Journal of Tropical Ecology (2002) 18:759–774. With 2 figures. Copyright © 2002 Cambridge University Press
DOI:10.1017/S0266467402002493 Printed in the United Kingdom

Seed bank and seed rain in a seasonal semi-deciduous forest in south-eastern Brazil

MARIA TEREZA GROMBONE-GUARATINI*[1] *and* RICARDO RIBEIRO RODRIGUES†

**Departamento de Botânica, Universidade Estadual de Campinas (UNICAMP), Cx. P. 6109, 13083-970, Campinas, São Paulo, Brasil*
†Departamento de Ciências Biológicas, Escola Superior de Agricultura Luiz de Queiróz, Cx. P 9, 13418-900, Piracicaba, São Paulo, Brasil
(Accepted 16th September 2001)

ABSTRACT. To examine the influence of seasonality on the abundance and composition of species in the community, we studied the seed rain and the seed bank in a seasonal, semi-deciduous forest in south-eastern Brazil. Soil samples (depth 3 cm, 0.25 m^2) were collected within a 1-ha plot in the dry seasons of 1996 and 1997 and the rainy season of 1997 (84 samples per collection). Thirty-five seed traps (0.25 m^2 each) were placed randomly in the forest from March 1997 to February 1998. The greatest density of seeds in the soil occurred in samples collected during the rainy season, the period which coincides with the main fruiting period in this forest. The Sørensen similarity index values for the seed bank composition among the three periods were high (> 0.50). The fallout of propagules was strongly seasonal, with more than half of the annual total number of seeds being caught in the two months around the end of the dry season and beginning of the rainy season. The mean density of seeds in the soil bank was nearly 86% lower than the seed rain density. There was no clear evidence of seasonal effects on species density and richness in this forest.

KEY WORDS: dispersal, phenology, seasonality, seed rain, succession, tropical forests

INTRODUCTION

Recent investigations into the natural processes which influence forest dynamics have shown that the soil seed bank is one of the principal sources of recruitment for new individuals in the initial stages of secondary succession (Butler & Chazdon 1998, Hall & Swaine 1980, Hopkins & Graham 1983, 1987; Young *et al.* 1987) and is partially responsible for dynamic changes that may

[1] Corresponding author.

occur during the development of vegetation (Lunt 1997). The species richness and abundance in seed banks may provide information on the potential of a community for regeneration (Williams-Linera 1993).

The composition of the seed bank reflects the richness of species present in the local vegetation or immediate vicinity (Saulei & Swaine 1988). However, there is evidence that disturbances and fragmentation may influence species richness and abundance in the soil (Graham & Hopkins 1990, Hopkins *et al.* 1990, Quintana-Ascencio *et al.* 1996, Young *et al.* 1987). Temporal alterations in the floristic composition of the community and seasonal variations in the fruiting and seed-dispersal types influence the abundance of seeds, species and plant life forms available in the soil of a community during the year and from year to year (Alvarez-Buylla & Martínez-Ramos 1990, Dalling & Denslow 1998, Dalling *et al.* 1997, 1998; Saulei & Swaine 1988, Young *et al.* 1987).

In tropical forests, the seasonal patterns of fruiting define the temporal variation in the flux of propagules to a determined area during the year and between different years (Foster 1985, Frankie *et al.* 1974, Morellato 1995, White 1994). The flux of propagules is fundamental in determining the potential population of a particular habitat (Harper 1977), and the lack of seed dispersal is a limiting factor in forest regeneration (Holl 1999). As a result the course of succession is intimately related to the seasonal patterns of seed arrival (Young *et al.* 1987). Investigations of seed rain may provide useful information on the abundance, spatial distribution, density and richness of species.

Autochthonous and immigrant propagules contribute to the ecological changes in a community and are fundamental for natural regeneration (Hofgaard 1993). Whereas autochthonous seeds maintain the floristic forest mosaic, allochthonous seeds may make the floristic composition more homogeneous if they are widely dispersed, or may produce floristic heterogeneity if the pattern of dispersal is patchy (Martínez-Ramos & Soto-Castro 1993).

Many studies have investigated the seed bank composition and quantified the seed rain in tropical forests under distinct disturbances, and in vegetation of different ages (Augspurger & Franson 1988, Denslow & Gomez Diaz 1990, Hopkins *et al.* 1990, Quintana-Ascencio *et al.* 1996, Saulei & Swaine 1988, Williams-Linera 1993, Young *et al.* 1987). The influence of seasonal variation of the seed rain on the composition and abundance of the soil seed bank has not yet been investigated (Butler & Chazdon 1998).

In this study, we investigated the origin of the propagules in the seed rain and examined whether there was any temporal variation in the seed rain as a function of phenological patterns of the community in a seasonal semi-deciduous forest in south-eastern Brazil, and whether there was a relationship between the composition of the seed rain, the seed bank and the local flora. We hypothesized that the seed population composition could vary during the year as a function of the phenological patterns of the community and that collecting soil samples at different times of the year would provide a more complete understanding of the species abundance and richness in the soil seed bank.

MATERIALS AND METHODS

Study area

The study was conducted in the Santa Genebra Municipal Reserve which belongs to the José Pedro de Oliveira Foundation and is situated in the district of Barão Geraldo, just north of the city of Campinas, São Paulo, Brazil (22°49′45″S and 47°06′33″W). The reserve has an area of 251.8 ha and altitude of 580–610 m. The forest is surrounded by agricultural areas and houses. The forest is a mosaic of successional stages where the intact canopy of large trees is adjacent to gaps and secondary growth areas.

The regional climate is characterized by a dry, cool season (April–September) when the rainfall is less than 70 mm mo^{-1} and the mean temperatures vary from 17.3 °C to 20.3 °C and a hot, humid season (October–March) when the rainfall is greater than 120 mm mo^{-1} and mean temperatures vary from 21.3 °C to 23.3 °C. The reserve has seasonal reproductive and growth rhythms seen as the loss of leaves in the driest months (July–August) followed by the emergence of new leaves at the beginning of the humid season (October–November) (Morellato 1995).

The vegetation is classified as tropical, semi-deciduous forest (Leitão Filho 1995) and is characterized by emergent trees up to 25 m tall, such as *Cariniana legalis*, *Aspidosperma polyneuron* and *Hymenaea courbaril*, and by a discontinuous canopy 15–18 m tall characterized by trees such as *Cedrela fissilis* and *Aspidosperma ramiflorum*. The understorey shrubs *Actinostemom klotzschii*, *Trichilia elegans* and *Hybanthus atropurpureus* are common. The families Leguminosae, Rubiaceae and Myrtaceae are each represented by several species.

