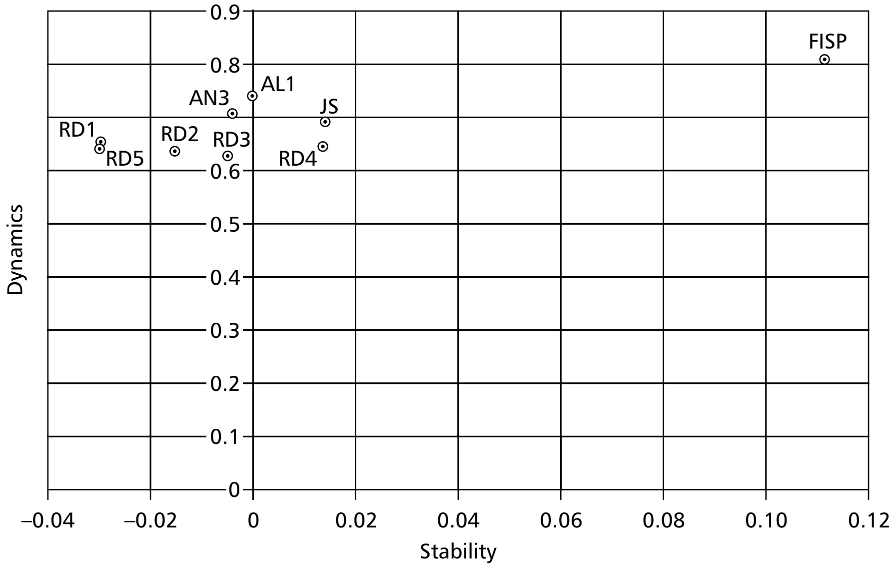

Fig. 5 — Stability and dynamics values for permanent sample plots. Inclusion criteria dbh ≥ 10 cm. AL1, Allpahuayo, Peru, Phillips (1996); AN3, plot 2 in Añangu, Ecuador, Korning & Balslev (1994a, b); FISP, this study; JS, Jatum Sacha, Ecuador, Phillips & Gentry (1994); RD1 to RD5, Ducke Reserve, Manaus, Brazil, Rankin-de-Merona *et al.* (1990).

TABLE 2

Tree dynamics in permanent sample plots in forest types under climatic conditions similar to study area in FISP reserve. Average anual temperature between 17°C and 21°C, average total anual precipitations from 1200 mm to 2400 mm and no more than 2 months of drought period. T = average anual temperature (°C); pp = average total anual pluvial precipitation (mm); dbh = diameter at breast height minimu for inclusion; Plot = plot size (ha); Per = average period between census (year); dens. = density (trees/ha); BA = basal area (m^2/ha); sps = total species; M = mortality rate (%/yr); $T_{0.5}$ = stand half life (years); R = recruitment rate (%/yr); T_2 = doubling time (years). FISP, this study; SGn, Santa Genebra Farm, Brazil (Santos *et al.*, 1996); UFLA, Reserve at Universidade Federal de Lavras, Brazil (Oliveira Filho *et al.*, 1994, 1997); Q_1 and Q_2, Montane forests plots in Queensland, Australia (Phillips & Gentry, 1994); Ki, Kibale, Uganda (Kasanene, 1987, *apud* Phillips *et al.*, 1994; LM2 and LM3, low montane forests plots in Venezuela (Carey *et al.*, 1994).

