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Effects of distinct types of disturbance on seed rain in the Atlantic forest of NE Brazil

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Abstract In disturbed sites, some groups of seeds might be excluded from the seed rain due to their dispersal modes or seed size, and some groups might be successful as a result of disturbance effects. In the present study, we examined the seed rain in natural treefall gaps and in an area of regenerating forest following an accidental burning, which occurred 4 years before this study. Both of these disturbed areas were compared with nearby forest understorey. The number of seeds, number of species, and proportion of wind-dispersed seeds were compared between these disturbed and undisturbed areas. The treefall gaps have received lower numbers of seeds and species than the nearby understorey, but the number of wind-dispersed seeds did not differ between these areas. The lowest seed number observed in treefall gaps can be attributed to a lower number of animal-dispersed seeds, suggesting that animals may be avoiding treefall gap areas. A higher number of seeds and a lower number of species were observed in the burned area when compared to the adjacent understorey. The high number of small-sized seeds and of wind-dispersed seeds in the burned area was almost surely a consequence of the local production of the pioneer plants established after the burning. In this study, substantial differences were observed in the characteristics of the seed rain at disturbed sites, when compared with undisturbed understorey. However, these two distinct types of disturbance showed quite differing patterns, as treefall gaps received lower number of seeds while the burned area received a higher number of seeds, with a greater proportion of wind-dispersed seeds. The exception was for species richness, which was quite low at both these disturbed sites.

Keywords Fire · *Miconia mirabilis* · Natural treefall gaps · Seed size · Understorey · Wind-dispersed seeds

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Introduction

Tropical forests are subject to natural disturbances that vary in intensity, frequency, and area affected (Connell 1978). These disturbances produce distinct effects on the principal sources of forest regeneration—the seed rain, the seed bank, the growth of individuals present before the disturbance (advanced regeneration), as well as the resprouting of stems and roots—thus strongly influencing the species composition of these communities (Uhl et al. 1988; Schupp et al. 1989). With the exception of plants that reproduce vegetatively, these regeneration sources are all dependent on the arrival of seeds (over short, medium, or long-term periods), thus underlining the importance of evaluating the characteristics of the seed rain in tropical forests. Nonetheless, research addressing community-wide seed rain patterns in tropical forest is rare (Hardesty and Parker 2002)

A majority of the studies on seed rain have been undertaken in two contrasting situations: either within the undisturbed understorey of a tropical forest (Jackson 1981; Foster 1982; Martinez-Ramos and Soto-Castro 1993; Penhalber and Mantovani 1997; Harms et al. 2000; Grombone-Guaratini and Rodrigues 2002) or in abandoned pastures (Young et al. 1987; Holl 1999; Cubiña and Aide 2001; Holl 2002). However, in order to better understand the role of the seed rain in relation to the dynamics of tropical forests following disturbance, it is also important to analyse the characteristics of the seed rain in intermediate situations of natural and/or anthropogenic disturbances, like treefall gaps and burned areas without the previous cut of vegetation. This analysis will enable us to determine if some groups of seeds are being excluded from disturbed areas due to their dispersal modes, seed size, or species composition, and if some groups are more successful as a result of disturbance effects. Changes in the composition and abundance of seeds in the seed rain will have strong effects on the future vegetation community and on future seed bank composition (Young et al. 1987; Walker and Neris 1993). After a strong disturbance like landslides or anthropogenic activities of slash and burn, the seed bank may become depleted, either by massive germination of the seeds, or by the loss of a large number of seeds (as by burning) (Whitmore 1983; Hopkins and Graham 1984; Saulei and Swaine 1988; Garwood 1989; Miller 1999). Seed bank renewal will depend on the seed rain.

Hypotheses concerning expected changes in seed rain characteristics in intermediate natural disturbances, such as natural treefall gaps, have been proposed and need to be tested. Two major topics are concerned to dispersal mode and to seed size. In relation to dispersal mode, it has been suggested that some frugivorous birds concentrate their activities in treefall gaps and that seeds dispersed by these birds would be disproportionately deposited there (Levey 1988; Schupp et al. 1989; Wenny and Levey 1998). On the other hand, wind-dispersed seeds may be deposited in larger numbers in treefall gaps than in the forest understorey. Schupp et al. (1989) has suggested that air flow at the boundary between the understorey and open areas, together with the morphological structure of wind-dispersed seeds, may facilitate their dispersal into gaps. Studies on these topics (Augspurger and Franson 1988; Loiselle et al. 1996) have not, however, been conclusive. In relation to seed size, smaller numbers of large, non wind-dispersed seeds would be expected in treefall gaps. Large vertebrates may avoid new gaps (Forget and Sabatier 1997), and as these animals are dispersal agents for large animal-dispersed seeds, gaps might be expected to receive relatively fewer of these seeds (Schupp et al. 1989). However, as pointed by Wenny (2001), seed rain into different patches in the forest is still poorly understood at the community level.

The effects of anthropogenic fire disturbances on the characteristics of the seed rain have been investigated on sites subjected to slash and burn agriculture (Carriere et al. 2002) or pasture (Holl 1999; Holl et al. 2000). A drastic reduction in the number of seeds in the seed rain was observed at burned sites due to greater resulting distances to seed sources and the reduced presence of disperser animals (Holl et al. 2000). At sites where burning was not preceded by the clearing of the vegetation or by agricultural use (for example, mature forests burned by accidental fires), some differences in the characteristics of the seed rain could be expected. At these sites, some trees remain alive after the fire and by acting as perches (Willson and Crome 1989; Woods 1989; Holl 2002) they would favour the arrival and permanence of disperser animals bringing diaspores from neighbouring areas. Generally, accidental fires do not affect all forest area, and the remaining forest can function as a seed source. Additionally, as a result of the increased availability of light and nutrients (Vinha et al. 1983; Uhl and Jordan 1984; Canham and Marks, 1985) after burning, established pioneer species could produce large numbers of seeds and attract a greater number of disperser (Levey 1988; Clark et al. 2004). Pioneer species demonstrate a frequent (or even continuous) production of large quantities of small seeds (Foster and Janson 1985) that are dispersed by the wind or by small animals (Whitmore 1983). Therefore, it would be expected larger numbers of small seeds in a forest burned by accidental fires.

