SEEDLINGS DYNAMICS IN UNDISTURBED AND ADJACENT FIRE DISTURBED FOREST IN THE GRAN SABANA, SOUTHERN VENEZUELA

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SUMMARY

In the Gran Sabana, southern Venezuela, the conversion of large forest areas to a mosaic of forest, bush vegetation and savanna ("savannization") is a critical environmental issue associated with forest fires. Little is known about the behaviour of the seedling community in undisturbed and fire impacted forests in this region. Recruitment, survival and growth of seedlings was followed over a 6 year period in permanent quadrats established in undisturbed and adjacent fire-disturbed (secondary) forest. At the beginning of the study, secondary forest showed lower (P<0.05) values of seedling abundance and tree seedling richness than undisturbed forest. Abundance and species richness of tree seedling in both forests changed very little over the study period, which is associated to the partial balance between initial tree seedlings mortality rate (44-66%) and newly recruited tree seedlings survival rate (47-54%). At the end of the study ~80% of the recruited seedlings in undisturbed forest corresponded to tree species, whereas in secondary forest the proportions of tree (47%) and non-tree (53%) seedlings were rather similar. Growth in height during the 6 year period was considerably higher in secondary forest than in undisturbed forest (P<0.05). It is concluded that in undisturbed forest the succession process is relatively at a standstill, whereas in secondary forest this process advances very slowly.

In the Gran Sabana (southern Venezuela), forest disturbances and the conversion of large forest areas to a mosaic of forest, bush vegetation and savanna ("savannization") are critical environmental issues associated with forest fires. From a climatic point of view, the Gran Sabana should be covered by evergreen montane forests (Huber, 1995), but the actual vegetation cover appears as a complex mosaic consisting of several vegetation types in which the savanna and bush vegetation predominate, and forests appear only as scattered fragments of limited extension (Hernández, 1994). According to Fölster *et al*. (2001) and Dezzeo *et al*. (2004), the current vegetation mosaic in the Gran Sabana represents a transitional stage in a long term savannization process that is originally triggered by fire, but is essentially conditioned by soil chemical stress and episodic drought stress. High acidity, low basic cations and a high amount of toxic elements in the soils limit the microbial activity in this region and are responsible for the accumulation of organic matter on the soils surface (Priess and Fölster, 2001), making the forests highly susceptible to fire, especially in exceptionally dry years.

The current expansion of the savanna at the expense of forests in the Gran Sabana is evidenced by the presence of secondary shrubland and savannas with large and still standing burned tree trunks. Vegetation studies in this region (Fölster, 1986; Fölster, 1992; Fölster, 1994; Hernández, 1999) indicate that forest fires tend to trigger a degradational succession, which may pass through several phases of woody regrowth, each containing less biomass, ending in a secondary bush or a bush savanna. No indication of an intermittent impact of fire has been observed. If the observations are correct, forests in this region are fragile systems.

To understand the forest fragility in the Gran Sabana information is needed about regeneration dynamics over time. Regeneration is a key process to warrant the future of species in the forest community and involves recruitment, survivorship and growth of a very large number of species that may differ

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in their modes of life and the roles they play in the community (Bazzaz, 1991). The regeneration process can be affected by disturbances that frequently imply changes in environmental factors such as light, temperature, moisture, nutrients and wind levels, which influence abundance and composition of seedlings and saplings in the forest understory (Whitmore, 1998; Barnes *et al*., 1998).

Numerous studies on the impact of disturbances on regeneration have been carried out in tropical regions. However, few of them have been focused on the long-term monitoring of seedlings and saplings (e.g. Uhl *et al*., 1988; Turner, 1990; Nepstadt *et al*., 1996; Rettenmaier and Fölster, 1999; Rodríguez *et al*., 2004; Capers *et al*., 2005; Khumbongmayum *et al*., 2005; Dupuy and Chazdon, 2006), although these studies are necessary to better understand the effect of perturbation on tropical forest dynamics.

The present work focuses on what is really occurring with the regeneration stratum in fire disturbed forest and how is the behaviour of this stratum in the undisturbed forest. To do this, stand-level variation in seedling dynamics over a 6-yr period was compared in undisturbed and adjacent fire-affected forests that differ from each other with respect to structure, species composition, biomass and organic layer on the soil surface, but are relatively similar with respect to mineral soil characteristics. Our objectives were 1) to determine how recruitment, survival and growth in height of tree and non-tree seedlings differ between undisturbed and adjacent fire-disturbed forests, and 2) to test whether the densities of tree and non-tree seedlings in the fire-disturbed forest become more similar in time than those of the undisturbed forest.

