Acta Botanica Brasilica 28(3): 392-403. 2014.
doi: 10.1590/0102-33062014abb3344

Litter production and seed rain in semideciduous forest fragments at different successional stages in the western part of the state of Paraná, Brazil

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Received: 30 August, 2013. Accepted: 18 March, 2014

ABSTRACT

We documented litter production and seed rain in fragments of semideciduous forest (SDF) in the western part of the state of Paraná, Brazil: a late successional fragment (LF); an early successional fragment (EF); and a reforested late successional fragment (RLF). In each fragment, we established three permanent plots with four litter traps each, corresponding to 12 litter traps per fragment. Botanical material was collected monthly between June 2011 and May 2012. We sorted the material by category: leaves; branches; reproductive structures; and miscellaneous. We analyzed the seed rain using the reproductive structures. Annual production was highest (11,560 kg.ha^{-1}) in the LF, followed by the RLF, with 9330 kg.ha^{-1}, and the EF, with 7838 kg.ha^{-1}. The RLF yielded 7167 diaspores, from 33 species, compared with 4751 diaspores, from 38 species, for the EF; in both fragments, pioneer and anemochorous species predominated. The LF yielded 2173 diaspores, from 49 species, among which late secondary and climax species with zoochorous dispersal predominated. We observed asynchrony in the frequency of diaspore production of trees and lianas. Our data describe the dynamics of plant assemblages in SDF fragments and provide information on successional stages, dispersion syndromes, patterns of asynchrony, deciduousness, reproductive periods, and resource availability for frugivores.

Key words: Litterfall, semideciduous forest, succession, zoochory

Introduction

Habitat loss and fragmentation deriving from expanding agricultural pressure have significant effects on natural landscapes (Tabarelli & Gascon 2005). Such effects can be biotic or abiotic. Examples of abiotic effects include changes in microclimate, soil erosion, and river siltation (Borges *et al.* 2004). Biotic effects include changes in species composition and abundance, as well as in ecological interactions, resource availability, and seed dispersal, together with changes in population dynamics, which can reduce genetic variability and increase the rate of local extinction (Scariot *et al.* 2005). These effects increase as fragments become smaller and more distant from each other (Fahrig 2003). Detailed studies of ecological communities and processes in fragments are needed in order to understand the dynamics of such assemblages.

Studies on the phytosociology, litterfall, and seed rain of fragmented and restored forests are important for understanding and classifying the stages of forest succession. Combining these methods results in a greater amount of information on ecological succession and is considered a more efficient way to evaluate forest dynamics than is the use of any single method (Martins 2001; Magnago *et al.* 2012). In analyses of fragmented or restored forests, these methods can also assess resource productivity or lack of sustainability (Brancalion *et al.* 2012). They can also help determine whether goals established for these areas have been reached or if additional measures are needed for their conservation and management (Rodrigues & Gandolfi 2009).

Litter deposited on the soil surface acts as an open system, since it receives material mostly from the vegetation, which is decomposed and returned to the soil in the form of organic matter (Ewel 1976). It also reflects the nutrient cycling and productive capacity of forests, because its production varies with forest type, climate, altitude, rainfall, temperature, topography, the presence of deciduous species, successional stage, and other factors (Figueiredo Filho *et al.* 2003). Therefore, litter analysis has been used by many authors as a way to compare areas at different successional stages and

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restored areas (Martins & Rodrigues 1999; Werneck *et al.* 2001; Moreira & Silva 2004; Pezzatto & Wisniewski 2006; Machado *et al.* 2008; Menezes *et al.* 2010; Pimenta *et al.* 2011).

Seed rain refers to the arrival of diaspores on soil through dispersal, leading to the formation of seed banks and seedling establishment (Araujo 2002). This process helps parameterize models of population recruitment with the arrival of allochthonous or autochthonous diaspores (Loiselle *et al.* 1996) and provides information about the abundance, richness, and spatial distribution of species in a particular area (Grombone-Guaratini & Rodrigues 2002). Despite their importance, such studies are scarce in Brazil and have mostly focused on the southeastern and southern regions of the country (Penhalber & Mantovani 1997; Grombone-Guaratini & Rodrigues 2002; Campos *et al.* 2009; Araujo *et al.* 2004). Studies combining analyses of litter production and seed rain are virtually nonexistent (Araujo 2002; Gondim 2005).

Quantifying litter production and seed rain can reveal important features of ecological processes and ecosystem sustainability throughout ecological succession (Brancalion *et al.* 2012). In that context, the objective of this study was to quantify litter production and seed rain in three fragments of semideciduous forest, each at a different successional stage.

Materials and Methods

Study area

All of the fragments studied were in the western part of the state of Paraná, Brazil (Fig. 1). We studied two forest fragments in the Santa Maria Biodiversity Corridor. The first was a 242-ha late successional fragment (LF) of native forest in the Santa Maria Farm's Private Nature Reserve (25°29'32.83"S; 54°21'41.38W). The second was a 26.7-ha early successional fragment (EF) of gallery forest along the Bonito River (25°27'29.36"S; 54°21'15.21"W). In addition, we studied a part of a reforested late successional fragment (RLF) in the Itaipu Reservoir Protected Area (25°40'10.33"S; 54°39'47.55"W), that was established in 1979 and comprises approximately 58,000 ha.

According to the Köppen classification system, the climate of the region is type Cfa (subtropical humid mesothermal), with a mean annual temperature of 21°C. Mean temperatures are above 22°C in summer and below 18°C in winter. The rainfall is usually well distributed throughout the year, with a slight reduction during the winter, and the mean annual precipitation is approximately 1800 mm (IAPAR 2012).