In order to describe the characteristics of the seed rain, and to test some of the hypotheses that have been put forward concerning the nature of seed dispersal in environments that have experienced different degrees of disturbance, we examined the seed rain in an area of regenerating forest following accidental burning (without previous vegetation clearing) and in natural treefall gaps in an old-growth forest. Both of these disturbed areas were compared with nearby undisturbed forest understorey. This represents the first study in Brazil (and apparently in the Neotropics) of the seed rain in areas affected by accidental fires. Specifically, we sought to answer the following questions, according to the hypotheses presented above: Are there differences in the number of seeds and in the number of species arriving in the seed rain between disturbed and undisturbed areas? Are these differences due to preferential dispersal of seeds from a specific size class or from a specific dispersal mode (i.e. wind-dispersed seeds)? Additionally, we discuss the arrival pattern of the most abundant species in the seed rain based on the available information about the vegetation in each area.

Methods

Study area

This study was undertaken in the Una Biological Reserve, located in the municipality of Una, Bahia, Brazil (15°10′ S and 39°03′ W). The Reserve is situated within the Brazilian Atlantic Forest domain, one of the ten most endangered biomes of the world (Mittermeier et al. 1999; Myers et al. 2000). Although forest fragmentation process is strongly increasing in this region, studies about regeneration sources are scarce. The Una Biological Reserve occupies approximately 7,022 ha, and 78% of its area is considered well-conserved forest (Marques et al. 2002). The remaining areas were recently disturbed or are undergoing regeneration. The climate is classified as type Af in the system of Köppen, and is characterized by the absence of a definite dry period and a yearly total rainfall greater than 1,300 mm (Mori et al. 1983). Vegetation is classified as tropical moist forest following Holdridge life zones (Hartshorn 1991).

The western portion of Reserve in which this study was undertaken is dominated by a tall and very humid forest. The canopy is composed of 25–30 m trees, with occasional emergent trees reaching up to 40 m (Amorim et al. unpublished data). Representative tree families include Myrtaceae, Sapotaceae, Fabaceae, and Chrysobalanaceae. In the understorey, common plants are palms (genera *Bactris* and *Genoma*), herbaceous species of the families Maranthaceae and Rubiaceae, and ferns. There is also a very rich epiphytic flora (Amorim et al. unpublished data).

Sampling areas

A total of 24 sampling areas were divided equally among four areas: Natural treefall gaps (G); Understorey adjacent to the treefall gaps (UG); Burned forest (B), and the understorey of a forest near the burned area (UB).

All natural forest gaps were mapped and measured by the method proposed by Runkle (1982) within a 3.5 ha. (Area 1, Fig. 1a, b) of old-growth forest within the Una Biological Reserve. Six of the largest and most recent

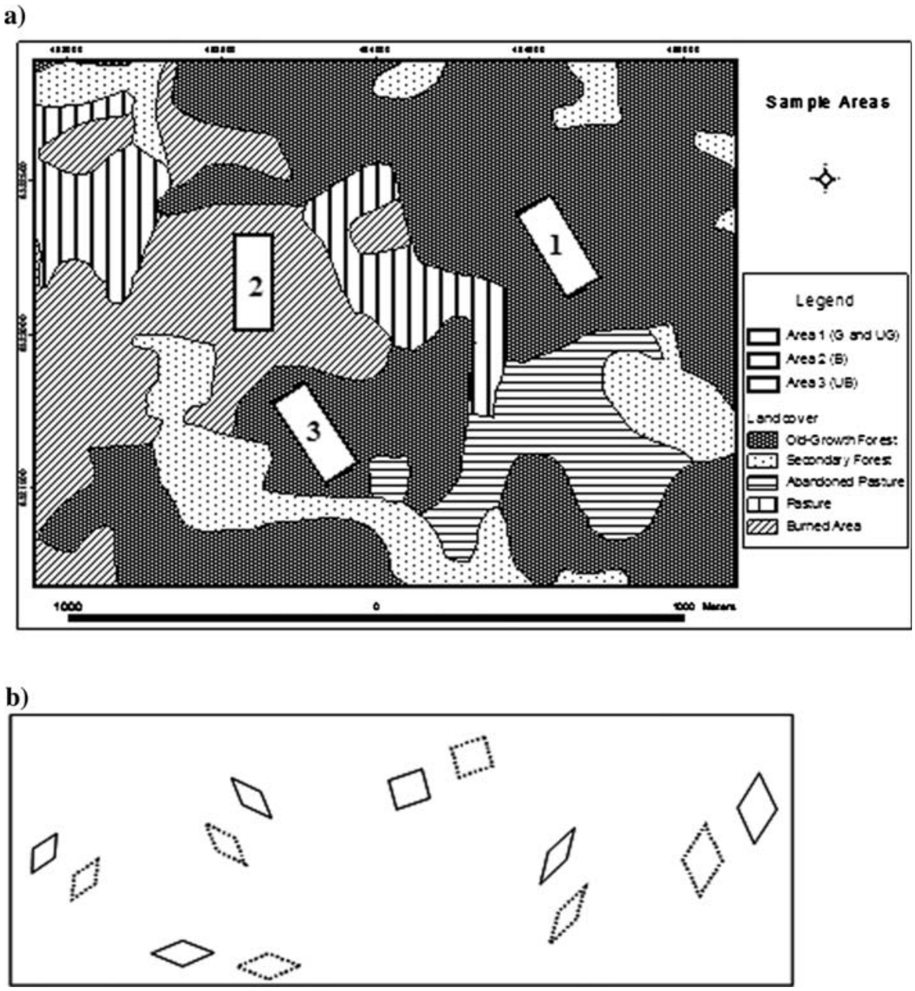

Fig. 1 Sample areas within Una Biological Reserve. (**a**) Land cover in the study site (Marques et al. 2002) and the location of sample areas: Area 1—Treefall gaps (G) and understorey near gaps (UG) plots; Area 2—Burned area (B) plots; Area 3—Understorey near burned area (UB) plots. (**b**) Schematic distribution of plots within the areas. Continuous figures indicate treefall gaps (G) plots in Area 1, burned (B) plots in Area 2, and understorey near burned area (UB) plots in Area 3. Dashed figures indicate understorey near gaps (UG) plots in Area 1