Study area

The study was carried out in the Gran Sabana, an elevated (800-1500masl) plateau of 18000km^2 located in southern Venezuela (04º45'-05°30'N and 60°30'-61°22'W). The climate has been classified as tropical very humid premontane, with mean annual precipitation of 2200-4000mm and mean temperature of 17-24°C (Galán, 1984). Precipitation is distributed unevenly throughout the year, with a mean monthly rainfall >60mm during the dry season (Dec-Mar), which implies that there is no drought stress during this season (Walter and Medina, 1971). Soils are derived from Precambrian sediments of the Roraima Group and are in an advanced phase of weathering (Fölster *et al*., 2001).

The potential vegetation of the region is considered to be evergreen montane forests (Huber, 1995), but the actual vegetation is dominated by savannas with irregularly interspersed forest fragments. This vegetation cover is associated with forest fires without intentional land use change by the sparse human population. Several of the savannas in the region are secondary, originated and maintained by repeated fires (Huber, 1990; Huber, 1995). According to EDELCA (1986) the study region suffers from at least 2000 fires each year, and they are in great part started by the indigenous population, who set fire for multiple purposes. In many places grass savannas with huge charred standing and fallen trunks of the former forests provide evidence of the savannization process in the region (Fölster, 1986; Huber, 1990).

Field work was conducted in a site differentially affected by uncontrolled forest fires occurring at least 5 years before the beginning of this study. There is no registered information about the fire history of the site, and the information gathered was obtained through interviews with residents of the region. The site is covered by unburned primary tall forest (undisturbed forest) and fire-disturbed forest (secondary forest). None of these forests was affected by fire during the study period of six years. The dominant tree species in undisturbed forest are *Dimorphandra macrostachya* Benth and *Euterpe* sp., while in secondary forest predominate *Vismia guianensis* (Aubl.) Choisy, *Myrcia* sp. and *Clusia* sp. (Dezzeo *et al*., 2004). The structure of undisturbed forest shows large differences compared to that of secondary forest (Table I). The soils under both forests are sandy soils, with low pH, base saturation and P concentration, and high concentration of Al (Dezzeo *et al*., 2004). Undisturbed forest did not show any evidence of fire damage. In secondary forest, however, the large and still standing charred stumps, the abundance of charcoal and burned trunks on the forest floor, and the absence of an organic surface layer (Table I), the latter being typical of undisturbed forest in the region, point to the strong impact of fire. Due to the presence of large and still standing burned tree trunks in secondary forest, it is possible to suppose that before the fire event(s) this secondary forest had a rather similar structure to that of undisturbed forest.

Methods

The selected areas of undisturbed and secondary forests were separated ~600m from each other. The undisturbed forest had a closed canopy, while the canopy of secondary forest was very open. At each selected area of both forests, 18 permanent quadrats of 1m^2 each were set in May 1999. The quadrats were established at least 5m apart to guarantee independence between them. The four corners of each quadrat were marked by wooden stakes driven into the ground. In each quadrat all individuals >5cm and <100cm in height were considered seedlings at the beginning of the study. During the initial census in May 1999, each plant within the quadrat was carefully tagged with a numbered aluminium plate and its height measured. Seedlings were identified according to the local name by an experienced field assistant and specimens were collected for plant identification. In most cases the seedlings were identified to the level family or genus. More precise identification is difficult as the flora of the forests of the Gran Sabana is poorly known. Each labelled seedling was assigned to the tree or non-tree plant group. Tree species were defined as those capable of reaching at least 10cm in DBH as adults. In the group of non-tree or understory seedlings were included all small shrubs, lianas and herbs, including members of Pteridaceae, Araceae, Orchidaceae, Poaceae, Cyperaceae, Sellaginelaceae, and Zingiberaceae.