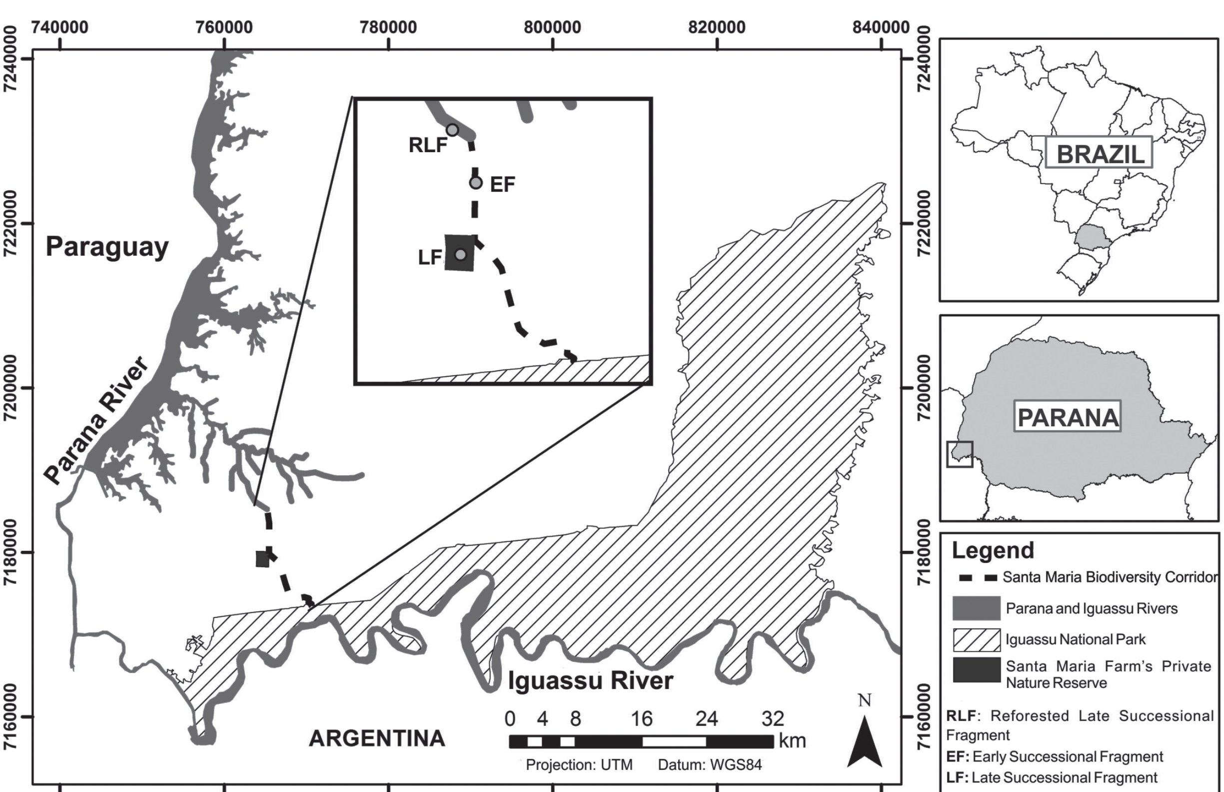

Figure 1. Map showing the three fragments of semideciduous forest studied in the western part of the state of Paraná, Brazil.
Source: ArcGIS 10 (ESRI 2010).

All three fragments are located on the third Paraná plateau in the Paraná River Basin (Maack 2012), composed of dikes of basic rock originating from the basaltic magmatism phase of the Mesozoic (MINEROPAR 2008). The predominant soils in the region are Oxisols and Ultisols. The vegetation type is semideciduous forest (SDF), in which 20-50% of the species are deciduous (IBGE 2012).

Litter production

In each fragment, we established three permanent plots (20 × 20 m). In each plot, we randomly distributed four 0.5 × 0.5 m litter traps with nylon mesh (1 mm^2), corresponding to 12 litter traps per fragment. Traps were installed in May 2011. Litter was collected monthly from June 2011 to May 2012 and taken to the laboratory, where it was dried in an oven for 48 h at 70°C. Subsequently, each sample was sorted into the following categories: leaves; branches; reproductive structures (flowers, fruits, and diaspores); and miscellaneous (animal remains, feces, etc.) Litter was weighed, by category, on a precision balance, and the values were converted to $kg.ha^{-1}.day^{-1}$.

Seed rain

We analyzed seed rain using the reproductive structures in the litter. Fruits and diaspores were identified with the aid of taxonomic literature, exsiccata, and seed collections at the herbarium of Western Paraná State University and in the Herbarium of the Municipal Botanical Museum, in Curitiba, Brazil (code, MBM). Plant family identification followed the Angiosperm Phylogeny Group III guidelines (APG III 2009), and species author names were checked against the List of Species in the Flora of Brazil (Forzza *et al.* 2013).

We estimated seed counts for each species using the average number of seeds per fruit. Those averages were derived from the literature (Lorenzi 2002; Carvalho 2006) and from fruits sampled to count the seeds. Values were then adjusted to obtain average numbers of $diaspores.day^{-1}$. Diaspores were classified according to dispersal syndrome (van der Pijl 1982): anemochory, autochory, or zoochory. The frequency of occurrence of each dispersal syndrome was also calculated for each fragment. After identification, species were classified according to growth form: trees (including shrubs), herbs, or lianas. Species were also classified according to successional category (Budowski 1965): pioneer, early secondary, late secondary, or climax.

Data analyses

To evaluate the total litter and seed rain production in each fragment, a chi-square goodness-of-fit test was used. To perform a temporal assessment of monthly litter production, we used repeated measures ANOVA. We used two-way ANOVA to compare the litter production of the respective fragments in each grouping. When significance was detected in these analyses ($p<0.05$), Tukey's test was performed. Analyses were performed with Statistica software, version 7.0 (Statsoft, Tulsa, OK, USA).

For the diaspore data of the seed rain, we calculated the absolute density and relative density of each species in each fragment. The Shannon-Wiener diversity index (H') and Pielou's evenness index (J') were calculated, and diversity values were compared among the three fragments with a t-test (Zar 1999). These analyses were performed using Past software, version 2.12 (Hammer *et al.* 2001). The frequencies of species and diaspores in different growth forms were compared among the three fragments by the chi-square goodness-of-fit test.

To test for associations between growth form and successional categories among the three fragments, the number of diaspores was evaluated by multivariate discriminant analysis for each of the classifications, and the vector significances analyzed by the Wilks' Lambda method using XLSTAT 2012 software, version 1.01 (Addinsoft 2012). The axes were defined as latent variables statistics, established according to the correlations of the explanatory variables in each fragment.

