

The need for full inventories of tree modes of disturbance to improve forest dynamics comprehension: An example from a semideciduous forest in Brazil

Adriana M.Z. Martini ^{a,b,d,*}, Renato A.F. Lima ^b,
Geraldo A.D.C. Franco ^c, Ricardo R. Rodrigues ^b

^a Universidade Estadual de Santa Cruz, Departamento de Ciências Biológicas, Rodovia Ilhéus-Itabuna, Km 16, Ilhéus, CEP 45650-000, BA, Brazil

^b ESALQ-USP, LCB, Laboratório de Ecologia e Restauração Florestal, Av. Pádua Dias 11, Piracicaba, CEP 13018-900, SP, Brazil

^c Instituto Florestal do Estado de São Paulo, Seção de Ecologia Florestal Divisão de Dasonomia, Rua do Horto 93, Tremembé, São Paulo, CEP 02377-000, SP, Brazil

^d Universidade Federal de São Paulo, Campus Diadema, Rua Prof. Artur Riedel, 275, Diadema, CEP 09972-270, SP, Brazil

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Abstract

A study was carried out to characterize the general pattern of tree mortality and damage in an old-growth semideciduous seasonal forest in the Caetetus Ecological Station, southeastern Brazil, and to assess species-specific patterns of mode and frequency of disturbances. We counted all disturbance events promoted by trees or parts of them larger than 20 cm in diameter within a 10.24 ha plot and recorded their mode of disturbance, basal diameter, age class, presence of re-sprouts and, whenever possible, their species. A total of 743 disturbance events were recorded inside the studied plot. Of these events, 650 were occasioned by entire trees (33% uprooted, 28% dead-standing, 26.5% snapped, 10.5% inclined and 2% complex events) while 93 were due to parts of trees (60.2% branch-falls and 39.8% stem-fall from multi-stemmed trees). Dead-standing trees were predominant in the recent age class, while uprooted trees predominated in the oldest age class. Probably, a large fraction of the trees in this forest die standing and then fall, exposing their roots. We found that considering all modes of disturbance is quite important, otherwise forest disturbance rates might be underestimated by approximately 25%. Even when usually neglected modes of disturbance were excluded from the estimates, this forest revealed a high disturbance rate compared to other forests. Some species showed damage and death rates greater than expected by chance, while others species showed significantly lower rates. A high proportion of re-sprouting was observed in this forest and the species presenting the greatest re-sprouting proportion were also the most abundant in the study area, corroborating the idea that this ability can be important to increase their competitive potential, especially in forest with high disturbance rates.

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1. Introduction

Forest dynamics are usually thought of as being determined principally by tree deaths. Studies on this topic are usually concerned with estimating either forest turnover rates based on canopy openness, or tree mortality rates based on long-term monitoring of forest communities. Three major modes of tree

mortality are generally recognized in both types of studies: uprooted, snapped, and standing dead trees. Each of these categories has different implications for forest dynamics and the sequential replacement of plant species (Putz et al., 1983; Schaetzl et al., 1989a; Lugo and Scatena, 1996; Arriaga, 2000; Gale and Hall, 2001).

Tree uprooting is usually associated with physical factors affecting root anchorage, such as wind, steep slopes, shallow soils, or soil saturation (Schaetzl et al., 1989b; Gale and Hall, 2001), although biotic factors (*e.g.* disease or pathogens affecting the root system), as well as root architecture are also important (Schaetzl et al., 1989b). Uprooting produces the largest impact on forest structure in comparison with other

* Corresponding author at: ESALQ-USP, LCB, Laboratório de Ecologia e Restauração Florestal, Av. Pádua Dias 11, Piracicaba, CEP 13018-900, SP, Brazil. Tel.: +55 19 3429 4431x231; fax: +55 19 3429 4431x231.

E-mail address: amzmartini@uol.com.br (A.M.Z. Martini).

modes of disturbance because it increases light intensity at the forest floor and disturbs the soil. Furthermore, uprooted trees can provoke changes in species composition during natural regeneration by causing the death of a large number of previously established plants and by exposing buried dormant seeds in the soil (Putz et al., 1983; Schaetzl et al., 1989b). On the other hand, a standing dead tree will gradually and slowly release bound nutrients both above and below ground and cause less impact on established plants. This mode of disturbance results more directly in increased growth rates of established plants rather than in changes in species composition. This mode of death is usually caused by pathogens, lightning, fire, or flooding (Putz et al., 1983; Arriaga, 2000).

The snapping of the tree trunk will tend to have intermediate effects on forest dynamics, with the height of stem breakage as a key factor in determining its impact on the surrounding vegetation. Stem breakage near the tree crown will resemble the effects of a standing dead tree, but the impact on established plants of breaks located nearer ground level will be more similar to those caused by an uprooted tree. Some of the physical factors responsible for uprooting trees can also cause trunk snapping, and a main difference between these two modes of death is whether the weakest point exposed to the lateral forces lies along the tree bole or with the soil anchorage (Putz et al., 1983; Gale and Barford, 1999).

Although these three basic modes of death are very important, they do not cover the entire range of natural disturbances in a forest. Disturbances promoted by the death of one stem of a multi-stemmed tree, branch falls, or inclined trees have commonly been neglected in previous studies (Carey et al.,

1994; Korning and Balslev, 1994; Strasberg et al., 1995; Gale and Barford, 1999; Gale and Hall, 2001; Lin et al., 2004). Additionally, some trees remain alive after damages being able to re-sprout after snapping, or to maintain their crowns entirely alive after fall. Studies of forest dynamic that omit these situations will underestimate the disturbance regime (Paciorek et al., 2000). The dynamic of species replacement will be affected by the re-sprouting abilities of individual plants. For example if a canopy tree snaps but then re-sprouts it will be in a positional advantage over smaller trees (Putz et al., 1983) and will be able to fill the gap faster than species regenerating from seeds (Matelson et al., 1995; Negrelle, 1995; Paciorek et al., 2000).

