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## Growth and development of the thinning canopy in a post-hurricane tropical rain forest in Nicaragua

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### Abstract

The effect of catastrophic disturbance on forest structure was studied for 10 years subsequent to the landfall of Hurricane Joan in 1988. Four sites within the damage area and one control site outside of the area were established in the early 1990s and positions and sizes (DBH and crown height) were measured annually. Results of the study are reported in the context of the debate between equilibrium versus non-equilibrium models of tropical forest dynamics. Equilibrium models imply some sort of niche segregation on a species to species basis, whereas non-equilibrium models emphasise chance and history in the development of canopies. In either case, the details of the dynamics of building and thinning after a disturbance are key to resolve the debate. Physical aspects of the developing canopy began with a severely damaged forest with effectively no canopy at all. Two distinct canopies had developed 4 or 5 years after the disturbance; (1) a larger but diffuse canopy made up of the tress that had survived the hurricane standing and had begun resprouting high in their damaged crowns and (2) a 'thinning canopy' of very densely packed crowns of small individual trees, resulting from the growth of surviving saplings and seedlings and trees that had sprouted near to the ground. Competitive thinning has begun to occur in this dense lower canopy. Since the disturbance, the increase in number of species has been great, ranging from 134 to 208% over what would be expected in a mature forest. Mortality patterns in the thinning canopy suggest that trees are not dying at random and thus supports a niche-based model of forest regeneration. Qualitative analysis of the thinning canopy also suggests that some species have come to occupy the upper position in the canopy (and are thus likely to be competitive dominants) while other species have come to occupy the lower position (and are thus likely to be competitively suppressed). A qualitative model is proposed illustrating where, during the process of regeneration, various authors have emphasized either a niche (equilibrium) or non-niche (non-equilibrium) model. It is suggested that in the building phase of the post-disturbance forest a non-niche interpretation is most appropriate while in the thinning phase a niche interpretation may be warranted. © 2001 Elsevier Science B.V. All rights reserved.

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## 1. Introduction

Attempts to explain the coexistence of large numbers of tree species in tropical forests may be categorized into equilibrium and non-equilibrium explanations (Connell, 1978; Zagt and Werger, 1998). Equilibrium explanations include gap partitioning models (e.g. Orians, 1982; Brokaw, 1985; Denslow, 1987) and models of compensatory mortality (Janzen, 1970; Connell, 1971; Wills, 1996). Non-equilibrium models emphasize chance and historical effects (Chesson and Warner, 1981; Shmida and Wilson, 1985; Hubbell and Foster, 1986), and most recently, incorporate the concept of recruitment limitation (Hurt and Pacala, 1995; Hubbell et al., 1999). It has recently been suggested that "... chance processes contribute highly to the initial species composition of gaps ... [and] ... are probably in most cases strong enough to even out the effect of species-specific growth and survival characteristics. Once the species composition of a patch is determined (soon after gap formation), regeneration will be dominated by predictable processes based on species-specific differences in growth and survival ..." (Zagt and Werger, 1998). Chance processes are largely associated with non-equilibrium explanations while predictable processes are largely associated with equilibrium explanations, in this context. Thus, the interpretation of Zagt and Werger (1998) suggests that both equilibrium and non-equilibrium forces may be at play, but operative at different stages of post-disturbance succession.

The study of light gaps caused by treefalls has been common (e.g. Bauer, 1964; Vandermeer et al., 1974; Denslow, 1980; Pickett, 1983; Barton, 1984; Brandani et al., 1988; Denslow et al., 1990; Brown and Whitmore, 1992), most often associated with the potential for light gaps to act as the disturbance that drives either the equilibrium or non-equilibrium interpretation of species diversity. At a larger scale, periodic storms act to increase the extent and rate of tree falls, sometimes on a massive scale (Blumenstock et al., 1961; Canham and Loucks, 1984; Boucher, 1990; Brokaw and Walker, 1991; Peterson and Pickett, 1995). The pattern of succession following catastrophic storm damage has been of interest both for its own sake and because it may represent a convenient way of understanding post-damage succession

generally, from individual tree-fall to hurricane damage (Vandermeer et al., 1996). Damage from a large and strong storm represents an exceptionally large light gap and is thus one end of a scale that begins with a single tree-fall.

The landfall of Hurricane Joan in 1988 caused extreme physical damage over an extensive area (estimated as 500,000 ha) of the Caribbean coast of Nicaragua (Vandermeer et al., 1990; Yih et al., 1991). Post-disturbance successional processes in this region have been studied since 1989 (Boucher et al., 1994; Vandermeer et al., 1995, 1996, 1997, 1999; Boucher, 1997; Boucher and Mallona, 1997; Granzow et al., 1998), concentrated in five locations, four within the area of damage and one 'control' site well outside of the damage area, as discussed more fully in Section 2.

The pattern of early post-storm succession can be thought of as a two stage process (Vandermeer et al., 1996) in which the damage event leads to initial building of a low-statured, but very dense canopy, followed by the thinning of individuals from that canopy through the process of competition (Fig. 1). The original forest contains the upper canopy and the advanced regeneration — the seedling and sapling layer. After the hurricane, the damaged forest contains a few standing trees that begin resprouting high above the ground, plus felled trees that begin resprouting at about the same general height as the saplings that survived the hurricane. During the building phase (also called the 'innovation phase' (Oldeman, 1990), or the 'stand initiation stage' (Oliver and Larson, 1990), or sak'aab by some Mayans (Chen, 1987)), growth is rapid for all individuals since the entire area is bathed in light. But rapidly the trees that resprouted at a relatively low height, the surviving saplings, and some of the faster growing seedlings form a dense canopy at a much lower height than the original canopy. In this dense canopy it can be assumed that there is much competition for light.

As this canopy develops, some individuals will come to dominate while others will become suppressed, due to the normal processes of competition (mainly for light, although root competition may also be important) (Westoby, 1982; Weiner and Thomas, 1986; Weiner, 1990). Since this canopy is where competition will eventually act to thin the populations to some density approximately equal to the original stem density, we refer to it as the 'thinning canopy' or

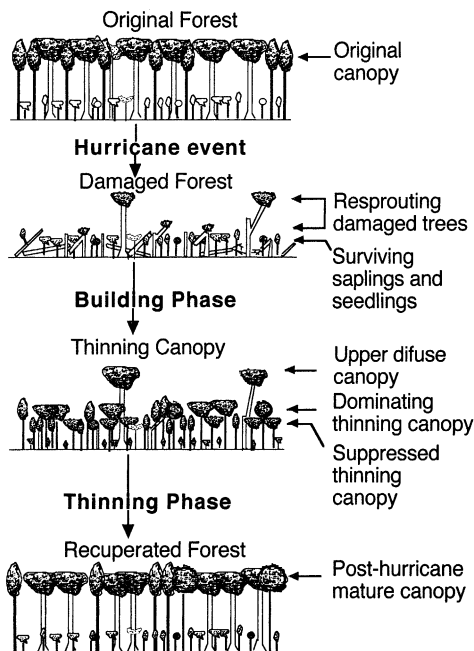


Fig. 1. Diagrammatic representation of the development and dynamics of the thinning canopy. The top diagram represents the structure of the forest before the hurricane. The second diagram shows the intense physical damage experienced by the forest from the hurricane. The third diagram is after the thinning canopy has been 'built' (after the building phase). Finally the fourth diagram shows the recuperated forest, with the same physical structure as the original canopy, but with a different set of species and a different distribution of individuals within the species. The absence of such features as a mid story or light gaps is a result of the attempt to simplify the explanation of post-hurricane succession and does not imply that such complicating features are not important.

the 'thinning phase' (also called the 'aggradation phase' (Bormann and Likens, 1979; Oldeman, 1990), or the 'stem exclusion stage' (Oliver and Larson, 1990), or Kambal-hubche' by some Mayans (Chen, 1987)). As the process of thinning begins, we can expect that within the thinning canopy it will be possible to identify two subcanopies, one associated with the individuals that are beginning to dominate the competition process and the other associated with the individuals that are being suppressed by competition. All of these ideas are illustrated in Fig. 1.

As we have argued elsewhere (Vandermeer et al., 1996) the damage event, as it applies to ecological processes, is most conveniently thought of not as the

result of the hurricane alone, but rather as the combination of initial damage plus the building phase. We propose that the growth of individuals to form the thinning canopy (the building phase) is a random process while the differential growth and survival of individuals as the thinning canopy grows are species-specific processes. We have already presented evidence that the building phase is a random process (Vandermeer et al., 1996) but in the present work we document that there are species-specific aspects of growth and survivorship involved with the early stages of thinning.

## 2. Methods

An initial expedition was made to the area in February of 1989 and two of the permanent plots were established at this time (two of the three plots at the Bodega site). Another site was visited in 1989 and incorporated into the study for a 4-year period (Vandermeer et al., 1990, 1995, 1996), before the permanent plots there were abandoned because of vandalism. We do not report on that site in the present manuscript.