Site	Latitude, longitude	Altitude (m)	T (°C)	pp (mm)	dbh (cm)	Plot (ha)	Per (yrs)	dens. (trees/ha)	BA (m^2/ha)	sps	M (%/yr)	$T_{0.5}$ (year)	R (%/yr)	T_2 (year)
FISP	23°39’S, 46°37’WG	790	19.0	1477	8	1.00	5.6	737	16.63	87	1.67	41.2	3.46	20.4
SGn	22°50’S, 7°06’WG	690	20.7	1347	5	1.00	12.0	1463	24.9	103	3.44	19.7	–	–
UFLA	21°14’S, 44°58’WG	925	19.4	1529.7	5	5.04	4.8	1295.04	19.77	136	2.64	25.9	3.09	22.8
Q_1	17°02’S, 145°03’EG	730	20.8	1800	10	0.41	32.2	956	69.6	108	0.67	103.6	0.40	176.0
Q_2	16°47’S, 145°03’EG	945	20.0	1750	10	0.20	15.7	935	–		1.35	50.8	0.95	73.2
Ki	0°27’N, 30°25’WG	1440	20.0	1700	13	49.8	1.67	752	–	56	0.68	102.4	–	–
LM2	8°42’N, 71°30’WG	1500	19.5	1800	10	0.25	17.0	664	–	–	1.52	45.3	1.13	61.6
LM3	8°42’N, 71°24’WG	1900	17.0	2000	10	0.25	17.0	560	–	–	2.28	30.1	1.10	63.4

The first hypothesis was raised in a previous study (Struffaldi-de-Vuono, 1985) which considered induced mortality by atmospheric pollution caused by a steel mill (De Vuono *et al*., 1988). Were this the case, stricter emissions controls starting at the end of the eighties could be enabling some of the populations to recover after drastic reductions of phytotoxic aerial pollutants followed by several years of leaching of pollutants.

The second hypothesis involves climatic changes in the metropolitan area of São Paulo over the past century. The average annual temperature in the city has increased 2°C in the 20th century (Lombardo, 1985). At the meteorological station in the FISP reserve the average annual temperature increased from 17.1°C in 1929 to 19°C in 1995. This temperature rise was followed by a reduction of fog and less frequent but heavier periods of rainfall (Lombardo, 1985).

A third explanation involves the interactions among many factors (pollutants, climatic change, fragmentation) and a non linear response of plants to the stress.

The mortality rate in this study, 1.56%/yr (for dbh ≥ 10 cm, like compared sites), was very close to the mean value for 65 other studies of tropical and sub-tropical forests (Phillips, 1996). Among these, 50% of the values were between 1.13% and 2.10%/yr. Mortality at FISP varied greatly among species, from none for several species to 4.14%/yr. for *Maytenus robusta.*

The recruitment rate at FISP was greater than the highest figures in the literature: 3.44%/yr in Gajabuih, Indonesia (Phillips & Gentry, 1994). Elevated recruitment rates were reported after periods of acute disturbance (Lugo & Scatena, 1996; Boucher & Mallona, 1997) or chronic disturbance, such as in especially dry years (Condit *et al.,* 1996), in secondary stands (plot 2 in Milton *et al*., 1994; selectively logged area in Elouard *et al*., 1997) and/or forest edges (Laurence *et al*., 1998).

In various studies there were no significant differences in M between diameter classes (Swaine *et al*., 1987a; Gentry & Terborgh, 1990; Rankin-de-Merona *et al*., 1990; Carey *et al*., 1994; Korning & Balslev, 1994a), but in others (Briscoe & Wadsworth, 1979; Matelson *et al*., 1995; Taylor *et al*., 1996) lower dbh classes had higher mortality and recruitment, as was the case in FISP, where the differences were due to mortality among the *Maytenus robusta* population and recruitment of *Psychotria nemorosa* trees.