In the present study, we carried out an exhaustive sampling of all modes of disturbance occasioned by trees in a semideciduous seasonal forest. Specifically, we addressed the following questions: How many modes of disturbance caused by trees can be found and what is the predominant mode in this forest? What is the proportion of damaged trees that re-sprouted and/or remained alive? Is the presence of re-sprouting associated with any particular mode of disturbance? What are the overall mortality and damage rates of trees in this forest? What are the mortality, damage and resprouting rates of the most abundant tree species encountered in this forest?

2. Study area

The Caetetus Ecological Station (EEC) is a state reserve located in central western São Paulo State, Brazil ($22^{\circ}41'S$ – $22^{\circ}46'S$ and $49^{\circ}10'W$ – $49^{\circ}16'W$) (Fig. 1). The reserve covers an area of 2178 ha and is predominantly occupied by old-growth

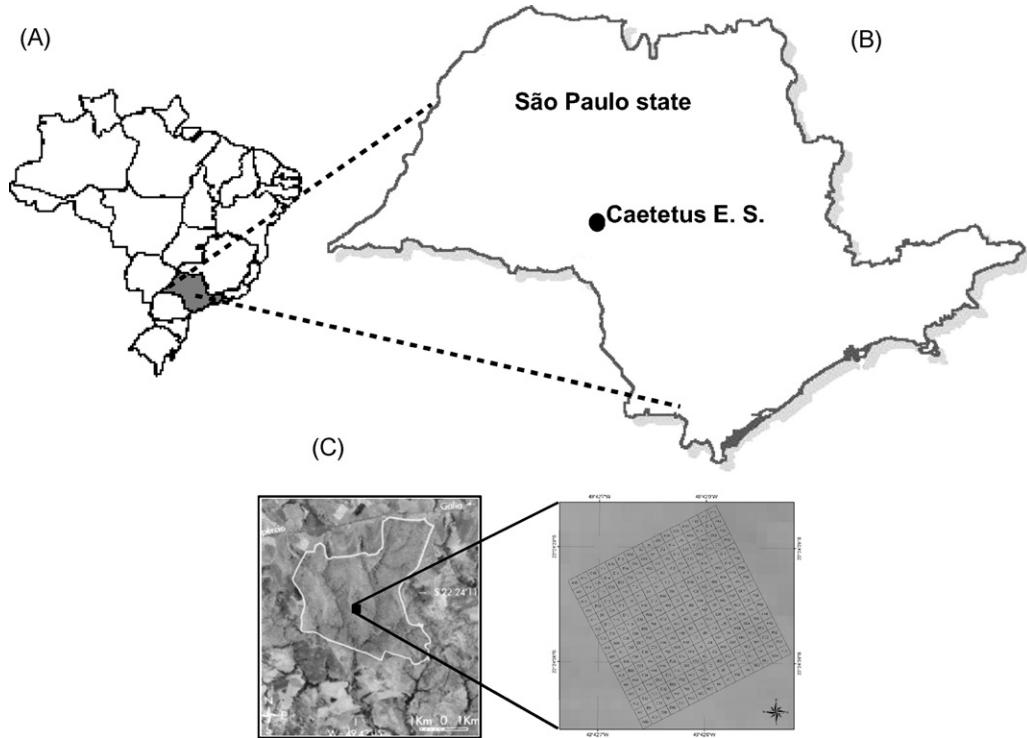


Fig. 1. Map of the study area with the location of: (A) São Paulo state at Brazil; (B) Caetetus Ecological Station (EEC) in São Paulo state; (C) the permanent plot in the EEC.

semideciduous seasonal forest, with an average canopy height ranging from 25 to 30 m. The local climate is classified as type Cwa in the system of Köppen, and is characterized by the occurrence of a definite dry winter and an average annual rainfall of approximately 1400 mm. During the dry season (April–September), the mean monthly rainfall is usually below 60 mm and the occurrence of extended dry periods in some years is very common. The average annual temperature is 21 °C (Sentelhas et al., 2005). According to Astolpho et al. (2004), the annual probability of the occurrence of frost events vary between 20% and 40%. The terrain at the station is relatively flat, with elevations ranging between 550 and 650 m above sea level. In a regional context, the EEC is located in a large valley bottom (Pires-Neto et al., 2005), where the occurrence of strong winds is relatively common.

A permanent plot of 10.24 ha – 320 m × 320 m, divided in 256 sub-plots of 20 m × 20 m – was established in 2002, in an area of old-growth forest in a central location at this ecological station (Fig. 1C), as part of the project “Diversidade, dinâmica e conservação em florestas do Estado de São Paulo: 40 ha de parcelas permanentes” within the program BIOTA/FAPESP (www.biota.org.br). The predominant soils in the plot are the red-yellow Argisols (Ultisols), with small patches of Arenosols and Fluvisols (Entisols). The elevation within the plot varies from 570 to 610 m. In the 2005 census, 12,039 individuals >5 cm dbh were sampled, and the basal area was 36.78 m²/ha. A total of 148 species, 110 genera, and 44 families were recorded inside the plot. The richest families were Myrtaceae, Euphorbiaceae, Fabaceae, Mimosaceae, and Rutaceae.

3. Material and methods

All disturbance events promoted by trees or parts of trees (including fallen branches or stems from multi-stemmed trees) with basal diameter >20 cm were counted between February and March 2005 in a 10.24 ha permanent plot of semideciduous seasonal forest. The term “event” was used referring to each dead or damaged tree or each tree fallen parts, irrespective if it was related to a single or a multiple disturbance episode. We recorded the disturbance mode, basal diameter, age class, trees status as “dead” or “alive”, and the presence of re-sprouts for each disturbance event.