In February of 1990 six plots (100 m × 10 m) were located in two sites chosen to represent extremes of hurricane damage, one in the center of the damage area (Bodega) and one near the edge of the damaged area (Fonseca) (Fig. 2). The three plots at each of the sites are separated by at least 500 m and thus sample slightly different forests. Each plot was given an arbitrary name, Ernesto, Colibri, and Katarina at Bodega and Judy, Luvi, and Molly at Fonseca. Two of the plots at Bodega were originally censused in the pilot study in February of 1989. In 1994 two additional sites were added, with a single plot (50 m × 30 m) at each. These are the La Union site and the Loma de Mico site. In 1996, for comparative purposes, two additional plots (50 m × 30 m) were established at a site well outside of the damaged area (Kurinwás) (Fig. 2).

All trees greater than 3.2 cm DBH (10 cm in circumference) in all plots were located, identified, permanently marked and measured. Identifications were initially made in the field, verified later in the herbarium, and voucher specimens collected for all species and deposited in herbaria (HNMN, MICH,

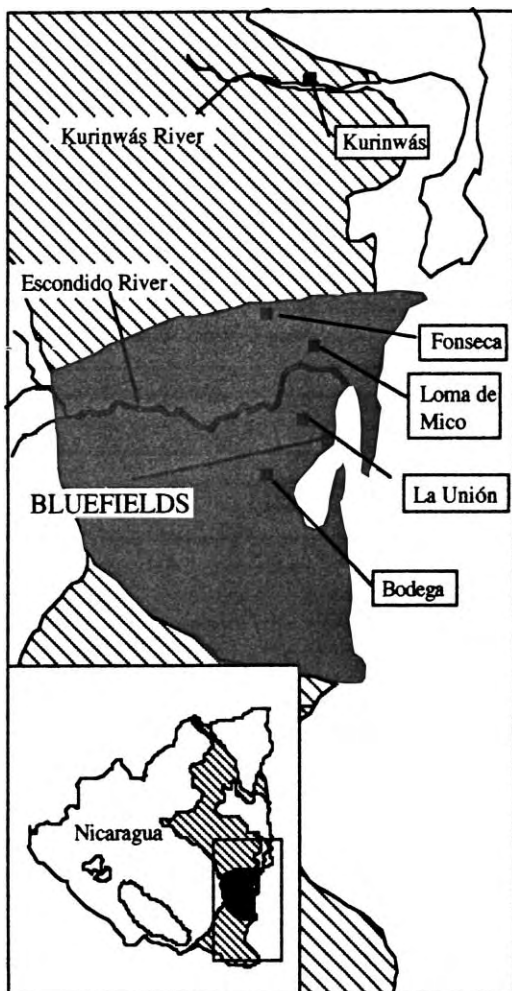


Fig. 2. Location of study sites, area of intensive damage from Hurricane Joan (shaded area) and extent of original lowland rain forest (hatched area).

and INB). Trees were marked with a small numbered aluminum tag affixed with an aluminum nail. The position at which breast height diameters were measured was indicated with spray paint. The height of the tallest living foliage on the tree being measured, was measured with 15 m telescoping poles for small trees and with a hypsometer for trees greater than 15 m, at all sites save Kurinwás. All trees have been measured once per year in 1990–1998 (always in February or March), except those in the control plots (Kurinwás) which were measured once only, in 1996.

Numbers of individuals and of species are all represented as species per 0.1 ha, the size of most of the plots. At the Kurinwás, La Unión, and Loma de Mico sites each 50 m × 30 m plot was 1.5 times the size of the plots at the other sites. Species richness was thus calculated as the average of all combinations of two of the three 50 m × 10 m subplots for each of the 50 m × 30 m plots (thus each calculation was of the number of species per 0.1 Ha). Pooling all plots at all sites, a total of 3140 individual trees were marked and 256 species encountered over the course of this 9 year study.

It is worth commenting on some of the peculiarities of each of the four main sites in the study. Fonseca is located about 5 km east of the Kama River. When the permanent plots were set up they were in a matrix of extensive forest. In the past 10 years forest clearing has been massive and today the permanent plots stand in an island of forest bordered by pastures and migratory slash and burn agriculture. While there is ostensibly a 100 m border of forest around the three permanent plots, thus making an island of forest perhaps 1500 m in diameter, at some points trails and roads come quite close (within 10 m) to the plots. A small fire in 1995 damaged the first 10 m of the third transect (Molly), and occasional vandalism (tags removed from trees) has been experienced in the second of the three plots (Judy). The soils at Fonseca are generally well drained.

Loma de Mico is on the edge of a large north–south upland area that had been cleared for pastures in the 1950s. The forest is in a low-lying area adjacent to this pasture and the plot is within an extensive matrix of forest extending eastward from the pastures. The soils are poorly drained and the area is frequently inundated during the wet season, although it is not classified by local people as a swamp forest. There is an obvious preponderance of the palm *Astrocaryum alatum* and an abundance of the economically important tree *Carapa guianensis*, both of which are species commonly associated with poorly drained areas (McHargue and Hartshorne, 1981; Hartshorn, 1983).

The plot at La Unión is located about 1 km from the banks of the Caño Negro River. The forest is located on a natural island of well-drained soils in a sea of swamp forest (dominated by *Raphia taedigera*). While there has been much clearing in the area for agriculture, the area in which the plot is located is

approximately 30 ha, although its natural state is as an island of upland forest in a sea of swamp forest. The surrounding swamp forest suffered a severe fire in 1989 as a consequence of the hurricane damage (Urquhart, 1997), although the forest outside of the swamp did not burn. Occasional acts of vandalism (tag removal) have occurred at this site also. The plot at this site is located on the leeward side of a small hill, which probably afforded substantial protection from the most severe effects of the hurricane (Vandermeer et al., 1996).

The plots at Bodega are located about 3 km south of the Kukra River, and are within a matrix of forest that was very extensive in 1989 but has been somewhat degraded since that time. A 100 m border around the area where the plots are located maintains a continuous forest matrix at least 1500 m in diameter and the islands of agriculture around the area have not yet completely fragmented the remaining forest. The plots are located about 3 km from the banks of the Kukra River, on well-drained soil. One of the plots (Katarina) is located on the border of an extensive swamp (originally dominated by *Pterocarpus officianalis*) and has been repeatedly subjected to fires spreading out from the now degraded swamp. As a consequence, that particular plot has had its ultimate 30 m abandoned, and is thus only 70 m long. Projections of species per 0.1 ha for Katarina were made with a power function ( $S = aA^b$ , where  $S$  denotes the number of species and  $A$  is area) and a log function ( $S = a + b \log(A)$ ) (Condit et al., 1996; He and Legendre, 1996). The power function always gave a larger prediction than the log function, so the average value of the two was used as an estimate of the number of species per 0.1 ha for that damaged plot.

### 3. Results

#### 3.1. Physical aspects of the thinning canopy

The density of stems (>3.2 cm DBH) continued increasing rapidly for the first 5 or 6 years after the hurricane, but has leveled off and begun to decrease within the past 3 years (Fig. 3a). The increase in numbers of individuals was only partially due to the invasion of pioneers, as discussed below. Most of the increase was from resprouting individuals that were

damaged in the hurricane (Vandermeer et al., 1995), and saplings and seedlings that had survived the hurricane.

The physical aspects of the canopy can be most easily visualized by the distribution of heights of individual trees. In Fig. 4 heights of individual trees are plotted against position in the plot (where position is taken as the spatial point along the long axis of each of the plots), for all four sites. When heights were first measured in 1994, there was a clear pattern that included a low-statured dense canopy at approximately 7 m high, plus an upper diffuse canopy that ranged from 8 to 30 m. The diffuse upper canopy consisted of the trees that survived the hurricane standing and began the process of resprouting high up on their trunks or damaged crowns. This canopy provided a diffuse shade below. The lower canopy consisted of the trees that had resprouted from fallen individuals, from individuals that had been truncated below 7 m, and from the seedlings and saplings that had survived the hurricane. The lower canopy had developed under the diffuse shade of the upper canopy, a shade that was perhaps effective in creating patches of vine-free territory in which the individuals of the lower canopy could thrive. Aerial photographs taken in 1989 and 1994 in the vicinity of Bluefields (Fig. 5a and b) show the development of these two canopies clearly, from the extremely damaged forest with many trunks still standing in 1989 (Fig. 5a) through the individual trees emerging from what appears to be a lower uniform canopy (Fig. 5b). The standing trunks (Fig. 5a) formed the diffuse upper canopy and the resprouting of felled trees and growth of saplings and seedlings formed the low-statured thinning canopy (Fig. 5b). An aerial photograph taken in 1999 (Fig. 5c) shows how the distinct two canopy structure has changed, with the taller trees of the lower canopy growing to merge with the original upper canopy.