(estimated age between 1 and 4 years old) gaps were chosen for study. The areas of these six treefall gaps (G) varied from 65.4 to 260.9 m^2. The linear distances between treefall gaps varied from 25 to 300 m.

Adjacent to each gap, a sampling plot of same shape and size was established (total of six) in the forest understorey (UG), with the borders of these plots at a minimum distance equivalent to the larger diameter of that respective gap (Area 1, Fig. 1a,b). The minimum distance between understorey and gap plots was ca. 25 m, and the maximum was 50 m.

Six sampling plots were also established within the area of forest burned (B) during an accidental fire in February 1995, *i.e.* 4 years before this study (Area 2; Fig. 1a). The fire was of medium intensity, which allowed some canopy trees to survive, although the understorey vegetation was completely eliminated. The vegetation was 3–4 m tall at the start of the study, with some pioneers trees (predominately *Miconia mirabilis* (Aubl.) L. O. Williams [Melastomataceae], *Cecropia pachystachya* Trécul [Cecropiaceae], and *Henriettea succosa* (Aubl.) DC. [Melastomataceae]) already at a reproductive stage (pers. obs.). This burned area was located approximately 1 km from Area 1 (Fig. 1a). This intervening 1 km between Area 1 and the burned area is a mosaic of sucessional patches, composed of abandoned pastures, late sucessional forest fragments, and riparian forests not burned in the accidental fire.

Additionally, six other sampling plots were established in the forest understorey (UB) of an old-growth forest located approximately 200 m from the burned area (Area 3, Fig. 1a).

In order to minimize the influence of plot size and the spatial configuration of the samples, the plots in the burned area and in the forest understorey near the burned area were laid out (Fig. 1b) with the same spatial pattern and the same sizes and shapes as the six gaps of Area 1.

Seed data collection

Six seed traps of 0.25 m^2 (50 × 50 cm, and 10 cm above the ground) were randomly located within each of six sampling plots in each area, for a total of 144 traps in all four areas studied. Material was collected monthly from the traps (between January and December, 1999), and subsequently dried and handled in the laboratory. All diaspores > 1 mm were classified, counted, measured, and then stored in alcohol. Only mature diaspores that did not break when squeezed were considered. Diaspores demonstrating signs of predation, or those that were soft or empty were not considered.

Seeds were identified with the aid of field collections as well as by comparison with specimens stored at the CEPEC herbarium, according to the classification system elaborated by Cronquist (1981), with modifications by APG (1998). Nonetheless, part of the material could not be fully classified due to the small amount of herbarium specimens from the region with mature fruits. These seeds were separated into morphospecies. Seeds not identified, but showing small morphological variations, were considered to be of only one morphospecies. This generates a conservative estimate of the number of species actually present. Thus, the term ''species'' as utilized here refers to all fully identified species, as well as the morphospecies.

Material collected in the burned area (B) and in the forest near the burned area (UB) during October was lost due to an accidental fire in the drying oven.

Data analysis

Data from the six seed traps in each sample plot were grouped together for all analyses involving number of seeds and number of species.

Permutation tests (Manly 1997) were used to compare each disturbed area and the adjacent understorey (*i.e.* G vs. UG, and B vs. UB). This method was preferred to *t*-test or non-parametric tests due to the small number of samples, and also because part of the data was not normally distributed. The variables tested were: (i) the mean number of seeds; (ii) the mean number of species; (iii) the mean number of wind-dispersed seeds; (iv) the mean number of species with wind-dispersed seeds. The observed mean differences were compared with the distribution found by randomly reallocating plots to areas. The significances of the observed differences were estimated as the proportion of the random datasets that had a mean difference equal or greater than the observed value. As in conventional *t*-test, this permutation procedure tests the null hypothesis that all plot are samples of the same population (Manly 1997).

For each permutation test, 1,000 datasets were generated by random shuffling with the Resampling Stats software (2001). Treefall gaps (G) and the adjacent understorey (UG) were sampled in a paired design (see above), and in this case, plots were shuffled only within pairs.

For non wind-dispersed species, seeds were classified into three size-classes according to the length of their major seed axis: Small = 1.0–5.0 mm long; Medium = 5.0–15 mm long; Large > 15 mm. The mean number of seeds and species were compared between the areas for each size class, following the procedures described above.

A Detrended Correspondence Analysis (DCA) of seed abundance (excluding uniques, i.e. species that have occurred in only one plot) was performed for each plot in order to analyse the similarity of seed species composition among plots in similar habitats.

Results

In one year, 19,591 seeds belonging to 139 species were sampled in the 144 seed-traps. The mean number of seeds per plot was significantly lower in treefall gaps (G) than in the understorey adjacent to the gaps (UG), as more than twice as many seeds were captured in the understorey (Fig. 2a). The opposite was observed in the fire-disturbed area, and the mean number of seeds was significantly higher in the burned area (B) than in the understorey adjacent to the burned area (UB). The two types of disturbed areas - treefall gaps (G) and the burned area (B)–received significantly lower mean number of seed species (Fig. 2b) than their adjacent understorey areas (UG and UB, respectively).