Soil seed bank

For this study, an area considered to be late secondary forest situated in the central region of the reserve was chosen. A permanent plot (200 m × 50 m) in this area was subdivided into 100 equal plots of 10 m × 10 m, to give a total sample area of 1 ha. The 100 plots, each with an area of 100 m^2, were further divided into subplots of 0.25 m^2 to give 40 000 subplots which represented the sample units. In the dry season (August) of 1996 and 1997 and the rainy season (March) of 1997, 84 soil samples were collected (0.25 m^2, 0.03 m deep, with a total sample area of 21 m^2 and a volume of 0.63 m^3). The precise locations of the subplots were obtained by measuring the coordinate distances from the boundaries of the plots. Each sample was placed in a black polythene bag which was then labelled, sealed and transported to the laboratory. Within 36 h of collection, the samples were placed in the nursery at the Departamento de Ciências Florestais da Escola Superior de Agricultura Luis Queiróz, since germination in the nursery occurred more rapidly than in the greenhouse (M. T.

Grombone-Guaratini, *pers. obs.*). Germination experiments were performed using wooden boxes measuring 0.5 m × 0.5 m, with a 3-cm layer of vermiculite under the soil to facilitate drainage. The surface layer of leaves collected was sieved with a mesh sieve (4.76 mm) to prevent larger particles on the soil surface from affecting the germination process.

The samples of the 1996 dry season, the 1997 rainy season and the 1997 dry season were incubated with maximum temperature fluctuations of 14.0–30.6 °C, 14.2–29.9 °C and 15.3–31.7 °C, respectively. The samples were placed under full lighting in the nursery, since most seeds of the species present in this type of forest germinate in direct sunlight (I. Válio, *pers. comm.*). To provide ideal germination conditions, the samples were kept humid. To obtain a measure of the number of viable seeds in the soil (Brown 1992, Gross 1990, Heerdt *et al.* 1996), the number of seedlings that emerged was counted weekly for 18 wk. Each seedling identified was removed from the box. After 8 wk of observation, all the seedlings were removed and the soil stirred to promote germination of seeds that may have remained buried or shaded. The number of new seedlings was again scored over the next 10 wk. Five control samples with vermiculite alone were randomly chosen for the experiment.

A few common weeds (*Cuphea mesostemon* Kohne, *Emilia sonchifolia* DC., *Euphorbia prostrata* Ait. and *Oxalis* sp.) germinated in the boxes with vermiculite but were excluded from the analysis. The young seed-bank plants were identified based on specialized literature and with help from experts as well as by consulting herbarium collections.

Seed rain

In the same area, 35 subplots were randomly chosen by simple sampling without reposition. The traps (0.50 × 0.50 m) were constructed with a wooden base and a cover of fine-mesh nylon and were installed 10 cm above the soil. The total sampled area was 8.75 m^2. The inside of the traps was lined with fabric containing 70% polyester and 30% cotton to facilitate removal of the collected material. This fabric was chosen for its poor retention of moisture over a prolonged period thereby reducing the possibility of the collected material rotting in the trap.

The contents of the traps were collected monthly from March 1997 to February 1998. Once in the laboratory the material was sorted with the help of a magnifying glass and the diaspores were preserved in 70% alcohol for later identification. Only apparently viable propagules (with no signs of predation or empty seeds) were included in the analysis (Foster 1985). Immature fruits were considered as aborted and were not included in the count since they would not be effective in increasing the population size (Stephenson 1981). The species found in the traps were classified according to their life form (trees, shrubs, herbs and climbers) and their manner of dispersal (van der Pijl 1982). The principal vertebrate agents of dispersal in this study were birds and mammals. The material collected was identified by comparison with a desiccated fruit collection, from the same area and by comparison with material in the herbarium collection of the Universidade Estadual de Campinas (UEC). The help of experts was also sought when necessary.

Vegetation composition and structure

From 1996 to 1998, all plants with flowers and/or fruit in the study area were collected and identified.

Data analysis

After square-root transformation, ANOVA followed by Tukey's multiple comparison test (Zar 1999) was used to compare the soil seed density of different periods of collection. The K^2-test was used to assess the normality in the population distribution (Zar 1999).

Floristic similarity between (1) the species lists from the three seed-bank samples and (2) the flora of the seed rain and the flora of the forest area studied (taking into consideration all life forms found in the forest and in the seed bank) was computed using Sørensen's Index (Mueller-Dombois & Ellenberg 1974). To verify the species similarity among the studied months an agglomerative hierarchical clustering analysis was performed, using the Sørensen's Index and unweighted paired group arithmetic averaging (UPGMA) using the FITOPAC package (Shepherd 1995). The densities (D) and absolute frequencies (f) were calculated for seed-bank and seed-rain species as $D = n / A$ and $f = 100 \times (p/P)$ when n was the number of individuals of each species, A was the sampled area (m^2), p was the number of samples with each species and P was the total number of samples (Mueller-Dombois & Ellenberg 1974). ANOVA followed by Tukey's multiple comparision test (Zar 1999) was used to compare the soil seed density of different periods of collection. We used χ^2-test to compare different dispersal mechanisms of trapped species in the seed rain (Zar 1999).

RESULTS

Seed bank

The density of the germinated seeds in the soil was 32.3 ± 31.6 seeds m^{-2} in the dry season of 1996, 49.6 ± 43.8 seeds m^{-2} in the rainy season of 1997 and 46.3 ± 68.2 seeds m^{-2} in the dry season of 1997. The seed density of the soil during the dry season of 1996 was significantly lower than in the rainy season of 1997 ($F = 5.97$, $df = 2$, $P < 0.05$), but there was no difference between the wet and dry seasons of 1997. *Trema micrantha*, a tree characteristic of the early stages of succession, was the most abundant species since it had the highest absolute density in the three periods sampled (Appendix 1).