Among the more abundant populations, *Guapira opposita* (Vell.) Reitz (Nyctaginaceae), *Amaioua guianensis* Aubl. (Rubiaceae), *Psychotria nemorosa, Guatteria australis* increased their populations over the period. These are understorey species (Klein, 1980), as are *Plinia glomerata* and *Myrcia pubipetala,* which were among those with the most marked population decline. The decline of *Maytenus robusta*, however, was the greatest. It is classified variously as a gap colonizer (Costa & Mantovani, 1995), a late secondary (Klein, 1980) and an early secondary (Gandolfi *et al*., 1995). Canopy and sub-canopy species in our study, such as *Coccoloba warmingii*, *Ouratea semiserrata* and *Pera glabrata* were in steady state. This latter species is classified as an early secondary (Costa & Mantovani, 1995; Tabarelli & Mantovani, 1997) or a secondary (Klein, 1980); no references were found for the first two. Data for the dynamics of these species are only available for *Maytenus robusta* and *Amaioua guianensis*. Both were sampled by Felfili (1995) at Águas Claras Farm, in the Brazilian central plateau. For *Maytenus robusta*, an M value of 2.7%/yr was recorded, lower than that measured in the community (3.44%yr^{-1}). Also in this study M of 3.1%yr^{-1} was recorded for *Amaioua guianensis*. None of the 22 *Amaioua guianensis* individuals died at FISP over the period between surveys.

In a forest undergoing successional change it is expected that understorey, shade tolerant populations should become more common, as the canopy recovers, but at FISP, this was not observed: in the case of understorey tree species, the population included individuals within the highest and lowest λ values. The inclusion criterion (dbh ≥ 8 cm) ensured that only adult trees were sampled, thus offering a partial picture of this population. In addition the understorey vegetation (Gomes & Mantovani, 2001), seedlings, and seed banks (Penhalber, 1995) were sampled and the results also contributed for interpretation of our study. In the first census, where individuals with dbh ≥ 2.5 cm in subplots were also surveyed, *Guatteria australis* and *Plinia glomerata* were not recorded. All the other species listed above were surveyed and *Amaioua guianensis* and *Guapira opposita* were the most abundant in the size class (2.5 ≤ dap < 8 cm). No seeds for *Guatteria australis, Plinia glomerata* and *Myrcia pubipetala* were recorded in the seed rain samples (Penhalber & Mantovani, 1997). In the seedling bank all the species were poorly represented except for *Maytenus robusta* and *Psychotria nemorosa* (Penhalber, 1995). Using the dbh size distributions of these populations when they were studied in the first survey (Gomes & Mantovani, 2001) a population decline was expected for *Plinia glomerata* and *Maytenus robusta*.

The results in this study confirm the prediction for *Plinia glomerata*. The number of trees that died and were recruited, however, was small – six and two respectively – and a future census will be needed to confirm this trend. For *Maytenus robusta* however, the process was much more pronounced than expected. Therefore, understorey species had very different population trends: an accentuated decline for some and a vigorous increase for others.

Classification systems that place species into ecological groups present several problems when applied to tree species in montane rain Atlantic Forests. Among the rich terminology found in the literature for designating ecological groups (Clark & Clark, 1987), the classification system proposed by Schulz (1960), which distinguishes understorey species as "partial shade-bearers" and "shade-bearers" was more appropriate for species in the FISP plot. According to this classification, *Maytenus robusta* and *Plinia glomerata* would be in the second group and *Guapira opposita, Psychotria nemorosa* and *Amaioua guianensis* would be in the first. Classification by ecological groups had its origin in field observations of stratification in the forest and the subjective human perception of "exposure to light". More objective classification systems will likely emerge when the physiology of plants representing each ecological group is studied, especially in regard to their responses at each life stage to environmental factors.

Rare species have higher mortality and recruitment rates in permanent plots in lowland tropical rain forests (Hubbell & Foster, 1983, 1986a, b, c, d, 1990; Manokaran & Kochummen, 1987; Okali & Ola-Adams, 1987; Swaine *et al.,* 1987a, b; Hall, 1991; Welden *et al.,* 1991; Primack & Hall, 1992; Condit *et al.,* 1995). This is partly due to the rarity of gap-loving species that have high growth, recruitment and mortality rates. Large gaps are rare even in this type of forest and, therefore, gap-specialized species are also rare. However, since not all rare species are gap-specialized, species belonging to other ecological groups may be found among the rare species. In the FISP study, the changes under way in the community made it difficult to interpret dynamics of rare group species. Many rare species will become common under more steady state conditions, and, perhaps, occasional and common species will become rare. Note that definition of rare species is subjective.