The general temporal pattern for the thinning canopy, visible qualitatively in the data for Bodega (Fig. 4d), is for the canopy to slowly increase in average height, and for the spread around that average height to also increase. This is as expected from the basic ideas of dominance and suppression (Weiner, 1990). Some trees are beginning to spread above the rest of the canopy, others remain below the canopy. The first category may be those that are 'dominating' in the competitive process, while those below may be

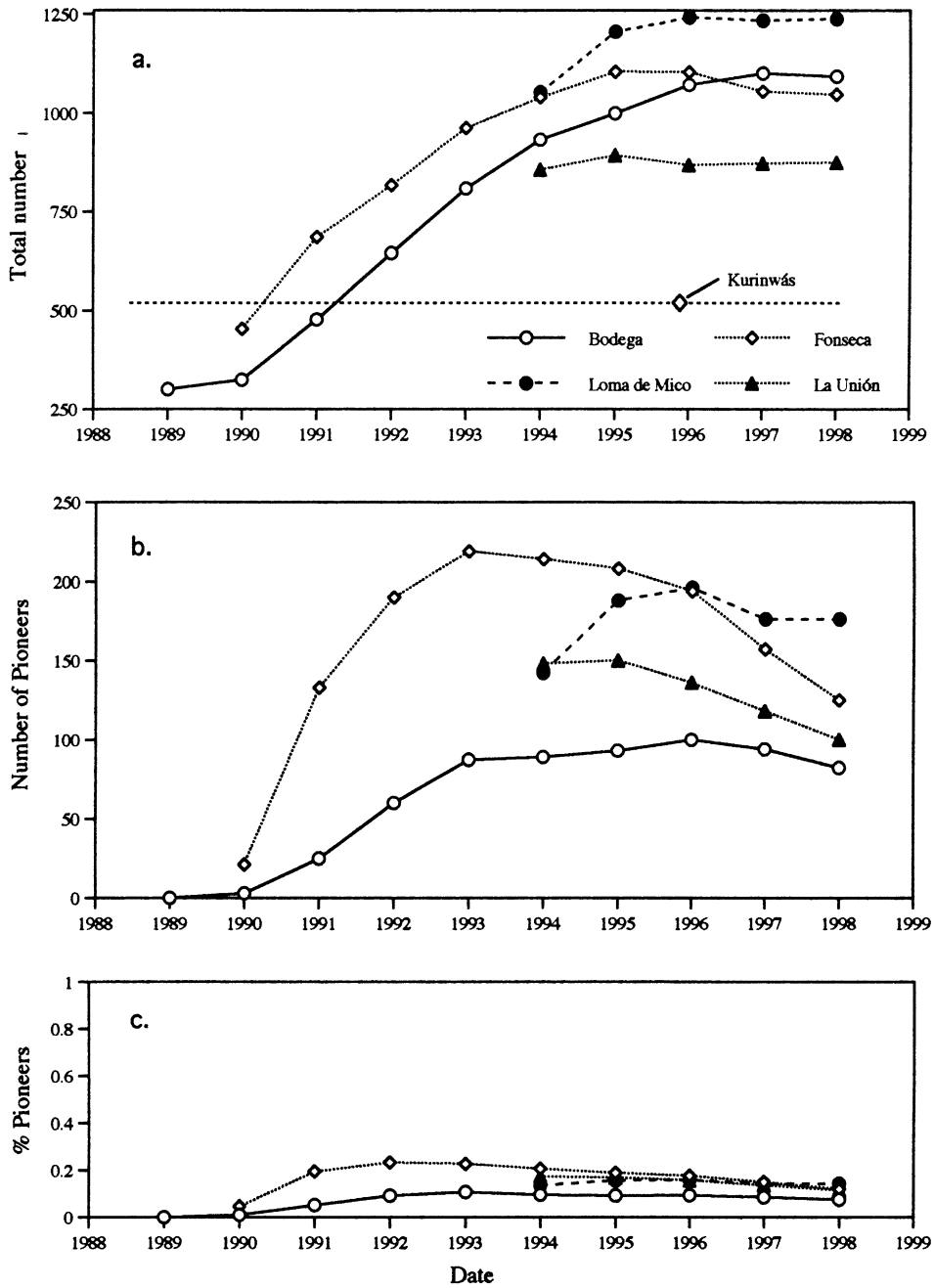


Fig. 3. Number of trees/ha (stems > 3.2 cm DBH) in each year of the study. (a) All species at each of the five sites. (b) Number of individuals of pioneer species at each of the four damaged sites (note difference in ordinate scale in comparison with graph in a). (c) Proportion of pioneers — number of individuals belonging to pioneer species divided by total number of individuals in the plot.

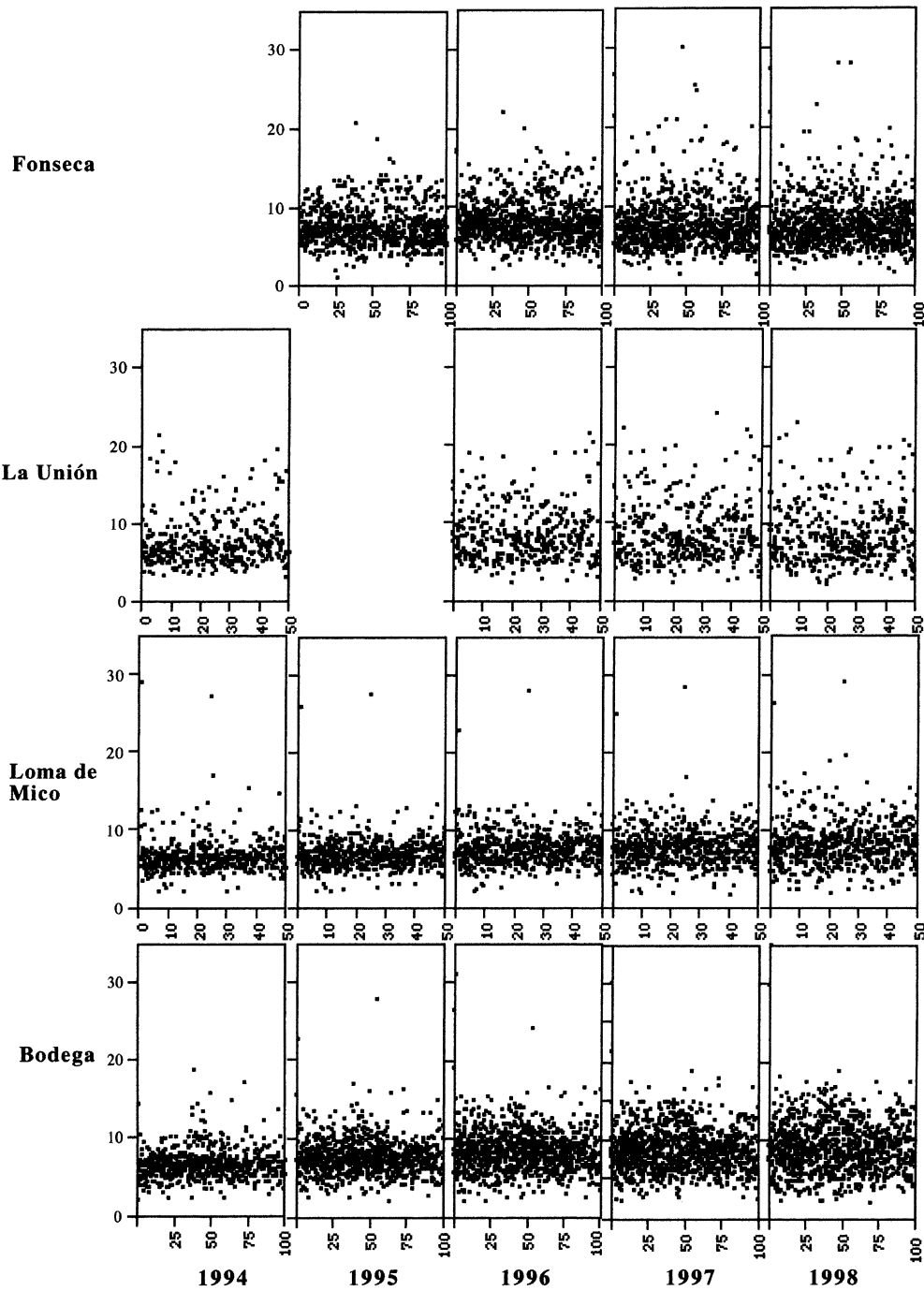


Fig. 4. Graphs of height vs. position along the long axis of the plot (100 m for Fonseca and Bodega, 50 m for La Unión and Loma de Mico). The basic tendency for higher variance as time progresses is obvious at all sites. Heights were not taken for all sites in 1994 and 1995. Figures for Loma de Mico and Bodega for 1994 and 1995 are only partially complete, representing sub samples (not random, but not biased with respect to height) in each year. The subsamples from 1995 were significantly smaller than those for 1994, explaining the obvious lowered density of points for 1995.