The disturbance modes were defined as follows: (i) Uprooted: entire trees that had fallen exposing their roots. Their boles were horizontally positioned; (ii) snapped – entire trees that had their trunks broken at any height; (iii) standing – entire trees that had died while standing or trees that had lost the largest portion of their crowns; (iv) inclined – entire trees, dead or alive, that had inclined to a steep angle at which crown displacement created a canopy opening; (v) stem – the dead stem (>20 cm diameter) of a multi-stemmed tree; (vi) branch – the loss of part (>20 cm diameter) of the crown of a tree; (vii) complex – entire trees that could not be classified into the categories described above, usually because the same tree demonstrated two or more disturbance categories. In order to define if a damaged tree as “dead” or “alive”, each tree was carefully inspected to verify the presence of any living tissue. If

at the time of the inspection, the tree had any living tissue, it was classified as damaged, but not dead.

Three disturbance age classes (that is, time since tree disturbance) were defined based on the information available from a previous inventory conducted in 2002 in the permanent plot, and from visual inspection of the damaged tree in relation to their leaves and buds, and to the degree of wood decay. Events were classified as age 3 (old) when the tree was recorded as already dead or damaged in the first inventory. When the tree was alive and not damaged in the first inventory the event was considered intermediate (age 2) or fresh (age 1). These latter two classes were distinguished by the presence of well-preserved bark and thin twigs on the terminal branches of the tree or the part of the tree (stem or branch) in age class 1. For some analyses, the classes 2 and 1 were grouped together into a single class (Recent).

3.1. Data analysis

The number of events observed in each disturbance mode was compared among the three age classes. The chi-square test was employed to determine if disturbance modes were equally distributed in each age class. A chi-square test was also used to verify possible differences in the proportions of trees with re-sprouts among the disturbance modes. Branches were excluded from this analysis. The diameter distributions of trees (or parts of trees) were compared between the disturbance modes by inspection of the median confidence intervals in notched box-plots. Non-overlapping confidence intervals indicated an absence of similarity in their distributions.

A chi-square test was also performed to test if some of the most abundant species inside the plot (at least 10 individuals with diameter at breast height >19.1 cm) at the 2002 census demonstrated differences in the number of dead trees when compared with the expected numbers obtained under the null hypothesis that all species have the same mortality rates. We calculate, at first, the overall mortality rate for the whole plot as the “exponential mortality coefficient” (λ) cited by Sheil et al. (1995), being:

$$\lambda = \log e \left(\frac{N_0/N_1}{t} \right),$$

where N_0 and N_1 are the total trees counts at the beginning and end, respectively, of the measurement interval, t . The measurement interval between the first inventory and this study was not homogeneous for the whole permanent plot, then the t value used for the whole plot (hereafter t_w) was the mean time between the two surveys (2002 and this study) for each of the 256 sub-plots of 20 m × 20 m.

In order to estimate the expected number of dead trees for each species, the λ value obtained for the whole plot (hereafter λ_w) was applied to the initial number of individuals of each species observed in the 2002 census. However, an additional correction was needed because the measurement interval for each species was not equal to the whole plot interval (t_w). The calculation of the mean time for each species (t_i) was made including only the plots where the species was present in the

2002 census. Then, for each species (i) the expected number of dead trees ($Dexp_i$) was calculated as follows

$$Dexp_i = N_{0i} - \left(\frac{N_{0i}}{e^{\lambda_w t_i}} \right),$$

where N_{0i} is the number of individuals of each “ i ” species at the first census, λ_w the mortality coefficient for the whole plot, and t_i is the specific mean time for each species.

The observed numbers were then compared to these corrected expected values. The overall chi-square value was calculated and, if significant, the largest deviations were presented, indicating which species showed the most important differences in their mortality proportion. The same test was performed with the damage rates, i.e. the proportion of trees in this size class that were damaged (including damaged trees that remained alive and trees that died).

4. Results

Of the 743 disturbance events recorded in the 10.24 ha plot, 650 (87.5%) were occasioned by entire trees, while 93 (12.5%) were due to either stems from multi-stemmed plants (37) or to branches (56). Among the 650 events produced by entire trees, 33% were uprooted trees, 28% standing trees, 26.5% snapped trees, 10.5% inclined trees, and 2% complex trees. The distribution of the disturbance mode was significantly different ($\chi^2 = 56.43$, d.f. = 10, $p < 0.001$) among the three age classes. Uprooted trees were predominant in the oldest age class, but were weakly represented in the intermediate class (only 12.6% of trees were uprooted in this age class). On the other hand, standing and inclined trees were proportionally more common in the fresh and intermediate age classes, respectively (Fig. 2). In a period of 2.2 years (t_w mean measurement time between the two census for the whole plot), 222 disturbance events had occurred within the plot, resulting in an average of 9.85 events/ha/year (2.84 standing, 2.49 snapped, 1.51 inclined, 1.24 uprooted, and 0.18 complex trees/ha/year, 0.89 branches/ha/year, and 0.71 stems/ha/year).

Uprooted trees demonstrated larger diameters than fallen branches, standing trees, and inclined trees, but did not differ

significantly from snapped trees or the stems of multi-stemmed plants (Fig. 3A). Branches, inclined trees and standing trees demonstrated the smallest diameters, and did not differ significantly among themselves. Snapped trees did not differ from standing trees, but they were significantly thicker than inclined trees (Fig. 3A). Trees with re-sprouts did not differ in diameter from trees without re-sprouts, for any disturbance mode (Fig. 3B).