Results and discussion

Litter production

The highest annual litter production occurred in the LF, where 11,560 $kg.ha^{-1}$ were collected, followed by the RLF, with 9330 $kg.ha^{-1}$, and the EF, with 7838 $kg.ha^{-1}$ (χ^2=732,8; $p<0.05$). The finding that annual litter production was highest in the LF corroborates those of other studies of late successional SDFs (Vital *et al.* 2004; Pezzatto & Wisniewski 2006). The lower density and basal area of species in the EF (Gris 2011) is related to the lower annual litter production in early successional forest (Pinto *et al.*, 2009). The annual litter production of the RLF evaluated in the present study was higher than that reported in studies conducted in other reforested areas of SDFs in southern Brazil, including the 5341 $kg.ha^{-1}$ reported by Pimenta *et al.* (2011) and the 6636 $kg.ha^{-1}$ reported by Moreira & Silva (2004). That difference might be due to the fact that, in the RLF studied here, the proportions of deciduous or semideciduous species and exotic species are higher than expected for a typical SDF (Gris 2011; IBGE 2012). In addition, the high abundance of the semideciduous exotic species *Psidium guajava* L. might have contributed to the larger litter production in the RLF. However, that same factor could slow restoration processes. One of several useful methods to connect natural forest blocks is the re-establishment of habitat strips, which seems to be more effective when native trees are used (Sayer *et al.* 2004). Native trees are more likely to support local fauna and ecological processes, as well as to improve ecosystem structure and functioning, than are exotic species.

The proportional distribution of litter by category was similar among the fragments studied (F=26.4; p>0.05). Leaves predominated, followed by branches, reproductive structures, and miscellaneous litter (Tab. 1). According to Pagano & Durigan (2009), leaves represent the main component of the litter and determine the total production. Werneck et al. (2001) and Pezzatto & Wisniewski (2006) also stated that leaves tend to comprise the highest percentage of litter in early successional forests. This is attributable to the rapid growth and leaf renewal of pioneer species (Martins & Rodrigues 1999), which are fairly representative in such forests (Gris 2011).

In the LF, the months with the highest litter production were August (53.36 $kg.ha^{-1}.day^{-1}$) and September (56.76 $kg.ha^{-1}.day^{-1}$). As shown in Fig. 2A, mean monthly litter production was significantly higher in September than in June, December, January, April, and May (F=3.11; p<0.05). Similar results were obtained by Vital et al. (2004) and Pimenta et al. (2011). August and September were also the months with the highest leaf production (33.49 $kg.ha^{-1}.day^{-1}$ and 37.4 $kg.ha^{-1}.day^{-1}$, respectively (Fig. 2B). The September mean was significantly higher than those of June, December, January, April, and May (F=2.82; p<0.05). The increased litter production close to September is typical of an SDF, because the reduced photoperiod, temperature, and rainfall in the austral winter months result in increased leaf fall (Pagano & Durigan 2009; IBGE 2012).

As can be seen in Fig. 2A, the EF showed non-significant variation in litter production throughout the year (F=3.11; p>0.05). Litter production in the leaf category varied over the months (F=2.82; p<0.05), being significantly higher in July than in December and May (Fig. 2C). According to Gris (2011), 64% of the tree species in this forest fragment are pioneers, which undergo constant leaf loss throughout the year (Budowski 1965).

In the RLF, litter production peaked in November (61.59 $kg.ha^{-1}.day^{-1}$; F=3.11; p<0.05), due to increased leaf and branch production (Fig. 2A, D). The high leaf production from August to November resulted in high litter production (Fig. 2D). The duration of the leaf fall was longer in the RLF than in the two other fragments studied, a finding that is probably due to the higher proportional richness of deciduous and semideciduous species. These results contrast with those presented for late successional SDFs by Vital et al. (2004), Pimenta et al. (2011), and Pagano & Durigan (2009), suggesting that the RLF was not typical of an SDF.

Seed rain

The total seed rain sampled in the three fragments studied was 14,091 diaspores. These were sorted to 75 morphospecies, of which we identified 56 to the species level, 10 to the genus level, and five to the family level. Four morphospecies remained undetermined (Tab. 2).

Species richness was highest (49 species) in the LF, where diversity was significantly higher than in the other fragments (H'_{LF}=2.69 vs. H'_{EF}=1.61 and H'_{RLF}=1.17; p<0.05). Evenness was also highest in the LF (J'_{LF}=0.70 vs. J'_{EF}=0.44 and J'_{RLF}=0.33). However, the total number of diaspores collected was lower in the LF than in the EF and RLF (2173 vs. 4751 and 7167), as was the absolute density (7,243,333vs. 15,836,667 and 23,890,000 $diaspores.ha^{-1}$).

In the EF, 4751 diaspores of 38 species were collected. Nearly 87% of the diaspores collected belonged to pioneer species, which is consistent with the smaller size and the isolation patterns of the EF (Tab. 2). In addition, the seed rain in the EF was dominated by a few pioneer species (especially *Cecropia pachystachya* Trécul), as previously noted by Pivello *et al.* (2006).

The total number of diaspores collected was highest in the RLF (n = 7167), which also exhibited the greatest absolute density (2389 $diaspores.day^{-1}$) and the lowest species richness (33 species). The high abundance of diaspores belonging to a small number of species is characteristic of reforested areas, particularly those planted with pioneer tree species, as observed by Martins *et al.* (2012). In the RLF, pioneer species accounted for 97% of the diaspores, the species *Casearia sylvestris* Sw. and *Helietta apiculata* Benth. alone accounting for 84.34% (Tab. 2).

Diaspores of the exotic species *Leucaena leucocephala* (Lam.) de Wit and *Psidium guajava* (National Invasive Species Database for Brazil 2012) were also found in RLF. These species were used in the reforestation project in the Itaipu Reservoir Protected Area. That project, reportedly the largest in the world, used exotic species, which was common practice in the 1970s. However, the consequences

Table 1. Annual litter production in three semideciduous forest fragments in the western part of the state of Paraná, Brazil, by litter category.

