# Atlantic Forest succession over calcareous soil, Parque Estadual Turístico do Alto Ribeira - PETAR, SP[1]

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**ABSTRACT** - (Atlantic Forest succession over calcareous soil, Parque Estadual Turístico do Alto Ribeira - PETAR, SP). The forest succession after abandonment of slash-and-burn agriculture over calcareous soil in Brazilian Atlantic Forest was assessed. This is one of the world's most threatened Biome, with only 8% remaining. The study area is located over calcareous soil inside the Alto Ribeira Touristic State Park (PETAR), southeast Brazil. The phytossociological survey showed a successional pattern dominated by species of Leguminosae, especially *Piptadenia gonoacantha* (Mart.) J.F. Macbr. This species occurs in calcareous soils as a substitute of *Tibouchina pulchra* (Cham.) Cogn. (Melastomataceae) that is the most usual dominant tree species in early succession over acidic soil, which is the most common situation in this Biome. These results are important for a better understanding of Neotropical forest biodiversity and characterize a unique genetic bank in this highly endangered Biome. They are also decisive to support actions regarding rehabilitation of degraded lands and a potential tool for Neotropical forest sustainable management, both inside and around the conservation unit.

**RESUMO** - (Sucessão de Mata Atlântica sobre solos calcários, Parque Estadual Turístico do Alto Ribeira - PETAR, SP). Foram levantadas as características da sucessão florestal após abandono de campo cultivado em agricultura de subsistência sobre solos calcários na Mata Atlântica brasileira. Este é um dos biomas mais ameaçados do mundo, que apresenta apenas 8% de remanescentes. A área de estudo está localizada sobre solo calcário no Parque Estadual Turístico do Alto Ribeira (PETAR), sudeste do Brasil. O levantamento fitossociológico indicou padrão de sucessão dominado por Leguminosae, especialmente *Piptadenia gonoacantha* (Mart.) J.F. Macbr. Esta espécie ocorre sobre solo calcário, substituindo a espécie arbórea dominante em início de sucessão sobre solos ácidos, *Tibouchina pulchra* (Cham.) Cogn. (Melastomataceae), sendo que esta é a situação mais comum neste Bioma. Estes resultados são importantes para um melhor conhecimento da biodiversidade da floresta neotropical e caracteriza um banco genético único neste bioma altamente ameaçado. São também decisivos no suporte de ações de reabilitação de áreas degradadas e um instrumento potencial para manejo auto-sustentado da floresta neotropical, tanto dentro dos limites da unidade de conservação, quanto em suas áreas de entorno.

Key words - Secondary succession, Brazilian Atlantic Forest, tropical calcareous soil, *Piptadenia gonoacantha*, slash-and-burn agriculture

## Introduction

The Brazilian Atlantic Forest is considered one of the three most threatened ecosystems on Earth. Once covering more than a million squared kilometers, today the forest is reduced to less than 8% of the original cover (SOS Mata Atlântica 1998). It is considered by The Conservation International as one of world's biodiversity hot spots (Myers *et al.* 2000). São Paulo State, SE Brazil, had more than 82% of its area covered by forest. Today, the remnants are around 7% of its original distribution (SOS Mata Atlântica 1998), occurring mainly in the mountainous region near the shore.

The Atlantic Forest is a complex of ecosystems that belongs to the Atlantic Dominion which includes a Dense Ombrophylous Forest (IBGE 1992, Joly *et al*. 1999) on slopes and mountain tops, especially in SE Brazil. This physiognomy is characterised as evergreen "hygrophyllous forest" (Torres *et al*. 1997), with high diversity and endemism indexes (Mori *et al*. 1981), and is considered as the richest forest for Orchidaceae and the most ancient diversity center for South America (Brieger 1969). In the Dense Ombrophylous Forest from southern and southeastern Brazil, the most common angiosperm families in terms of number of species (considering low and high altitude areas, below and above 700 m

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high, respectively) are: Myrtaceae, Leguminosae, Rubiaceae, Melastomataceae, Lauraceae, Sapotaceae, Euphorbiaceae, Moraceae and Annonaceae (Oliveira Filho & Fontes 2000). Studies carried out in secondary forests over acidic and oligotrophic soils in this type of forest indicated the species *Tibouchina pulchra* (Cham.) Cogn. (Melastomataceae), an endemic genus (Veloso 1982), as one of the most important trees, if not the most, in these communities (Loefgren 1898, Leitão Filho *et al.* 1993, Tabarelli *et al.* 1993, 1994, 1999, Torezan 1995).

The gap-phase dynamics is the fundamental basis for studying the forest growth cycle and it is the beginning of the regenerative cycle. Disturbance created by gaps, that alter environmental conditions, triggers a construction phase characterised by species colonisation and growth following a continuum of ecophysiological response that induce cicatrization (Brokaw 1985). The final stage is the mature phase, where a new gap may restart the growth cycle (Whitmore 1984). The essential characteristic of shifting cultivation ("roça") is that slash-and-burn clearings are small (usually < 1ha), and seed dispersal distances are short. During recovery phase, ecosystem function does not appear to be severely disrupted, and in this way, the abandoned "roças" are similar in behaving like big gaps (Uhl *et al.* 1990). Surveys of long-term succession in the Amazon produced a model on how tropical forest develops on abandoned farm sites, which could help in the design of ecologically sustainable uses of rain forest, *e.g.* through a natural succession-mimic aproach (Subler & Uhl 1990), that prevent nutrient losses, protecting fragile soils while conserving the forest biological diversity (Gomez-Pompa & Burley 1991).

Although difficult to be defined, secondary forests are estimated in a worldwide basis to cover between 530 (FAO 1996) to 600 million ha. (Brown & Lugo 1990), roughly 33% of total tropical forest (7% in Latin America). Based in this fact, Chazdon (1998) suggests that tropical secondary forests are now being recognised for their value in the conservation of biological diversity. Emrich *et al.* (2000) affirm that secondary forests are an inexpensive and site-appropriate form of reforestation and have in principle a high regenerative potential. They can fulfil a whole range of functions that can benefit humanity, including forestry uses (fuelwood, timber, non-timber forest products, tourism), agricultural uses (agro-forestry systems) and environmental protection

functions (water, soil and climate protection including $CO_2$ sink functions and the conservation of biodiversity). With respect to carbon dioxide sequestration, a very important global issue nowadays, secondary forests are likely to mitigate global change due to the facts that plants are at early stages of development, showing higher $CO_2$ assimilation and growth rates and that tree species are suitable for wood processing at older stages.

In the present work we performed the characterization of the species composition occurring in the main phases that drive the forest succession after slash-and-burn agriculture over calcareous soil through a phytosociological inventory. We observed a new pattern of Atlantic Forest succession related to the occurrence of calcareous soils, where legumes (especially *Piptadenia gonoacantha*) are dominant. This information will contribute to the knowledge about Atlantic Forest biodiversity and regeneration, and could help to develop a forest recovery model to support regional rehabilitation and management actions.