Re-sprouts were found on 17.9% of the trees (excluding branches), but the proportion of re-sprouted trees was significantly different among the different modes of disturbance. For events involving only entire trees, snapped trees showed the highest proportion (26.7%) of re-sprouting, while only 5.1% of the uprooted trees had re-sprouted. The loss of a stem in a multi-stemmed plant was strongly associated with the occurrence of resprouting. Eighty-one percent of the trees in this disturbance mode had re-sprouted (Fig. 3B). The species with highest proportions of re-sprouted trees in the recent age classes were *Ocotea indecora* Schott ex Meisn. (74%), *Centrolobium tomentosum* Guill. ex Benth. (46.7%), *Aspidosperma polyneuron* Müll. Arg. (42.9%), and *Metrodorea nigra* A. St.-Hil. (20.7%). Disturbance events involving entire trees in which the tree remained totally alive were restricted to inclined (50% of the events) and uprooted (1% of the events) disturbance modes.

M. nigra, and *O. indecora* were more damaged (including trees that remained alive and trees that had re-sprouted) than would be expected from the overall damage rate for the plot (11.01% in 2.2 years, or $\lambda_w = 0.053$), while the species *Astronium graveolens* Jacq., and the group *Syagrus* spp (including the species *S. rommanzofiana* (Cham.) Glassman and *S. oleracea* (Mart.) Becc.) demonstrated less damaged individuals than expected (Table 1). The overall chi-square result for damage data was 74.09; d.f. = 27, $p < 0.001$. The species *M. nigra* and *Croton floribundus* Spreng. had a higher mortality rate than expected for the total plot (5.89% in 2.2 years, or $\lambda_w = 0.027$). On the other hand, *O. indecora* and *Chrysophyllum gonocarpum* (Mart. & Eichler) Engl. had a lower mortality rate than expected, with no dead individuals observed during the study period in spite of their high abundances in the first inventory in 2002 (165 and 80 individuals with dbh > 19.1 cm, respectively) (Table 1). All damaged individuals of *O. indecora* in the recent age class had survived, including uprooted and snapped trees, which had re-sprouted vigorously. The overall chi-square result for death data was 54.460; d.f. = 27; $p = 0.001$. *Cecropia glazioui* Snelth. demonstrated a high proportion of dead individuals (62.5%), but was not included in these analyses as only eight individuals (dbh > 19.1 cm) were recorded in the first inventory.

It was only possible to accurately identify a few species of trees with unique characteristics of bark, wood, and/or trunk form that had died before the first inventory (age class 3). Among these, only three species (*A. polyneuron*, *C. tomentosum*, and *O. indecora*) and one palm genera (*Syagrus*, including two species *S. rommanzofiana* and *S. oleracea*) had sufficient numbers of individuals to allow analysis of the distribution of the modes of disturbance between all age classes. A higher proportion of uprooted trees of *A. polyneuron* was observed in the older age class than in the recent age class, while the proportion of standing

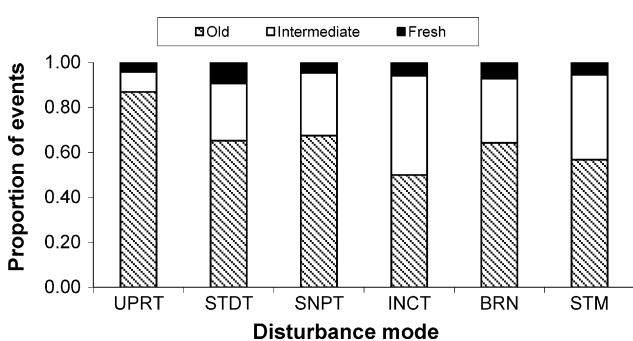


Fig. 2. Distribution of the proportion of events recorded for each disturbance mode in each of the three age classes. Disturbance modes: UPRT – uprooted trees ($n = 214$), STDT – standing trees ($n = 184$), SNPT – snapped trees ($n = 172$), INCT – inclined trees ($n = 68$), BRN – Branches ($n = 56$), STM – stems from multi-stemmed trees ($n = 37$).