TABLE I
STRUCTURAL ATTRIBUTES OF VEGETATION IN UNDISTURBED FOREST AND FIRE-DISTURBED SECONDARY FOREST

Variable	Undisturbed forest	Secondary forest
[a] Number of species >2.5cm dbh/0.1ha	45	28
[a] Number of trees 2.5-10cm dbh/0.1ha	340	103
[a] Number of trees >10cm dbh/0.1ha	106	13
[a] Basal area >10cm dbh (m^2/ha^{-1})	40	2.0
[a] Basal area <10cm dbh (m^2/ha^{-1})	7.0	2.0
[a] Number of dead standing trees >5cm dbh/0.1ha	32	36
[b] Total biomass (Mg/ha)	411	13
[a] Organic surface layer (Mg/ha)	227	0
[a] Maximum height of the trees (m)	30	16

[a] From Dezzeo *et al*. (2004); [b] from Dezzeo and Chacón (2005).

Every year (from May 1999 to May 2005) censuses were conducted to measure growth of the tagged plants, to count and tag newly recruited seedlings, and to count the previously tagged seedlings that had died. These records give detailed information about the fate of each individual plant in the sample from one year to the next. In May 2004 the census could not be carried out. The collected data was used to evaluate species richness of tree seedlings (number of species per m^2), seedling abundance by plant group (number of stems per m^2), seedling dominance of tree species (number of stems of a species in relation to the number of all other species per m^2), mortality (number of seedlings that died divided by the total number of seedlings censed per m^2), recruitment (the new appearance of seedlings during the inter-census period), and growth (the increase in height of each seedling during the study period). The survival rate of the initial censured seedlings was calculated as the number of seedlings that survived from 1999 to 2005, divided by the number of seedlings present in 1999. The tagged plants >1m in height during the study period were not excluded from the analysis.

Unreplicated forest sampling was used because it was difficult to delimit more plots of disturbed and undisturbed forests presenting exactly the same characteristics. Thus, it must be acknowledged that pseudo-replications could be a limitation in the present study, as in many other published studies related to plant regeneration. However, it is also admitted that the absence of forest replications should not be a serious problem since the plots were delimited for the purpose of identifying major vegetation types and, furthermore, there are spatial and temporal replications within each plot for analysis of seedling dynamics. Hurlbert (1984) recognized that the most common type of controlled experiments in field ecology involves a single replicate per treatment and stated that this is neither surprising nor bad.

Analysis of variance was used to determine whether mean seedling density, recruitment, survival and growth in height differed between sites and whether it changed within sites during the study period. Quadrats were used as replication units and data were log transformed when they did not meet the homogeneity of variance assumptions of ANOVA. A Tukey Honest Significant Difference (HSD) test was used when statistical differences (P<0.05) were found. Growth data did not meet the homogeneity of variance assumptions of ANOVA and data transformations did not remedy this fact. Therefore, for this data a Kruskall Wallis test was used to evaluate site differences. All statistics were computed using Statistica for Windows 6.0 (Statistica, 2001).

TABLE II
ABUNDANCE* AND TREE SEEDLING RICHNESS** IN THE SAMPLED AREA AT THE BEGINNING (MAY 1999) AND AT THE END (MAY 2005) OF THE STUDY

Variable	Undisturbed forest	Secondary forest
Tree seedlings abundance in 1999	26.6 ±9.0 a 1	5.3 ±3.3 b 1
Tree seedlings abundance in 2005	24.5 ±8.8 a 1	6.6 ±3.5 b 1
Non-tree seedlings abundance in 1999	5.2 ±3.6 a A	14.9 ±11.4 b A
Non-tree seedlings abundance in 2005	3.2 ±3.6 a B	11.3 ±5.0 b A
Tree richness in 1999	7.0 ±1.1 a +	3.5 ±2.0 b +
Tree richness in 2005	6.8 ±1.0 a +	3.8 ±2.3 b +

* Mean number of plants/m^2 ±SD. ** Mean number of tree species/m^2 ±SD. Within a row, values sharing the same lower case letter did not differ significantly. Within a column, values sharing the same number, capital letter, or plus symbol did not differ significantly (ANOVA, p<0.05).

Results

Seedling abundance and species richness

Initial tree seedling abundance was significantly higher (P<0.05) in undisturbed forest than in fire affected (secondary) forest. In contrast, initial non-tree seedling abundance was significantly lower (P<0.05) in undisturbed forest compared to that in secondary forest (Table II). Tree seedling abundance remained statistically similar within each forest over the 6-year period, while non-tree seedling abundance decreased significantly (P<0.05) in undisturbed forest, and remained similar in secondary forest.