## Material and methods

Study site - The study area is located in São Paulo State, southeastern of Brazil, at the Ribeira de Iguape Watershed, inside of the Parque Estadual Turístico do Alto Ribeira - PETAR (24°31'43" S; 48°41'09" W), approximately 380 km southwest from São Paulo City, the biggest metropolitan area in South America (figure 1). This protected area (35712 ha) together with other state parks comprise more than 270000 ha of continuous Atlantic Forest in Conservation Units. This area was inscribed as Natural Site on the World Heritage List (www.unesco.org/whc/sites/893.htm). Regional climate is tropical hyperhumid without a dry period with mean annual precipitation around 1800 mm, evenly distributed throughout the year (34% summer and 17% winter of total annual precipitation) and mean annual temperature between 17-19 °C (max. 23 °C; min. 14 °C) (Gutjahr 1993). Geologically it has a pre-Cambrian basement with many metamorphic degrees, mainly metasediments silicic-argillaceous and epimetamorphic calcareous. The relief is very mountainous with karstic plateaus and intrusive granites. The study site is located at 500-600 m above sea level over calcareous substrate, which comprises around 40% of the park area (figure 1), classified as Cambisols associated with Chernozems (Camargo *et al.* 1986, FAO-ISRIC-ISSS 1998). When compared with an acidic soil originated from a silicic-argillaceous substrate close to the study area (Torezan 1995), the eutrophic calcareous soil showed higher pH (pH = 6), saturation of bases (V% = 79), organic matter (OM% = 5) and calcium content (9.5 mEq/100 ml), and much less exchangeable acidity (2.6 mEq/100 ml).
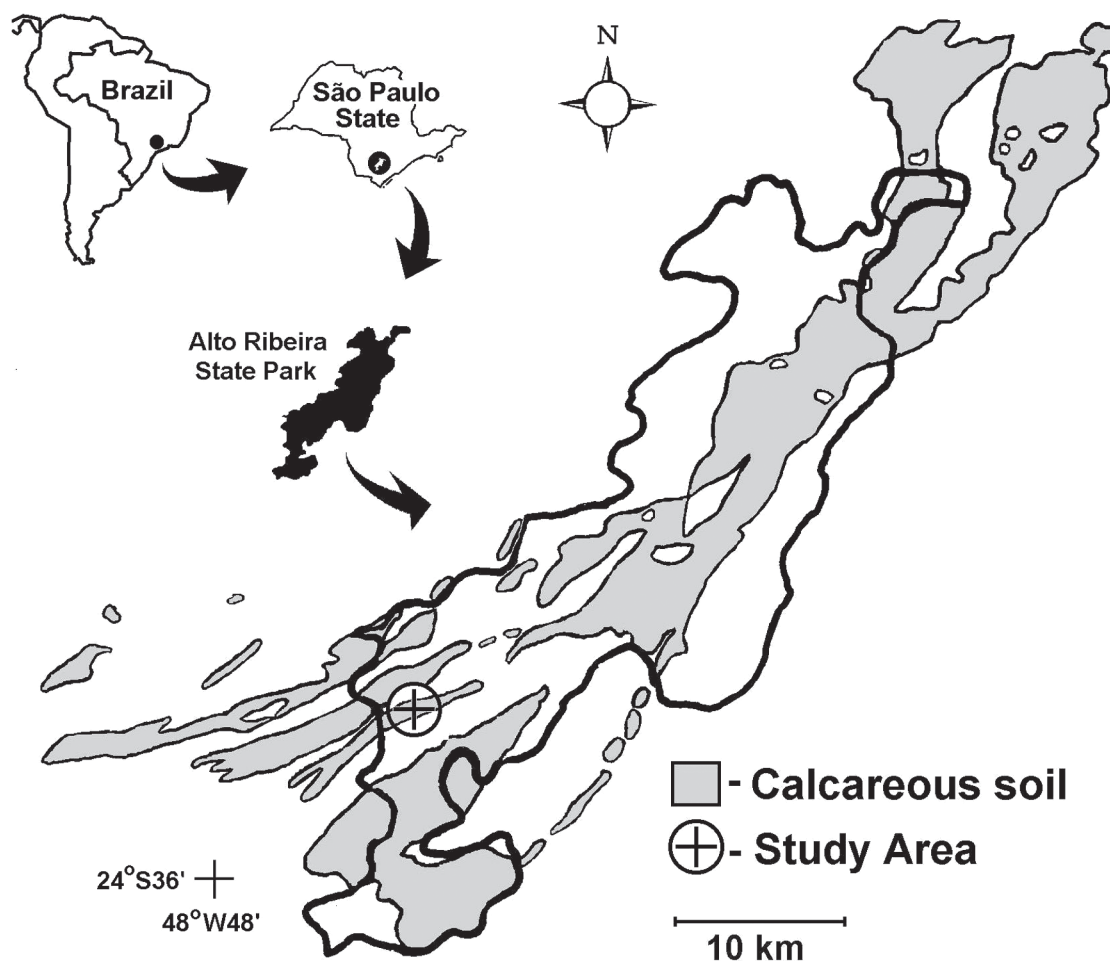
Figure 1. Localization of the study area and occurrence of calcareous soil.

Forest survey - The study area was chosen through field observations, interviews with the farmer who abandoned the crop areas, analysis of aerial photographs from 1962, 1973, 1981 and 1997 (figures 2-5), and LANDSAT TM 5 orbital image of 1990. Scales varied between 1:25 000 and 1:50 000. The phytossociological survey was carried out in three different adjacent spots corresponding to different times of abandonment after slash-and-burn agriculture: Phase I (PI) with 15 years; Phase II (PII) with 25 years; and Phase III (PIII) with more than 36 years without disturbance and probably never clear-cut (figure 2). The inventory was made using transects 50 m long and 20 m wide (0.1 ha). The inclusion criterion was trunk perimeter at breast height ≥ 15 cm. All individuals were labelled, measured in height and perimeter, mapped and sampled for taxonomic identification. The vouchers were deposited at the Herbarium of São Paulo Forestry Institute (SPSF). Tree heights (m) were measured by an opti-meter Ranging 120, Ranging Inc. Species binomials were standardized according to Missouri Botanical Garden (http://mobot.org/ W3T/Search/vast.html) and New York Botanical Garden (http://www. nybg.org/search).

The Relative Dominance (RDo) is an index to assess relative space occupation and is estimated by the relative basal area of all individuals belonging to one species or family. The basal area was calculated by converting perimeter to basal area in $cm^2$. The Species Relative Density (RDi) is an index to assess the species relative distribution. The sum of these two parameters gives the Coverage Index for each Species (CIi) (Müller-Dombois *et al.* 1974).

RDoi = (BAi x 100)/ΣBAn
RDi = (Ni x 100)/Nm
CIi = RDoi + RDi
Where:
RDoi - Species Relative Dominance
BAi - Species Basal Area
ΣBAn -Total Basal Area
RDi - Species Relative Density
Ni - Species Number of individuals
Nn - Total Number of individuals
CIi - Species Coverage Index