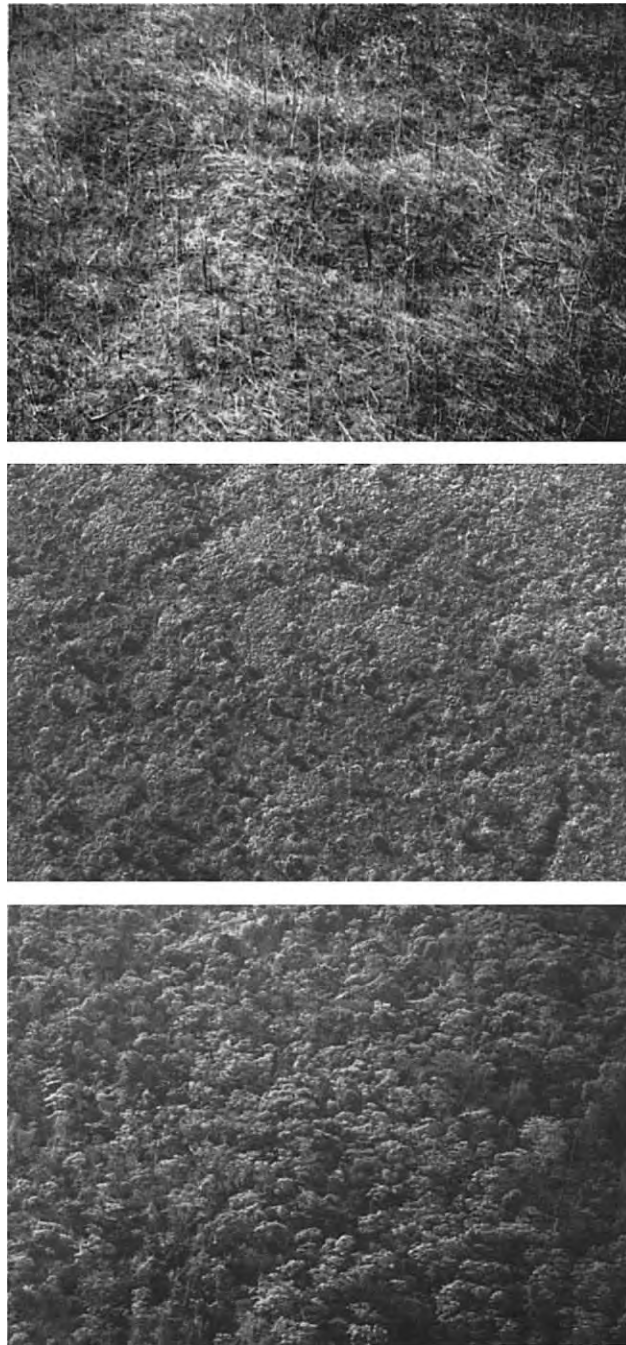


Fig. 5. Aerial photographs of canopy near Bluefields. Top photo is of the forest in February of 1989, four months after the hurricane. The extent of physical damage is obvious. Middle photo is of the forest in February of 1994, 5 years after the hurricane. The pattern of emergent trees standing above a relatively uniform canopy is obvious. The emergent trees represent the individuals that survived the hurricane standing and began resprouting high in the canopy. The uniform canopy below them is the dense thinning canopy that has developed after 6 years of post-hurricane succession. Bottom photo is of the forest in February of 1999, 10 years after the hurricane. Division into a thinning canopy and emergent trees is no longer obvious (see text).



becoming ‘suppressed’ by that same competitive process. Such an analysis is most commonly applied to plant monocultures (Westoby, 1982; Weiner and Thomas, 1986; Weiner, 1990), but is equally appropriate here, except for the species that are truly understory tree species. A key question, discussed in a later section, is whether the species composition of the ‘dominating’ half of the canopy is the same as that of the ‘suppressed’ half, something we would expect if a tree’s competitive success in the thinning canopy is random with respect to its identity. Of course all species that are by nature understory species will fall out of this analysis as ‘suppressed’ species. As of the present date the thinning canopy is still short enough that most of these understory trees are probably still well below their maximum height.

Furthermore, it is clear that the trees that made up the upper diffuse canopy in 1994 have slowly been incorporated into the upper half of the thinning canopy as the larger of the trees making up the thinning canopy grow. It appears that the larger trees of the thinning canopy grow more rapidly than the smaller trees in the upper diffuse canopy. In the present time it is difficult to distinguish the upper diffuse canopy from the lower thinning canopy, and we shall simply refer to the overall canopy as the thinning canopy when talking about its status in 1998.

The mean tree height, which gives a measure of the mean height of the general canopy, is shown for all four sites in Fig. 6. As reflected in the raw data (Fig. 4), mean heights have been increasing rapidly, at a rate of about 0.5 m per annum. The canopy height (mean tree height) in 1994 was 7.1 m, whereas today the mean for three of the sites (eliminating Fonseca — see below) is 8.8 m. More interesting, from the point of view of competition, is the vertical spread of the canopy. Using the Gini coefficient (Weiner and Thomas, 1986) as a measure of vertical spread, it is evident that the spread has been increasing (Fig. 7), as would be expected if some of the trees are dominating and others becoming suppressed (the Gini coefficient measures the relative equality of the distribution, so it decreases as the variability increases). In all of the above it is clear that Fonseca is an unusual site, most notable in Figs. 4 and 6, where it is alone showing a non-monotonic relationship of average height over time. The dramatic decline in 1997 is most likely due to the effects of Hurricane Caesar which passed over the coast at

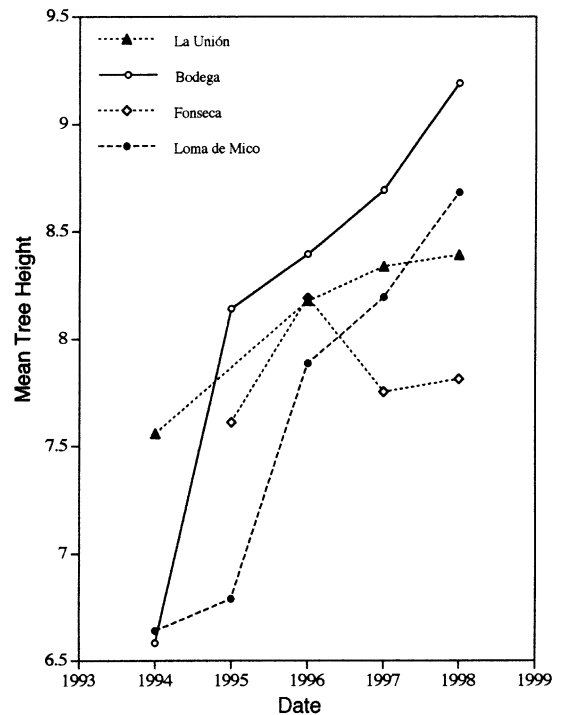


Fig. 6. Mean tree heights as a function of time. The decline at the site Fonseca is probably due to the effects of Hurricane Caesar (see text).

almost exactly the same latitude as Fonseca in late 1996 (Ruiz, 1997). During the data collecting of 1997 it was obvious that there had been some storm damage, although much less than the damage from Joan in 1988. Local people also reported that the forest had been damaged by the hurricane, and we are convinced that the unique nature of Fonseca, visible in both Fig. 4a and Fig. 6, is due to this particular disturbance event.

### 3.2. The role of pioneers in the thinning canopy

Our earlier work emphasized the direct regeneration hypothesis. This hypothesis states that post-disturbance succession will proceed to form the mature canopy from the existing trees, without significant intervention by pioneers (Vandermeer et al., 1989, 1995; Boucher, 1990; Yih et al., 1991). This hypothesis is to be contrasted with earlier expectations that the very large light gap opened up by the hurricane would provide an ideal site for the dominance of

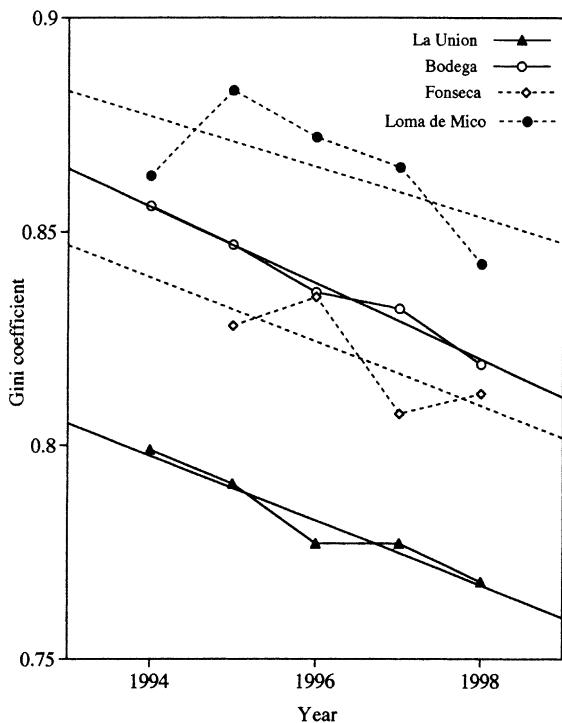


Fig. 7. Gini coefficient of tree heights as a function of time. Straight lines are linear regressions at each of the four sites.

pioneering species, and that the successional process would begin with a forest composed mainly of such species.