The undisturbed forest quadrants showed a significantly higher value (P<0.05) of initial tree species richness than that of secondary forest. The tree species richness did not change within the sites over the 6-year period (Table II). At the beginning of the study *Dimorphandra macrostachya* Benth. and *Licania heteromorpha* Bentham were the most abundant seedling species in undisturbed forest, representing 60% of the total tree seedling abundance (Table III). Contrary to undisturbed forest, secondary forest showed no clear dominant species in terms of relative abundance at the beginning of the study. Over the 6-year period, the same group of species in both undisturbed and secondary forest remained as the most dominant species in terms of relative abundance.

In the group of non-tree seedlings, individuals of Poaceae and Cyperacae (monocots species) were not found in undisturbed forest, neither at the beginning nor at the end of the study. In secondary forest, however, the abundance of monocots was 12% at the beginning and 10% at the end of the period. The fern *Pteridium aquilinum* (L.) Kuhn was absent from undisturbed forest, while in secondary forest this species presented an abundance of 9% at the beginning and 8% at the end of the study.

Mortality and recruitment

Over the 6-year study period, the absolute values of survival of the initially counted tree and non-tree seedlings were significantly higher (P<0.05) in

TABLE III
TREE SPECIES THAT COMPRISED AROUND 60% OF THE TOTAL ABUNDANCE IN THE SAMPLED AREA OF UNDISTURBED AND SECONDARY FORESTS AT THE BEGINNING (MAY 1999) AND AT THE END (MAY 2005) OF THE STUDY PERIOD

Species	Relative abundance (%)			
	Undisturbed forest		Secondary forest	
	1999	2005	1999	2005
Dimorphandrama Macrostachya Benth.	39	30	7	8
Licania heteromorpha Bentham.	21	27	-	-
Miconia sp.	-	-	17	14
Myrcia sp.	-	-	16	12
Byrsonima sp.	-	-	9	6
Clusia sp.	-	-	8	13
Vismia guianenesis (Aubl.) Choisy	-	-	7	9

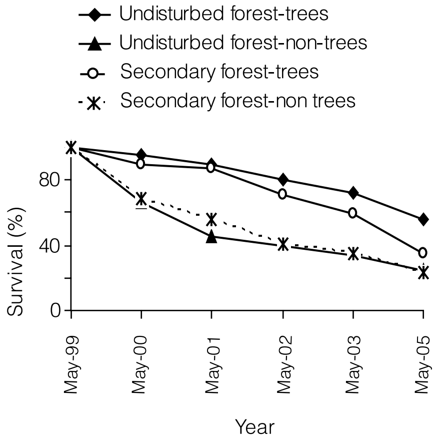

Figure 1. Survival over time for the initial labeled tree and non-tree seedlings in undisturbed and secondary forests.

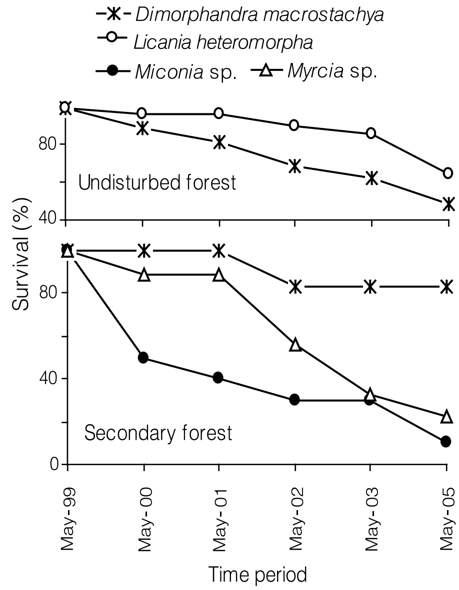

Figure 2. Survival over time for the most abundant species in undisturbed and secondary forests.

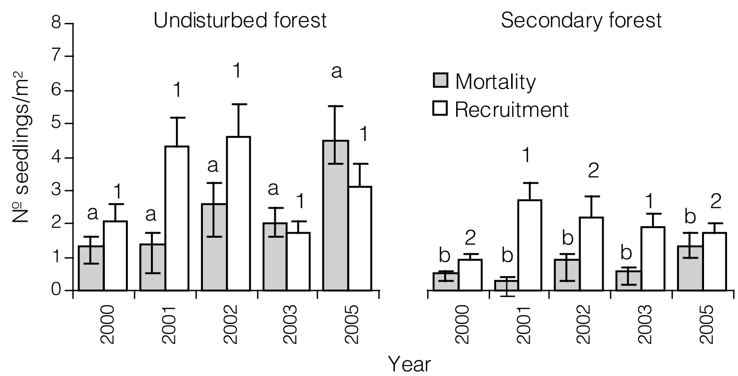

Figure 3. Values (mean ± SE per m²) of the initial censused tree seedlings mortality over the study period and of the newly recruited tree seedlings during the same period in the studied forests. For each year, different letters between forest types indicate significant differences in mortality and different numbers between forest types indicate significant differences in recruitment (ANOVA, *P*< 0.05 or Kruskall Wallis, *P*<0.05).