Dynamic processes that predominate in lowland tropical rain forests cannot be automatically applied to the type of forest in the FISP reserve. Tropical forests contain a number of distinctive pioneer species, dependent on large gaps for germination and growth, and "gap-phase dynamics" prevail in these forests. Authors such as Pascal & Pelissier (1996), Swaine *et al.* (1990), Uhl (1982), who have worked in other forest types, recognize that different dynamic processes may be more common. Perhaps, in low stature forests the rule is that dead trees are replaced with young understorey individuals, saplings or vegetative growth from neighboring plants and rarely by recruitment of a pioneer tree in a gap. Low stature tropical and sub-tropical forests (montane forests, forests on sandy sediment, and deciduous forests), although less diverse than lowland rain forests, are common in various parts of the world, and of great interest for the conservation of biodiversity.

Acknowledgments — The first author received financial support from Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP), Brasil (Grant N. 94/1294-5).

REFERENCES

ARAGAKI, S. & MANTOVANI, W., 1998, Caracterização do clima e da vegetação de remanescente de floresta no planalto paulistano. *An. IV Simp. Ecos. Brasil.*, *3*: 25-36.

BOUCHER, D. H. & MALLONA, M. A., 1997, Recovery of the rain forest tree *Vochysia ferruginea* over 5 years following hurricane Joan in Nicaragua: a preliminary population projection matrix. *For. Ecol. Manage, 91*: 195-204.

BRISCOE, C. B. & WADSWORTH, F. H., 1979, Stand structure and yield in the Tabonuco forest of Puerto Rico, pp. B79-B89. *In*: H. T. Odum & R. F. Pigeon (eds.), *A tropical rain forest*. USA Atomic Energy Comission, Tenessee, 1678p.

CAREY, E. V., BROWN, S., GILLESPIE, A. J. R. & LUGO, A. E., 1994, Tree mortality in mature lowland tropical moist and tropical lower montane moist forest of Venezuela. *Biotropica, 26*(3): 255-265.

CLARK, D. A. & CLARK, D. B., 1987, Análisis de la regeneración de árboles del dosel en bosque muy húmedo tropical: aspectos teóricos y práticos. *Rev. Biol. Trop., 35*(supl. 1): 41-54.

CONDIT, R., HUBBELL, S. P. & FOSTER, R. B., 1993, Short-term dynamics of a neotropical forest. *Bioscience, 42*(11): 822-828.

CONDIT, R., HUBBELL, S. P. & FOSTER, R. B., 1995, Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. *Ecol. Monogr., 65*(4): 419-439.

CONDIT, R., HUBBELL, S. P. & FOSTER, R. B., 1996, Changes in tree species abundance in a Neotropical forest: impact of climate change. *J. Trop. Ecol., 12*: 231-256.

CONNELL, J. H., TRACEY, J. G. & WEBB, L. J., 1984, Compensatory recruitment, growth, and mortality as factors maintaining rain forest tree diversity. *Ecol. Monogr., 54*(2): 141-164.

COSTA, L. G. S. & MANTOVANI, W., 1995, Dinâmica sucessional da floresta mesófila semidecídua em Piracicaba (SP). *Oecologia brasiliensis, 1*: 291-305.

COSTA, M. P. D. & MANTOVANI, W., 1992, Composição e estrutura de clareiras em mata mesófila na bacia de São Paulo, SP. *Rev. Inst. Flor. SP, 4*: 178-183.

DE VUONO, Y. S., LOPES, M. I. M. S. & DOMINGOS, M., 1988, Alterações provocadas pela poluição atmosférica na fertilidade do solo da Reserva Biológica do Instituto de Botânica, São Paulo, Brasil. *Rev. Bras. Bot., 11*(1/2): 95-100.