Litter category	Fragment		
	LF	EF	RLF
Leaves ($kg.ha^{-1}$), mean (%)	6705 aA (58)	5880 aA (75)	6502 aA (69)
Branches ($kg.ha^{-1}$), mean (%)	3010 aB (26)	1410 aB (18)	2119 aB (23)
Reproductive structures ($kg.ha^{-1}$), mean (%)	1466 aBC (13)	432 aB (6)	613 aB (7)
Miscellaneous ($kg.ha^{-1}$), mean (%)	379 aC (3)	117 aB (1)	96 aB (1)

LF – late successional fragment; EF – early successional fragment; RLF – reforested late successional fragment.
Means followed by the same lower-case letters in the same row or by the same upper-case letters in the same column do not differ significantly (p<0.05) by Tukey's test.

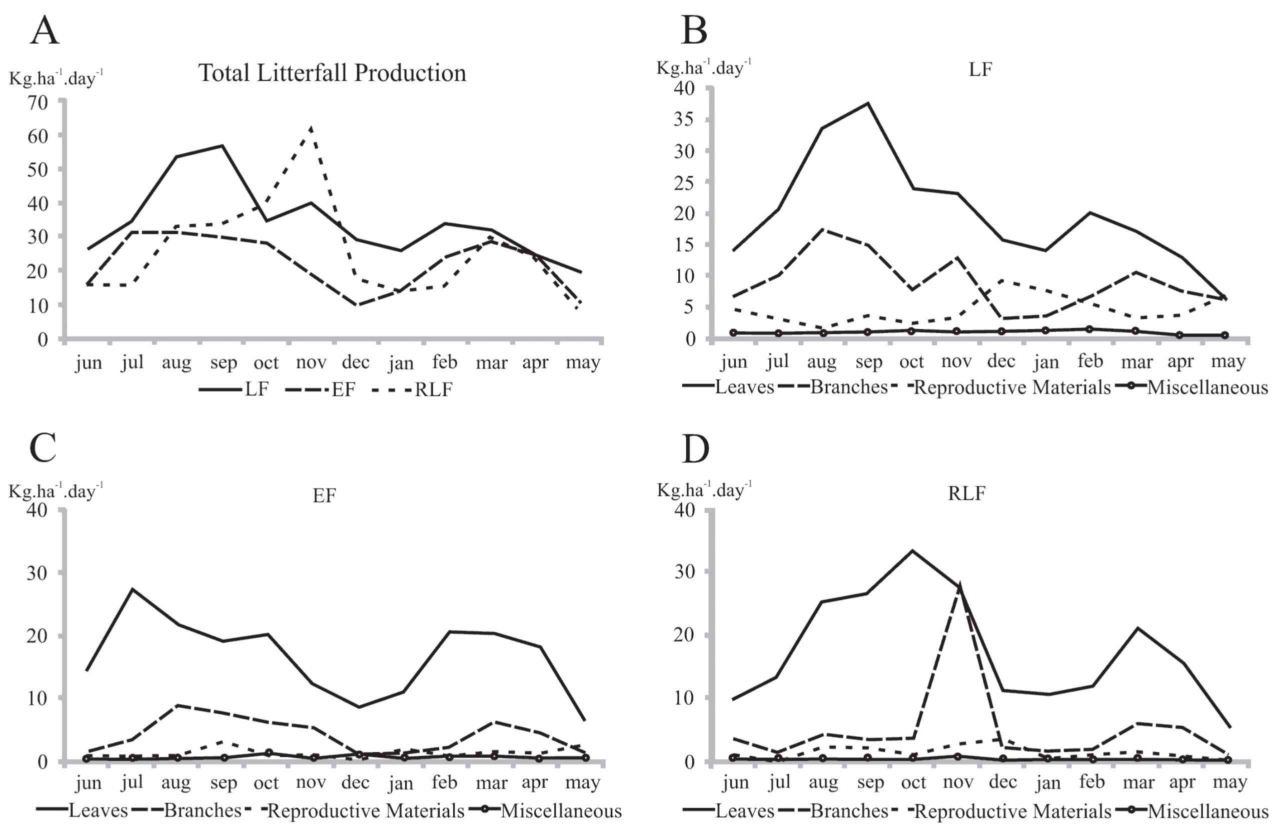

Figure 2. A) Total litter production (in kg.ha⁻¹.day⁻¹) in three semideciduous forest fragments in the western part of the state of Paraná, Brazil. B), C), and D) Litter production, by category, in the late successional fragment (LF); early successional fragment (EF), and reforested late successional fragment (RLF).

Table 2. Species in the seed rain of three semideciduous forest fragments in the western part of the state of Paraná, Brazil.

FAMILY	SPECIES	GF	SC	DS	Fragment					
					LF		EF		RLF	
					N	RD	N	RD	N	RD
Anacardiaceae	*Schinus terebinthifolius* Raddi	T	P	Zoo	0	0.00	145	3.05	4	0.06
Apocynaceae	*Condylocarpon isthmicum* (Vell.) A.DC.	L	-	Ane	8	0.37	3	0.06	0	0.00
	Forsteronia sp.	L	-	Ane	8	0.37	15	0.32	31	0.43
	Rauvolfia sellowii Müll.Arg.	T	P	Zoo	2	0.09	0	0.00	0	0.00
	Tabernaemontana catharinensis A. DC.	T	P	Zoo	0	0.00	1	0.02	1	0.01
Aquifoliaceae	*Ilex paraguariensis* A.St.-Hil.	T	C	Zoo	2	0.09	16	0.34	0	0.00
Araliaceae	*Dendropanax cuneatus* (DC.) Decne. & Planch.	T	ES	Zoo	22	1.01	45	0.95	0	0.00
	Schefflera calva (Cham.) Frodin & Fiaschi	T	C	Zoo	2	0.09	0	0.00	1	0.01
Arecaceae	*Euterpe edulis* Mart.	T	C	Zoo	80	3.68	1	0.02	0	0.00
	Syagrus romanzoffiana (Cham.) Glassman	T	C	Zoo	85	3.91	45	0.95	0	0.00
Asteraceae	*Mikania* sp.	L	-	Ane	120	5.52	434	9.13	7	0.10
Bignoniaceae	*Fridericia* sp.	L	-	Ane	18	0.83	161	3.39	7	0.10
	Handroanthus impetiginosus Mattos	T	C	Ane	1	0.05	7	0.15	0	0.00
	Handroanthus ochraceus (Cham.) Mattos	T	C	Ane	15	0.69	11	0.23	15	0.21
	Jacaranda micrantha Cham.	T	P	Ane	9	0.41	2	0.04	0	0.00
	Pyrostegia sp.	L	-	Ane	0	0.00	1	0.02	0	0.00

Continues

Table 2. Continuation.