Species richness and life-form distribution

Forty-one species were identified in the seed bank of the 1996 dry season, 39 species in the rainy season of 1997 and 37 species in the dry season of 1997. The similarity values for the seed bank composition in the three periods sampled were high (1996 dry vs. 1997 rainy: SI = 0.53, 1996 dry vs. 1997 dry: SI = 0.58, 1997 dry vs. 1997 rainy: SI = 0.53) and the small differences are due to a few species that fruited in only one season (Table 1). Together trees and shrubs represented the greatest species richness and abundance in the seedlings germinated from soil samples of the three periods (Table 2).

Seed rain

From March 1997 to February 1998, 3865 propagules of 54 species in total were identified in the 35 traps installed in the forest. The density of seed deposition during this period was 442 ± 493 propagules m^{-2}. The densities and absolute frequencies, life forms, successional stages and manner of dispersal of the samples

Table 1. Fruiting season, dispersal agent and number of tree and shrub seeds found in the 84 seed bank samples collected in the Santa Genebra Municipal Reserve, in August 1996 (dry season), March 1997 (rainy season) and August 1997 (dry season).

Species	Fruiting period	Dispersal mechanism	Number of seeds		
			Dry/1996	Rainy/1997	Dry/1997
Trees					
Aspidosperma polyneuron	Jul–Oct	Wind	3	–	–
Cecropia glaziouii	Jan–Dec	Mammals/birds	7	8	26
Cecropia hololeuca	Jan–Dec	Mammals/birds	8	4	8
Cecropia pachystachya	Jan–Dec	Mammals/birds	16	15	7
Celtis tala	Unknown	Mammals	17	21	23
Chorisia speciosa	Jul–Sept	Wind	1	–	–
Cordia cf. *trichotoma*	Nov–Dec	Birds	5	5	5
Croton floribundus	Nov–Jan	Ballistic	–	4	–
Croton priscus	Nov–Feb	Ballistic	–	77	21
Esenbeckia febrifuga	Mar–Sept	Ballistic	2	–	–
Galipea multiflora	Mar–Jul	Ballistic	2	–	7
Miconia discolor	Nov–Apr Jul–Sept	Birds	–	1	–
Piptadenia gonoacantha	Jul–Sept	Wind	6	–	6
Senna macranthera	Apr–Aug	Wind	–	2	–
Syagrus romanzoffianum	Jan–Dec	Mammals/birds	–	–	1
Trema micrantha	Jan–Dec	Birds	170	435	351
Trichilia clausseni	Oct–Feb	Birds	–	1	–
Urera baccifera	Apr–Jun	Birds	10	3	8
Zanthoxylum rhoifolium	Dec	Birds	4	2	1
Zanthoxylum cf. *monogynum*	Oct–Dec	Birds	–	–	4
Zanthoxylum cf. *hiemale*	Feb	Birds	–	11	–
Shrubs					
Hybanthus atropurpureus	Jan–Dec	Ballistic	50	137	95
Piper sp.	–	Mammals	2	–	–
Solanum alternatopinnatum	–	Birds	3	–	–
Solanum granuloso-leprosum	Jan–Dec	Mammals	12	8	9
Solanum hirtellum	April	Mammals	–	–	1
Solanum variabile	Unknown	Mammals	1	–	–
Wissadula amplissima	Unknown	Ballistic	7	7	9

Table 2. The diversity and relative abundance of different growth forms in the samples of soil seed bank collected in the Santa Genebra Municipal Reserve. The plants are grouped according to their life forms.

Life form	Seedlings					
	Dry season/1996		Rainy season/1997		Dry season/1997	
	% of seeds	No. of species	% of seeds	No. of species	% of seeds	No. of species
Herbs	6.5	10	4.8	12	3	12
Climbers	21.8	12	4.6	10	22.6	8
Trees	47.8	12	68.8	12	55.5	12
Shrubs	16.9	7	17.2	5	14.7	5
Unknown	6.9	0	4.6	0	4.2	0
Total	100	41	100	39	100	37

are shown in Appendix 2. Most of the species (48.1%) sampled in the seed rain had a low absolute frequency (≤ 10%) and most (61.1%) were represented by a small number of diaspores per unit area. Most diaspores collected belonged to species of climbers (48.2%) followed by trees (29.6%), shrubs (9.3%) and herbs (5.6%); four morphotypes (7.4%) could not be characterized (Appendix 2).

The fallout of propagules measured in the Santa Genebra Municipal Reserve over a 1-y period was strongly seasonal, with more than half of the annual total number of seeds being caught in the 2 mo around the end of the dry season and beginning of the rainy season. The mean number of diaspores showed two peaks: the highest between August and September and a lower one in January. The smallest monthly mean of diaspores (0.94 ± 3.14) occurred in February and the largest in September (52.8 ± 86.5) (Figure 1a). Considering the number of species, high peaks occurred in August and September and smaller ones in May and June (Figure 1b). The species composition of seed rain differed substantially and the fusion in the clustering analysis clearly separated two groups (Figure 2). On the right side of the dendrogram, the wet months built up one group. On the left the dry months built up another cluster.

There was variation in the number of species associated with the three dispersal mechanisms ($\chi^2 = 6.05$, df = 2, $P < 0.05$). The contents of the traps consisted predominantly of wind-dispersed species (57.4%, 31 species), followed by animal-dispersed species (29.6%, 16 species) and ballistically dispersed species (9.3%, 5 species); 3.7% (2 species) could not be characterized (Appendix 2).

Climber species were caught in the traps mainly from May to November i.e. during the entire dry season and at the beginning of the rainy season. Propagules of tree species were recorded predominantly during the rainy season, from September to January.

Seed rain and vegetation composition and structure

The number of species in the studied area was 205, and consisted of 85 trees, 37 treelets, 36 climbers, 32 shrubs and 15 herbs (Grombone-Guaratini 1999). Nearly 70% (39 species) of the species found in the seed rain coincided with the composition of the local flora. The similarity between the seed rain and the community composition was 0.42.