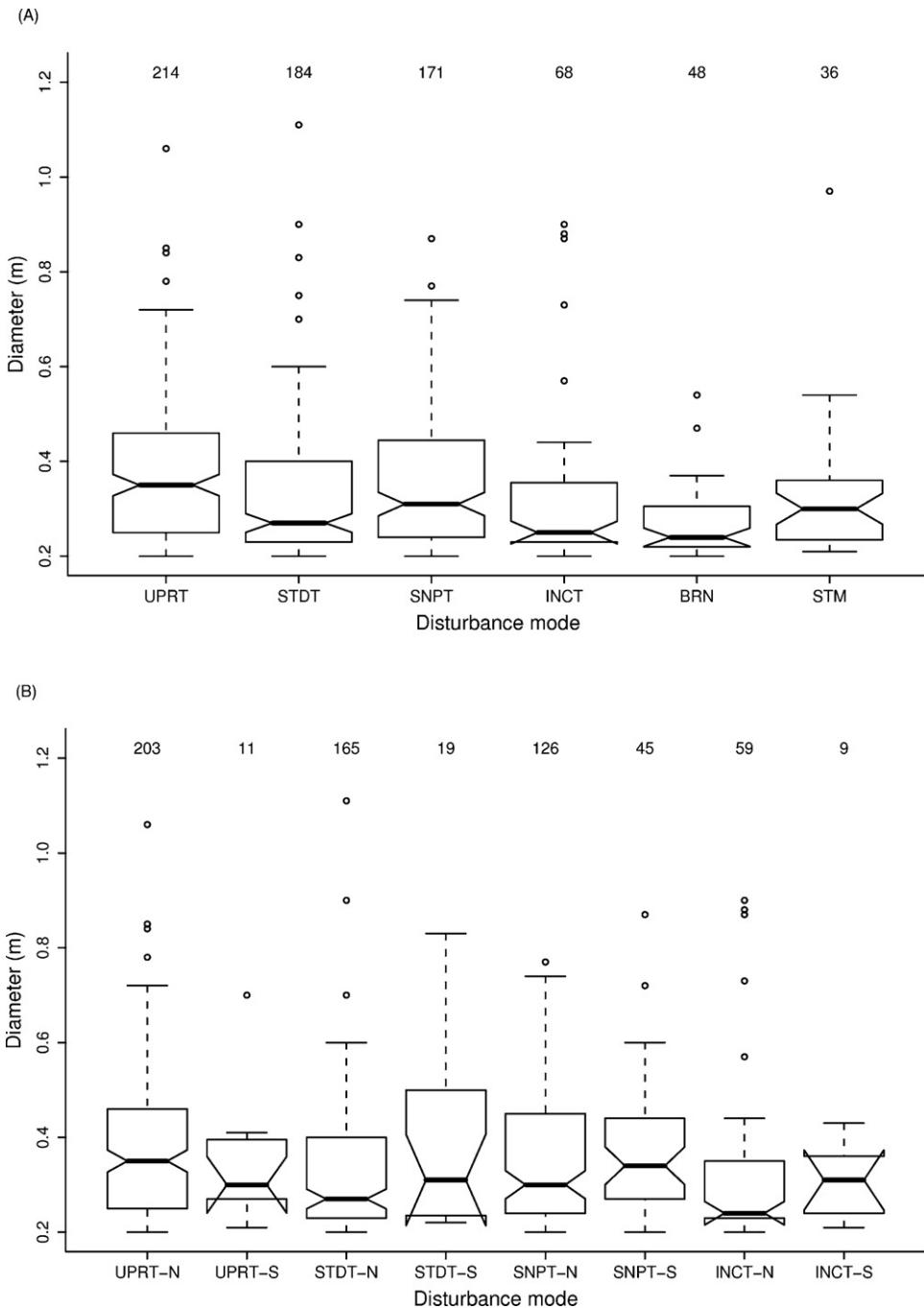


Fig. 3. Diameter distribution of trees, or parts of trees, sampled in each disturbance mode (A), and (B) regarding only trees with (-S) or without (-N) re-sprouts. The center vertical line marks the sample median. The length of each box shows the range within which the central 50% of the values fall, with the box edges at the first and third quartiles. Whiskers show the range of values that fall within 1.5 times the length of the box. Boxes are notched (narrowed) at the median and return to full width at the lower and upper confidence interval values. Outlier values are plotted as empty circles. An extreme value (>1.5 m) was not presented in the graphic to enhance the visualization of the differences. The number of events of each disturbance mode is shown above each box (see codes for the disturbance modes in Fig. 1).

trees was highest in the recent class for both *A. polyneuron* and *C. tomentosum* (Fig. 4). Additionally, a greater proportion of inclined trees was observed for *A. polyneuron*, *O. indecora*, and *Syagrus* spp in the recent rather than in the older age class (Fig. 4).

5. Discussion

The semideciduous seasonal forest examined demonstrated disturbance events that could be separated into seven

categories, three of which – uprooting, snapping, and standing dead – have regularly been recorded in earlier studies (Carey et al., 1994; Korning and Balslev, 1994; Gale and Barford, 1999; Gale and Hall, 2001; Lin et al., 2004). The exclusion of the events provoked by branches, inclined trees, stems from multi-stemmed trees, and complex trees can result in the underestimation of the forest disturbance by approximately 25%. Although some studies have employed a more ample definition of disturbance events (Rankin De Merona et al., 1990; Van Der

Table 1

The 28 most abundant tree species (dbh > 19.1 cm) in the 2002 census of a 10.24 ha plot of semideciduous forest and the observed numbers of damaged and dead individuals in the second census

Species	Number of trees alive in 2002	Observed number of damaged trees	Expected number of damaged trees	Damage deviation	Observed number of dead trees	Expected number of dead trees	Death deviation
<i>Syagrus</i> spp	243	16	26.98	4.467(–)	14	14.43	0.013
<i>Aspidosperma polyneuron</i>	169	14	18.52	1.105	8	9.9	0.366
<i>Centrolobium tomentosum</i>	166	14	18.43	1.064	7	9.86	0.827
<i>Ocotea indecora</i>	165	26	17.47	4.168(+)	0	9.33	9.329(–)
<i>Croton floribundus</i>	162	20	17.68	0.304	16	9.45	4.538(+)
<i>Metrodorea nigra</i>	90	29	9.82	37.437(+)	15	5.25	18.102(+)
<i>Chrysophyllum gonocarpum</i>	80	5	8.47	1.421	0	4.52	4.523(–)
<i>Astronium graveolens</i>	67	2	7.47	4.005(–)	1	3.99	2.245
<i>Balfourodendron riedelianum</i>	52	4	5.53	0.423	3	2.95	0.001
<i>Esenbeckia leiocarpa</i>	46	4	5.3	0.319	4	2.84	0.476
<i>Savia dyctiocarpa</i>	45	1	5.37	3.558	1	2.88	1.227
<i>Piptadenia gonoacantha</i>	44	8	4.99	1.82	5	2.67	2.036
<i>Machaerium stipitatum</i>	35	2	3.69	0.773	0	1.97	1.97
<i>Acacia polyphylla</i>	31	3	3.51	0.075	2	1.88	0.008
<i>Ceiba speciosa</i>	26	0	3.02	3.02	0	1.62	1.617
<i>Gallesia integrifolia</i>	24	0	2.52	2.518	0	1.34	1.345
<i>Parapiptadenia rigida</i>	21	0	2.26	2.263	0	1.21	1.209
<i>Cedrela fissilis</i>	20	1	2.23	0.678	1	1.19	0.031
<i>Holocalyx balansae</i>	18	3	1.88	0.667	2	1	0.989
<i>Lonchocarpus cultratus</i>	17	2	1.75	0.035	0	0.93	0.935
<i>Campomanesia xanthocarpa</i>	16	2	1.69	0.055	1	0.9	0.01
<i>Trichilia clausenii</i>	16	2	1.72	0.044	1	0.92	0.007
<i>Patagonula americana</i>	15	0	1.56	1.56	0	0.83	0.833
<i>Peltorphorum dubium</i>	15	3	1.62	1.168	1	0.87	0.02
<i>Cabralea canjerana</i>	13	1	1.41	0.121	0	0.74	0.738
<i>Diatenopteryx sorbifolia</i>	13	2	1.38	0.276	1	0.76	0.079
<i>Urena baccifera</i>	12	1	1.38	0.106	0	0.74	0.74
<i>Inga striata</i>	11	2	1.14	0.641	1	0.61	0.248