## Results

The analysis of historical series of aerial photography from the study site was critical for definition of the age of each forest fragment studied, *i.e.* the time elapsed from the abandonment of the crop field, when it occurred. For the forest fragment called PIII, it was possible to determine that it was not cut since 1962, and probably long before that, as we could see from the size of trees occuring at that time, resulting in an estimate of more than 36 years in 1998. With respect to the fragment called PII, it was possible to define the time elapsed after the area had been abandoned, corresponding to aproximadetely 25 years in 1998. For the fragment called PI, the time elapsed after the abandonment of the crop field was estimated through interviews with the farmer and by analysis of aerial photography from 1981 (not shown),
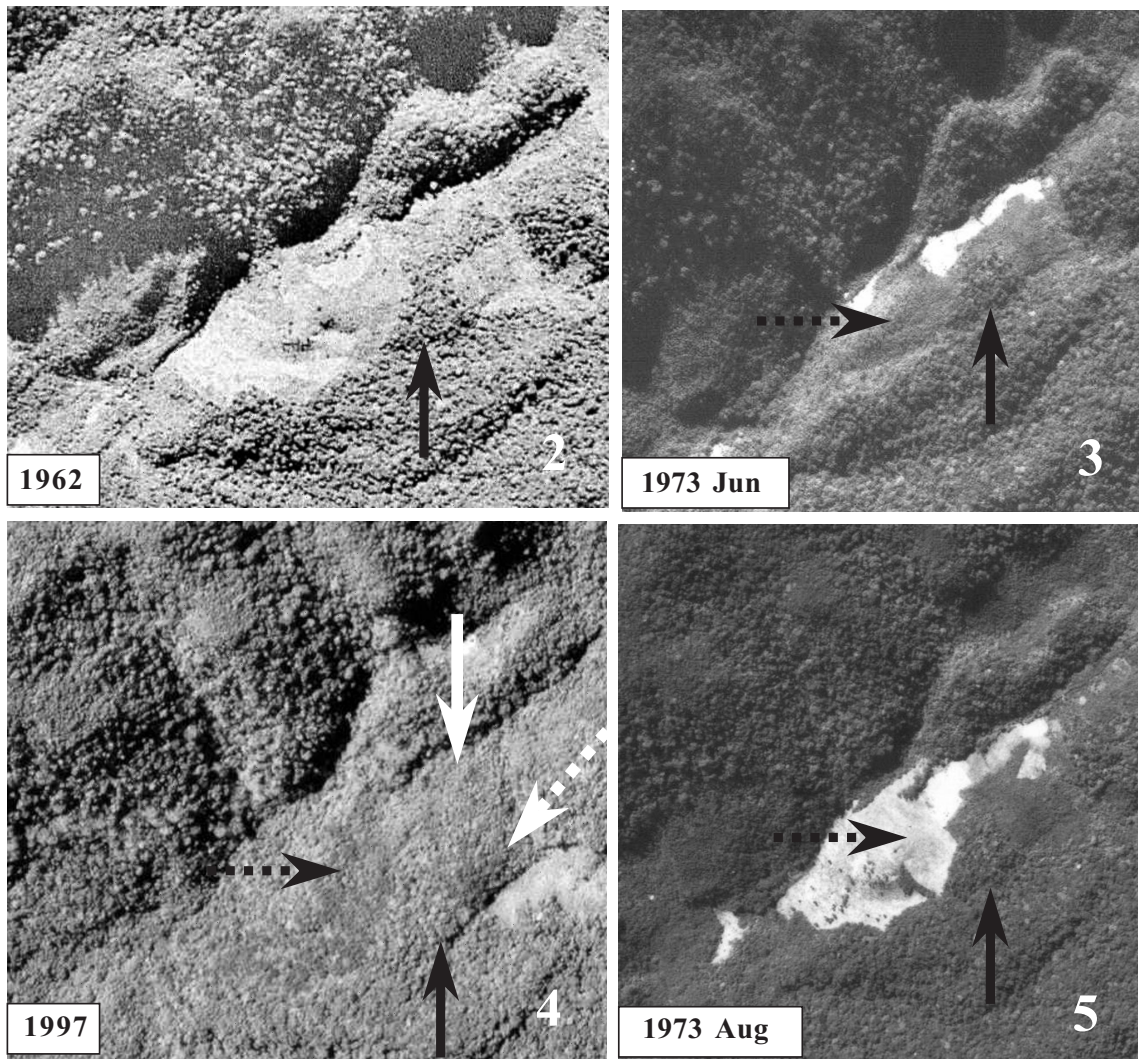


Figure 2-5. Historical series of aerial photography showing the evolution of the vegetation cover in the study area. 2. Aerial photo (1962) showing a forested area, which remains uncut (black arrow) throughout the time comprehended by our study. 3 and 5. Aerial photos from two different periods in 1973 (June and August, respectively) showing a forest fragment cut (dotted arrow) and the uncut fragment (black arrow). 4. Aerial photo (1997) showing the successional phases inventoried: white arrow-phase I (15 years after abandonment); white dotted arrow-phase II (25 years); black arrow-phase III (36 + years); the black dotted arrow indicates a regeneration area dominated by *Piptadenia gonoacantha*, similar to the area where phase II was inventoried.

and resulted in approximately 15 years.

Considering the complete survey, including all areas studied, were registered 34 families (two unidentified), 75 genera (seven unidentified), and 87 species (six unidentified) (table 1).

The phytossociological survey indicated a decrease in tree density along succession: PI - 1940 ind.ha$^{-1}$; PII - 1690 ind.ha$^{-1}$; and PIII - 1520 ind.ha$^{-1}$. The Species Relative Dominance (RDoi) and Coverage Index (CIi) indicates that, besides a single exception (*Myrsine coriacea*; CIi), top positions are occupied by species belonging to Leguminosae (table 1, figure 6).

PI is dominated by *Piptadenia gonoacantha* and *Symplocos laxiflora* in respect to RDoi. The CIi follows the RDo pattern, with *P. gonoacantha* as the main species (Figure 6). In this area, 38 species (two unidentified) belonging to 33 genus (one unidentified) and 21 families were sampled. The family Leguminosae was the most important with respect to Relative Dominance, Coverage Index, number of individuals ($n_i = 48$) and number of species ($n_{sp} = 8$), following by Lauraceae ($n_i = 13$; $n_{sp} = 6$) and Annonaceae ($n_i = 22$; $n_{sp} = 4$) (figure 7).

PII is dominated by *P. gonoacantha* and *M. coriacea*, both with increased RDoi related to the former stage. Here, the CIi indicates that *M. coriacea* showed a slightly higher value, which is correlated with its higher number of individuals that occur mainly in the forest understorey (figure 6). In this stage, 29 (three unidentified) species, 28 genus and 15 families were sampled, which represents a clear decrease in family and species diversity. The family Leguminosae was the first in importance with respect to number of species ($n_{sp} = 7$) and Relative Dominance, and second with respect to number of individuals ($n_i = 25$) and Coverage Index. The family Myrsinaceae was the first with respect to number of individuals ($n_i = 43$) and because of that, also with respect to Coverage Index. It is important to notice that this latter family was represented by only one species, which is typical of the understorey habitat. Melastomataceae ($n_i = 18$; $n_{sp} = 4$), Piperaceae ($n_i = 18$; $n_{sp} = 2$) and Euphorbiaceae ($n_i = 11$; $n_{sp} = 3$) were also important (figure 7).