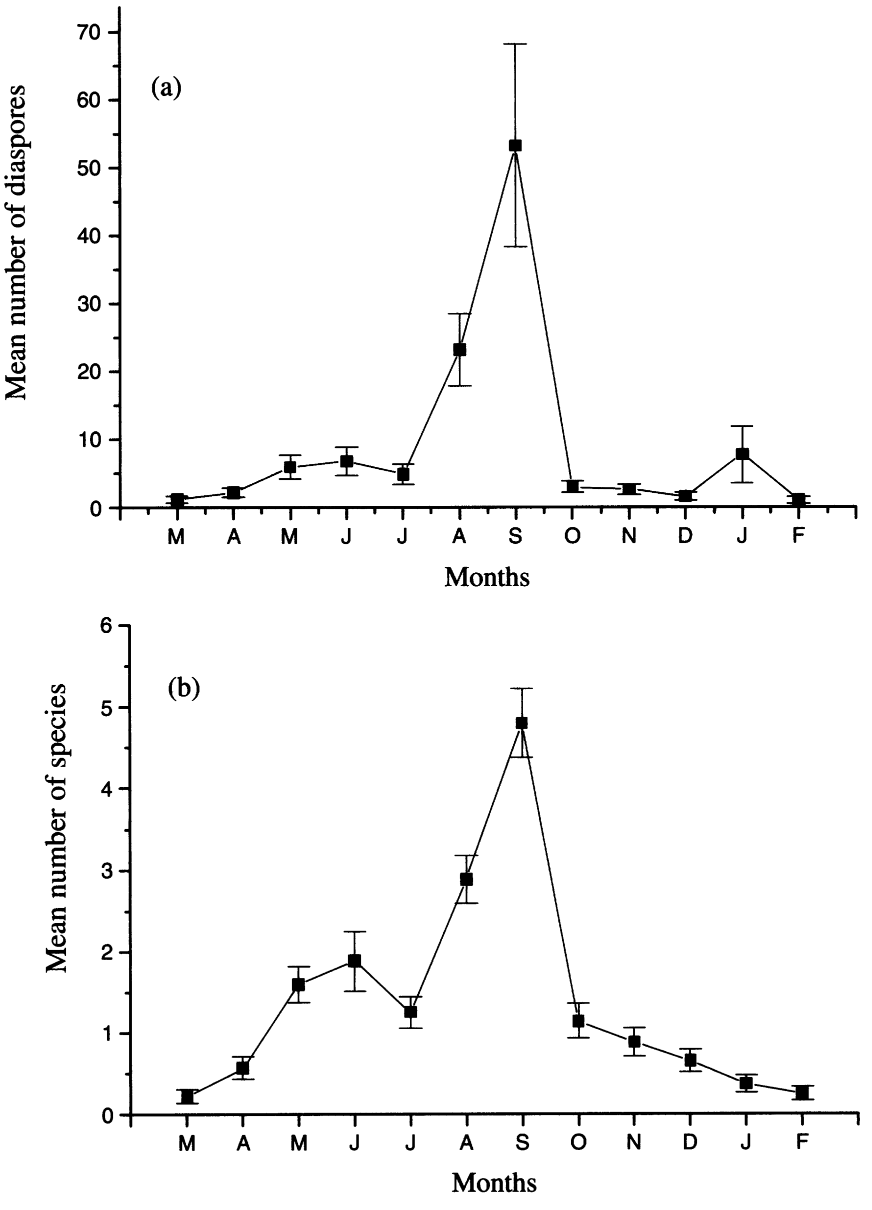

Figure 1. Mean number of seeds (a) and species (b) per month in the 35 seed traps from March 1997 to February 1998. Vertical lines represent the standard deviation above and below the mean.

DISCUSSION

Seed bank

The densities of viable seeds in the soil samples of the three periods were lower than those reported in other studies conducted in tropical forests, including semi-deciduous forests (742–1069 seeds m^{-2}, Hopkins & Graham 1983, Putz 1983) and Brazilian Atlantic montane (872 seeds m^{-2}, Baider *et al.* 1999) or

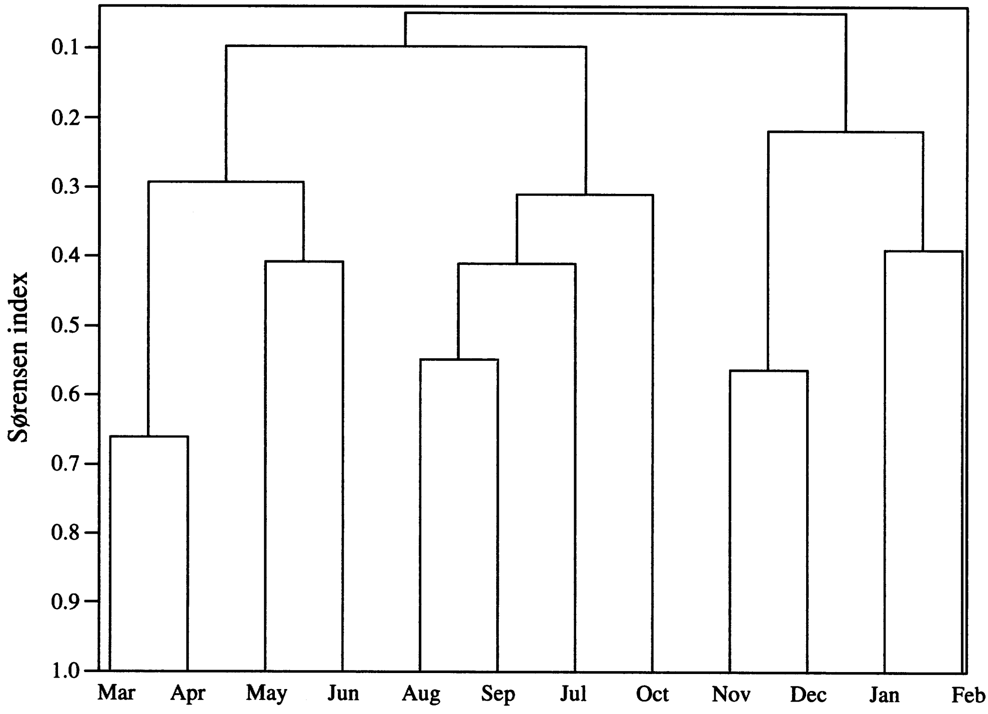

Figure 2. Dendrogram from UPGMA clustering analysis of seed rain composition from March 1997 to February 1998 based on Sørensen index values.

gallery (372 seeds m^{-2}, Grombone-Guaratini 1993) forests. These discrepancies may partly reflect the lack of methodological standardization which limit ecological comparisons (Butler & Chazdon 1998, Dalling *et al.* 1998), but may also result from variations in the forest structure and species composition, seed rain at different locations and length of seed dormancy (Dalling *et al.* 1997, 1998).