FAMILY	SPECIES	GF	SC	DS	Fragment					
					LF		EF		RLF	
					N	RD	N	RD	N	RD
Boraginaceae	*Cordia americana* (L.) Gottschling & J.S.Mill.	T	P	Ane	1	0.05	0	0.00	13	0.18
	Cordia ecalyculata Vell.	T	P	Zoo	2	0.09	1	0.02	0	0.00
	Cordia trichotoma (Vell.) Arráb. ex Steud.	T	LS	Ane	122	5.61	217	4.57	10	0.14
Celastraceae	*Hippocratea volubilis* L.	L	-	Ane	5	0.23	1	0.02	0	0.00
Combretaceae	*Combretum fruticosum* (Loefl.) Stuntz	L	-	Ane	0	0.00	0	0.00	1	0.01
Euphorbiaceae	*Alchornea triplinervia* (Spreng.) Müll.Arg.	T	LS	Zoo	23	1.06	0	0.00	0	0.00
	Euphorbiaceae sp.	-	-	-	0	0.00	5	0.11	11	0.15
Fabaceae	*Albizia polycephala* (Benth.) Killip ex Record	T	P	Aut	1	0.05	0	0.00	7	0.10
	Dalbergia frutescens (Vell.) Britton	L	-	Ane	1	0.05	0	0.00	53	0.74
	Fabaceae sp.	-	-	-	3	0.14	0	0.00	0	0.00
	Inga marginata Willd.	T	ES	Zoo	16	0.74	0	0.00	3	0.04
	Leucaena leucocephala (Lam.) de Wit**	T	-	Aut	0	0.00	0	0.00	303	4.23
	Parapiptadenia rigida (Benth.) Brenan	T	ES	Aut	2	0.09	35	0.74	35	0.49
	Peltophorum dubium (Spreng.) Taub.	T	P	Ane	0	0.00	0	0.00	7	0.10
	Senegalia polyphylla (DC.) Britton & Rose	T	P	Aut	4	0.18	0	0.00	19	0.27
Lauraceae	Lauraceae sp	-	-	-	1	0.05	0	0.00	2	0.03
	Nectandra megapotamica (Spreng.) Mez	T	C	Zoo	6	0.28	3	0.06	0	0.00
	Ocotea diospyrifolia (Meisn.) Mez	T	P	Zoo	235	10.81	0	0.00	0	0.00
	Ocotea sp.	T	-	Zoo	0	0.00	0	0.00	3	0.04
Malvaceae	*Heliocarpus popayanensis* Kunth	T	P	Ane	24	1.10	0	0.00	0	0.00
	Luehea divaricata Mart.	T	ES	Ane	0	0.00	110	2.32	1	0.01
Malpighiaceae	*Heteropterys intermedia* (A.Juss.) Griseb.	L	-	Ane	0	0.00	32	0.67	0	0.00
Meliaceae	*Cedrela fissilis* Vell.	T	LS	Ane	42	1.93	0	0.00	0	0.00
	Guarea kunthiana A.Juss.	T	LS	Zoo	19	0.87	0	0.00	0	0.00
Moraceae	*Maclura tinctoria* (L.) D.Don ex Steud.	T	LS	Zoo	3	0.14	0	0.00	56	0.78
	Sorocea bonplandii (Baill.) W.C.Burger et al.	T	LS	Zoo	52	2.39	0	0.00	0	0.00
Myrsinaceae	*Myrsine umbellata* Mart.	T	ES	Zoo	2	0.09	0	0.00	0	0.00
Myrtaceae	*Eucalyptus* sp.**	T	-	Ane	0	0.00	2	0.04	0	0.00
	Psidium guajava L.*	T	-	Zoo	0	0.00	0	0.00	398	5.55
Nyctaginaceae	*Pisonia aculeata* L.	L	-	Zoo	87	4.00	0	0.00	0	0.00
Poaceae	*Andropogon* sp.	H	-	Ane	0	0.00	17	0.36	1	0.01
	Lasiacis ligulata Hitchc. & Chase	H	-	Ane	0	0.00	17	0.36	0	0.00
	Poaceae sp. 1	-	-	-	11	0.51	17	0.36	0	0.00
	Poaceae sp. 2	-	-	-	0	0.00	2	0.04	0	0.00
	Zea mays L.**	H	-	Zoo	0	0.00	1	0.02	0	0.00
Polygonaceae	*Ruprechtia laxiflora* Meisn.	T	LS	Ane	111	5.11	0	0.00	0	0.00
Rhamnaceae	*Gouania ulmifolia* Hook. & Arn.	L	-	Zoo	642	29.54	19	0.40	0	0.00
Rosaceae	*Prunus myrtifolia* (L.) Urb.	T	ES	Zoo	3	0.14	0	0.00	23	0.32
Rubiaceae	*Psychotria carthagenensis* Jacq.	T	LS	Zoo	0	0.00	2	0.04	10	0.14
Rutaceae	*Balfourodendron riedelianum* (Engl.) Engl.	T	LS	Ane	5	0.23	0	0.00	0	0.00
	Esenbeckia febrifuga (A.St.-Hil.) A. Juss. ex Mart.	T	ES	Aut	0	0.00	4	0.08	0	0.00
	Helietta apiculata Benth.	T	P	Ane	0	0.00	0	0.00	1097	15.31

Continues

Table 2. Continuation.