ELOUARD, C., PASCAL, J.-P., PÉLISSER, R., RAMESH, B. R., HOULLIER, F., DURAND, M., ARAVAJY, S., MORAVIE, M.-A. & GIMARET-CARPENTIER, C., 1997, Monitoring the structure and dynamics of a dense moist evergreen forest in the Western Ghats (Kodagu District, Karnataka, India). *Trop. Ecol., 38*(2): 193-214.

FELFILI, J. M., 1995, Growth, recruitment and mortality in the Gama gallery forest in central Brazil over a six-year period (1985-1991). *J. Trop. Ecol., 11*: 67-83.

GANDOLFI, G., LEITÃO-FILHO, H. F. & BEZERRA, C. L. F., 1995, Levantamento florístico e caráter sucessional das espécies arbustivo-arbóreas de uma floresta mesófila semidecídua no município de Guarulhos, SP. *Rev. Bras. Biol., 55*(4): 753-767.

GENTRY, A. H. & TERBORGH, J., 1990, Composition and dynamics of the Cosha Cashu "mature" floodplain forest, pp. 542-64. *In*: A. H. Gentry (ed.), *Four neotropical rainforests*. Yale University Press, New Haven, 627p.

GOMES, E. P. C., 1998, *Dinâmica do componente arbóreo de um trecho de mata em São Paulo, SP*. Doctoral Dissertation, Universidade de São Paulo, São Paulo, 312p.

GOMES, E. P. C. & MANTOVANI, W., 2001, Size distributions in a warm temperature forest tree populations in São Paulo, Southeastern Brazil. *Naturalia, 26*: 131-158.

HALL, P., 1991, *Structure, stand dynamics and species compositional change in three mixed dipterocarp forests of northwest Borneo*. Ph.D. Thesis, Boston University, Boston, 701p.

HARTSHORN, G. S., 1980, Neotropical forest dynamics. *Biotropica,* (Supl.): 23-30.

HARTSHORN, G. S., 1990, An overview of neotropical forest dynamics, pp. 585-590. *In*: A. H. Gentry (ed.), *Four neotropical rainforests*. Yale University Press, New Haven, 627p.

HOEHNE, F. C., KUHLMANN, M. & HANDRO, O., 1941, *O Jardim Botânico de São Paulo*. Empresa Gráfica da Revista dos Tribunais, São Paulo, 656p.

HUBBELL, S. P., CONDIT, R. & FOSTER, R. B., 1990, Presence and absence of density dependence in a neotropical tree community. *Philos. Trans. R. Soc. Lond. (B. Biol. Sci.), 330*: 269-281.

HUBBELL, S. P. & FOSTER, R. B., 1983, Diversity of canopy trees in a neotropical forest and implications for conservation, pp. 25-41. *In*: S. Sutton, T. Whitmore & A. Chadwick (eds.), *Tropical rain forest: ecology and management*, Blackwell, Oxford, 498p.

HUBBELL, S. P. & FOSTER, R. B., 1986a, Biology, chance, and history and the structure of tropical rain forest tree communities, pp. 314-329. *In*: J. Diamond & T. Case (eds.), *Community ecology*. Harper and Row, Nova York, 665p.

HUBBELL, S. P. & FOSTER, R. B., 1986b, Canopy gaps and the dynamics of a neotropical forest, pp. 77-96. *In:* M. J. Crawley (ed.), *Plant ecology*. Blackwell Scientific Publications, Oxford, 496p.

HUBBELL, S. P. & FOSTER, R. B., 1986c, Commonness and rarity in a neotropical forest: implications for tropical tree conservation, pp. 205-231. *In*: M. Soulé (ed.), *Conservation biology*. Sinauer, Sunderland Massachusetts, 584p.