We attributed the significant differences in the seed bank density between dry season of 1996 and rainy season of 1997 to (1) temporal variation in the seed rain as a function of the forest phenology which may have influenced the composition of the soil seed bank and (2) differences in the meteorological conditions during the two sampling seasons which led to selective germination of the seeds in the soil. According to Vázquez-Yanes & Orozco-Segovia (1996), tropical pioneer seeds kept under high moisture conditions showed better viability than those maintained in drier conditions. This phenomenon may result in a shift in the soil seed density. However, there was no difference in the seed densities of the 1997 rainy and dry seasons. This unexpected result may be a consequence of the increased precipitation during the 1997 dry season (22.6 mm compared to 4.3 mm for the 1996 dry season).

The total number of seeds that germinated was greater in the seed-bank samples collected in the rainy season, a period which coincided with the preferred season for dispersal (Morellato 1995, Penhalber & Mantovani 1997).

Seasonal and annual fluctuations in seed production may partially influence the soil seed density (Butler & Chazdon 1998, Dalling *et al.* 1997, 1998; Putz & Appanah 1987). Since seed production varies between years and throughout the year, studies which evaluate the seasonal availability of seeds could provide models for assessing how the course of succession is influenced by the time of the year in which a disturbance occurs.

The methods used to analyse the seed composition of the soil may also have introduced some variation. Thus direct germination may underestimate the seed bank density and diversity if ideal conditions for germination are not available (Brown 1992, Gross 1990). Variations in temperature and solar radiation during the periods in which the samples remained in the nursery may have influenced the results obtained. However, the photoperiod in the tropics varies little and the daily changes in temperature are generally greater than the seasonal variations (Wright 1991); in addition our aim was to express the potential of natural germination in an attempt to determine the differences that occur between the different times of the year.

The abundance of trees and shrubs in the seed bank in the Santa Genebra Municipal Reserve (64.7–86%) was comparable to those of other tropical forest seed banks. Hall & Swaine (1980) reported that shrubs and trees made up 83% of the individuals that germinated in the seed-bank samples collected in Ghana. Lawton & Putz (1988) stated that trees and shrubs represented 77% of the soil seed community in the Monteverde Cloud Forest Reserve, Costa Rica. In the El Triunfo Biosphere Reserve, Chiapas, Mexico, Williams-Linera (1993) reported that 59.2% of the germinated seeds were woody plants. In contrast, a seed bank composed predominantly by herbaceous species (76%) in which tree and shrub components accounted for just 14% of the total seedlings was described in a gallery forest in Brazil (Grombone-Guaratini 1993). A larger proportion of seeds from herbaceous species may have reflected an excessive input of herbaceous species from surrounding open, disturbed vegetation (Dalling & Denslow 1998). The abundance of tree species probably varies according to the degree of forest fragmentation. In addition, the structure and composition of the local plant community may also influence the seed-bank composition.

The proportion of seeds from climbers was greater during the dry season, a period which coincides with the fruiting peak of this life form in this forest (Morellato & Leitão Filho 1996). Climbers are colonizers of clearings (Gentry 1983), and their richness is characteristic of seasonal semi-deciduous forest (Leitão Filho 1995). The high density of some species may be stimulated by disturbances that occur in the vicinity (Whitmore 1978).

Seed rain

The observations about seasonality in the seed rain agree with those of other studies which monitored seed rain in tropical forests throughout the year

(Jackson 1981, Penhalber & Mantovani 1997). Favourable germination conditions and the availability of dispersal agents may exert strong selective pressures which could influence fruiting and determine the seasonal model of fruit production (Foster 1985).

The low frequency of most species suggests that a large spatial variation in the distribution of propagules exists in this forest. The analysis of seed flow in plant communities has shown that seed rain is spatially heterogeneous (Augspurger & Franson 1988, Denslow & Gomez Diaz 1990, Rabinowitz & Rapp 1980, Young *et al.* 1987). The abundance and spatial distribution of species in fruit may play an important role in the diversity of seed rain, and could account for variation in the composition of seeds that fall in different locations in the forest (Martínez-Ramos & Soto-Castro 1993). The spatial distribution of seed rain depends on the mode of dispersal (Rabinowitz & Rapp 1980) and on the availability and efficiency of the dispersal agent.

The abundance of diaspores also showed a seasonal variation which depended on the dispersal agent. Wind-dispersed species were deposited in the traps mainly during the dry season and at the beginning of the rainy season, whilst animal-dispersed species were present in a greater number during the rainy season. These data are compatible with those reported by Frankie *et al.* (1974) for Costa Rica and by Foster (1985) for Panama, and reflect the fruiting pattern described for seasonal semi-deciduous forests (Morellato 1995). Thus, at the beginning of the rainy season, wind-dispersed fruits are still efficiently dispersed, but decrease thereafter because of rain, budding and the growth of leaves in the upper layers.

Penhalber & Mantovani (1997) suggested that a high percentage of wind-dispersed seeds was indicative of a certain degree of perturbation in a forest. We disagree with this proposal since our results have shown that some of the wind-dispersed propagules in the seed rain originated from autochthonous tree species corresponding to intermediate and final stages of succession (Table 1). Seasonal semi-deciduous forests lack a continuous canopy because approximately 68% of the tree species in the upper layer (canopy) are deciduous during the dry season (Morellato 1995).

Considering the life forms, climbers represented the greatest number of propagules in the seed rain. Climbers are abundant in this type of vegetation (Leitão Filho 1995) and most of those in the Santa Genebra Reserve are wind dispersed (Morellato & Leitão Filho 1996). Climbers and trees were the most frequent life forms in the seed rain in a tropical forest in Mexico, probably because they are able to produce a large number of propagules per unit area (Martínez-Ramos & Soto-Castro 1993).

Approximately 70% of the propagules were autochthonous. The number of seeds captured in the traps probably reflected the fruiting of species in the immediate vicinity of the site (Saulei & Swaine 1988).

Seed bank vs. seed rain

The mean density of seeds in the soil bank in both periods was nearly 86% lower than the seed-rain density. A smaller reduction (71%) was reported by Rabinowitz & Rapp (1980). The probable explanations for this finding include intense predation or rapid germination of the diaspores as soon as they reach the soil. The vertical transport of seeds, the activity of vertebrates and the percolation of rain water are also possible causes for the loss of seeds in the soil (Saulei & Swaine 1988). In the present study, the different methods used to count seeds in the seed bank and in the seed rain may have contributed to the large difference between these two; the specific method for assessing apparently viable seeds may have overestimated the seed-rain content.