Only 19 (13.7%) of the total number of species of seeds sampled were wind-dispersed, accounting for a total of 899 seeds (4.63%). Of these 19 species, 11 belonged to the Asteraceae family, and the others to Apocynaceae (2 species), Bignoniaceae, Bromeliaceae, Malpighiaceae, Poaceae, and Sapindaceae, plus one unidentified species.

Wind-dispersed seeds were homogeneously distributed between the treefall gaps and the understorey near gaps, both in terms of the number of seeds and the number of species (Fig. 3). Very high numbers of wind-dispersed seeds were sampled within the burned area plots (Fig. 3a), although the number of species of wind-dispersed seeds did not differ between the burned area and the adjacent understorey.

The smallest size class (Small) contained more than half (56.3%) of the non wind-dispersed species. This class also accounts for 98.5% of the total number of non wind-dispersed seeds, due to very large numbers of seeds of a few very abundant species. Treefall gaps received a lower number of non wind-dispersed small seeds than did the adjacent understorey, but these areas did

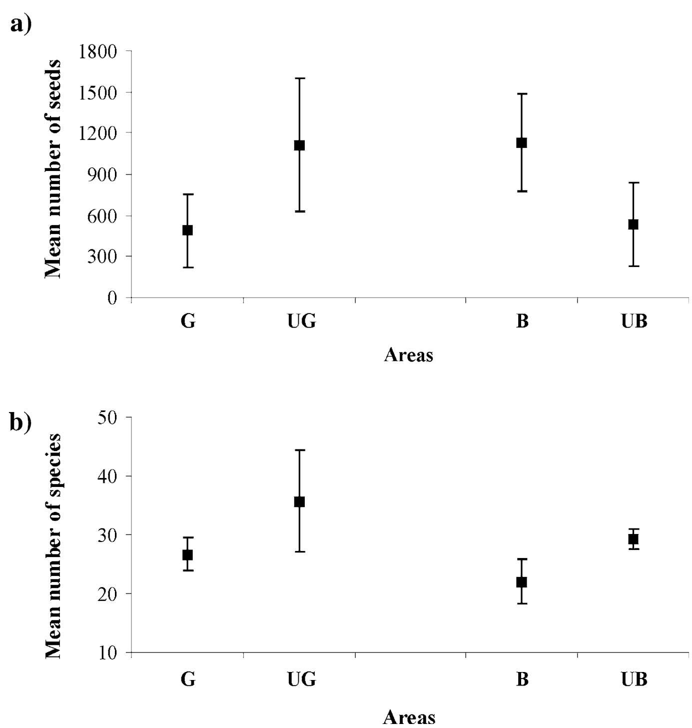

Fig. 2 Comparisons of the seed rain in disturbed areas and their adjacent understorey. (**a**) Mean number of seeds (G × UG: $P = 0.028$; B × UB: $P = 0.013$). (**b**) mean number of species (G × UG: $P = 0.027$; B × UB: $P = 0.002$). Legends: G— Treefall gaps ($n = 6$); UG—Understorey near gaps ($n = 6$); B— Burned area ($n = 6$); UB—Understorey near burned area ($n = 6$). The bars represent standard deviation

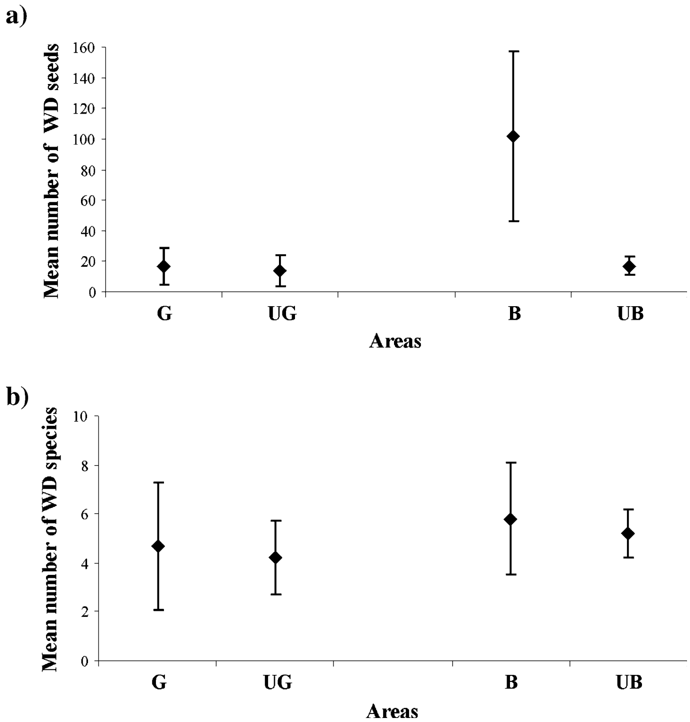

Fig. 3 Distribution of wind dispersed (WD) seeds in the seed rain in disturbed areas and their adjacent understorey. (**a**) Mean number of wind-dispersed seeds (G × UG: $P = 0.674$; B × UB: $P = 0.019$). (**b**) mean number of species of wind-dispersed seeds (G × UG: $P = 0.882$; B × UB: $P = 0.651$). The bars represent standard deviation. For legends see figure 2

not differ in the number of medium-sized seeds (Table 1). The high standard deviation observed for the medium-sized seeds encountered in treefall gaps (Table 1) was due to a single treefall gap that received 36 seeds of a single species of the Myrtaceae family. The number of species with small size class seeds was only slightly lower in treefall gaps while the number of species with medium-sized seeds, on the other hand, was significantly lower in these same gaps (Table 1).