undisturbed than in secondary forest (Table IV). The survival rate (proportion of the initially counted cohort that survived the 6-year period) of tree seedlings was 56% in undisturbed forest and 34% in secondary forest, while for non-tree seedlings the survival rate was 25% in undisturbed and 23% in secondary forest (Figure 1). In undisturbed forest, the species with the highest initial value of seedling abundance (*Dimorphandra macrostachya*) (Table III) showed a survival rate of 48% (Figure 2). The survival rate of *Licania heteromorpha*, the other important species in undisturbed forest, was around 20% higher than that of *D. macrostachya*. In secondary forest *D. macrostachya* showed very low abundance (Table III) and this abundance showed few changes during the study period (Figure 2).

Absolute values of newly recruited tree seedlings and survival of these new seedlings over time were significantly different (P<0.05) between undisturbed and secondary forests (Table IV). In the case of non-tree species, the mean values of newly recruited seedlings and their survival over time were significantly higher (P<0.05) in secondary forest than that in the undisturbed one (Table IV). Survival rates of newly recruited seedlings (proportion of recruited seedlings alive at the end of the study period) fluctuate between 47-54% for tree seedlings and between 21-34% for non-tree seedlings (Table IV). In undisturbed forest, the highest proportion (86%) of recruited seedlings alive at the end of the study was represented by tree seedlings, whereas in secondary forest the proportion of tree (53%) and non-tree (47%) seedlings at the end of the study were relatively similar (Table IV).

The high mortality of the initially counted and labelled seedlings in undisturbed and secondary forests was in part compensated by newly recruited plants. Considering the values of initial abundance of seedlings and their survival over time, as well as the abundance of the newly recruited seedlings and their survival (Table IV), undisturbed forest lost 19% of their original tree seedling abundance, and 54% of their original non-tree seedling abundance. Secondary forest did not lose tree seedlings, but gained 8% of its original value of tree seedling abundance. This forest, however, lost 54% of its original non-tree seedling abundance.

In undisturbed forest, recruitment was 38-67% higher than mortality in 2000, 2001 and 2002, while in 2003 and 2005 mortality was 15-31% higher than recruitment (Figure 3). In contrast, recruitment in secondary forest was always higher (24-68%) than mortality.

Growth in height

At the start of the study, mean height of the labelled tree seedlings was significantly higher (P<0.05) in undisturbed forest (26.6 ±7.2cm) than in secondary forest (17.7 ±4.1cm). At the end of the study, however, mean height of the

TABLE IV
ABUNDANCE AND MORTALITY OF THE INITIAL LABELED SEEDLINGS AND OF THE RECRUITED SEEDLINGS PER m² OVER THE 6-YEARS STUDY PERIOD FOR TREE AND NON-TREE SPECIES

Tree species	Undisturbed forest	Secondary forest
Abundance of initial seedlings*	26.6 ±9.0 a	5.3 ±3.3 b
Survival of initial censed seedlings*	14.8 ±5.7 a	1.8 ±0.9 b
Mortality rate (%) of initial seedlings	44.3	66.0
New recruited seedlings*	12.7 ±7.8 ab	8.3 ±3.4 b
Survival of new recruited seedlings*	6.8 ±4.9 ab	3.4 ±2.1 b
Mortality rate (%) of new recruited seedlings	46.5	53.1
Survival rate (%) of new recruited seedlings	53.5	46.9
Non-tree species		
Abundance of initial seedlings*	5.2 ±3.6 a	14.9 ±11.4 b
Survival of initial censed seedlings*	1.3 ±0.8 a	3.4 ±2.5 b
Mortality rate (%) of initial seedlings	75.0	77.1
New recruited seedlings*	3.2 ±2.2 a	16.8 ±5.5 b
Survival of new recruited seedlings*	1.2 ±0.7 a	3.8 ±2.4 b
Mortality rate (%) of new recruited seedlings	65.6	79.2
Survival rate (%) of new recruited seedlings	34.4	20.8

* Mean number of plants/m² ±SD.
Different letters in a row indicate significant differences between vegetation types (ANOVA, P<0.05 or Kruskall Wallis, P<0.05).