Analysis of the similarity between the seed-rain flora and the total flora of the study area showed that there were few species in common. The presence of some species in the seed rain and seed bank only during their period of fruiting (*Zanthoxylum monogynum*, *Piptadenia gonoacantha*, *Trichilia claussenii* and *Senna macranthera*), suggests that these species remain in the soil for only a brief period, thus making the seed bank transitory. The species that were present in the seed bank and absent from the seed rain may accumulate seeds in the soil for a long period of time (*Cecropia* sp. and *Trema micrantha*).

Although there were differences in the species composition of the seed rain among the several studied months and significant differences between the seed densities of the 1996 dry season and the 1997 rainy season, there was no clear evidence of seasonal effects on species density and richness in this forest. Our data emphasize the importance of the seed bank and seed rain as potential sources of new individuals and species for recruitment. Furthermore, the availability of propagules and dispersal agents throughout the year ensures the structural re-establishment of the vegetation following disturbance. Investigations of vegetation structure, spatial and temporal patterns of seed rain, and the influence of both of these on the composition of the seed bank may provide important information for the conservation and management of tropical forests.

ACKNOWLEDGEMENTS

I. Valio, C. J. Burrows and D. Kennedy provided critical suggestions which improved the quality of this manuscript. The authors thank Vera N. Solferin, Flávia F. de Jesus and Stephen Hyslop for reviewing the English and Rodrigo A. S. Pereira for statistical advice and the Fundação José Pedro de Oliveira for granting permission to work on the Santa Genebra Municipal Reserve. M.T.G.G. was supported by Coordenadoria de Aperfeiçoamento de Pessoal de Ensino Superior (CAPES) and Conselho Nacional de Pesquisa (CNPq).

LITERATURE CITED

ALVAREZ-BUYLLA, E. & MARTÍNEZ-RAMOS, M. 1990. Seed bank and seed rain in the regeneration of a tropical pioneer tree. *Oecologia* 84:314–325.

AUGSPURGER, C. K. & FRANSON, S. E. 1988. Input of wind-dispersed seeds into light-gaps and forest sites in a neotropical forest. *Journal of Tropical Ecology* 4:239–252.

BAIDER, C., TABARELLI, M. & MANTOVANI, W. 1999. O banco de sementes de um trecho de Mata Atlântica. *Revista Brasileira de Biologia* 59:319–328.

BROWN, D. 1992. Estimating the composition of a forest seed bank: a comparison of the seed extraction and seedling emergence methods. *Canadian Journal of Botany* 70:1603–1612.

BUTLER, B. J. & CHAZDON, R. L. 1998. Species richness, spatial variation, and abundance of the soil seed bank of a secondary tropical rain forest. *Biotropica* 30:214–222.

DALLING, J. W. & DENSLOW, J. S. 1998. Soil seed bank composition along a forest chronosequence in seasonally moist tropical forest, Panama. *Journal of Vegetation Science* 9:669–678.

DALLING, J. W., SWAINE, M. D. & GARWOOD, N. C. 1997. Soil seed bank community dynamics in seasonally moist lowland tropical forest, Panama. *Journal of Tropical Ecology* 13:659–680.

DALLING, J. W., SWAINE, M. D. & GARWOOD, N. C. 1998. Dispersal patterns and seed bank dynamics of pioneer trees in moist tropical forest. *Ecology* 79:564–578.

DENSLOW, J. S. & GOMEZ DIAZ, A. E. 1990. Seed rain to tree-fall gaps in a neotropical rain forest. *Canadian Journal of Forest Research* 20:642–648.

FOSTER, R. B. 1985. The seasonal rhythm of fruitfall on Barro Colorado Island. Pp. 151–172 in Leigh, E. G., Rand, A. S. & Windsor, D. M. (eds). *The ecology of a tropical forest*. Smithsonian Institution Press, Washington, DC.

FRANKIE, G. W., BAKER, H. G. & OPLER, P. A. 1974. Comparative phenological studies of trees in tropical lowland wet and dry forest sites of Costa Rica. *Journal of Ecology* 62:881–913.

GENTRY, A. H. 1983. Dispersal ecology and diversity in neotropical forest communities. *Sonderbaende Naturwissenschaftlichen Vereins* 7:303–314.

GRAHAM, A. W. & HOPKINS, M. S. 1990. Soil seed banks of adjacent unlogged rainforest types in north Queensland. *Australian Journal of Botany* 38:261–268.

GROMBONE-GUARATINI, M. T. 1993. *Banco de sementes de uma floresta ripária no Rio Mogi Guaçú, SP.* Masters thesis, Institute of Biology, State University of Campinas, Campinas, SP.

GROMBONE-GUARATINI, M. T. 1999. *Aspectos da dinâmica de um trecho de floresta estacional semidecidual.* Doctoral thesis, Institute of Biology, State University of Campinas, Campinas, SP.

GROSS, K. L. A. 1990. Comparison of methods for estimating seed numbers in the soil. *Journal of Ecology* 78:1079–1093.

HALL, J. B. & SWAINE, M. D. 1980. Seed stocks in Ghanaian forest soils. *Biotropica* 12:256–263.

HARPER, J. L. 1977. *Population biology of plants*. Academic Press. London. 892 pp.

HEERDT, G. N. J., VERWEIJ, G. L., BEKKER, R. M. & BAKKER, J. P. 1996. An improved method for seed bank analysis: seedling emergence after removing the soil by sieving. *Functional Ecology* 10:144–151.

HOFGAARD, A. 1993. Seed rain quantity and quality, 1984–1992, in a high altitude old-growth spruce forest, northern Sweden. *New Phytologist* 125:635–640.

HOLL, K. D. 1999. Factors limiting rain forest regeneration in abandoned pasture: seed rain, seed germination, microclimate, and soil. *Biotropica* 31:229–242.

HOPKINS, M. S. & GRAHAM, A. W. 1983. The species composition of soil seed banks beneath lowland tropical rainforests in North Queensland, Australia. *Biotropica* 15:90–99.

HOPKINS, M. S. & GRAHAM, A. W. 1987. The viability of seeds of rainforest species after experimental soil burials under tropical wet lowland forest in north-eastern Australia. *Australian Journal of Ecology* 12:97–108.