FAMILY	SPECIES	GF	SC	DS	Fragment LF N	LF RD	EF N	EF RD	RLF N	RLF RD
Salicaceae	*Casearia sylvestris* Sw.	T	P	Zoo	20	0.92	465	9.79	4948	69.04
Sapindaceae	*Cupania vernalis* Cambess.	T	ES	Zoo	0	0.0	1	0.02	2	0.03
	Diatenopteryx sorbifolia Radlk.	T	ES	Ane	0	0.00	20	0.42	62	0.87
	Matayba elaeagnoides Radlk.	T	P	Zoo	141	6.49	0	0.00	0	0.00
	Serjania sp.1	L	-	Ane	0	0.00	29	0.61	25	0.35
	Serjania sp.2	L	-	Ane	133	6.12	0	0.00	0	0.00
Sapotaceae	*Chrysophyllum gonocarpum* (Mart. & Eichler ex Miq.) Engl.	T	LS	Zoo	1	0.05	0	0.00	0	0.00
	Chrysophyllum marginatum (Hook. & Arn.) Radlk.	T	P	Zoo	1	0.05	0	0.00	0	0.00
Solanaceae	*Cestrum bracteatum* Link & Otto	T	P	Zoo	51	2.35	0	0.00	6	0.08
	Solanum granuloso-leprosum Dunal	T	P	Zoo	28	1.29	0	0.00	0	0.00
	Solanum sp.	T	-	Zoo	1	0.05	0	0.00	0	0.00
Styracaceae	*Styrax leprosus* Hook. & Arn.	T	P	Zoo	0	0.00	6	0.13	0	0.00
Urticaceae	*Cecropia pachystachya* Trécul	T	P	Zoo	0	0.00	2857	60.13	0	0.00
Undetermined 1	5 diaspores	-	-	-	0	0.00	0	0.00	5	0.07
Undetermined 2	1 diaspore	-	-	-	1	0.05	0	0.00	0	0.00
Undetermined 3	1 diaspore	-	-	-	1	0.05	0	0.00	0	0.00
Undetermined 4	1 diaspore	-	-	-	0	0.00	1	0.02	0	0.00

GF – growth form; T – tree; L – liana; H – herb; SC – successional category; P – pioneer; ES – early secondary; LS – late secondary; C – climax; DS – dispersal syndrome; Ane – anemochory; Aut – autochory; Zoo – zoochory; LF – late successional fragment; EF – early successional fragment; RLF – reforested late successional fragment; N – abundance; RD – relative density.
* Species exotic to the local flora.
** Species exotic to Brazil.

of reforestation with exotics remain unknown (Durigan & Engel 2012).

In the LF, the daily production of diaspores was highest in the months of September (27% of the total annual production), October (12%), and November (13%), as shown in Fig. 3. In SDFs, fruiting typically peaks between September and November (Penhalber & Mantovani 1997; Grombone-Guaratini & Rodrigues 2002; Araujo *et al.* 2004). In the areas studied, these months correspond to the end of the cold, dry winter season and to an increase in seed dispersal. In the EF, the daily production of diaspores was highest in the months of March (53% of the total annual production) and October (17%), *Cecropia pachystachya* accounting for 97% and 51% of the diaspores collected in March and April, respectively. *Cecropia pachystachya* is a pioneer species that fruits in March and April, producing thousands of diaspores (Carvalho 2006), which explains its dominance in the seed rain. When data on *C. pachystachya* were excluded, the daily production of diaspores in the EF was highest in September, October, and November, as is typical in SDFs (Penhalber & Mantovani 1997; Grombone-Guaratini & Rodrigues 2002; Araujo *et al.* 2004).

In the RLF, the daily production of diaspores was highest in the months of October (41% of the total annual production), November (19%) and March (8%), and showed atypical fruiting dynamics in comparison with the other SDF fragments studied (Fig. 3), due to the presence of pioneer, deciduous, and semideciduous species in proportions different from those normally found in SDFs, as well as to the introduction of exotic species (Gris 2011). This use of exotics hinders the restoration of natural ecological processes (Rodrigues & Gandolfi 2009). In addition, the prevalence of *Casearia sylvestris* diaspores in October (98%) and November (95%), together with that of those of *Helietta apiculata* in March (80%), resulted in fruiting peaks different from those observed in the other fragments analyzed in the present study and in other studies of SDFs (Penhalber & Mantovani 1997; Grombone-Guaratini & Rodrigues 2002; Araujo *et al.* 2004).

Of the species identified in the LF, 57% were zoochorous, 36% were anemochorous, and 7% were autochorous, proportions similar to those reported in other studies of late successional SDFs (Carmo & Morellato 2009; Penhalber & Mantovani 1997). Zoochorous species contribute to plant-frugivore interactions, which provides stability in the ecosystem and allows for diaspore dispersal (Silva 2008). This pattern was reversed in EF and RLF. In the EF, 50% of the species were anemochorous, 44% were zoochorous,

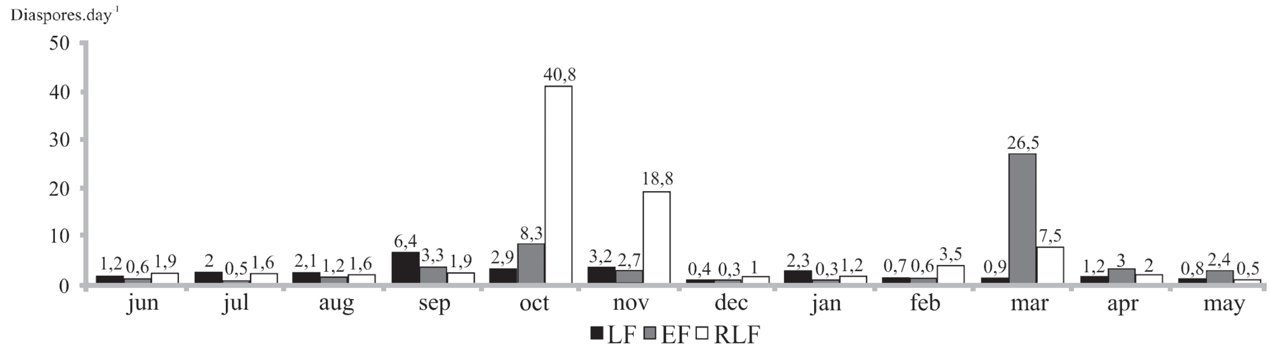

Figure 3. Mean daily diaspore collection (in diaspores.day^{-1}) between June 2011 and May 2012 in three semideciduous forest fragments in the western part of the state of Paraná, Brazil: late successional fragment (LF); early successional fragment (EF), and reforested late successional fragment (RLF).

and 6% were autochorous. In the RLF, nearly 47% of species were anemochorous, 40% were zoochorous, and 13% were autochorous. According to Howe & Smallwood (1982), a higher incidence of anemochory is characteristic of forest without a continuous canopy, as was the case in our fragments (data not shown). These results seem to indicate a lower availability of resources for frugivores. Garcia *et al.* (2014) recommend the inclusion of zoochorous "keystone" species to increase the availability of resources for frugivores and accelerate the restoration process, especially in the early stages of succession.