Of the many pioneer species easily observable along streams and in old agricultural areas near the study sites, only 10 species were actually observed in the permanent plots — *Castilla elastica*, *Cecropia insignis*, *Cecropia obtusifolia*, *Croton smithianus*, *Guettarda combsii*, *Isertia haenkeana*, *Miconia argentea*, *Ochroma pyramidale*, *Piper auritum*, and *Solanum rugosum*. Other pioneer species never occurred in the permanent plots despite their abundance in nearby open areas — e.g. *Cordia alliodora*, *Tabernamontana* sp., *Miconia serrata* and *Miconia argentea*. Of the 10 pioneer species, the only ones that occurred in large numbers were *Cecropia obtusifolia*, *Croton smithianus*, *Guettarda combsii*, *Isertia haenkeana*, and *Piper auritum* (Table 1). Furthermore, it is not possible to generalize about their occurrence, since each site had a characteristic pattern of pioneer influx. In Bodega *Croton smithianus* and *Isertia haen-*

*keana* almost totally dominated the pioneer community. In La Union *Cecropia obtusifolia* and *Piper auritum* were the two dominants. In Loma de Mico *Guettarda combsii* was by far the most abundant, with *Croton smithianus* and *Isertia haenkeana* common. In Fonseca *Croton smithianus* was the most abundant, with *Cecropia obtusifolia* and *Isertia haenkeana* common.

Each of the five common pioneers has peculiar natural history characteristics. *Cecropia obtusifolia* is bird and bat dispersed, grows to upper canopy heights and appears to be able to maintain itself in older canopies if it is initially able to get above the thinning canopy. It has a characteristic association with ants (Ferguson et al., 1995) enabling it to grow relatively uninhibited by vines, which are attacked and killed by the ant mutualists. *Croton smithianus* also grows to upper canopy height if in appropriate circumstances, and is wind dispersed. *Guettarda combsii* is bird dispersed and seems capable of maintaining itself in a closed canopy forest situation, contrary to usual expectations of pioneering species. We include it as a pioneer simply because of its common occurrence in nearby open agricultural areas. *Isertia haenkeana* is most commonly seen as a large shrub in open areas, but in the forest it attains the status of a small tree, seemingly not having the capability of getting above even a relatively low canopy. It is bird dispersed and evidently not very shade tolerant. *Piper auritum* is dispersed by bats and, like *Guettarda combsii*, seems capable of surviving under low light conditions.

It is worth emphasizing that these 10 pioneers, and even the five most abundant of them, never came close to dominating the growing canopy. In Fig. 3 we plot the number of stems over time for (a) total number of stems of all species, (b) number of stems of the 10 pioneer species, and (c) the percentage of pioneers over time. It is clear that after the 10 year period in question, the pioneers are dying, as expected (Fig. 3b). But most importantly, these pioneers never represented a significant fraction of the stems growing to become the thinning canopy (Fig. 3c). In Fig. 3a we also have plotted the stem density of the site at Kurinwas (not damaged by the hurricane), for comparative purposes. Presuming the stem density does not change significantly over such a short time span in an old growth forest, we have only censused the plots at Kurinwas once.

Table 1  
Abundance (number of individuals per hectare) of pioneer species at all sites

Site	Date	<i>C. elastica</i>	<i>C. insignis</i>	<i>C. obtusifolia</i>	<i>C. smithianus</i>	<i>G. combsii</i>	<i>I. hankeana</i>	<i>M. argentea</i>	<i>O. pyramidalis</i>	<i>P. auritum</i>	<i>S. rugosa</i>
Bodega	1989	0	0	0	0	0	0	0	0	0	0
Bodega	1990	0	0	0	0	0	0	0	0	0	3
Bodega	1991	0	0	0	20	0	1	0	0	0	4
Bodega	1992	0	1	4	42	0	9	0	0	0	4
Bodega	1993	0	1	6	54	0	22	0	0	0	4
Bodega	1994	0	1	6	52	0	29	0	0	0	1
Bodega	1995	0	1	7	53	0	30	0	0	1	1
Bodega	1996	0	1	7	55	0	34	0	0	2	1
Bodega	1997	0	2	5	54	0	29	0	0	4	0
Bodega	1998	0	2	3	49	0	24	0	0	4	0
La Un.	1994	2	4	84	2	0	6	0	2	48	0
La Un.	1995	2	4	82	0	0	6	0	2	54	0
La Un.	1996	2	4	74	0	0	6	0	2	48	0
La Un.	1997	2	2	58	0	0	6	0	2	48	0
La Un.	1998	0	2	46	0	0	6	0	0	46	0
LdM	1994	0	0	2	40	86	34	0	0	0	0
LdM	1995	0	0	2	40	126	40	0	0	0	0
LdM	1996	0	0	4	40	130	40	2	0	0	0
LdM	1997	0	0	2	40	122	30	2	0	0	0
LdM	1998	0	0	2	40	130	22	2	0	0	0
Fon	1990	0	2	4	15	0	0	0	0	0	0
Fon	1991	0	3	22	98	0	2	0	0	1	7
Fon	1992	0	3	35	126	10	11	0	0	1	4
Fon	1993	0	3	41	136	14	21	0	0	0	4
Fon	1994	0	3	44	117	17	32	0	0	0	1
Fon	1995	0	3	45	107	17	36	0	0	0	0
Fon	1996	0	2	39	98	17	38	0	0	0	0
Fon	1997	0	2	30	72	17	36	0	0	0	0
Fon	1998	0	1	18	57	17	32	0	0	0	0

### 3.3. Mortality patterns in the thinning canopy

The calculation of expected mortality, under the assumption of randomness, was as follows: for each of the four sites all actual cases of mortality were registered for the years 1996, 1997, and 1998. Population densities of each species were calculated based on an individual appearing in the yearly census in 1995, 1996 and/or 1997 (recall that individuals appear in the census when they reach a size of 3.2 cm DBH). General probability of mortality was calculated as the total 3 year mortality count (all mortality records of all species) divided by the total 3 year population density (number of individuals of all species alive in at least 1 of the 3 year census period). The population density of each species was multiplied by this expected mortality to determine the expected mortality of each species in the community. The analysis of mortality was aimed at testing the null hypothesis that individual trees die independently of their species identity, after the pioneer species had been eliminated from consideration. In the overall study we encountered only 10 species that clearly fall into the pioneer category (see above). These 10 species were eliminated from all data sets before initiating the data analysis of mortality patterns.

Goodness of fit tests were performed with a standard  $\chi^2$ -test, where expected categories were lumped until at least five mortality events were expected in a given category (species with fewer than five mortality events were lumped with other species with fewer than five mortality events and the expected mortality of those two or more species was compared to the actual mortality of those two or more species — for lumping, species were selected based on the number of mortality records, not on species identity). Degrees of freedom were calculated as two less than the number of categories used, the extra being because the mortality rate was estimated from the data (Sokal and Rohlf, 1981). At three of the four sites we reject the null hypothesis — trees are not dying randomly with respect to their species identity (Table 2).

Some species that do not fall within the limits of the original expectation from competitive neutrality are shown in Table 3. In no case did we observe a species with a reversal in bias from one locality to another, that is, each species had either greater than expected

Table 2

Analysis of mortality patterns for the four sites in this study. A significant chi square indicates deviation from the community drift hypothesis

Site	Chi square	Probability	df
Loma de Mico	6.048	>0.10	5
La Union	14.63	<0.01	4
Fonseca	210.74	<0.001	18
Bodega	30.26	<0.001	10

mortalities or less than expected mortalities at all sites in which it occurs.

In the case of Fonseca we see the overwhelming importance of *Goethalsia meiantha*, which exhibited much more mortality than expected by chance. If the analysis is repeated with this species removed, statistical significance becomes marginal ( $\chi^2=16.04$ , d.f.=10,  $0.1>P>0.05$ ). According to local informants this species is something of a pioneer, occurring in secondary forests and along streamsides and perhaps belongs in the pioneer category in the first place. Indeed according to these data it would appear to be a species whose place in the successional sequence has now passed. However, other authors report significant densities of the species in what is assumed to be old growth forests (Hartshorn, 1983; Lieberman et al., 1985).

The data from Bodega are especially influenced by *Vochysia ferruginea*, where eight mortalities were expected and only two observed. However, after eliminating this species from the data set the analysis remained significant ( $P<0.05$ ). *Vochysia ferruginea* is well known as a species with unusual behavior in this forest (Vandermeer et al., 1990; Boucher et al., 1994; Boucher and Mallona, 1997), with height and diameter increments that continue at a rapid rate even as the individual becomes larger. It is, as we have noted elsewhere (Boucher et al., 1994), neither in the obvious pioneer class nor in the obvious primary forest class, but rather appears to occupy its own special niche.