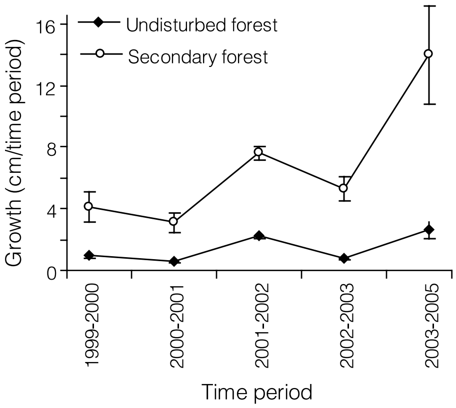

Figure 4. Values of growth (mean ± SE per m^2) in height (cm/year) of the initial censused tree seedlings over time in undisturbed and secondary forests.

initially labelled tree seedlings that survived over the 6-year period was significantly lower (P<0.05) in undisturbed (35.5 ±10.1cm) than in secondary forest (56.2 ±28.6cm). Total growth in height during the 6-year period was considerably higher (P<0.05) in secondary (39.7 ±19.4cm) than in undisturbed forest (7.6 ±2.1cm). Figure 4 shows that growth in height (cm/year) of tree seedlings over the study period was always significantly lower (P<0.05) in undisturbed than in secondary forest. In general, growth in height of the tree seedlings showed both decreases and increases over time (Figure 4).

Discussion

Measurements of seedling dynamics in this study were made in order to determine how survival, recruitment and growth of seedlings are progressing in fire-affected (secondary) forest and in adjacent undisturbed forest, and to test whether the density of tree and non-tree seedlings in the secondary forest become more similar over time to that of the adjacent undisturbed forest. At the beginning of this study, undisturbed forest showed a closed canopy while secondary forest showed a very open canopy and there were large differences in structure between them.

According to the results, the composition of the seedling community in terms of abundance and tree species richness appeared to change very little over the 6-year period in both undisturbed and secondary forests. In secondary forest, seedling abundance and tree seedling richness was significantly lower than those of undisturbed forest (Table II), indicating that the perturbation that considerably influenced the structural attributes of this forest was still substantially influencing the seedling community.

Higher tree seedling species richness and corresponding higher seedling abundance in undisturbed forest compared to the secondary forest are not surprising given the higher richness of tree species (Dezzeo *et al*., 2004) and the higher seed numbers in the soil (Flores and Dezzeo, 2005) of undisturbed forest. Similar patterns of higher seedling species richness and correspondingly higher seedling abundance have also been shown in other old-growth tropical forests (Denslow, 1995; Nicotra *et al*., 1999; Rettenmaier and Fölster, 1999). The tree seedling abundance found in undisturbed forest was very high compared to the range of values per m^2 reported for 5-100cm tall tree seedlings in continuous forests (9.5-17.2) and fragmented forests (5.5-15.3) in Brazil (Benítez-Malvido, 1998), and with the range of values (0.7-6.4 plants per m^2) reported for 10-50cm tall understory woody dicots in old-growth forests of four neotropical countries (Harm *et al*., 2004). Tree seedling abundance per m^2 in secondary forest was significantly lower than that in undisturbed forest, but still lies within the range of seedling abundance reported by Harm *et al*. (2004).

A high abundance of seedlings is a sign of successful seed germination and establishment (Ganesan and Siddappa, 2004). In undisturbed forest, the high values of seedling abundance found in the present study can be associated with the presence of a relatively thick litter layer above the soils of these forests (Table I). Litter influences the microclimate (Fowler, 1988) and nutrient cycling (McClaugherty *et al*., 1985; Cuevas and Medina, 1988) of forest soils, and can potentially increase the establishment of seedlings. According to Molofsky and Augspurger (1992), leaf litter should be considered an important factor in plant establishment and may help maintain higher seedling diversity in many tropical forests. In the case of secondary forest in the present study, the lower values of tree seedling abundance and tree seedling richness compared to undisturbed adjacent forest are probably consequences of several interacting factors.