HUBBELL, S. P. & FOSTER, R. B., 1986d, The spatial context of regeneration in a neotropical forest, pp. 395-412. *In*: M. J. Crawley, P. J. Edwards & A. J. Gray (eds.), *Colonization, succession, and stability*. Blackwell, Oxford, 482p.

HUBBELL, S. P. & FOSTER, R. B., 1987, La estructura espacial en gran escala de un bosque neotropical. *Rev. Biol. Trop., 35*(suplemento): 7-22.

HUBBELL, S. P. & FOSTER, R. B., 1990, Structure, dynamics and equilibrium status of old-growth forest on Barro Colorado Island, pp. 522-541. *In*: A. H. Gentry (ed.), *Four neotropical rainforests*. Yale University Press, New Haven, 627p.

HUBBELL, S. P. & FOSTER, R. B., 1992, Short-term dynamics of a neotropical forest: why ecological research matters to tropical conservation and management. *Oikos, 63*(1): 48-61.

KLEIN, R. M., 1980, Ecologia da flora e vegetação do Vale do Itajaí. *Sellowia, 32*: 165-389.

KNOBEL, M. G., 1995, *Aspectos da regeneração natural do componente arbóreo-arbustivo, de trecho da floresta da Reserva Biológica do Instituto de Botânica em São Paulo, SP.* Masters Thesis, Universidade de São Paulo, São Paulo, 123p.

KÖPPEN, W., 1948, *Climatologia.* Fondo de Cultura, México, 478p.

KORNING, J. & BALSLEV, H., 1994a, Growth rates and mortality patterns of tropical lowland tree species and the relation to forest structure in Amazonian Ecuador. *J. Trop. Ecol., 10*(2): 151-166.

KORNING, J. & BALSLEV, H., 1994b, Growth and mortality of trees in Amazonian tropical rain forest in Ecuador. *J. Veg. Science, 4*: 77-86

LAURENCE, W. F., FERREIRA, L. V., RANKIN-DE-MERONA, J. M. & LAURENCE, S. G., 1998, Rain forest fragmentation and the dynamics of Amazonian tree communities. *Ecology*, *79*(6): 2032-2040.

LIEBERMAN, D. & LIEBERMAN, M., 1987, Forest tree growth and dynamics at La Selva, Costa Rica (1969-1982). *J. Trop. Ecol., 3*: 347-358.

LIEBERMAN, D., HARTSHORN, G. S., LIEBERMAN, M. & PERALTA, R., 1990, Forest dynamics at La Selva Biological Station, Costa Rica, 1969-1985, pp. 509-521. *In*: A. H. Gentry (ed.), *Four neotropical rainforests.* Yale University Press, New Haven, 627p.

LOMBARDO, M. A., 1985, *A ilha de calor nas metrópoles: o exemplo de São Paulo.* Hucitec, São Paulo, 244p.

LUGO, A. E. & SCATENA, F. N., 1996, Background and catastrophic tree mortality in tropical moist, wet, and rain forests. *Biotropica, 28*(4a): 585:599.

MANOKARAN, N. & KOCHUMMEN, K. M., 1987, Recruitment, growth and mortality of tree species in a lowland dipterocarp forest in Peninsular Malaysia. *J. Trop. Ecol., 3*: 315-30.

MATELSON, T. J., NADKARNI, N. M. & SOLANO, R., 1995, Tree damage and annual mortality in a montane forest in Monteverde, Costa Rica. *Biotropica, 27*(4): 441-447.

MELHEM, T. S., GIULIETTI, A. M., FORERO, E., BARROSO, G. M., SILVESTRE, M. S. F., JUNG, S. L., MAKINO, H., MELO, M. M. R. F., CHIEA, S. C., WANDERLEY, M. G. L., KIRIZAWA, M. & MUNIZ, C., 1981, Planejamento para a elaboração da "Flora Fanerogâmica da Reserva do Parque Estadual das Fontes do Ipiranga (São Paulo, Brasil)". *Hoehnea, 9*: 63-74.