The burned area received a larger number of small seeds than did the understorey, but no

Table 1 Distribution of the mean number of seeds and species of non wind-dispersed seeds in the different size classes (length of the long-axis of the seed) in the disturbed areas and the adjacent understorey

	Treefall gaps ($n = 6$)	Understorey near gaps ($n = 6$)	*	Burned area[a] ($n = 6$)	Understorey near burned area[a] ($n = 6$)	*
Mean number of seeds (SD) per plot						
Small	458.8 (281.1)	1080.5 (477.9)	$P = 0.039$	1022.3 (333.2)	508.5 (305.8)	$P = 0.024$
Medium	10.5 (14.1)	15.5 (10.5)	$P = 0.469$	5.33 (7.8)	9.17 (6.3)	$P = 0.376$
Large	3 (5.4)	0.8 (1.2)	–	0.33 (0.8)	0.5 (0.5)	–
Mean number of species (SD) per plot						
Small	18 (3.5)	23.5 (5.8)	$P = 0.054$	15 (3.9)	19 (2.7)	$P = 0.081$
Medium	3.17 (1.9)	7.3 (3.7)	$P = 0.023$	0.8 (1.0)	4.5 (2.1)	$P = 0.009$
Large	0.8 (0.8)	0.7 (0.8)	–	0.3 (0.8)	0.5 (0.5)	–

Small = 1–5 mm long; Medium = 5.1–15 mm long; Large > 15.1 mm long,
* Probability estimated from 1,000 randomly permutated datasets.
[a] Total and mean numbers from 11 months

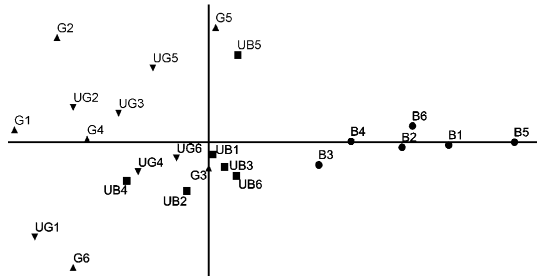

Fig. 4 Detrended correspondence analysis (DCA) ordination of plots, based on abundance of the seeds in the seed rain, but excluding uniques (i.e. species that have occurred in only one plot). (G—Treefall gaps, UG—Understorey near gaps, B—Burned area, UB—Understorey near burned area)

differences were observed between these two areas in terms of the number of medium-sized seeds nor in the number of species with small-sized seeds (Table 1). However, the number of species with medium-sized seeds was lower in the burned area than in the adjacent understorey. The numbers of seeds and species with large seeds were not statistically tested among areas due to the low numbers of seeds in this size class (Table 1).

Species composition and abundance

In the first axis of the DCA, the plots of the burned area (B) were grouped together in the right side, while the plots of the other three areas (G, UG and UB) were spread at the left side, suggesting a differentiation in the species composition of seed rain that arrived on the burned area (Fig. 4). This differentiation was essentially due to seeds that occurred exclusively or in a very high proportion on plots of the burned area, including seeds of the light demanding species such as *Lepidaploa cotoneaster* (Willd. Ex Spreng.) H. Rob. and *Baccharis* spp (Asteraceae), *Cecropia pachystachya* (Cecropiaceae) and some species of the Poaceae family. All of these species have seeds in the smallest size class. On the other hand, among the most important species in defining the plots on the left side of the first axis was *Evodianthus funifer* (Poit.) Lindman (Cyclanthaceae), a quite abundant species in treefall gaps and their adjacent understorey. Six out these 10 most important species have seeds in the medium and large size class. The second axis did not show any clear separation of plots.

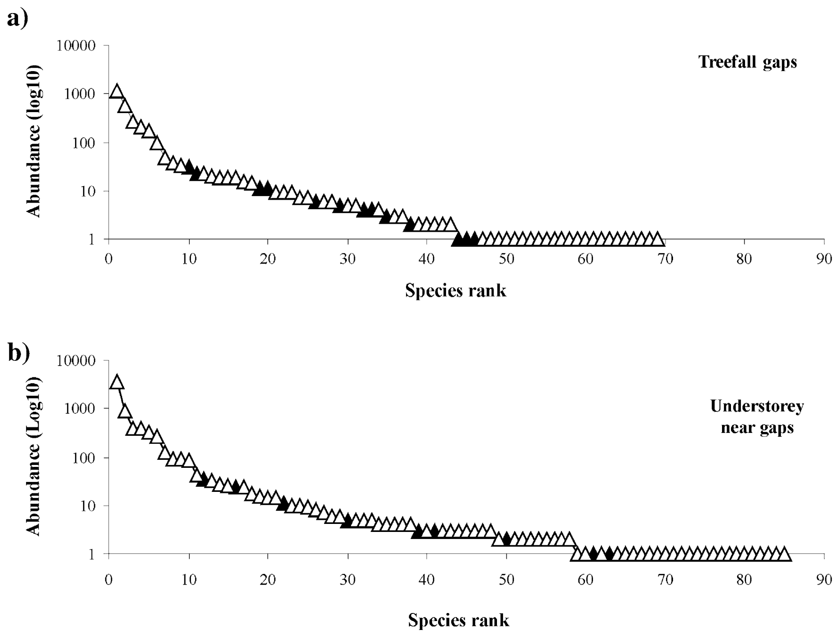

Fig. 5 Species abundance curves of the seeds sampled in the seed rain. (**a**) Treefall gaps (G) and (**b**) Understorey near treefall gaps (UG). Open triangles indicate non wind-dispersed species and filled triangles indicate wind-dispersed species