The La Union site is obviously influenced by the species *Hyeronima alchorneoides*, understood from other literature to be a species of old growth forest (Clark and Clark, 1992; Clark et al., 1993). Yet, according to Brokaw (personal communication) the species is highly heliophytic. It could be that the large

Table 3

Species with densities greater than 100 stems/ha that contributed to the significant chi squared values. Bold type indicates those species with lower than expected mortality, normal type those species with higher than expected mortality

Site	Species	Actual density	Expected mortality	Observed mortality
Fonseca	<i>Goethalsia meiantha</i>	45	5	20
Fonseca	<i>Croton schiedanus</i>	21	2	5
Fonseca	<i>Ardisia</i> sp.	13	1	4
	Total		8	29
Fonseca	<i>Hirtella guatemalensis</i>	18	2	0
Fonseca	<i>Galipea granulosa</i>	48	5	3
Fonseca	<i>Pseudolmedia spuria</i>	28	3	0
Fonseca	<i>Vochysia ferruginea</i>	65	7	3
	Total		17	6
Bodega	<i>Amaioua corymbosa</i>	20	1	4
Bodega	<i>Ardisia</i> sp.	15	1	3
Bodega	<i>Vismia macrophyllum</i>	18	1	3
	Total		3	10
Bodega	<i>Cupania glabra</i>	59	4	2
Bodega	<i>Miconia prasina</i>	74	6	3
Bodega	<i>Protium schippii</i>	36	3	0
Bodega	<i>Qualea paraensis</i>	42	3	0
Bodega	<i>Rinorea squamata</i>	56	4	1
Bodega	<i>Vochysia ferruginea</i>	104	8	2
	Total		28	8
La Union	<i>Hyeronima alchorneoides</i>	29	2	7
La Union	<i>Cordia bicolor</i>	7	1	3
	Total		3	10
La Union	<i>Lacistema aggregatum</i>	18	2	0
La Union	<i>Guatteria diospyroides</i>	20	2	0
La Union	<i>Casearia sylvestris</i>	23	2	0
La Union	<i>Dendropanax arboreus</i>	90	8	5
	Total		17	5

numbers of resprouts following the hurricane were unable to survive the dark understory of the thinning canopy. Thus, the standing adults that survived the hurricane were the survivors during the course of this study while the mortalities were concentrated among the smaller saplings and resprouts that could not survive the shade of the dense thinning canopy.

### 3.4. Qualitative analysis of the 1998 canopy

Considering the canopy in 1998 only, we can ask whether particular species tend to occupy particular positions in the canopy, or whether position in canopy is a random feature with respect to species identity. For each species at each of the four sites, number of individuals in the upper half of the canopy

(presumably the competitively dominating half) were tabulated separately from number of individuals in the lower half of the canopy (presumably the competitively suppressed half), where the upper half was defined as above the height of the median individual (of all individuals) at a particular site. Each species could then be classified as occurring more commonly in the upper half of the canopy or more commonly in the lower half of the canopy, based on how many of its individuals occurred in either upper or lower half. If more than 67% of the individuals occurred in the upper half of the canopy, the species was classified as an upper canopy species. If more than 67% of the individuals occurred in the lower half of the canopy, the species was classified as a lower canopy species. All other species were classified as 'medium', which is

Table 4a

Qualitative analysis of common species that are uniquely of either the upper half of the canopy (U) or lower half of the canopy (L)

Species	Fons.	LdeM.	Union	Bod.	summ	niche
<i>Guatteria recurvisepala</i>	U	U		U	UUU	heliophyte
<i>Vochysia ferruginea</i>	U	U		U	UUU	old growth canopy
<i>Croton smithianus</i>	U	U	–	U	UUU	pioneer
<i>Cecropia obtusifolia</i>	U	–	U	–	UU	pioneer
<i>Simarouba amara</i>	–	U	–	U	UU	heliophyte
<i>Casearia arborea</i>	–	–	U	U	UU	old growth canopy
<i>Swietenia macrophylla</i>	U				U	old growth canopy
<i>Miconia trinerva</i>		U			U	heliophyte
<i>Xylopia sericophylla</i>	–	U	–	–	U	heliophyte
<i>Carapa guianensis</i>	–	U		–	U	old growth canopy
<i>Trichospermum galleotii</i>		U		–	U	old growth canopy
<i>Hyeronima alchorneoides</i>			U	–	U	old growth canopy
<i>Cespedesia macrophylla</i>			U	–	U	old growth subcanopy
<i>Jacaranda copaia</i>	–	–	U	–	U	heliophyte
<i>Pourouma bicolor</i>			U	–	U	heliophyte
<i>Welfia regia</i>			U	–	U	old growth subcanopy
<i>Terminalia amazonia</i>	–			U	U	old growth canopy
<i>Vismia macrophylla</i>	–	–		U	U	heliophyte
<i>Qualea paraensis</i>	–			U	U	old growth canopy
<i>Galipea granulosa</i>	L			–	L	old growth subcanopy
<i>Prestoea</i>	L			–	L	old growth subcanopy
<i>Ardisia</i> sp.	–	L			L	heliophyte
<i>Sloanea tuerckhjeimii</i>	–	L			L	old growth canopy
<i>Miconia elata</i>	–	L		–	L	heliophyte
<i>Chione sylvicola</i>	–	L	–	–	L	old growth subcanopy
<i>Tetragastris panamensis</i>	–	L		–	L	old growth canopy
<i>Miconia tomentosa</i>	–	L			L	heliophyte
<i>Piper auritum</i>	–		L	–	L	pioneer
<i>Casearia sylvestris</i>			L	–	L	heliophyte
<i>Borojoa panamensis</i>				L	L	old growth canopy
<i>Unonopsis pittieri</i>	–	–		L	L	heliophyte
<i>Inga thibaudiana</i>		–	–	L	L	old growth canopy
<i>Astrocaryum alatum</i>	L	L	–		LL	old growth subcanopy
<i>Rinorea squamata</i>	L	–		L	LL	old growth canopy
<i>Bactris</i> sp.	–	L	L	–	LL	old growth subcanopy
<i>Lasistema aggregatum</i>	–	–	L	L	LL	old growth subcanopy
<i>Isertia haenkeana</i>	L	L	–	L	LLL	pioneer

Table 4b Qualitative analysis of species that are generally noncongruent or occur throughout the canopy (M)

<i>Inga cocleensis</i>	U	U		M	UUM	old growth canopy
<i>Byrsonima crassifolia</i>	M	U		M	UMM	heliophyte
<i>Mabea occidentalis</i>		U	M	M	UMM	old growth canopy
<i>Myrcia splendens</i>	–	U	–	M	UM	old growth canopy
<i>Guatteria diospyroides</i>	M		M	M	MMM	heliophyte
<i>Guettarda combsii</i>	M	M			MM	pioneer
<i>Cupania glabra</i>	M	M	–	M	MMM	old growth subcanopy
<i>Goethalsia meiantha</i>	M			–	M	heliophyte
<i>Protium schippii</i>	M	–	–	M	MM	old growth canopy
<i>Miconia prasina</i>	M	M		M	MMM	heliophyte
<i>Manilkara zapota</i>	M	–	–	–	M	old growth canopy
<i>Eugenia</i> sp.	–	M			M	old growth canopy
<i>Spachea correae</i>	–	M		–	M	old growth subcanopy
<i>Virola koschnyi</i>		–	M	–	M	old growth canopy

Table 4b (Continued)

Species	Fons.	LdeM.	Union	Bod.	summ	niche
<i>Dipteryx panamensis</i>	–		M	–	M	old growth canopy
<i>Viola multiflora</i>	–			M	M	old growth canopy
<i>Cordia bicolor</i>	–	–	–	M	M	old growth canopy
<i>Myrcia</i> sp.	–	–	–	M	M	old growth canopy
<i>Pseudolmedia spuria</i>	–	–	L	U	LU	old growth subcanopy
<i>Dendropanax arboreus</i>	U	–	M	L	LMU	old growth canopy
<i>Hirtella guatemalensis</i>	L	–	–	M	LM	old growth canopy
<i>Amaioua corymbosa</i>	M	L		L	LLM	old growth canopy

to say not having individuals either more likely in the upper or lower half of the canopy. Only those species that occurred at population densities of 33 ha or more were included in the analysis.

The results of this qualitative analysis are displayed in Table 4a and b, where U indicates a species of the upper half of the canopy, L of the lower half of the canopy, and M with individuals in both upper and lower canopy with relatively the same frequency (i.e. the percent in upper canopy between 33 and 67%). Cells with no entry indicate that the species did not occur in the plots at those sites, and a dash indicates that the species occurred but not at a high enough density to be included in the analysis.