PIII is dominated by *Schizolobium parahyba*, but its RDo is lower than that observed for the dominant species in PI and PII. Actually, some species can be seen with almost the same importance, like *Hymenaea courbaril*, *Ficus* sp., *Guapira opposita*

and *Aspidosperma ramiflorum* (figure 6). This reflects the higher diversity of PIII, where 58 species belonging to 53 genus (six unidentified) and 23 families (two unidentified) were sampled. CIi shows a slightly different pattern, where understorey species like *Euterpe edulis* and *Guapira opposita*, assumed higher importance because of higher number of individuals. Myrtaceae was the most important family with respect to number of individuals and species ($n_i = 23$; $n_{sp} = 11$). The Leguminosae was the most important with respect to Relative Dominance, and ranked second with respect to number of species
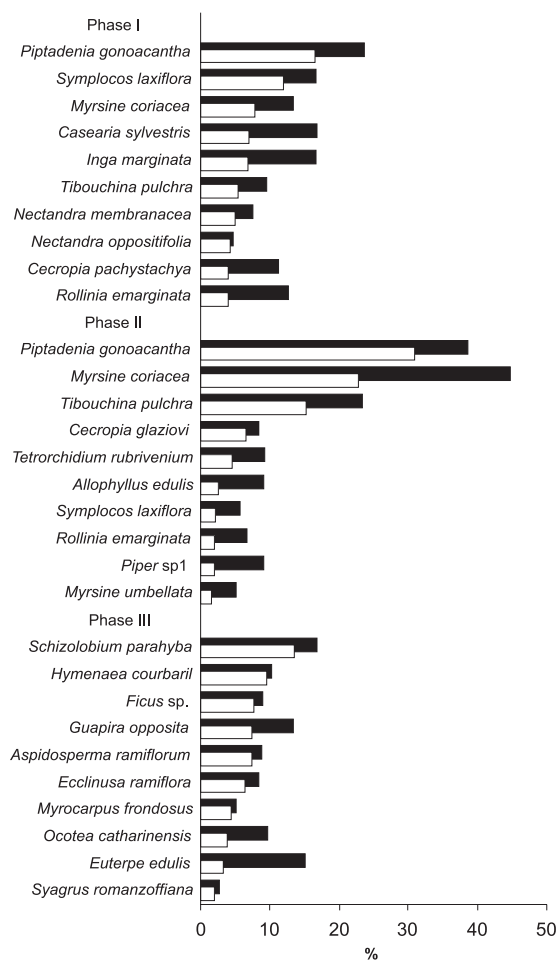


Figure 6. Distribution of the parameters - Coverage Index (■ CIi) and Relative Dominance (□ RDoi) among the species inventoried in the different successional phases. PI - phase I (15 years after abandonment of crop field); PII - phase II (25 years); PIII - phase III (36 + years).

Table 1. Occurrence of families and species in the successional phases sampled over calcareous soils at the Alto Ribeira Touristic State Park - PETAR, SP. Phase I - 15 years after abandonment of crop field; Phase II - 25 years; Phase III - 36 + years.

| Family/Species | Phase I | Phase II | Phase III |
|---|---|---|---|
| ANNONACEAE | | | |
| *Guatteria nigrescens* Mart. | X | | |
| *Rollinia sericea* (R.E. Fr.) R.E. Fr. | X | | X |
| *Rollinia emarginata* Schltdl. | X | X | |
| Annonaceae sp.1 | X | | |
| Annonaceae sp.4 | | | X |
| Annonaceae sp.5 | | | X |
| | | | |
| APOCYNACEAE | | | |
| *Aspidosperma polyneuron* Müll. Arg. | | | X |
| *Aspidosperma ramiflorum* Müll. Arg. | | | X |
| | | | |
| ARECACEAE | | | |
| *Euterpe edulis* Mart. | | | X |
| *Syagrus romanzoffiana* (Cham.) Glassman | | | X |
| | | | |
| ASTERACEAE | | | |
| *Verbesina* sp. | | X | X |
| | | | |
| BORAGINACEAE | | | |
| *Cordia trichotoma* (Vell.) Arráb. ex Steud. | X | | |
| | | | |
| BURSERACEAE | | | |
| *Protium heptaphyllum* (Aubl.) Marchand | | | X |
| | | | |
| CECROPIACEAE | | | |
| *Cecropia glaziovi* Snethlage | X | X | |
| *Cecropia pachystachya* Trécul | X | | X |
| *Coussapoa microcarpa* (Schott) Rizzini | | | X |
| | | | |
| CELASTRACEAE | | | |
| *Maytenus* cf. *evonymoides* Reisseck | | | X |
| | | | |
| CLETRACEAE | | | |
| *Clethra scabra* Pers. | X | | |
| | | | |
| CLUSIACEAE | | | |
| *Garcinia gardneriana* (Planch. & Triana) Zappi | | | X |
| | | | |
| EUPHORBIACEAE | | | |
| *Alchornea triplinervia* (Spreng.) Müll. Arg. | X | X | X |
| *Hyeronima alchorneoides* Allemao | | X | |
| *Margaritaria nobilis* L.f. | | | X |
| *Tetrorchidium rubrivenium* Poepp. | X | X | X |
| | | | |
| FLACOURTIACEAE | | | |
| *Casearia sylvestris* Sw. | X | X | |
| | | | |
| LAURACEAE | | | |
| *Beilschmiedia emarginata* (Nees) Kosterm. | | | X |
| *Endlicheria paniculata* (Spreng.) J.F. Macbr. | X | | X |
| *Nectandra megapotamica* (Sprengel) Mez | X | | X |
| *Nectandra membranacea* (Sw.) Griseb. | X | | |
| *Nectandra oppositifolia* Nees & Mart. | X | | X |

(cont.)

| Family/Species | Phase I | Phase II | Phase III |
|---|---|---|---|
| *Ocotea catharinensis* Mez | | | X |
| *Ocotea* sp. | X | | |
| *Persea venosa* Nees & Mart. ex Nees | X | | X |
| | | | |
| LEGUMINOSAE | | | |
| *Bauhinia forficata* Link | X | X | |
| *Dalbergia frutescens* (Vell.) Britton | | X | |
| *Hymenaea courbaril* L. | | | X |
| *Inga marginata* Willd. | X | X | X |
| *Lonchocarpus* muehlbergianus Hassl. | | | X |
| *Machaerium nyctitans* (Vell.) Benth. | X | | |
| *Machaerium lanatum* Tul. | X | | |
| *Machaerium stipitatum* (DC.) Vogel | | X | X |
| *Myrocarpus frondosus* Allemao | | | X |
| *Piptadenia gonoacantha* (Mart.) J.F. Macbr. | X | X | X |
| *Piptadenia paniculata* Benth. | X | X | |
| *Platymiscium floribundum* Vogel | X | X | |
| *Pterocarpus* cf. *rohrii* Vahl | | | X |
| *Schizolobium parahyba* (Vell.) S.F. Blake | X | | X |
| *Swartzia* aff. *acutifolia* Vogel | | | X |
| | | | |
| MALPIGHIACEAE | | | |
| *Byrsonima ligustrifolia* A. Juss. | | X | X |
| | | | |
| MELASTOMATACEAE | | | |
| *Leandra mosenii* Cogn. | | X | |
| *Miconia cinnamomifolia* (DC.) Naudin | | X | |
| *Miconia latecrenata* Triana | | X | |
| *Tibouchina pulchra* (Cham.) Cogn. | X | X | |
| Melastomataceae sp.1 | | | X |
| | | | |
| MELIACEAE | | | |
| *Cedrela fissilis* Vell. | | | X |
| *Guarea macrophylla* Vahl | | | X |
| *Trichilia lepidota* Mart. | | | X |
| | | | |
| MONIMIACEAE | | | |
| *Mollinedia clavigera* Tul. | | | X |
| Monimiaceae sp.1 | | | X |
| | | | |
| MORACEAE | | | |
| *Ficus* sp. | | | X |
| *Sorocea bonplandii* (Baill.) W.C. Burger, Lanj. & Wess. Boer | | | X |
| *Brosimum guianense* (Aubl.) Huber | | | X |
| | | | |
| MYRSINACEAE | | | |
| *Myrsine coriacea* (Sw.) R. Br. ex Roem. & Schult. | X | X | |
| *Myrsine umbellata* Mart. | | X | |
| | | | |
| MYRTACEAE | | | |
| *Calyptranthes concinna* DC. | | | X |
| *Campomanesia guaviroba* (DC.) Kiaerskow | X | X | X |
| *Eugenia cuprea* (O. Berg) Mattos | | | X |
| *Eugenia florida* DC. | | | X |
| *Eugenia riedeliana* O. Berg | | | X |
| *Gomidesia tijucensis* (Kiaersk.) D. Legrand | | | X |
| *Marlierea eugeniopsoides* (D. Legrand & Kausel) D. Legrand | | | X |
| *Myrceugenia myrcioides* (Cambess.) O. Berg | | | X |

(cont.)