The proportional contribution of trees to the species composition was similar among the fragments (LF=80%, EF=65%; RLF=77%; χ^2=2.34; *p*>0.05), as was that of lianas (LF=20%, EF=26%; RLF=20%; χ^2=4.20; *p*>0.05). Herbaceous species occurred only in the EF (9%) and RLF (3%). Nevertheless, the proportional contribution of each growth form to the total diaspore sample differed among the LF, EF, and RLF, trees accounting for 53%, 84%, and 98%, respectively and lianas accounting for 47%, 15%, and 2%, respectively; whereas herbs accounted for 1% in the EF.

In the LF, we observed asynchrony between the diaspore frequencies of trees and lianas, the frequency of the latter being highest from July to October, whereas that of the former was highest in the other months (Fig. 4A). In the EF, we also observed such asynchrony, although it was to a lesser degree (Fig. 4B). In the RLF, we detected no such asynchrony; in most months, tree species diaspores accounted for more than 90% of the sample (Fig. 4C). Engel *et al.* (1998) argued that asynchrony is characteristic of late successional SDFs, and that lianas are responsible for the high availability of fleshy fruits in austral winter.

With regards to the diaspores of trees, lianas, and herbs, the centroids obtained by discriminant analysis differed significantly among the fragments (F=2.48; *p*=0.033). The eigenvalue of the first axis was 0.31, explaining 64.19% of the variation. The first axis was defined as "vegetation size", in which negative scores refer to trees and positive scores refer to herbaceous species. The second axis had an eigenvalue of 0.17, explaining 35.80% of the variation, and was defined as "vegetation growth form". Tree and herbaceous species were represented by positive scores and lianas were represented by negative scores (Fig. 5A and 5B).

The discriminant analysis revealed that the three fragments differed in diaspore abundance of the various growth forms (Fig. 5A and 5B). Tree diaspores were dominant in the RLF, whereas diaspores of herbaceous and liana species were dominant in the EF. This is associated with the fact that the smaller size and greater openness of the EF creates an intense edge effect (Primack & Rodrigues, 2001; Fahrig 2003). In the LF, tree diaspores dominated, followed by those of lianas, which is characteristic of late successional SDFs (Fig. 4A). These two growth forms are important contributors to the maintenance of biodiversity and ecological processes, especially when asynchronous diaspore production is detected (Engel *et al.* 1998).

Among the tree species identified in the LF, we found that the successional stage was early primary (pioneer) in 38%, early secondary in 18%, late secondary in 24%, and climax in 21%, compared with 33%, 29%, 10%, and 29%, respectively, in the EF and 45%, 35%, 10%, and 10%, respectively, in the RLF. In terms of the proportional contribution of each successional stage to the total diaspore sample, pioneer, early secondary, late secondary, and climax species respectively accounted for 46%, 4%, 33%, and 17% in the LF, whereas pioneer species accounted for 87% and 97% of the diaspores in the EF and RLF, respectively. The centroids obtained by the discriminant analysis revealed a statistical difference among the successional stages of the tree species (F=3.66; *p*=0.002). The eigenvalue of the first axis was 1.05, explaining 92.77% of the variance. The first axis was defined as "successional stage", in which negative scores represented early successional forest and positive scores represented late successional forest. The eigenvalue of the second axis was 0.08, explaining 7.23% of the remaining variance. The second axis was defined as "successional categories"; positive scores representing early secondary, late secondary, and climax species, whereas negative scores represented pioneer species (Fig. 6A and 6B).

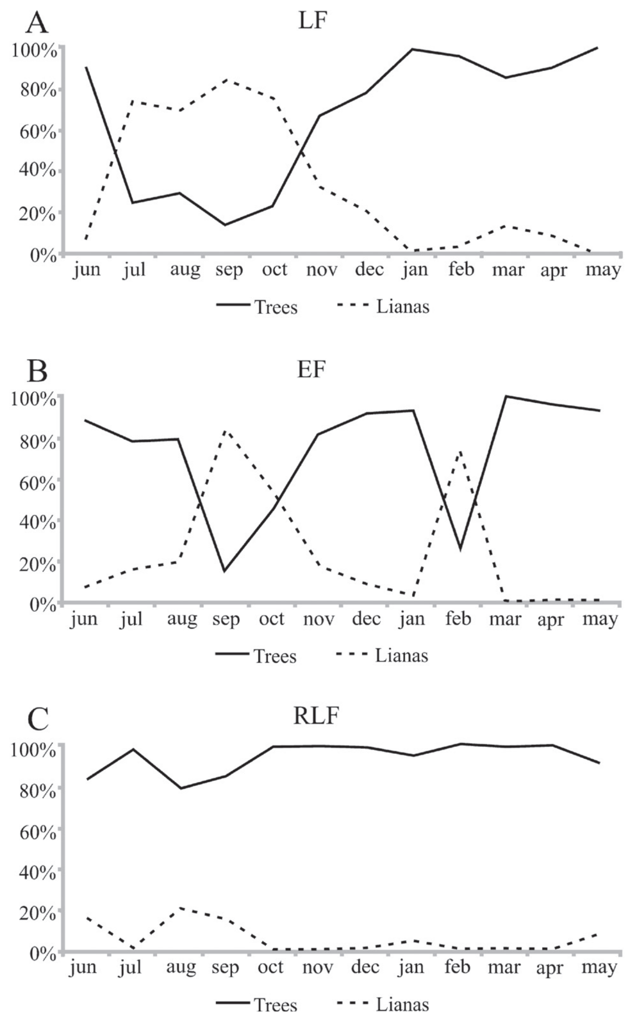

Figure 4. Frequencies of tree and liana seeds collected from June 2011 to May 2012 in three semideciduous forest fragments in the western part of the state of Paraná, Brazil: A) late successional fragment (LF); B) early successional fragment (EF); and C) reforested late successional fragment (RLF).