HOPKINS, M. S., TRACEY, J. G. & GRAHAM, A. W. 1990. The size and composition of soil seed banks in remnant patches of three structural rainforest in North Queensland. *Australian Journal of Ecology* 15:43–50.

JACKSON, J. F. 1981. Seed size as a correlate of temporal and spatial patterns of seed fall in a neotropical forest. *Biotropica* 13:121–130.

LAWTON, R. O. & PUTZ F. E. 1988. Natural disturbance and gap-phase regeneration in a wind-exposed tropical cloud forest. *Ecology* 69:764–777.

LEITÃO FILHO, H. F. 1995. A vegetação. Pp. 19–29 in Leitão Filho, H. F. & Morellato, L. P. (eds). *Ecologia e preservação de uma floresta tropical urbana – reserva de Santa Genebra*. Editora da Unicamp, Campinas, SP.

LUNT, I. D. 1997. Germinable soil seed banks of anthropogenic native grasslands and grassy forest remnants in temperate south-eastern Australia. *Plant Ecology* 130:21–34.

MARTÍNEZ-RAMOS, M. & SOTO-CASTRO, A. 1993. Seed rain and advanced regeneration in a tropical rain forest. *Vegetatio* 107/108:299–318.

MORELLATO, L. P. & LEITÃO FILHO, H. F. 1996. Reproductive phenology of climbers in a Southeastern Brazilian forest. *Biotropica* 28:180–191.

MORELLATO, P. C. 1995. As estações do ano na floresta. Pp. 37–41 in Leitão Filho, H. F. & Morellato, L. P. (eds). *Ecologia e preservação de uma floresta tropical urbana – reserva de Santa Genebra*. Editora da Unicamp, Campinas, SP.

MUELLER-DOMBOIS, D. & ELLENBERG, H. 1974. *Aims and methods of vegetation ecology*. John Wiley and Sons, New York. 574 pp.

PENHALBER, E. F. & MANTOVANI, W. 1997. Floração e chuva de sementes em mata secundária em São Paulo, SP. *Revista Brasileira de Botânica* 20:205–220.

PUTZ, F. E. 1983. Treefall pits and mounds, buried seeds, and the importance of soil disturbance to pioneer trees on Barro Colorado Island, Panama. *Ecology* 64:1069–1074.

PUTZ, F. E. & APPANAH, S. 1987. Buried seeds, newly dispersed seed, and the dynamics of a lowland forest in Malaysia. *Biotropica* 19:326–333.

QUINTANA-ASCENCIO, P. F., GONZALEZ-ESPINOSA, M., RAMIREZ-MARCIAL, N., DOMÍNGUEZ-VÁZQUEZ, G. & MARTÍNEZ-ICO, M. 1996. Soil seed banks and regeneration of tropical rain forest from milpa fields at the Selva Lacandona, Chiapas, Mexico. *Biotropica* 28:192–209.

RABINOWITZ, D. & RAPP, J. K. 1980. Seed rain in a North American tall grass prairie. *Journal of Applied Ecology* 17:793–802.

SAULEI, S. M. & SWAINE, M. D. 1988. Rain forest seed dynamics during succession at Gogol, Papua New Guinea. *Journal of Ecology* 76:1133–1152.

SHEPHERD, G. J. 1995. FITOPAC 1. *Manual do usuário*. Departamento de Botânica. Universidade Estadual de Campinas.

STEPHENSON, A. G. 1981. Flower and fruit abortion: proximate causes and ultimate functions. *Annual Review of Ecology and Systematics* 12:253–279.

VAN DER PIJL, L. 1982. *Principles of dispersal in higher plants*. Third edition. Springer-Verlag, Berlin. 215 pp.

VÁZQUEZ-YANES, C. & OROZCO-SEGOVIA, A. 1996. Comparative longevity of seeds of five tropical rain forest woody species stored under different moisture conditions. *Canadian Journal of Botany* 74:1635–1639.

WHITE, L. J. T. 1994. Patterns of fruit-fall phenology in the Lopé reserve, Gabon. *Journal of Tropical Ecology* 10:289–312.

WHITMORE, T. C. 1978. Gaps in the forest canopy. Pp. 639–655 in Tomlinson, P. B. & Zimmermann, M. D. (eds). *Tropical trees as living system*. Cambridge University Press, Cambridge.

WILLIAMS-LINERA, G. 1993. Soil seed banks in four low mountain forests of Mexico. *Journal of Tropical Ecology* 9:321–337.

WRIGHT, S. J. 1991. Seasonal drought and the phenology of understory shrubs in a tropical moist forest. *Ecology* 72:1643–1657.

YOUNG, K. R., EWEL, J. J. & BROWN, B. J. 1987. Seed dynamics during forest succession in Costa Rica. *Vegetatio* 71:157–173.

ZAR, J. H. 1999. *Biostatistical analysis*. Fourth edition. Prentice-Hall International Editions, New Jersey. 663 pp.

Appendix 1. The ten most frequent species in the seed bank of soil seed samples collected in the Santa Genebra Municipal Reserve. The number of individuals germinated (mean ± SD) and the density (D), absolute frequency (f) and life form of the species are shown (T: tree; S: shrub; H: herb; C: climber).

1996/dry season

Species	Number of individuals	Mean ± SD	D	f	Life form
Trema micrantha Blume	170	2.1 ± 6.8	8.3	46.9	T
Hybanthus atropurpureus (A. St. Hil.) Taub.	50	0.6 ± 1.2	2.4	30.1	S
Gouania virgata Reiss.	42	0.5 ± 2.0	2.0	16.9	C
Pfaffia paniculata (Mart.) O. Kuntze	22	0.3 ± 0.8	1.1	16.9	C
Ageratum conyzoides L.	17	0.2 ± 0.4	0.8	20.5	H
Celtis tala Gillies ex Planch.	17	0.2 ± 0.8	0.8	8.4	T
Cecropia pachystachya Tréc.	16	0.2 ± 0.5	0.8	14.5	T
Serjania sp.	14	0.2 ± 0.6	0.7	10.8	C
Mikania cordifolia (L.) Willd.	12	0.2 ± 0.6	0.6	9.6	C
Solanum granuloso-leprosum Dunal	12	0.2 ± 0.4	0.6	1.8	S