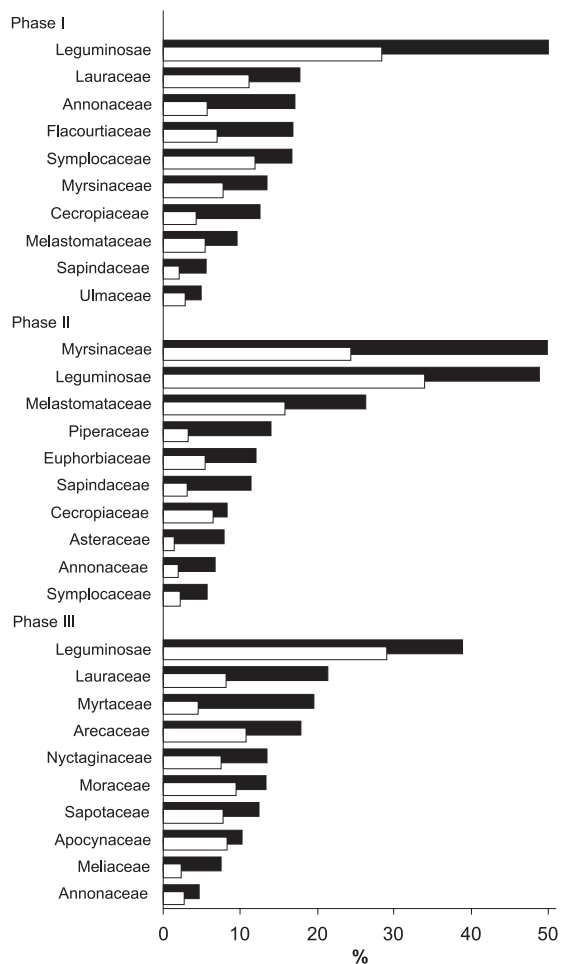| Family/Species | Phase I | Phase II | Phase III |
|---|---|---|---|
| *Myrcia formosiana* DC. | X | X | |
| *Myrcia pubipetala* Miq. | | | X |
| *Psidium cattleyanum* Sabine | | X | |
| Myrtaceae sp.1 | | | X |
| Myrtaceae sp.3 | | | X |
| NYCTAGINACEAE | | | |
| *Guapira opposita* (Vell.) Reitz | X | | X |
| OLACACEAE | | | |
| *Heisteria silvianii* Schwacke | X | | |
| PIPERACEAE | | | |
| *Piper* sp.1 | | X | |
| *Piper* sp.2 | | X | |
| PROTEACEAE | | | |
| *Roupala brasiliensis* Klotzsch | | | X |
| QUIINACEAE | | | |
| *Quiina glaziovii* Engl. | X | | |
| ROSACEAE | | | |
| *Prunus myrtifolia* (L.) Urb. | | | X |
| RUBIACEAE | | | |
| *Alibertia myrciifolia* Schum. | | | X |
| *Alseis floribunda* Schott | X | | X |
| *Bathysa meridionalis* Smith & Downs | | X | |
| *Posoqueria acutifolia* Mart. | | | X |
| *Psychotria* cf. *carthagenensis* Jacq. | | X | |
| *Rudgea* cf. *jasminoides* (Cham.) Müll. Arg. | | | X |
| SABIACEAE | | | |
| *Meliosma sellowii* Urb. | X | | |
| SAPINDACEAE | | | |
| *Allophyllus edulis* (A.St. Hil.) Radlk. | X | X | X |
| *Cupania oblongifolia* Mart. | X | X | |
| *Matayba guianensis* Aubl. | X | | |
| *Matayba juglandifolia* (Cambess.) Radlk. | | | X |
| SAPOTACEAE | | | |
| *Chrysophyllum inornatum* Mart. | | | X |
| *Ecclinusa ramiflora* Mart. | | | X |
| *Pouteria psammophila* (Mart.) Radlk. | X | | X |
| SYMPLOCACEAE | | | |
| *Symplocos laxiflora* Benth. | X | X | |
| ULMACEAE | | | |
| *Trema micrantha* (L.) Blume | X | X | |
| VERBENACEAE | | | |
| *Aegiphila* sp. | X | | |
| UNIDENTIFIED | | | |
| Sp.1 | | | X |
| Sp.3 | | | X |

Figure 7. Distribution of the parameters - Coverage Index (■ CIi) and Relative Dominance (□ RDoi) among the angiosperm families inventoried in the different successional phases. PI - phase I (15 years after abandonment of crop field); PII - phase II (25 years); PIII - phase III (36 + years).

($n_i$ = 15; $n_{sp}$ = 9). Lauraceae ($n_i$ = 20; $n_{sp}$ = 7) and Arecaceae ($n_i$ = 19; $n_{sp}$ = 2) were also important (figure 7).

Considering all inventories, the family Leguminosae was the most important in all aspects investigated (nº of individuals and species; Relative Dominance; Coverage Index). Other important families were Myrsinaceae, Myrtaceae, Annonaceae, Lauraceae and Melastomataceae (figure 8).

## Discussion

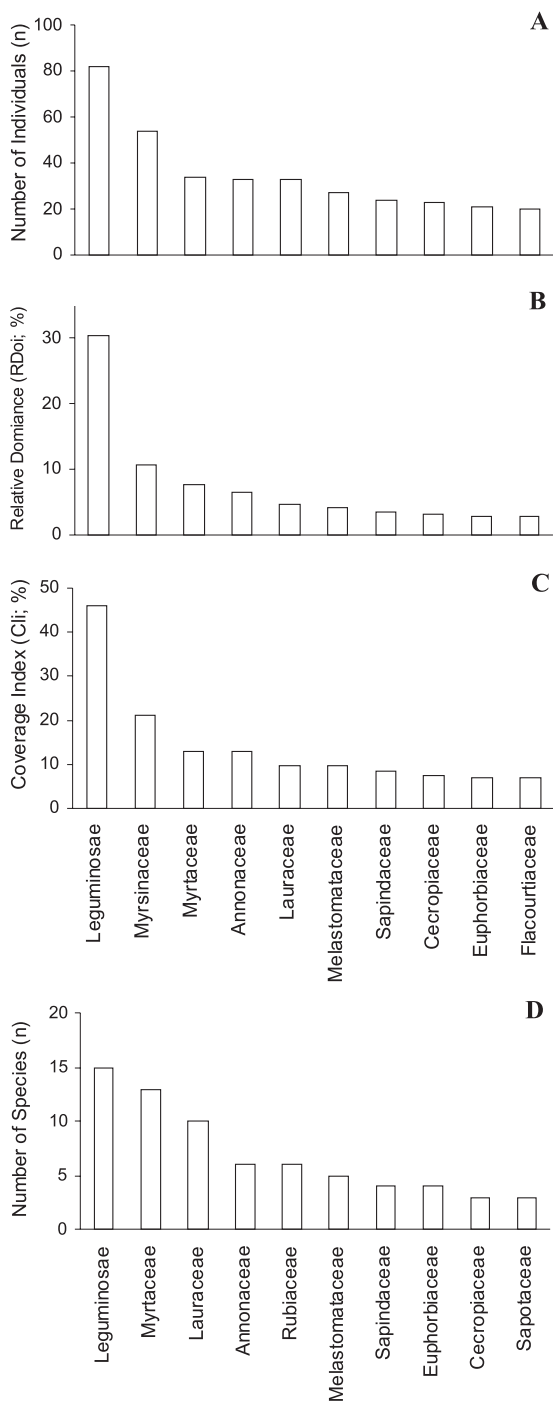The analysis of aerial photography was decisive to define the age of forest fragments in the study



Figure 8. Distribution of some parameters among the angiosperm families inventoried, considering all successional phases together. A. Number of Individuals (n); B. Relative Dominance (RDoi) (%); C. Coverage Index (CIi) (%); D. Number of Species (n).