MELHEM, T. S., MAKINO, H., SILVESTRE, M. S. F., CRUZ, M. A. V. & JUNG-MENDAÇOLLI, S. L., 1984, Planejamento para a elaboração da "Flora Polínica da Reserva do Parque Estadual das Fontes do Ipiranga (São Paulo, Brasil)". *Hoehnea, 11*: 1-7.

MILANEZ, A. I., BICUDO, C. E. M., VITAL, D. M. & GRANDI, R. A. P., 1990, Criptógamos do Parque Estadual das Fontes do Ipiranga, São Paulo, SP. *Hoehnea, 17*(2): 43-49.

MILTON, K., LACA, E. A. & DEMMENT, M. W., 1994, Successional patterns of mortality and growth of large trees in a Panamanian lowland forest. *J. Ecol., 82*(1): 79-87.

NASTRI, V. D. F., CATHARINO, E. L. M., ROSSI, L., BARBOSA, L. M., PIRRÉ, E., BEDINELLI, C., ASPERTI, L. M., DORTA, R. de O. & DA COSTA, M. P., 1992, Estudos fitossociológicos em uma área do Instituto de Botânica de São Paulo utilizados em programa de educação ambiental. *Rev. Insti. Flor. SP, 4*: 219-225.

OKALI, D. U. U. & OLA-ADAMS, B. A., 1987, Tree population changes in treated rain forest at Omo Forest Reserve, south-western Nigeria. *J. Trop. Ecol., 3*: 291-313.

OLIVEIRA FILHO, A. T., ALMEIDA, R. J., MELLO, J. M. & GAVILLANES, M. L., 1994, Estrutura fitossociológica e variáveis ambientais em um trecho da mata ciliar do córrego dos Vilas Boas, Reserva Biológica do Poço Bonito, Lavras (MG). *Rev. Bras. Bot., 17*(1): 67-85.

OLIVEIRA FILHO, A. T., MELLO, J. M. & SCOLFORO, J. R. S., 1997, Effects of past disturbance and edges on tree community structure and dynamics within a fragment of tropical semideciduous forest in south-eastern Brazil over a five-year period (1987-1992). *Plant Ecology, 131*(1): 45-66.

PASCAL, J. P. & PELISSIER, R., 1996, Structure and floristic composition of a tropical evergreen forest in south-west India. *J. Trop. Ecol., 12*: 191-214.

PENHALBER, E. F., 1995, *Dinâmica do banco de plântulas em um trecho de mata em São Paulo, SP.* Dissertação de Mestrado, Universidade de São Paulo, São Paulo, 124p.

PENHALBER, E. F. & MANTOVANI, W., 1997, Floração e chuva de sementes em mata secundária em São Paulo, SP. *Rev. Bras. Bot., 20*(1): 205-220.

PHILLIPS, O. L., 1996, Long-term environmental change in tropical forests: increasing tree turnover. *Envir. Cons., 23*(3): 235-248.

PHILLIPS, O. L., HALL, P., GENTRY, A. H., SAWYER, S. A. & VÁZQUEZ, R., 1994, Dynamics and species richness of tropical rain forests. *Proc. Natl. Acad. Sci. USA, 91*: 2805-2809.

PHILLIPS, O. L. & GENTRY, A. H., 1994, Increasing turnover through time in tropical forests. *Science, 263*: 954-958.

PINTO-COELHO, R. M., 2000, *Fundamentos em Ecologia.* Editora Médica, Porto Alegre, 252p.

PRIMACK, R. B. & HALL, P., 1991, Species diversity research in Bornean forests with implications for conservation biology and silviculture. *Tropics, 1*: 91-111.

PRIMACK, R. B. & HALL, P., 1992, Biodiversity and forest change in Malaysian Borneo. *Bioscience, 42*(11): 829-37.