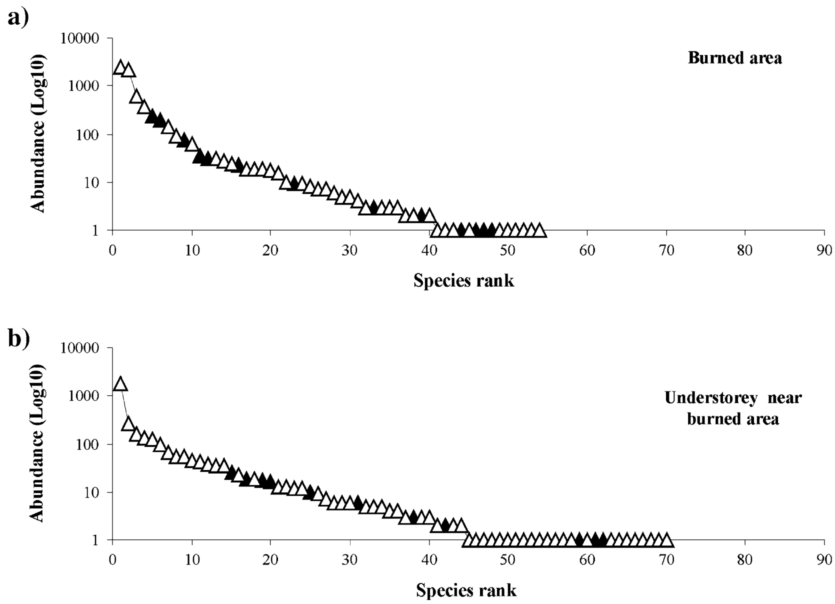

Fig. 6 Species abundance curves of the seeds sampled in the seed rain. (**a**) Burned area (B) and (**b**) Understorey near burned area (UB). Open triangles indicate non wind-dispersed species and filled triangles indicate wind-dispersed species

The distribution of abundance of species in the seed rain in treefall gaps was similar to that observed in the adjacent understorey (Fig. 5). However, the understorey area received a greater number of species and a higher number of seeds of *Miconia mirabilis* (the most abundant species in both areas) than treefall gaps (Table 2). On the other hand, the burned area showed a steeper curve than their adjacent understorey (Fig. 6), suggesting a strong dominance imposed by the two most abundant species, *Cecropia pachystachya* and *Miconia mirabilis*. It is also shown in these abundance curves that only in the burned area the wind-dispersed seeds were among the most abundant species.

An extreme abundance of *Miconia mirabilis* seeds was observed in all of the areas and one another species of Melastomataceae, *Henriettea succosa*, was among the most important species in the four areas (Figs. 5, 6 and Table 2). The proportion of rare species (represented by a single seed) was quite similar for the treefall gaps (38%) and the understorey near gaps (32%), but the burned area showed a lower proportion of rare species (26%) than the adjacent understorey (37%).

The ten most abundant species of seeds (Table 2) accounted for 84% of the total number of seeds collected in this survey. Seeds of species such as *Evodianthus funifer*, a hemi-epiphyte abundant in the forests of the region, and the morphospecies Unidentified-1, were found predominantly in the gaps and the understorey adjacent to the gaps. Seeds of *Cecropia pachystachya*, an arboreal species typically of disturbed environments, and *Lepidaploa cotoneaster*, a shrub species commonly found in open areas, were observed predominantly in the burned area. Seeds of the arboreal species *Henriettea succosa* were abundant in all of the areas (Table 2). The species *Solanum* sp1 is a peculiar case, as it was represented by a single fruit collected in the burned area, and contained 605 mature seeds.

Discussion

Treefall gaps and the adjacent understorey

The undisturbed area receiving the largest number of seeds was the understorey near the gaps (UG), with approximately 2 seeds > 1 mm/m^2/d. In a comparison with other studies undertaken in the understorey of tropical forests, some authors (Jackson 1981; Grombone-Guaratini and

Table 2 Number of seeds of the most abundant species sampled in the seed rain in disturbed areas and the adjacent understorey within the Una Biological Reserve, Bahia, Brazil

	Natural gaps	Understorey near gaps	Burned area	Understorey near burned area	Total
Miconia mirabilis (Aubl.) L. O. Williams (Melastomataceae)	1,175	3,529	2,212	1,765	8,681
Cecropia pachystachya Trécul (Cecropiaceae)	18	15	2,421	161	2,615
Evodianthus funifer (Poit.) Lindman (Cyclanthaceae)	581	911	4	54	1,550
Henriettea succosa (Aubl.) DC. (Melastomataceae)	170	327	373	270	1,140
Unidentified 1	263	389	19	97	768
Solanum sp1 (Solanaceae)	0	0	605	0	605
Rinorea guianensis Aublet (Violaceae)	32	273	1	133	439
Pogonophora schomburgkiana Miers ex Benth. (Euphorbiaceae)	4	388	0	0	392
Unidentified 2	203	28	5	34	270
Lepidaploa cotoneaster (Willd. ex Spreng.) H. Rob. (Asteraceae)	5	3	235	3	246

Rodrigues 2002; Hardesty and Parker 2002) described a lower number of seeds, with a minimum observed value of 0.35 seeds/m^2/d, while other authors (Walker and Neris 1993; Penhalber and Mantovani 1997, Holl 1999, Harms et al. 2000), described higher number of seeds, with a maximum observed value of 8.8 seeds/m^2/d. Although good comparisons between these studies is difficult due to the different sampling methods and collection efforts employed, as well as the differences in vegetation types, it can be seen that the numbers of seeds collected in the present study is within the range of values observed in other tropical forest sites.

The smaller number of seeds collected in gaps (0.89 seeds/m^2/d) when compared to the understorey was also observed by Devoe (1989 *apud* Walker and Neris 1993). This author encountered 0.78 seeds/m^2/d in gaps, and 2.55 seeds/m^2/d in the intact understorey, results that are very similar to those presented here. Loiselle et al. (1996) also reported a smaller number of seeds from the seed rain in gaps in relation to the adjacent understorey. These results are contrary to the expectation that gaps would receive a large number of seeds, whether animal dispersed (Levey 1988; Schupp et al. 1989; Wenny 2001), or wind-dispersed (Augspurger and Franson 1988; Schupp et al. 1989). Although differences were found in number of seeds and species, the species composition in gaps and their adjacent understorey seems to be similar. In fact, a large number of species (44) have occurred in both sites, and these species account for 71% and 80% of the total species composition of the treefall gaps and understorey, respectively, excluding the uniques (i.e. species that have occurred in only one plot) in each area.