1997/rainy season

Species	Number of individuals	Mean ± SD	D	f	Life form
Trema micrantha Blume	435	5.2 ± 9.8	20.7	75	T
Hybanthus atropurpureus (A. St. Hil.) Taub.	137	1.6 ± 2.9	6.5	38.0	S
Croton priscus Croizat	77	0.9 ± 2.8	3.7	16.7	T
Cecropia glazioui Sneth.	48	0.6 ± 1.3	2.3	28.6	T
Celtis tala Gillies ex Planch.	21	0.3 ± 0.7	1	14.3	T
Cecropia pachystachya Tréc.	15	0.2 ± 0.8	0.7	8.3	T
Conyza canadensis (L.) Cronquist	12	0.1 ± 0.4	0.6	11.9	H
Zanthoxylum chiloperone Mart. ex Engl.	11	0.1 ± 0.4	0.5	10.7	T
Rhynchosia phaseoloides Griseb.	10	0.1 ± 0.5	0.5	7.1	C
Pereskia aculeata Miller	8	0.1 ± 0.3	0.4	8.3	C

1997/dry season

Species	Number of individuals	Mean ± SD	D	f	Life form
Trema micrantha Blume	351	4.2 ± 11.9	16.7	54.8	T
Gouania virgata Reissk.	132	1.6 ± 3.0	6.3	41.7	C
Hybanthus atropurpureus (A. St. Hil.) Taub.	95	1.1 ± 1.8	45	45.2	S
Cecropia glazioui Sneth.	26	0.3 ± 0.7	1.2	21.4	T
Celtis tala Gillies ex Planch.	23	0.3 ± 0.8	1.1	16.7	T
Croton priscus Croizat	21	0.3 ± 1.2	1	9.5	T
Pfaffia paniculata (Mart.) O. Kuntze	18	0.2 ± 0.8	0.9	9.5	C
Mikania micrantha H.B.K.	17	0.2 ± 0.8	0.8	10.7	C
Serjania communis Camb.	10	0.1 ± 0.5	0.5	8.3	C
Solanum granuloso-leprosum Dunal	9	0.1 ± 0.4	0.4	7.1	S

Appendix 2. Phytosociological parameters of the species sampled in 35 traps set up in the Santa Genebra Reserve, Campinas, SP from March 1997 to April 1998. The species are organized according to their absolute frequencies. Bold names indicate species that were common among the flora of seed rain and the flora of the forest area.

Species	Number of diaspores	Density (diaspores m^{-2})	Absolute frequency	Dispersal
Climbers				
Urvillea ulmacea Kunth.	289	33.0	82.9	Wind
Serjania multiflora Camb.	221	25.3	65.7	Wind
Serjania reticulata Camb.	361	41.3	65.7	Wind
Pfaffia paniculata (Mart.) O. Kuntze	649	74.2	62.9	Wind
Serjania sp.	231	26.4	60	Wind
Serjania communis Camb.	137	15.7	48.6	Wind
Serjania grandiflora Camb.	28	32	34.3	Wind
Urvillea laevis Radlk.	55	6.3	28.6	Wind
Forsteronia rufa Muell. Arg.	16	1.8	25.7	Wind
Mansoa difficilis (Cham.) Bur. & K. Schum.	10	1.1	22.9	Wind
Mikania sp.	15	1.7	22.9	Wind
Arrabidea sp.	11	1.3	20	Wind
Gouania virgata Reiss.	56	6.4	17.1	Wind
Pyrostegia venusta (Ker-Gaw) Miers	9	1.0	14.3	Wind
Ipomoea sp.	5	0.6	11.4	Wind
Cuspidaria pterocarpha (Cham.) DC.	4	0.5	8.6	Wind
Adenocalimma bracteatum (Cham.) DC.	2	0.2	2.9	Wind
Dicella bracteosa (Juss.) Griseb.	3	0.3	2.9	Animal
Heteropteris aceroides Griseb.	1	0.1	2.9	Wind
Mikania cordifolia (L.) Wild.	41	4.7	2.9	Wind
Pithecoctenium sp.	6	0.7	2.9	Wind
Mendoncia puberula Mart.	2	0.3	5.7	Animal
Pereskia aculeata Miller	1	0.1	2.9	Animal
Shrubs				
Mapourea sessiliflora Muell. Arg.	40	4.6	31.4	Animal
Psychotria cathargenesis Jacq.	40	4.6	28.6	Animal
Hybanthus atropurpureus (A. St. Hil.) Taub.	9	1.0	11.4	Ballistic
Ixora gardneriana Benth.	25	2.9	11.4	Animal
Coffea arabica L.	2	0.2	5.7	Animal
Psychotria sp.	10	1.1	5.7	Animal
Psychotria vauthieri Muell. Arg.	1	0.1	2.9	Animal
Herbs				
Lasiacis ligulata Hitch. & Chase	8	0.9	8.6	Animal
Pharus sp.	17	1.9	2.9	Animal
Eupatorium hieracifolia (L.) Rafin.	32	3.7	2.9	Wind
Trees				
Vernonia diffusa Less.	867	99.1	80	Wind
Piptadenia gonoacantha (Mart.) Macbr.	28	3.2	40	Wind
Trichilia clausseni C. DC.	27	3.1	31.4	Animal
Cedrella fissilis Vell.	10	1.1	20	Wind
Croton priscus Croizat	294	33.6	17.1	Ballistic
Zanthoxylum monogynum St. Hil.	13	1.5	17.1	Animal
Esenbeckia leiocapa Engl.	21	2.4	14.3	Ballistic
Syagrus rhomanzoffiana (Cham.) Glassman	4	0.5	11.4	Animal
Esenbeckia febrifuga (St. Hil.) Juss.	11	1.3	8.6	Ballistic
Trichilia pallida Sw.	5	0.6	8.6	Animal
Galipea jasminiflora (A. St. Hil.) Engl.	2	0.3	5.7	Ballistic
Acacia polyphylla DC.	1	0.1	2.9	Wind
Cordia ecalyculata Vell.	2	0.2	2.9	Animal
Senna macranthera DC.	1	0.1	2.9	Wind
Zeyhera tuberculosa Burn.	1	0.1	2.9	Wind
Not classified				
Bignoniaceae sp1	20	2.3	28.6	Wind
Bignoniaceae sp2	3	0.3	8.6	Wind
Compositae sp1	6	0.7	5.7	Wind
Leguminosae sp1	1	0.1	2.9	Not identified
Leguminosae sp2	1	0.1	2.9	Not identified
Vernonia sp.	210	24	2.9	Wind