Chi-square deviations among the observed and expected (see methods for corrections used in this analysis) numbers of damaged and dead individuals are presented. Signs in parenthesis indicate, for the largest deviations, observed values greater (+) or lower (–) than expected.

Meer and Bongers, 1996; Segura et al., 2003), it was not possible to directly compare them with our results due to the different inclusion criteria and different classifications used.

Each type of disturbance results in different effects on the dynamics of natural forest regeneration (Putz et al., 1983; Lugo and Scatena, 1996; Gale and Barford, 1999; Arriaga, 2000), and a gradient of effects exist within the disturbance categories analyzed in the present study. One extreme of these effects is represented by uprooted trees, which have a very significant effect on forest structure (Schaetzl et al., 1989a,b) and can completely modify the species composition seen before and then after the disturbance event. The other extreme of this gradient is represented by inclined trees that remain alive and continue to use soil resources without provoking any real damage to the understorey vegetation, despite of the opening of canopy space directly below the initial position of the crown. As such, the principal effects of this type of disturbance will be on the growth rates of established species, and not on species composition. Other types of disturbances will have intermediate and more variable effects. For instance, snapped trees whose break point is closer the ground level will have effects more similar to those of uprooted trees. On the other hand, some branch falls were as large as some entire trees and might cause substantial canopy opening and understorey damage.

This was particularly true for branches of *A. polyneuron* in our study site.

Some authors have suggested that the prevalence of certain types of disturbances furnish information about the dynamics of a given forest. A predominance of uprooted trees, for example, would indicate a highly disturbed forest with a higher turnover rate than an area with a predominance of standing dead trees creating a fine-grained pattern of small gaps (Gale and Hall, 2001). When the complete suite of disturbance modes encountered in our sampling area were analyzed, uprooted, snapped and standing dead trees were found to be present in relatively equal proportions. However, when the disturbance events were separated into age classes, the most recent period (ca. 2.2 years) demonstrated a predominance of dead-standing trees, snapped trees, and inclined trees, that tend to produce smaller canopy openings. Studies in others semideciduous forests have shown the relevance of such small gaps on the forest disturbance regime (Brokaw and Scheiner, 1989; Dickinson et al., 2000; Martins and Rodrigues, 2002), but few have characterized gap creation in respect to the number of trees and disturbance modes involved.

However, in the older age class (the period previous to 2002), uprooted trees were much more abundant, representing 35.7% of all events. Four explanations are possible for the

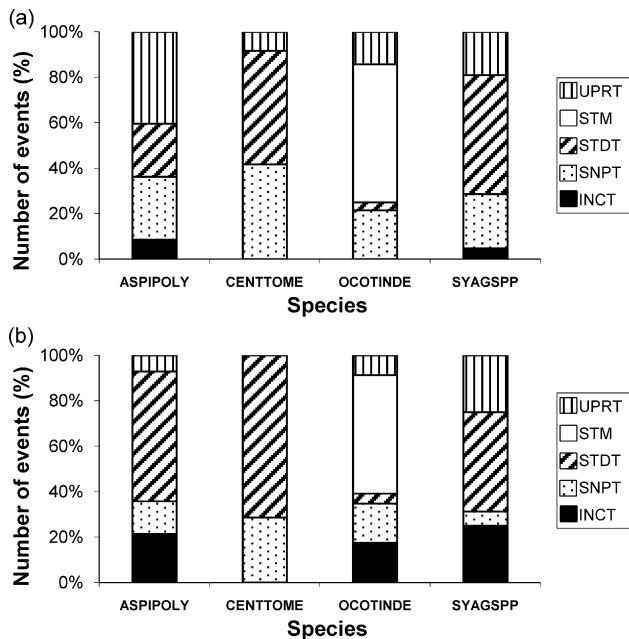


Fig. 4. Proportions of the disturbance modes of four tree species in a semideciduous forest. (a) Disturbance events that occurred before 2002 (Old); (b) Disturbance events that occurred between 2002 and 2005 (Recent). Species: ASPIPOLY – *Aspidosperma polyneuron*, CENTTOME – *Centrolobium tomentosum*, OCOTINDE – *Ocotea indecora*, SYAGSPP – *Syagrus* spp (including two species *S. romanzofiana* and *S. oleracea*). Disturbance Mode: UPRT – Uprooted trees, STDT – standing trees, SNPT – snapped trees, INCT – inclined trees, STM – stem from multi-stemmed trees.

observed differences between age classes. Firstly, a large fraction of the trees could die while standing or inclined, but then instead of slowly decaying while still erect they would fall and expose their roots, thus being classified as uprooted trees at the time of the survey. Lin et al. (2004) noted that some dead-standing trees recorded in their first survey appeared uprooted or snapped at the time of the second survey 4 years later. This tendency to fall and become uprooted instead of slowly decomposing may be associated with significantly larger individuals. As found here, Putz et al. (1983) and Arriaga (2000) observed that uprooted trees had larger diameters than trees in other disturbance modes. Putz et al. (1983) also observed that uprooted trees were to a great extent species with more resistant and higher density wood, features valid for *A. polyneuron* (Carvalho, 1994), that showed a high proportion of uprooted individuals in the oldest age class. Secondly, the largest proportion of uprooted trees in the oldest age class could also be explained by an “accumulation” effect, as this disturbance mode is associated with large individuals with denser and more resistant wood (Putz et al., 1983) that will decompose more slowly and remain for a long time in the forest floor.