It is clear that species are not distributed throughout the vertical strata of the canopy at random. Considering the sites in pairwise comparisons we tabulated the number of species that were congruent or non-congruent for each of the six possible comparisons. For example, in comparing Loma de Mico with La Union we find that *Bactris* sp. is congruent (it is a lower stratum species at both sites) whereas *Dendropanax arboreus* is non-congruent (it is an upper stratum species at Fonseca and a lower stratum species at Bodega — see Table 4b). Lumping all six comparisons (four sites, each compared with each other) we obtain

Table 5  
Pooled comparisons of species in strata at paired sites (see text for explanation).

At second site	At first site		
	Upper	Median	Lower
Upper	12	8	2
Median		13	4
Lower	9		9

the results in Table 5. A total of 34 comparisons were congruent (sum of elements in principal diagonal in Table 5) and 14 non-congruent (off-diagonal elements in Table 5), and a comparison of Table 5 with a table of equal expectations (eight expected in each of the six cells) provided a  $\chi^2$  of 11.75 ( $P < 0.05$ ). Thus, the pattern seems to be that a species will be ‘specialist’ in the upper canopy, ‘specialist’ in the lower canopy, or ‘generalist’ with respect to its position in the canopy.

Of the five pioneers registering enough individuals to be included in this analysis, two are found mainly in the upper half of the canopy (*Croton smithianus* and *Cecropia obtusifolia*), two are found mainly in the lower half of the canopy (*Piper auritum* and *Isertia haenkeana*), and one seems to occur throughout the canopy (*Guettarda combsii*). Both *Croton smithianus* and *Cecropia obtusifolia* are fast growing trees that are capable of reaching large sizes. Their presence mainly in the upper canopy is likely due to the fact that they are shade intolerant and, therefore, mainly those individuals that have grown to a height above the thinning canopy have avoided mortality. *Piper auritum* and *Isertia haenkeana* are small trees, mainly seen as shrubs in open areas. Both species have experienced dramatic mortalities in the past 3 or 4 years, and those that remain are likely to die soon also. Their presence mainly in the lower canopy is due to their small maximum size. *Guettarda combsii* appears to be far more shade-tolerant than the other four (indeed its classification as a pioneer is questionable on this basis), meaning that individuals that have reached the upper canopy as well as those remaining in the lower canopy survive equally well.

Fourteen non-pioneer heliophytes appear in the analysis. Those which occur mainly in the upper canopy appear to be species that are capable of

attaining large sizes while those which occur mainly in the lower canopy appear to be species that only reach smaller sizes (i.e. their position in the canopy may not be due to either dominance or suppression from competition). It is worth noting that the two species of *Guatteria* are quite distinct, *Guatteria recurvisepala* being a species of the upper canopy while *Guatteria diospyroides* occurs throughout the canopy. It appears that *Guatteria diospyroides* is more shade-tolerant than its congener and thus the smaller individuals in the forest have not experienced as much mortality. Indeed it is somewhat surprising to find three heliophytes in the median category (*Guatteria diospyroides*, *Goethalsia meiantha*, and *Miconia prasina*). *Goethalsia meiantha* is known to persist in old growth forests (Hartshorn, 1983) and, despite its commonness in open areas around streams and rivers, some smaller individuals seem to be surviving even in the dark understory of the thinning canopy (although the mortality rate of this species generally is very high — see previous section). *Miconia prasina* became especially abundant after the hurricane and in some areas (not in the permanent plots but rather in areas that appear to have been more degraded prior to the hurricane) can be seen as codominant with other heliophytes such as *Miconia impetolaris*, *Vismia macrophylla*, *Xylopia sericophylla*, and *Simarouba amara*. The fact that its smaller representatives have not been dying yet is something of a surprise — mortality rates for this species are generally much lower than what would be expected if mortalities occurred at random (see previous section).

Of the 10 presumed old growth (and thus non-heliophytic) species found in the upper half of the thinning canopy, eight are known as canopy trees and only two (*Cespedesia macrophylla* and *Welfia regia*) as subcanopy trees. *C. macrophylla* appears to reach its maximum adult size rapidly and is found in the upper half of the current thinning canopy only because that canopy is so low. We expect that this species will effectively retain its current stature as the canopy grows above it. *W. regia*, on the other hand, occurs in one of the sites in the upper half of the canopy seemingly because this site (La Unión) was relatively protected from the hurricane (see Section 2) and many adult *W. regia* survived the hurricane, making up the entire population currently in the thinning canopy. Clearly the canopy will eventually overtop these

individuals since they are currently near their maximum height (Vandermeer, 1983).

Of the eight old growth canopy species in the upper half of the canopy several seem worth comment. *Vochysia ferruginea* is an extremely abundant species in three of the four sites, and has been the subject of several previous detailed analyses (Boucher et al., 1994; Boucher and Mallona, 1997). It is a species capable of extremely rapid growth, but not a frequent resprouter. Indeed, its relative *Qualea paraensis* (also in the family Vochysiaceae) survived the hurricane quite well, experiencing significant damage from the storm but resprouting vigorously. *Vochysia ferruginea*, on the other hand, was devastated by the hurricane and the adults did not resprout at all. Yet it now dominates the thinning canopy in three of the four sites, having grown very rapidly from surviving seedlings and saplings (Vandermeer et al., 1995). *Carapa guianensis* is a species of poorly drained soils (McHargue and Hartshorne, 1981), explaining its abundance at the Loma de Mico site. *Hyeronima alchorneoides*, normally a species of old growth forest (Clark and Clark, 1992; Clark et al., 1993), is extremely abundant at La Unión and exhibited dramatic resprouting after the hurricane. Its current position in the upper thinning canopy is due in part to a massive mortality of the smaller individuals that were resprouts from fallen trees (see previous section).

Of the 12 old growth species found in the lower half of the thinning canopy, eight are subcanopy species. Presumably the four canopy species found here are currently represented by only young individuals.

In general the data presented in Table 4a and b suggest that species have already been essentially sorted out, with the canopy species dominating the upper levels of the thinning canopy and the subcanopy species more common in the lower levels of the thinning canopy.

#### 4. Discussion

The modern debate about tropical forest structure has centered mainly on the question of species diversity (e.g. Hubbell, 1997, 1999; Hubbell et al., 1999; Chazden et al., 1999). This debate has interesting historical antecedents. Ecological ideas about species diversity were probably initially conditioned by



Gauseian ideas of competitive exclusion. If two species were very similar in their ecological requirements, one of them would flourish, the other perish. This competitive exclusion principle (Hardin, 1960) suggested that in the case of trees, which seem to all do similar things, we might expect very few species in any one site. Such an expectation is well in accordance with the experience of ecologists familiar with temperate zone forest conditions, where indeed one or a few species dominate (e.g. beech forests, oak forests, etc). With this predisposition, the observation of a tropical forest with hundreds of species living together begs for explanation. To accommodate so many species in the same environment, it should thus be the case that large numbers of niches are available (Richards, 1952; Ashton, 1969). Hutchinson's (1961) paradox of the plankton was cast in a different setting, but recognized the same problem. If theoretical ecology suggested that a consort of similar species should be characterized by the dominance of one or a few species, how do we account for communities that clearly contain many (e.g. plankton, tropical trees)?

There are, we believe, two ways to resolve this paradox. First, it might be noted that the theoretical principles upon which the debate was first based are largely discredited by more modern theory. Second, several specific models have been proposed to recast the underlying problem such that the paradox never arises in the first place. The two approaches are closely related, although this fact does not seem to be always appreciated in the burgeoning literature on the subject.

At the theoretical level, modern ecology has gone beyond the early characterizations of population interactions. Armstrong and McGehee (1980) showed clearly that the Gauseian principle of one niche per species was conditioned on assumptions of linearity in the model. Two species could coexist indefinitely on a single resource if one merely added the biologically reasonable (essential?) assumption that consumers may become satiated with their food. Levins (1979) demonstrated the same idea in the more general context of non-linearity, showing that, metaphorically, one species could exist on a resource while another could exist on the square of the resource. Levins (1979) also demonstrated that a consequence of stochastic variation is likewise that a variety of species could exist on a single resource, similar to the Chesson and Warner (1981) lottery model. Abrams (1988)

clarified some of this debate in the provocatively titled 'How should resources be counted?'

Several studies have recently built on Levins' metapopulation model to show how competitive hierarchies in a metapopulation context can result in coexistence of large numbers of almost identical species (Nee and May, 1992; Tilman, 1994). Furthermore, recent literature on indirect effects in community networks (Paine, 1974; Vandermeer, 1980; Werner, 1992; Abrams et al., 1996; Vandermeer and Maruca, 1998) might suggest that the simple fact of having numerous species generates the potential for the sort of complexity that will allow yet more species to fit into the community. A trait-mediated indirect effect on species A by species C, for example, may prevent the competitive exclusion of A by B, which would occur in the absence of C. That is, it is the presence of the third species (C) that allows for the coexistence of the first two (A and B). The fact of multidimensionality (many species) itself may contain the mechanism for maintenance of large numbers of species together.