Table 2. Phytosociological survey in the three different phases of succession over calcareous soil - PETAR. Phase I - 15 years after abandonment of crop field; Phase II - 25 years; Phase III - 36 + years; RDi - species Relative Density; RDoi - species Relative Dominance; CIi - species Coverage Index; Ni - species number of individuals.

| Species | Family | Ni | RDoi | RDi | CIi |
|---|---|---|---|---|---|
| **Phase I** | | | | | |
| *Piptadenia gonoacantha* | Leguminosae | 14 | 16.5 | 7.2 | 23.7 |
| Dead | | 19 | 7.8 | 9.8 | 17.6 |
| *Casearia sylvestris* | Flacourtiaceae | 19 | 7.0 | 9.8 | 16.8 |
| *Inga marginata* | Leguminosae | 19 | 6.9 | 9.8 | 16.7 |
| *Symplocos laxiflora* | Symplocaceae | 9 | 11.9 | 4.6 | 16.6 |
| *Myrsine coriacea* | Myrsinaceae | 11 | 7.8 | 5.7 | 13.4 |
| *Rollinia emarginata* | Annonaceae | 17 | 3.9 | 8.8 | 12.7 |
| *Cecropia pachystachya* | Cecropiaceae | 14 | 4.0 | 7.2 | 11.2 |
| *Tibouchina pulchra* | Melastomataceae | 8 | 5.4 | 4.1 | 9.5 |
| *Nectandra membranacea* | Lauraceae | 5 | 4.9 | 2.6 | 7.5 |
| *Trema micrantha* | Ulmaceae | 4 | 2.8 | 2.1 | 4.9 |
| *Nectandra oppositifolia* | Lauraceae | 1 | 4.2 | 0.5 | 4.7 |
| *Bauhinia forficata* | Leguminosae | 4 | 2.0 | 2.1 | 4.1 |
| *Matayba guianensis* | Sapindaceae | 3 | 1.5 | 1.5 | 3.0 |
| *Myrcia formosiana* | Myrtaceae | 3 | 0.9 | 1.5 | 2.4 |
| *Tetrorchidium rubrivenium* | Euphorbiaceae | 2 | 1.1 | 1.0 | 2.1 |
| *Cordia trichotoma* | Boraginaceae | 3 | 0.5 | 1.5 | 2.1 |
| *Nectandra megapotamica* | Lauraceae | 3 | 0.5 | 1.5 | 2.0 |
| *Campomanesia guaviroba* | Myrtaceae | 3 | 0.4 | 1.5 | 2.0 |
| *Guatteria nigrescens* | Annonaceae | 3 | 0.4 | 1.5 | 2.0 |
| *Cupania oblongifolia* | Sapindaceae | 3 | 0.4 | 1.5 | 1.9 |
| *Schizolobium parahyba* | Leguminosae | 1 | 1.4 | 0.5 | 1.9 |
| *Alchornea triplinervia* | Euphorbiaceae | 3 | 0.3 | 1.5 | 1.8 |
| *Endlicheria paniculata* | Lauraceae | 2 | 0.5 | 1.0 | 1.5 |
| Annonaceae sp.1 | Annonaceae | 1 | 1.0 | 0.5 | 1.5 |
| *Meliosma sellowii* | Sabiaceae | 2 | 0.5 | 1.0 | 1.5 |
| *Pouteria psammophila* | Sapotaceae | 2 | 0.5 | 1.0 | 1.5 |
| *Cecropia glaziovi* | Cecropiaceae | 2 | 0.3 | 1.0 | 1.3 |
| *Piptadenia paniculata* | Leguminosae | 1 | 0.6 | 0.5 | 1.1 |
| *Persea venosa* | Lauraceae | 1 | 0.6 | 0.5 | 1.1 |
| *Platymiscium floribundum* | Leguminosae | 1 | 0.5 | 0.5 | 1.0 |
| *Aegiphila* sp. | Verbenaceae | 1 | 0.5 | 0.5 | 1.0 |
| *Rollinia sericea* | Annonaceae | 1 | 0.4 | 0.5 | 0.9 |
| *Machaerium lanatum* | Leguminosae | 1 | 0.4 | 0.5 | 0.9 |
| *Ocotea* sp. | Lauraceae | 1 | 0.4 | 0.5 | 0.9 |
| *Clethra scabra* | Clethraceae | 1 | 0.4 | 0.5 | 0.9 |
| *Heisteria silvianii* | Olacaceae | 1 | 0.3 | 0.5 | 0.9 |
| *Alseis floribunda* | Rubiaceae | 1 | 0.2 | 0.5 | 0.7 |
| *Guapira opposita* | Nyctaginaceae | 1 | 0.2 | 0.5 | 0.7 |
| *Allophyllus edulis* | Sapindaceae | 1 | 0.2 | 0.5 | 0.7 |
| *Quiina glaziovii* | Quiinaceae | 1 | 0.1 | 0.5 | 0.6 |
| *Machaerium nyctitans* | Leguminosae | 1 | 0.1 | 0.5 | 0.6 |
| **Phase II** | | | | | |
| *Myrsine coriacea* | Myrsinaceae | 37 | 22.8 | 21.9 | 44.7 |
| *Piptadenia gonoacantha* | Leguminosae | 13 | 30.9 | 7.7 | 38.6 |
| *Tibouchina pulchra* | Melastomataceae | 14 | 15.2 | 8.3 | 23.4 |
| *Tetrorchidium rubrivenium* | Euphorbiaceae | 8 | 4.5 | 4.7 | 9.3 |
| *Allophyllus edulis* | Sapindaceae | 11 | 2.6 | 6.5 | 9.1 |
| *Piper* sp.1 | Piperaceae | 12 | 1.9 | 7.1 | 9.0 |
| *Cecropia glaziovi* | Cecropiaceae | 3 | 6.5 | 1.8 | 8.3 |
| *Verbesina* sp | Asteraceae | 11 | 1.4 | 6.5 | 7.9 |
| *Rollinia emarginata* | Annonaceae | 8 | 2.0 | 4.7 | 6.7 |

(cont.)