Another possible explanation might be the occurrence of a catastrophic event, such as strong winds (Schaetzl et al., 1989b) that, associated to an extreme drought, could be responsible for uprooting trees over a wide time scale, especially large canopy and emergent individuals (Condit et al., 1995). In the EEC, there is a record of torrential rains associated with strong winds

that occasioned the fall of many trees in May 2002 (Rocha, 2003). However, the analysis of a historical series (SIGRH, 2007) of 66 years of records on rainfall showed that heavy rainfall events (*i.e.* above 80 mm/day) are historically common in the study site, happening at average intervals of 1.4 years. Therefore, the occurrence of such heavy rainfalls may not be a good explanation to the greater number of uprooted trees in the oldest age class.

Finally, an alternative possibility is that the recent age class actually contains a high number of standing dead and inclined trees, and not a low proportion of uprooted trees. The high mortality currently observed in these two categories might be associated with extreme climatic events such as frosts or extended droughts. However, the meteorological station located inside the EEC did not record any extreme weather events during the period between 11/2003 and 8/2005 (Sentelhas et al., 2005). On the other hand, several studies indicated changes in tree mortality and turnover rates in tropical forests as a consequence of global climatic changes (Williamson et al., 2000; Laurance et al., 2004; Lewis et al., 2004a,b). Only the consequences on the overall mortality rates were investigated until the present time, but different drivers of change (*sensu* Lewis et al., 2004a) could act more significantly on specific disturbance modes.

When only recent events (2002–2005) were considered, we observed an overall rate of 9.85 events/ha/year. In order to compare our results with data from other forests it was necessary to consider only that part of our data referring to entire trees, and excluding inclined trees. Considering then only entire trees damaged, there was 8.26 events/ha/year. Considering further only dead trees (that is, excluding individuals that remained alive) recorded during that same period, it was observed 4.79 events/ha/year. These values are greater than those observed by Milton et al. (1994) in a semideciduous forest in Panama (2.4–3.6 dead trees/ha/year; dbh > 19 cm). Gale and Barford (1999) surveyed all dead or damaged trees (trees that had lost stems or large branches) with dbh > 20 cm in a rain forest in Ecuador and recorded 39 dead or damaged trees/ha, a number considerably smaller than the 55.6 dead or damaged trees/ha (excluding inclined trees) found at our study site. Lugo and Scatena (1996) estimated the median of mortality rates for tropical forests as 1.6 percent/year for trees with dbh > 10 cm, but in the EEC forest the value for trees with dbh > 19.1 cm was 2.6 percent/year. The results presented above suggest that at least during the time period of this study, the semideciduous forest at the EEC was much more dynamic than other tropical forest sites.

A large fraction of the trees in the present study re-sprouted after being damaged, principally snapped trees and multi-stemmed trees. If these re-sprouted and living but damaged trees had not been recorded, approximately 25% of the disturbance events would have been ignored. In many cases these trees had considerable effects on the processes of natural forest regeneration by damaging the understorey vegetation or creating large canopy openings. The species that demonstrated the largest proportions of re-sprouting individuals were precisely the most abundant species with dbh > 19.1 cm: *O.*

indecora, *C. tomentosum*, *A. polyneuron*, *M. nigra*, and *C. floribundus*. The only exception was *S. romanoffiana*, a very abundant species lacking any capacity to re-sprout or to coppice. This strong relationship between species abundance and re-sprouting ability corroborates the idea that this capacity is an important determinant of a species' competitive ability (Matelson et al., 1995; Paciorek et al., 2000). Individuals that already occupy a canopy position but that suffer some sort of physical damage retain a significant competitive advantage if they have the capacity to re-sprout, for these plants already have large and well anchored roots and would have a height advantage in relation to the understorey plants (Putz et al., 1983). This capacity to re-sprout will influence the dynamics of species replacement after any disturbance event, as these same individuals may continue to occupy all, or a large part, of the affected area (Putz and Brokaw, 1989; Matelson et al., 1995; Negrelle, 1995; Paciorek et al., 2000).

Furthermore, it is important to consider that in some studies, trees that are counted as dead could re-sprout later. In these cases, the mortality rates might be overestimated. This could be particularly important in forests such as tropical dry forests, in which re-sprouting and coppicing have been considered two of the principal regeneration mechanisms (Murphy and Lugo, 1986).

Putz et al. (1983) observed a larger proportion of re-sprouting individuals in the smaller diameter classes ($\text{dbh} < 22 \text{ cm}$), although such relationship was not found in the present study. This might be attributable to the fact that only the large diameter class was analyzed in our study ($\text{dbh} > 19.1 \text{ cm}$). However, Segura et al. (2003) also found no relationship between tree diameter and survival after disturbance in plants with $\text{dbh} > 5 \text{ cm}$.