The number of wind-dispersed seeds and species recorded in gaps during this study was not larger than that observed in the adjacent understorey. In a study undertaken in a forest that had been strip-cut, Gorchov et al. (1993) found that wind-dispersed seeds were encountered at similar frequencies in the understorey of the forest and at the edge and the centre of the strip. Loiselle et al. (1996) encountered a larger total proportion of wind-dispersed seeds in gaps, although in two of the four sampling periods the numbers of wind-dispersed seeds were actually larger in the understorey. Although the work of Augspurger and Franson (1988) is often cited (Walker and Neris 1993; Guariguata and Pinard 1998; Wenny 2001; Shiels and Walker 2003) as an example of the greater occurrence of wind-dispersed seeds in gaps, the mean number of wind-dispersed seeds recovered did not, in fact, differ between the gaps and the understorey due to large variations among locations (Augspurger and Franson 1988). As such, there is no clear evidence at this time of the preferential dispersion of wind-dispersed species in gaps.

Treefall gaps received similar quantities of wind-dispersed seeds as those observed in the understorey. Hence, differences between these areas in terms of the total number of seeds are due to non wind-dispersed seeds. In tropical forests, a majority of the seeds are dispersed by animals (Jordano 1992; Morellato et al. 2000; Silva and Tabarelli 2000), and our results suggest that animals may be avoiding treefall gap areas. The lower number of small-sized seeds and the lower number of species with medium-sized seeds in gaps suggests that both small and large animals may be avoiding these areas. Gorchov et al. (1993) observed that the numbers of seeds and species dispersed by animals, especially birds, were lowest near the centres of open areas (strip-cut) within old-growth forest. The absence of trees in these gap centres must be an important factor determining the lower number of seeds encountered there, because of the absence of perches or shelters for animal dispersers, and/or the simple impossibility of having seeds fall directly from the (absent) canopy.

The burned area and the adjacent understorey

The largest numbers of seeds were sampled in this study within the most disturbed area (the burned area). This area differs from sites examined in previously published studies in that it was burnt by an accidental fire, without the vegetation having previously been cut. This situation allowed some canopy trees to survive, permitting these trees to serve as perches or shelters for disperser animals. Several studies have demonstrated large numbers of seeds deposited beneath the crown of remnant trees in disturbed areas (Willson and Crome 1989; Guevara and Laborde 1993; Carrière et al. 2002; Holl 2002). The burned area under consideration was inserted within a mosaic of continuous forest in advanced sucessional stages, riparian forests not affected by the fire, and forest fragments that could all be considered significant seed sources and sources of animal dispersers. Even in areas without remnant trees, Martínez-Garza and González-Montalgut (2002) found high numbers of seeds from fleshy-fruited species in the seed rain in a pasture that was crossed by riparian vegetation and surrounded by secondary forests.

Additionally, the four years interval between burning and the initiation of this survey allowed a number of species of herbaceous plants, shrubs, and pioneer trees to become established (Martini 2002) and reach reproductive age in the burned area (pers. obs.). Due to the sudden availability of nutrients released by the burnt plant material (Vinha et al. 1983; Uhl and Jordan 1984; Canham and Marks 1985), and the increased incidence of light due to the elimination of the canopy cover, these species are able to produce larger numbers of seeds and further attract a greater number of disperser animals (Levey 1988; Clark et al. 2004). In fact, as will be detailed below, a high proportion of the seeds sampled in the seed rain in the burned area was composed of seeds from pioneer species, such as *Miconia mirabilis, Cecropia pachystachya, Henriettea succosa* and *Lepidaploa cotoneaster*. As a result of the conditions described above, the burned area showed the most distinctive species composition in the seed rain, when compared to the other areas.

The only area that did show a significant greater number of wind-dispersed seeds was the burned area, principally due to the large number of seeds from the Asteraceae family (*Lepidaploa cotoneaster, Baccharis* spp., *Piptocarpha pyrifolia* Baker, and *Mikania salzmaniifolia* DC.). With the exception of *Piptocarpha pyrifolia*, all of the other species were exclusively high light-demanding species, and frequently encountered in disturbed areas in the Una Biological Reserve (Amorim et al., unpublished data). The greater abundance of these species in the seed rain in the burned area was almost surely more of a consequence of the local abundance of these plants in these areas (pers. obs.) that of any dispersal processes from outside areas.

Seeds from pioneer species are also largely responsible for the large numbers of small seeds arriving in the burned area. These results are in accordance with the expected for disturbed areas, *i.e.* that species in the initial stages of succession, which constitute the largest part of the reproductive vegetation, produce small seeds (Foster and Janson 1985). The lower numbers of species with medium-sized seeds observed in the burned areas would suggest a deficiency of large-bodied dispersers, as these animals would tend to avoid open areas (Schupp et al. 1989; Forget and Sabatier 1997; Guariguata and Pinard 1998).

As this study was initiated four years after the burn, it was not possible to determine the origin of the plants already established there (*i.e.* if they were derived from the seed bank that survived the burning or from the fresh seed rain), but it is reasonable to predict that the resulting medium-term community will be composed predominately by plant species with small and/or wind-dispersed seeds.