Although dispersal limitations seem to be unimportant in the secondary forest because the annual seed rain is seven times higher than in undisturbed forest (Flores and Dezzeo, 2005), new plant colonists may confront unfavourable microclimatic conditions due to the very open canopy of the secondary forest. An open canopy is not always beneficial for plant establishment, as it may lead to reduced soil moisture and increased soil temperature, such as occurs along the edges, where the relative humidity and temperature change drastically because of increased insolation and wind penetration (Camargo and Kapos, 1995; Kapos, 1989). This negative effect of an open canopy is probably enhanced in secondary forest due to the absence of the litter layer on the soils of this vegetation type. The presence of leaf litter in gaps or areas with very open canopy reduces the incoming radiation that reaches the soil surface and prevents large increases in soil temperature (Molofsky and Augspurger, 1992).

Another factor that could be interfering with tree seedling establishment and tree seedling richness in the secondary forest is the large abundance of non-tree seedlings (Table II), particularly ferns and monocots grasses (Poaceae and Cyperacea), which can impose barriers for tree regeneration (Aide *et al*., 1996; Cabin *et al*., 2002; Slocum *et al*., 2004).

Monocotyledonea species, particularly Poaceae and Cyperaceae, are the most important species in the savannas of the study region (Dezzeo *et al*., 2004; Ramírez *et al*., 2007). In the secondary forest quadrants of this study, the abundance of individuals of this taxonomic group over the study period suggests that this forest is involved in a savannization process and, therefore, it can be highly sensitive to future fire perturbations.

As mentioned before, time had no significant measurable effect on tree seedling abundance and richness, and on the most abundant tree seedling species in both undisturbed and secondary forests. The main reason for this result is that in the studied forests the mortality rate of initial tree seedlings (44-66%) was more or less balanced by the survival rate of newly recruited tree seedlings (47-54%; Table IV). According to the results, the most abundant species in undisturbed forest (*Dimorphandra macrostachya*) suffered the highest seedling mortality over the study period (~50%), while other species with lower seedling abundance as *Licania heteromorpha* showed lower mortality (~30%; Figure 2). Higher seedling mortality in species with higher seedling abundances has been considered as a community-level compensatory trend in seedling survival (Webb and Peart, 1999).

Tree seedling mortality in secondary forest was higher as compared to mortality in undisturbed forest (Table III). High mortality of light demanding seedlings such as those found in secondary forest has been related to herbivory and drought (Howe, 1990; Nepstad *et al*., 1991; Osunkoya *et al*., 1993). Shupp (1988) reported that because of seed and seedling predation, the probability of surviving to reproductive maturity may be significantly greater for a seed landing in the forest understory than for a seed dispersed into a gap. Competition with herbaceous species could be a significant factor leading to increased mortality in gaps (Dupuy and Chazdon, 2006). However, this cannot explain the higher tree seedling mortality found in secondary forest, because of the mortality of non-tree seedlings was also very high.

The better light conditions in secondary forest have considerably favoured the growth in height of the tree seedlings compared to the growth in undisturbed forest (Figure 2). The positive influence of an open canopy (forest gap) on seedling growth has been associated with relatively high levels of photosynthetically active radiation (Chazdon and Fetcher, 1984; Turner, 1990; Osunkoya *et al*., 1993).

The inter-annual variations in recruitment, mortality and growth observed in Figures 3 and 4 remain as yet unexplained, but are possibly related to inter-annual climatic variations. Unfortunately, no information on rainfall variation in the study site over the 6-year period is available and, therefore, the relationships between rainfall and inter-annual peaks of recruitment, mortality and growth can not be confirmed.

Conclusion

Although the results indicate that in undisturbed forest the behaviour of the seedling community is very dynamic in terms of recruitment and mortality, the few changes registered in the absolute values of seedling abundance, tree seedling richness and growth in height over time seem to indicate that the succession process in the undisturbed forest is, relatively, at a standstill. The differences in seedling dynamics between undisturbed and adjacent secondary forests are related to the fact that the secondary forest showed an open canopy, a soil surface without litter layer and very low abundance of large trees, tree species richness and biomass. The fact that secondary forest gained 8% of its original value of tree seedling abundance over the 6-year period (Table IV) could be considered indicative of some advance in the succession process, although in this secondary forest tree seedling richness did not change significantly (P<0.05) during this time. However, if the high abundance of non-tree seedlings in this forest (~70% of all seedlings) and its small change over the time are taken into account, it can be speculated that recovery of the secondary forest may take even longer, probably until the organic layer on top of the soil can be developed. According to Dezzeo *et al*. (2004) the organic surface layer plays an important role in maintaining the fertility of the soils in undisturbed forests, and their absence on the soils of secondary forest is a critical factor determining the capacity of this vegetation type to recover from fire disturbance. The development of strategies to control the use of fire or the implementation of effective fire suppression practices in the region is of fundamental importance for the forest conservation in the Gran Sabana.