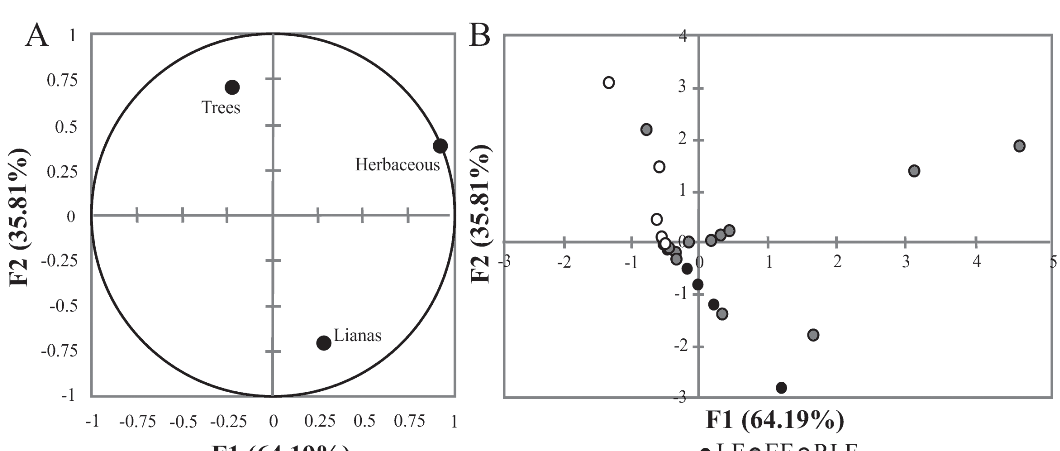

Figure 5. Ordination diagrams of discriminant analysis for growth form in three semideciduous forest fragments in the western part of the state of Paraná, Brazil: late successional fragment (LF); early successional fragment (EF), and reforested late successional fragment (RLF). A) Growth forms distributed on axis for data explanation. B) Distributions of growth forms in the fragments.
First axis: vegetation size. Second axis: vegetation growth form.

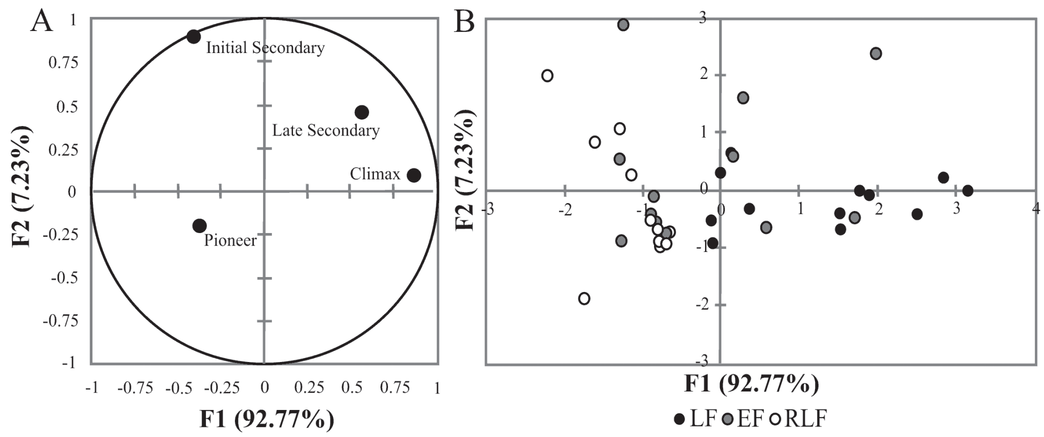

Figure 6. Ordination diagrams of discriminant analysis for successional categories in three semideciduous forest fragments in the western part of the state of Paraná, Brazil: late successional fragment (LF); early successional fragment (EF), and reforested late successional fragment (RLF). A) Successional categories distributed on axis for data explanation. B) Distributions of successional categories in the fragments.
First axis: successional stages. Second axis: successional categories.

We observed that, in the LF, diaspores were produced mainly by late secondary and climax species, whereas, in the EF and RLF, they were produced mainly by pioneer and early secondary species (Fig. 6A and 6B). According to a floristic and phytosociological study of these same fragments, conducted by Gris (2011), the predominant sources of diaspores were late secondary and climax species (accounting for 35% and 42%, respectively) in the LF; pioneer and early secondary species (accounting for 64% and 29%, respectively) in the EF; and pioneers and early secondary species (accounting for 66% and 29%, respectively) in the RLF. Pioneer species tend to reproduce quickly, producing a large number of diaspores (Budowski 1965; Martins *et al.* 2012).

Conclusions

The three study areas have different characteristics in terms of litter production and seed rain, the LF showing characteristics of late successional SDF and the EF showing characteristics of early successional SDF. The restored forest was not a typical SDF, probably because of the species planted in the area and their ecological characteristics. Analyses of litter production and seed rain are important for characterizing the stages of ecological succession and, as such, complement floristic and phytosociological studies. Together, these analyses help describe the dynamics of plant assemblages in SDF fragments, because they provide information on successional stages, dispersal syndromes, patterns of asynchrony, deciduousness, reproduction periods, and availability of resources for frugivores and pollinators. Such information can also reveal important features of regeneration potential, ecological processes, ecological succession and ecosystem sustainability, which are essential for biodiversity conservation and management of fragmented areas.

Acknowledgments

We would like to thank the Fazenda Santa Maria for allowing us access to the site. We are also grateful to the staff of the Municipal Botanical Museum of Curitiba, as well as to the other botanists who aided in the identification of the diaspores. This study received financial support from the *Programa Parque Tecnológico Itaipu Ciência e Tecnologia* (PTI C&T, Itaipu Technology Park Science and Technology Program; master's scholarship to MAGT) and from the Western Paraná State University *Centro de Ciências Biológicas e da Saúde* (CCBS, Center for Biological and Health Sciences).

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