The number of seeds collected in the understorey of the forest near the burned area (UB) was less (1.08 seeds/m^2/d) than in the understorey near the gaps (UG). This difference was probably determined by the non wind-dispersed seeds as the number of wind-dispersed seeds was very similar to that observed in the treefall gaps and the adjacent understorey. It is also important to note that the species composition in the understorey near the burned area is more similar to that observed in the understorey near gaps and in gaps than to the species composition observed in the burned area. Therefore, the proximity to the burned area could be negatively affecting the number of seeds arriving in the seed rain in the adjacent intact forest. Nearby disturbances may affect seed dispersal by altering the abundance of vertebrates or by inducing behavioural changes in disperser species (Guariguata and Pinard 1998). Spatial or temporal changes in frugivorous activities and/or in the fruiting pattern of plants may affect the structure and/or composition of the seed rain that falls in different forest locations (Martinez-Ramos and Soto-Castro 1993).

Abundant species in the seed rain

In a comparison between the most abundant species observed in the seed rain with most abundant plants encountered in the natural regeneration of these same areas studied by Martini (2002), some species deserve special attention either because they showed distinct dispersal strategies or because they showed strong discrepancies between the number of observed seeds and the established plants.

Seeds of *Miconia mirabilis*, a pioneer treelet, were encountered in large numbers in all of the plots in all four areas, including the two understorey and the gaps. However, reproductive individuals of this species are almost absent in the forest understorey or even in treefall gaps (pers. obs.). Although there is no available information about the species composition of the overstorey of these areas, individuals of this species between 0.2 and 5 m tall were not encountered in gaps or in the understorey of the forest (Martini 2002). In light of the fact that the nearest reproductive individuals were found only in the forest edges, that were at least 100 m distant from the sampling plots (pers. obs.), the high frequency and abundance of seeds of this species in the seed rain in gaps as well as in the understorey indicates that disperser animals are actively transporting seeds produced at the forest edge into the forest interior. Future studies of dispersal agents, seed banks, and the capacity of these seeds to remain dormant and accumulate in the soil would certainly increase our understanding of the regeneration strategy of this outstanding pioneer species, and its role in the communities studied.

Seeds of *Cecropia pachystachya* were recorded in almost all of the plots (23 out of 24), but 93% of the total number of seeds was found in the burned area, indicating a strong effect of local production. Young plants (from 0.2 to 5 m tall) were only found in the burned area (Martini 2002) and reproductive adults were abundant in the burned area, but extremely rare in the other three areas (pers. obs.). In newly burned forest plots in Venezuela, Uhl and Jordan (1984) found a strong dominance of *Cecropia filicifolia* in the regeneration community. This species appears to be very similar to *Cecropia pachystachya*, in that both are fast-growing pioneer species and are dispersed primarily by birds and bats. These authors suggest that the observed abundance of *C. filicifolia* is due to a rich supply of seeds, the availability of protected microhabitats for establishment (*e.g.* beside logs), and the availability of light and nutrients at that site. Very similar conditions were found in our study area for *Cecropia pachystachya*.

The understorey adjacent to the burned area received a larger number of seeds of *Cecropia pachystachya* than the treefall gaps and the adjacent understorey. This suggests an influence of the proximity to the burned area, probably due to the smaller distances to be covered by the disperser animals that would be carrying seeds produced by adult plants growing in the burned area. The quite low number of seeds of *Cecropia pachystachya* in the treefall gaps and the adjacent understorey suggests that their disperser animals are not being able to penetrate into this patch of the forest.

Additionally, species such as *Euterpe edulis* Mart. (Arecaceae) and *Psychotria purpurascens* Müll. Arg. (Rubiaceae) were common plants established in all four areas (Martini et al. in press), although they were either not registered at all in the seed rain, or at most by a single seed in a gap plot (*Euterpe edulis*). Among the ten most abundant species in the seed rain, only a single species (*Evodianhtus funifer*) was well represented among the plants established in these areas, except for the burned area (Martini 2002). A larger number of seeds and plants of this species were encountered in the gaps, and the understorey adjacent to them, than in the other areas.

Only in the burned area did the two most abundant seed species (*Miconia mirabilis* and *Cecropia pachystachya*) coincide with the frequency of the small and medium-sized plant species established there. It is possible that in the burned area the seed rain, as well as the smaller individuals that became established there, are simply a result of the predominance of mature reproductive plants of those species in the same area, as was observed by Walker and Neris (1993) and by Saulei and Swaine (1988).

These results suggest a weak relationship between the seed rain composition and the composition of small and medium-sized plants in the undisturbed areas (UG and UB) and in the area with natural disturbance (G). Other studies have also noted a weak relationship between species in the seed rain and young individuals (Martinez-Ramos and Soto-Castro 1993) and adults (Saulei and Swaine 1988; Penhalber and Mantovani 1997; Harms et al. 2000; Hardesty and Parker 2002) growing in their study areas. It must be stressed, however, that sampling was undertaken for only a single year, while many tropical forest species show varying patterns of fruiting in different years (Schupp 1990; Davies and Ashton 1999; Wright et al. 1999; Newstrom et al. 1994).

Although the data presented here is based on a small numbers of plots in each area, both the numbers of seeds and the numbers of species found in the seed rain were high, and the overall results appear to be consistent. This is the first study concerning seed rain in treefall gaps and fire-disturbed areas in the Brazilian Atlantic Forest, one of the most endangered biomes in the world. Knowledge concerning regeneration sources in disturbed areas can provide useful information for the management and conservation of this forest.

In this study, substantial differences were observed in the characteristics of the seed rain at disturbed sites, when compared with undisturbed forest understorey. However, these two distinct types of disturbance (natural treefall gaps and fire-disturbed area) showed quite differing patterns in terms of the total number of seeds encountered and totals of wind-dispersed seeds. It is noteworthy that species richness was quite low at both these disturbed sites.

In addition to seeking explanations for these observed differences, it will be instructive to evaluate the consequences of these differences on the future plant community. Continuous analyses of the composition of established plants and the seed rain will be necessary in order to understand these relationships.

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