| Species | Family | Ni | RDoi | RDi | CIi |
|---|---|---|---|---|---|
| *Symplocos laxiflora* | Symplocaceae | 6 | 2.2 | 3.6 | 5.7 |
| *Myrsine umbellata* | Myrsinaceae | 6 | 1.5 | 3.6 | 5.1 |
| *Piper* sp.2 | Piperaceae | 6 | 1.3 | 3.6 | 4.9 |
| *Piptadenia paniculata* | Leguminosae | 4 | 0.9 | 2.4 | 3.3 |
| *Cupania oblongifolia* | Sapindaceae | 3 | 0.5 | 1.8 | 2.3 |
| *Inga marginata* | Leguminosae | 2 | 0.9 | 1.2 | 2.1 |
| *Campomanesia guaviroba* | Myrtaceae | 2 | 0.8 | 1.2 | 1.9 |
| *Bauhinia forficata* | Leguminosae | 2 | 0.6 | 1.2 | 1.8 |
| *Machaerium stipitatum* | Leguminosae | 2 | 0.4 | 1.2 | 1.6 |
| *Miconia cinnamomifolia* | Melastomataceae | 2 | 0.4 | 1.2 | 1.5 |
| Dead | | 2 | 0.3 | 1.2 | 1.5 |
| *Hyeronima alchorneoides* | Euphorbiaceae | 2 | 0.2 | 1.2 | 1.4 |
| *Psidium cattleyanum* | Myrtaceae | 2 | 0.2 | 1.2 | 1.4 |
| *Alchornea triplinervia* | Euphorbiaceae | 1 | 0.7 | 0.6 | 1.3 |
| *Casearia sylvestris* | Flacourtiaceae | 1 | 0.3 | 0.6 | 0.8 |
| *Trema micrantha* | Ulmaceae | 1 | 0.2 | 0.6 | 0.8 |
| *Bathysa meridionalis* | Rubiaceae | 1 | 0.2 | 0.6 | 0.8 |
| *Myrcia formosiana* | Myrtaceae | 1 | 0.2 | 0.6 | 0.8 |
| *Leandra mosenii* | Melastomataceae | 1 | 0.1 | 0.6 | 0.7 |
| *Miconia latecrenata* | Melastomataceae | 1 | 0.1 | 0.6 | 0.7 |
| *Byrsonima ligustrifolia* | Malpiguiaceae | 1 | 0.1 | 0.6 | 0.7 |
| *Psychotria* cf. *carthagenensis* | Rubiaceae | 1 | 0.1 | 0.6 | 0.7 |
| *Dalbergia frutescens* | Leguminosae | 1 | 0.1 | 0.6 | 0.7 |
| *Platymiscium floribundum* | Leguminosae | 1 | 0.1 | 0.6 | 0.7 |
| Phase III | | | | | |
| *Schizolobium parahyba* | Leguminosae | 5 | 13.47 | 3.3 | 16.8 |
| *Hymenaea courbaril* | Leguminosae | 1 | 9.58 | 0.7 | 10.2 |
| *Ficus* sp. | Moraceae | 2 | 7.69 | 1.3 | 9 |
| *Guapira opposita* | Nyctaginaceae | 9 | 7.45 | 5.9 | 13.4 |
| *Aspidosperma ramiflorum* | Apocynaceae | 2 | 7.43 | 1.3 | 8.7 |
| *Ecclinusa ramiflora* | Sapotaceae | 3 | 6.44 | 2 | 8.4 |
| *Myrocarpus frondosus* | Leguminosae | 1 | 4.44 | 0.7 | 5.1 |
| *Ocotea catharinensis* | Lauraceae | 9 | 3.77 | 5.9 | 9.7 |
| *Euterpe edulis* | Arecaceae | 18 | 3.23 | 11.8 | 15.1 |
| *Syagrus romanzoffiana* | Arecaceae | 1 | 2.05 | 0.7 | 2.7 |
| Dead | | 3 | 2 | 2 | 4 |
| Melastomataceae sp.1 | Melastomataceae | 1 | 1.93 | 0.7 | 2.6 |
| *Endlicheria paniculata* | Lauraceae | 4 | 1.64 | 2.6 | 4.3 |
| *Allophyllus edulis* | Sapindaceae | 2 | 1.64 | 1.3 | 3 |
| *Nectandra megapotamica* | Lauraceae | 2 | 1.66 | 1.3 | 3 |
| Myrtaceae sp.3 | Myrtaceae | 1 | 1.55 | 0.7 | 2.2 |
| *Protium heptaphyllum* | Burseraceae | 1 | 1.52 | 0.7 | 2.2 |
| *Trichilia lepidota* | Meliaceae | 3 | 1.23 | 2 | 3.2 |
| *Roupala brasiliensis* | Proteaceae | 1 | 1.22 | 0.7 | 1.9 |
| *Coussapoa microcarpa* | Cecropiaceae | 2 | 1.22 | 1.3 | 2.5 |
| *Brosimum guianense* | Moraceae | 2 | 1.18 | 1.3 | 2.5 |
| Annonaceae sp.5 | Annonaceae | 1 | 1.12 | 0.7 | 1.8 |
| *Prunus myrtifolia* | Rosaceae | 2 | 1.11 | 1.3 | 2.4 |
| *Maytenus* cf. *evonymoides* | Celastraceae | 3 | 0.98 | 2 | 3 |
| *Piptadenia gonoacantha* | Leguminosae | 1 | 0.97 | 0.7 | 1.6 |
| Annonaceae sp.4 | Annonaceae | 1 | 0.92 | 0.7 | 1.6 |
| *Tetrorchidium rubrivenium* | Euphorbiaceae | 2 | 0.88 | 1.3 | 2.2 |
| *Cedrela fissilis* | Meliaceae | 3 | 0.87 | 2 | 2.8 |
| *Chrysophyllum inornatum* | Sapotaceae | 3 | 0.82 | 2 | 2.8 |
| *Aspidosperma polyneuron* | Apocynaceae | 1 | 0.8 | 0.7 | 1.5 |
| *Rollinia sericea* | Annonaceae | 1 | 0.64 | 0.7 | 1.3 |
| *Margaritaria nobilis* | Euphorbiaceae | 2 | 0.6 | 1.3 | 1.9 |

(cont.)