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DINÁMICA DE PLÁNTULAS EN UN BOSQUE NO PERTURBADO Y EN EL BOSQUE ADYACENTE PERTURBADO POR EL FUEGO EN LA GRAN SABANA, SURESTE DE VENEZUELA

Nelda Dezzeo, Saúl Flores y Noemí Chacón

RESUMEN

En la Gran Sabana, al sureste de Venezuela, la conversión de extensas áreas boscosas a un mosaico de bosque, vegetación arbustiva y sabana ("sabanización") es un asunto ambiental crítico asociado con incendios forestales. Poco se conoce acerca del comportamiento de la comunidad de plántulas en bosques no perturbados y en bosques afectados por el fuego en la región. El reclutamiento, supervivencia y crecimiento de plántulas fue seguido durante un período de 6 años en cuadratas permanentes establecidas en bosque no perturbado y bosque adyacente perturbado por el fuego (secundario). Al comienzo del estudio, el bosque secundario mostró valores menores (P<0,05) de abundancia de plántulas y riqueza de plántulas arbóreas que el no perturbado. La abundancia y riqueza de especies de plántulas arbóreas en ambos tipos de bosque variaron muy poco a lo largo del periodo de estudio, lo cual está asociado con el balance parcial entre tasa de mortalidad de plántulas marcadas al inicio del estudio (44-66%) y tasa de supervivencia de nuevas plántulas arbóreas reclutadas (47-54%). Al final del estudio ~80% de las plántulas reclutadas en el bosque no perturbado correspondió a especies arbóreas, mientras que en el secundario la proporción de plántulas arbóreas (47%) y no arbóreas (53%) fue similar. El crecimiento en altura durante el período de 6 años fue considerablemente mayor en el bosque secundario que en el no perturbado (P<0,05). Se concluye que en el bosque no perturbado el proceso de sucesión esta relativamente paralizado, mientras que en el bosque secundario este proceso avanza muy lentamente.

DINÂMICA DE PLÂNTULAS EM FLORESTA NÃO PERTURBADA E FLORESTA ADJACENTE PERTURBADA PELO FOGO NA GRAN SABANA, SUDESTE DA VENEZUELA

Nelda Dezzeo, Saúl Flores e Noemí Chacón

RESUMO

Na Gran Savana, ao sudeste da Venezuela, a conversão de extensas áreas florestais a um mosaico de floresta, vegetação arbustiva e savana ("savanização") é um assunto ambiental crítico associado com incêndios florestais. Pouco se conhece sobre o comportamento da comunidade de plântulas em florestas não perturbadas e em florestas afetadas pelo fogo na região. O recrutamento, sobrevivência e crescimento de plântulas foi seguido durante um período de 6 anos em blocos permanentes estabelecidos em floresta não perturbada e floresta adjacente perturbada pelo fogo (secundário). No começo do estudo, a floresta secundária mostrou valores menores (P<0,05) de abundância de plântulas e riqueza de plântulas arbóreas que a não perturbada. A abundância e riqueza de espécies de plântulas arbóreas em ambos os tipos de florestas que variaram muito pouco ao longo do período de estudo, o qual está associado com o balanço parcial entre taxa de mortalidade de plântulas marcadas no inicio do estudo (44-66%) e taxa de sobrevivência de novas plântulas arbóreas recrutadas (47-54%). No final do estudo ~80% das plântulas recrutadas na floresta não perturbada correspondeu a espécies arbóreas, enquanto que na secundária a proporção de plântulas arbóreas (47%) e não arbóreas (53%) foi similar. O crescimento em altura durante o período de 6 anos foi consideravelmente maior na floresta secundária que na não perturbada (P<0,05). Conclui-se que na floresta não perturbada o processo de sucessão está relativamente paralisado, enquanto que na floresta secundária este processo avança muito lentamente.