This recent theoretical literature perhaps suggests the need for a re-examination of the original basis of the competitive exclusion principle. If non-linearities, or stochasticity or metapopulation structure or multidimensionality can result in many species coexisting, perhaps the need for a special theory to account for many species living together is only necessary because of the historical inertia of excessively linear thinking. However, since only the credulous seriously expect to see the linear outcome of Lotka–Volterra-like models in nature, the question remains as to precisely which deviations from those naive linear expectations do in fact account for the observations.

Two broad classes of explanation have emerged in recent years. On the one hand there are explanations that are based on some notion of the ecological niche, assuming the necessity of at least one niche per species and asking whether, or how, large numbers of niches could exist when it seems on first blush that trees all do the same thing. On the other hand there are explanations that presume, at the extreme, that all the trees indeed are in the same niche and that other forms of population dynamics permit coexistence. For convenience we refer to these two classes as niche and non-niche models, and note that they correspond essentially to the categories of equilibrium and non-equilibrium of Zagt and Werger (1998) as described in

Section 1, or the ‘niche-assembly’ versus ‘dispersal-assembly’ models recently summarized by Hubbell (1997, 1999).

Niche models (equilibrium models) can be categorized as of two types (Wills et al., 1998), direct and indirect. Direct niche models view the subdivision of the environment either into spatially diverse units, based usually on edaphic factors (Clark and Clark, 1992; see also review in McLaughlin and Roughgarden, 1993), or into temporally distinct units, based on some form of disturbance (where the formation of treefall light gaps is conceptualized as a disturbance) followed by succession (Vandermeer et al., 1974; Orians, 1982; Denslow, 1987; Alvarez-Buylla and Martinez-Ramos, 1992). Indirect niche models formulate the problem of niche variability as a consequence of the action of the species utilizing the niche. Wills et al. (1997) refer to these models as density-dependent models since the creation of a type of niche is dependent on the density of the species involved. They are based on either abiotic factors (e.g. local depletion of nutrients (Kenkel, 1988) or build up of toxins (Putman and Tang, 1986)) or biotic factors (e.g. pest species are more likely to attack individuals within conspecific clumps (Janzen, 1970) or diseases are more likely to decimate a dense population than a sparse one (Wills, 1996; Hubbell, 1999)).

Non-niche models (non-equilibrium models) are generally of two categories, disturbance models and metapopulation models. Disturbance models share the general feature that competitive exclusion is avoided by some intervening event. The most popular of the disturbance models is the intermediate disturbance hypothesis, simultaneously formulated by Connell (1978) and Huston (1979), in which it is postulated that too weak a disturbance will have little consequence, too strong a disturbance will directly eliminate species, leaving the intermediate forms of disturbance as the likely candidate for deterring the inexorable tendency towards competitive dominance by one or a few species. The community drift model of Hubbell and Foster (1986), although not explicitly formulated in this manner, can be thought of as an application of the intermediate disturbance hypothesis to tropical rain forests (Vandermeer, 1996; Vandermeer et al., 1996). Metapopulation models are based on the basic formulation of Levins (1969) and are applied to the problem of tropical forest diversity by concep-

tualizing the subunits as approximately the size of an area occupied by an individual adult tree (Nee and May, 1994; Tilman, 1994). Hastings (1980) provides an approach that combines the disturbance factor with the metapopulation context.

The present study seeks to distinguish between the niche (equilibrium) and non-niche (non-equilibrium) approach to the problem, following the schema of Zagt and Werger (1998). We have divided the post-disturbance successional process into two main stages, the building phase and the thinning phase. Zagt and Werger (1998) review copious data relative to these two stages, but effectively recognized a broader range of phenomena in their analysis. Their analysis begins before the occurrence of the disturbance, with the arrival of seeds and germination of seedlings, proceeding to the establishment of the advanced regeneration (the seedlings and saplings in the pre-disturbance forest understory). Recent emphasis on recruitment limitation (and/or dispersal-assembly) focuses on this stage (Hubbell, 1999; Hubbell et al., 1999), and emphasizes the assembly of the understory community before the occurrence of the disturbance. Our work proceeds from a later point in the process, looking at the pattern in the post-disturbance environment. In Fig. 8 we summarize what we believe to be the overall pattern, from the arrival of the seed at a point in space to the domination of that point by an adult tree. Zagt and Werger (1998) emphasize both ends of this spectrum, providing evidence for a niche-based model at the level of seedling growth and survival, but not at the level of initial seed dispersal, and finding little evidence of a niche based model at the other end of the spectrum, the mortality of adult trees. Hubbell and coworkers (Hubbell, 1999; Hubbell et al., 1999) have recently emphasized the seed dispersal end of the spectrum and their earlier work (Wills et al., 1997), failed to find evidence for a niche model in terms of mortality of adult trees. As suggested by Zagt and Werger (1998), most studies emphasize either the early stages of the overall process (the left hand side of Fig. 8) or the late stages (right hand side of Fig. 8), either with seedling establishment or growth and mortality in an old growth forest. Our work, on the contrary, focuses on the intermediate stage, the post-disturbance dynamics.

Our earlier work on recruitment into the thinning canopy (Vandermeer et al., 1996), focusing on

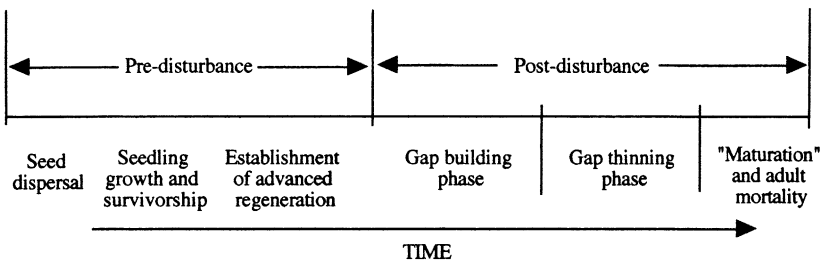


Fig. 8. Generalized pattern of forest regeneration, with regard to the effect of disturbance.

recruitment from the lower strata rather than initial recruitment of seeds and seedlings, strongly supported the non-niche framework for the building phase of post disturbance succession. Here we report on the initial stage of the thinning process (the 'gap thinning phase' in Fig. 8), and find evidence for a niche-based interpretation.

With reference to Fig. 8, we tentatively suggest that recruitment-like events (seed dispersal and growth of advanced regeneration into a post-disturbance environment) are likely to be non-niche phenomena, while the process of growth and survival of seedlings and especially of small trees in the thinning canopy, are more likely to be niche phenomena. Thus, seeds are effectively randomly dispersed, possibly affected by recruitment limitation, and the resultant seedlings grow and survive differentially depending on their specific identities. When a disturbance occurs (a simple treefall or multiple treefalls generated by a storm) the recruitment of the understory into the thinning canopy is random, but the final growth and survivorship in that canopy depends on species identity. This interpretation is in line with the schema of Zagt and Werger (1998) and emphasizes that the niche versus non-niche dichotomy may not be appropriate since both may apply but at different stages of the process.

It is also worth noting that these data are consistent with recent metapopulation models based on competitive hierarchies (Nee and May, 1992; Tilman, 1994; Tilman et al., 1994). If a competitive hierarchy exists, as thinning proceeds we should see the poorer competitors eliminated before the stronger competitors, which is to say, there should be pattern in the way growth and mortality occur in the thinning canopy. The basic framework of Kohyama (1992), also a competitive hierarchy model, is also consistent with the patterns we observe.

The evidence offered in this article is another example in the growing literature that rejects a strict non-niche interpretation of tropical forest dynamics (e.g. Alvarez-Buylla and Martinez-Ramos, 1991, 1992; Clark et al., 1992; Terborgh et al., 1996; Hubbell, 1999; Hubbell et al., 1999). Our data clearly show that species are not randomly distributed along a successional gradient, at least for the initial stages of that gradient (i.e. within 10 years after disturbance). Furthermore, this observation is not a consequence of Swain and Whittmore's (1988) provisional rough-cut of the pioneer/primary forest dynamic (since we eliminated the pioneers from the mortality analysis). Rather, as suggested originally by Alvarez-Buylla and Martinez-Ramos (1991), and reinforced by Hubbell (1995), these two categories may represent extremes on a 'continuum of tree life histories'. The data reported herein offer strong support to the idea that there are specific niches, above and beyond the pioneer/primary forest dichotomy, associated with the successional gradient, much as suggested by Alvarez-Buylla and Martinez-Ramos (1992) and earlier authors (Vandermeer et al., 1974; Orians, 1982; Denslow, 1987)). The data presented here, in combination with our earlier work (Vandermeer et al., 1996), strongly support the position of Zagt and Werger (1998) that a non-niche (non-equilibrium) interpretation applies to the building phase (see Fig. 1 and/or Fig. 8) while a niche (equilibrium) interpretation applies to the thinning phase.

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