| Species | Family | Ni | RDoi | RDi | CIi |
|---------|--------|----|------|-----|-----|
| *Pouteria psammophila* | Sapotaceae | 1 | 0.53 | 0.7 | 1.2 |
| *Campomanesia guaviroba* | Myrtaceae | 2 | 0.53 | 1.3 | 1.8 |
| *Sorocea bonplandii* | Moraceae | 2 | 0.51 | 1.3 | 1.8 |
| *Persea venosa* | Lauraceae | 1 | 0.47 | 0.7 | 1.1 |
| *Myrceugenia myrcioides* | Myrtaceae | 4 | 0.43 | 2.6 | 3.1 |
| *Eugenia cuprea* | Myrtaceae | 5 | 0.42 | 3.3 | 3.7 |
| *Nectandra oppositifolia* | Lauraceae | 1 | 0.38 | 0.7 | 1 |
| *Gomidesia tijucensis* | Myrtaceae | 1 | 0.38 | 0.7 | 1 |
| *Marlierea eugeniopsoides* | Myrtaceae | 3 | 0.36 | 2 | 2.3 |
| *Myrcia pubipetala* | Myrtaceae | 3 | 0.33 | 2 | 2.3 |
| *Verbesina* sp. | Asteraceae | 3 | 0.3 | 2 | 2.3 |
| *Alibertia myrciifolia* | Rubiaceae | 2 | 0.3 | 1.3 | 1.6 |
| *Garcinia gardneriana* | Clusiaceae | 2 | 0.25 | 1.3 | 1.6 |
| *Cecropia pachystachya* | Cecropiaceae | 2 | 0.23 | 1.3 | 1.5 |
| *Posoqueria acutifolia* | Rubiaceae | 1 | 0.21 | 0.7 | 0.9 |
| *Matayba junglandifolia* | Sapindaceae | 1 | 0.2 | 0.7 | 0.9 |
| *Inga marginata* | Leguminosae | 2 | 0.23 | 1.3 | 1.5 |
| *Eugenia florida* | Myrtaceae | 1 | 0.2 | 0.7 | 0.9 |
| *Beilschmiedia emarginata* | Lauraceae | 2 | 0.16 | 1.3 | 1.5 |
| *Guarea macrophylla* | Meliaceae | 2 | 0.15 | 1.3 | 1.5 |
| *Machaerium stipitatum* | Leguminosae | 1 | 0.14 | 0.7 | 0.8 |
| *Pterocarpus* cf. *rohrii* | Leguminosae | 2 | 0.13 | 1.3 | 1.4 |
| *Eugenia riedeliana* | Myrtaceae | 1 | 0.12 | 0.7 | 0.8 |
| *Byrsonima ligustrifolia* | Malpighiaceae | 2 | 0.12 | 1.3 | 1.4 |
| *Alchornea triplinervia* | Euphorbiaceae | 1 | 0.12 | 0.7 | 0.8 |
| Sp.3 | | 1 | 0.11 | 0.7 | 0.8 |
| Sp.1 | | 1 | 0.09 | 0.7 | 0.7 |
| Monimiaceae sp.1 | Monimiaceae | 1 | 0.07 | 0.7 | 0.7 |
| *Mollinedia clavigera* | Monimiaceae | 1 | 0.07 | 0.7 | 0.7 |
| *Lonchocarpus muehlbergianus* | Leguminosae | 1 | 0.07 | 0.7 | 0.7 |
| *Swartzia* aff. *acutifolia* | Leguminosae | 1 | 0.07 | 0.7 | 0.7 |
| *Calyptranthes concinna* | Myrtaceae | 1 | 0.07 | 0.7 | 0.7 |
| *Alseis floribunda* | Rubiaceae | 1 | 0.07 | 0.7 | 0.7 |
| Myrtaceae sp.1 | Myrtaceae | 1 | 0.06 | 0.7 | 0.7 |
| *Rudgea* cf. *jasminoides* | Rubiaceae | 1 | 0.05 | 0.7 | 0.7 |
| Lauraceae sp.1 | Lauraceae | 1 | 0.05 | 0.7 | 0.7 |

area. This methodology proved to be a useful tool in the selection of forested areas to exemplify the succession dynamics or chronosequence that occurs in the study site. Our analysis was favoured by the occurrence of two sets of photos in 1973, where in an interval of two months we identified an area of cut forest, which corresponds in December 1997 to a forest fragment with 24.5 years old.

The phytosociological survey carried out in the chronosequence was considered sufficient to achieve the main objective of this work, *i.e.*, the characterization of the main species involved in the secondary succession process at the study site. The transect with 0.1 ha used to assess the successional stages produced a relatively fast and accurate result, as suggested by Shugart (1984), who indicates a surface area around 0.1 ha adequate for application of "gap models". However, to assess the tree species diversity (species richness, abundance and Shannon diversity) it would be recommended a larger sampling area as suggested by He *et al*. (1996).

The species composition along the forest succession phases at the study site indicates a different pattern of forest succession, where *Piptadenia gonoacantha* (Mimosaceae) substitutes the species generally found at the initial succession of Atlantic Forest over acidic soils, *Tibouchina* spp. (Melastomataceae) (Loefgren 1898, Leitão Filho *et*

*al*. 1993). The occurrence of this kind of soil represents a typical situation in the Atlantic Forest, where most soils are usually found to be acidic, highly leached and nutrient deficient, although there is great diversity of specific soil types within the humid tropics (Jordan 1985).

The results indicate that *P. gonoacantha* only occurs over the calcareous soil, while *T. pulchra* showed a marked decrease in importance when compared with the successional dynamics outside the limestone area, *e.g.* in an area close to the study site (Torezan 1995, Godoy 2001). This suggests a competitive exclusion, where *P. gonoacantha* a superior competitor in this kind of environment, displaces the species *T. pulchra.*

The occurrence of angiosperm families showed a clear dominance of Leguminosae throughout succession and a decrease of importance of Melastomataceae in the more mature forest. In the early succession, Symplocaceae and Flacourtiaceae were important because the high number of individuals of a single species *Symplocos laxiflora* and *Casearia sylvestris*, respectively. In the intermediary stage, Myrsinaceae was important because of the number of individuals of *Myrsine coriacea*, an understorey species, showing clearly the beginning of stratum development. The importance of Leguminosae is due to the highest basal area shown by the relative dominance. The most important species was *P. gonoacantha* that accounted for more than 30% of total basal area of the community and more than 90% of the basal area from leguminous species.

In the older stage, Leguminosae was again the most important family, accounting for almost 30% of total basal area and showing the occurrence of nine species. Lauraceae and Myrtaceae were also important because the high number of individuals and species.

Considering the inventory as a whole, Leguminosae was the most important family followed by Myrsinaceae, Myrtaceae, Annonaceae, Lauraceae, Rubiaceae and Melastomataceae, which is, except for the dominance of Leguminosae, a similar result as found by Leitão Filho *et al*. (1993) for secondary forest in areas protected from air pollution in Cubatão, São Paulo. In addition, these families are considered by Oliveira Filho & Fontes (2000), except Myrsinaceae, as having the highest number of species on the flora of areas of Ombrophylous Dense Forest.

Despite of the fact that calcareous soils cover more than 30% of earth's surface (Marschner 1995), their occurrence is less than 7% in the Brazilian territory (Karmann 1994). In addition, the main areas of karst landscape in Brazil are situated in dry and/or seasonal zones, where dominant vegetation are Cerrado and Deciduous Seasonal Forest. Whitmore (1984) indicates that karst landscape is absent of the humid tropics of Africa and it is rare in Latin America, except for Caribbean region. The author also describes karst occurrence in a small part of the tropical Far East (China, Indo-Chine, Sumatra, Malaya, Sarawak, Java and New Guinea), where the forests over limestone have several characteristic species occurring in habitats normally drier than the surrounding areas, stressing that acidic soils are common because peat occurrence.

The Atlantic Forest over calcareous soil found at the study site is important for Neotropical Forest Biodiversity because it is probably the only site where it occurs in Brazil, being a very important genetic bank of threatened species such as *Ocotea catharinensis* Mez - Lauraceae (SBB 1992); *Aspidosperma ramiflorum* Müll. Arg. - Apocynaceae; *Myrocarpus frondosus* Allemao - Fabaceae; *Chrysophyllum inornatum* Mart. - Sapotaceae; and *Euterpe edulis* Mart. - Arecaceae (www.bdt.org.br/redflora/).

These results provided a background to study the forest architectural growth, successional dynamics and species regeneration strategies, and for the study of ecophysiology of nitrogen use strategies by tree species and the relations with successional status (Aidar 2000).

The characterization of this locally restricted Atlantic Forest successional pattern is decisive in supporting actions taken to rehabilitate degraded lands, and can be a potential tool for sustainable tropical forest management, including the potential to serve as carbon offset mechanism (Silver *et al*. 2000), both inside and around the Alto Ribeira Touristic State Park boundaries.

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