RANKIN-DE-MERONA, J. M., HUTCHINGS, R. W. & LOVEJOY, T. E., 1990, Tree mortality and recruitment over a five-year period in undisturbed upland rainforest of the central Amazon, pp. 573-583. *In*: A. H. Gentry (ed.), *Four neotropical rainforests.* Yale University Press, New Haven, 627p.

SANTOS, F. A. M., TAMASHIRO, J. Y., RODRIGUES, R. R. & SHEPHERD, G. J., 1996, The dynamics of tree populations in a semideciduous forest at Santa Genebra Reserve, Campinas, SE Brazil. *Supplement to Bulletin of the Ecological Society of America* (1996 Annual Combined Meeting Ecologists/Biologists as Problem Solvers, Abstracts, Providence, Rhode Island), *77*(3): 389.

SCHULZ, S. P., 1960, Ecological studies on the rain forest in northern Suriname. *Ver. K. ned. Akad. Wet. (A. natd.), 53*: 1-267.

SHEIL, D., 1995a, A critique of permanent plot methods and analysis with examples from Budongo Forest, Uganda. *For. Ecol. Manage., 77*(1): 11-34.

SHEIL, D., 1995b, Evaluating turnover in tropical forests. *Science, 268*: 894.

SHEIL, D. & MAY, R., 1996, Mortality and recruitment rate evaluations in heterogeneous tropical forests. *J. Ecol., 84*: 91-100.

SHEIL, D., BURSLEM, D. F. R. P. & ALDER, D., 1995, The interpretation and misinterpretation of mortality rates measures. *J. Ecol., 83*: 331-333.

STRUFFALDI-DE-VUONO, Y. S., 1985, *Fitossociologia do estrato arbóreo da floresta da Reserva Biológica do Instituto de Botânica (São Paulo-SP).* Tese de Doutorado, Universidade de São Paulo, São Paulo, 213p.

SWAINE, M. D., HALL, J. B. & ALEXANDER, I. J., 1987a, Tree populations dynamics at Kade, Ghana (1968-1982). *J. Trop. Ecol., 3*: 331-45.

SWAINE, M. D. & LIEBERMAN, D., 1987, Notes on the calculation of mortality rates. *J. Trop. Ecol., 3*: ii-iii.

SWAINE, M. D., LIEBERMAN, D. & PUTZ, F. E., 1987b, The dynamics of tree populations in tropical forest: a review. *J. Trop. Ecol., 3*: 359-366.

SWAINE, M. D., LIEBERMAN, D. & HALL, J. B., 1990, Structure and dynamics of a tropical dry forest in Ghana. *Vegetatio, 88*: 31-51.

TABARELLI, M. & MANTOVANI, W., 1997, A regeneração de uma floresta tropical montana após corte e queima (São Paulo-Brasil). *Rev. Brasil. Biol., 59*(2): 239-250.

TAYLOR, D. M., HAMILTON, A. C., WHYATT, J. D., MUCUNGUZI, P. & BUKENYA-ZIRABA, R., 1996, Stand dynamics in Mpanga Research Forest Reserve, Uganda, 1968-1993. *J. Trop. Ecol., 12*: 583-597.

TEIXEIRA, C. B., DOMINGOS, M., REBELLO, C. F. & MORAES, R. M., 1992, Produção de serapilheira em floresta residual da cidade de São Paulo: Parque Estadual das Fontes do Ipiranga. *Rev. Inst. Flor. SP, 4*: 785-789.

UHL, C., 1982, Tree dynamics in a species rich tierra firme forest in Amazonia, Venezuela. *Acta Cient. Venez., 33*: 72-77.

WELDEN, C. W., HEWETT, S. W., HUBBELL, S. P. & FOSTER, R. B., 1991, Sapling survival, growth, and recruitment: relationship to canopy height in a neotropical forest. *Ecology*, *72*(1): 35-50.