It was observed that uprooted trees demonstrated the largest diameters, followed by snapped trees and stems of multi-stemmed trees. The large diameters of uprooted trees may help explain the large number of these individuals recorded in the oldest age class, as cited above. On the other hand, rapid growing trees, such as the pioneer species, tend to have low density wood (Swaine et al., 1987; Swaine and Whitmore, 1988) and be more prone to snapping, and thus being less likely to attain great sizes. Inclined trees demonstrate smaller diameters than plants in other disturbance mode (except branches), probably reflecting the fact that they do not have sufficient weight or canopy area to fall over and carry other trees with them. These small individuals tend to remain supported by the vegetation around them for periods as long as 5 years (Putz et al., 1983) while their wood slowly deteriorates.

The analyses discussed above considered the entire set of plants damaged or died within the survey area. However, it could be expected that the patterns of tree mortality in a forest are related to some aspects of life history of particular species (Strasberg et al., 1995), thus the analysis of the most abundant species can be very informative. In fact, among the most abundant species in the study area, some of them stood out as demonstrating significantly different rates of death or damage.

M. nigra showed a large proportion of damaged individuals and a high mortality rate in the size class analyzed. *M. nigra* is a

sub-canopy, late-secondary species that is extremely abundant in the smaller diameter classes, representing approximately 50% of all individuals with $\text{dbh} > 5 \text{ cm}$ in the sampling area (unpublished data). However, this species is considerably less abundant in the larger size class analyzed ($\text{dbh} > 19.1 \text{ cm}$), representing less than 5% of all plants surveyed. The high rates of damage and death observed are probably associated with the processes of senescence in this species, as senescent individuals will be less resistant to attacks by pathogens (Franklin et al., 1987).

O. indecora, demonstrated a high percentage of damaged plants, but a very low number of dead individuals, principally due to its capacity to re-sprout. Not a single individual of this species was found to have died in the more recent age class (2002–2005), but many (52%) had lost one or more of their larger stems ($>20 \text{ cm}$ of basal diameter). Of the total number of individuals of this species that suffered some type of damage, only 5 (8%) had died, and all of those individuals in the oldest age class, indicating that even though individuals are highly subject to damage, mortality rates are low. *O. indecora* is a very abundant late-secondary species in the study area, and its capacity to resist damage seems to be strongly associated with the maintenance of dense populations in this community. Studies have shown that re-sprouting is an important survival strategy in the family Lauraceae (Matelson et al., 1995; Paciorek et al., 2000), and especially in the genus *Ocotea* (Matelson et al., 1995; Negrelle, 1995).

Croton floribundus, on the other hand, demonstrated an intermediate proportion of damaged individuals in the study area as a whole, but 80% of these damaged individuals had died, resulting in a very significant mortality rate. A large proportion of the damaged individuals of this species (50%) snapped, which is probably associated with the fact that this is a fast-growing pioneer species with relatively light wood (0.6 g/cm^3 , see Lorenzi (1992)). According to Putz et al. (1983), trees with less dense and weaker wood can "compensate" for their greater tendency to break with a capacity to re-sprout. However, the capacity to re-sprout does not seem to be responsible for maintaining the high abundance of *C. floribundus* because its mortality rate was actually relatively high when it becomes damaged. This may be related to the type of re-sprouting seen in this species, in which a majority of the new sprouts occur close to trunk breakage point, while in *O. indecora*, for example, sprouting occurs predominantly at trunk base (unpublished data).

For *Syagrus* spp., the number of damaged individuals was less than expected, but the percentage of damaged individuals that had subsequently died was extremely high (87.5%), and only two inclined individuals were observed to be still alive. These results indicate that the chances of damaging individuals of the genus *Syagrus* is relatively small, but once damaged, the effects are essentially lethal. Paciorek et al. (2000) observed that the lack of axillary buds in the majority of the palm species impedes re-sprouting. Exceptions include the clonal palms that can sprout from basal buds, but the two species of *Syagrus* (both late-secondary) growing in the study area do not have that capacity. In the oldest age class, a majority (53%) of the

individuals of *Syagrus* died while still standing. Gale and Barford (1999) also observed a predominance of dead-standing (47%) individuals of the palm *Iriartea deltoidea* Ruiz & Pavon in Ecuador, with a low percentage of uprooted individuals, possibly related to the fact that this species has stilt roots.

Although other abundant species did not demonstrate death or damage rates different from the expected (e.g. *C. tomentosum* and *A. polyneuron*), the differences found between damage and death rate of the most abundant species have some implications for the management of these species. Some species seem to be more “resilient” (with high damage rate but low mortality), such as *O. indecora*, while others seem to be more “resistant” (with low damage rates), such as *Syagrus* spp and *A. graveolens*. Another group of species appear to have high recruitment rates that compensate the high mortality rates observed, such as *M. nigra* and *C. floribundus*. Besides management practices implications, these distinct strategies observed among the most abundant species are quite important to understand the processes underlying the dominance of some species in the studied forest as well as in other semideciduous forests.

6. Conclusions

The present study emphasizes the importance of a complete inventory of disturbance events in order to be able to analyze the dynamic of a forest. Forest dynamics rates evaluated only on the basis of the numbers of entire trees (that is, excluding branches, inclined trees, and stems from multi-stemmed trees) or based only on tree mortality without considering resprouting, may be underestimating rates of forest dynamics by up to 25%. This underestimation will become quite significant in studies of seasonal forests where multi-stemmed individuals are numerous and re-sprouting represents an important survival strategy for many species, such as seen with *Ocotea indecora* in this study. The dominance of the most abundant species in the area appears to be achieved by distinct strategies related to the balance between their re-sprout ability and their damage and mortality rates. According to the overall results presented here, the studied forest is very dynamic. The high winds typical of their geomorphologic context (large valley bottom), associated with the strong water shortage period and with the heavy rains frequently observed in the rainy season, typical of a seasonal and subtropical region, might be important factors in determining the structure and dynamic of this forest.

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