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Height dynamics of the thinning canopy of a tropical rain forest: 14 years of succession in a post-hurricane forest in Nicaragua

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Abstract

Understanding the maintenance of the large diversity of tree species in a tropical rain forest has become something of a holy grail. Among the many factors thought to be involved is disturbance. One hypothesis is that repeated disturbance sets the process of competition anew, thus that competitive exclusion never occurs. In the context of a forest massive damage from storms is potentially the source of the damage that could preserve species diversity. After damage from a storm the canopy of the forest begins with a rapid growth, known as the building phase. Soon a very dense canopy is formed, called the ''thinning canopy'' which dictates the subsequent dynamic process of competition, where those individuals located near the top of the canopy will have a competitive advantage over those in the subcanopy. We here report on the first 14 years of the development and dynamics of the thinning canopy after the catastrophic hurricane damage occasioned by the landfall of Hurricane Joan in October 1988 in the general area of Bluefields, Nicaragua. The overall pattern of growth is clear, where larger trees have been growing and smaller ones more-or-less stagnant, for the past 8 years. The upper canopy was somewhere on the order of 11–18 m in 1996 and is somewhere between about 15 and 22 m in 2003. The dynamic pattern reflects the basic story of growth into the thinning canopy followed by intense competition where some individuals overtop others, thus creating a platykurtic distribution with a skewed bias towards smaller individuals, because of the few individuals overtopping the others. Mortality rates were between 7 and 33 stems per thousand per year, and were concentrated in individuals located beneath the canopy.
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1. Introduction

A central concern of community ecology is how some communities contain very large numbers of species while others contain so few. The main question comes from the famous paradox that some organisms appear to have similar niches and thus should, according to classical theory, exhibit competitive exclusion, yet seem to coexist in apparent perpetuity, the classical example being plankton (Hutchinson, 1961). The tree community of a tropical rain forest is another striking example. Tropical rain forests may contain hundreds of species of trees coexisting in the same area that would contain only 10 or 20 species in a temperate forest. Understanding the maintenance of so many species, seemingly with very similar niches, has

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become something of a holy grail (Hubbell and Foster, 1986). (The evolutionary origin of this diversity is quite another question and is not part of the present work (e.g., Ricklefs and Schluter, 1993)).

Among the many factors thought to be involved with the maintenance of species diversity is disturbance (Connell, 1978; Huston, 1979, 1995; Miller, 1982; Mooney and Gordon, 1983; Sousa, 1984; Pickett and White, 1985; Burslem and Whitmore, 1999). Disturbance in forests may range from the simple light gap formation resulting from a toppled tree, to the massive damage done by large storms or fires (Stearns, 1949; Spurr, 1956; Gómez-Pompa et al., 1972; Oliver and Stephens, 1977; Crow, 1980; Dunn et al., 1983; Canham and Loucks, 1984; Flanagan, 1988; Foster, 1988; Merens and Peart, 1992; Peterson and Pickett, 1995; Molino and Sabatier, 2001). The fundamental idea, known as the intermediate disturbance hypothesis (Connell, 1978; Huston, 1979), is that while species with similar niches may be expected to exclude each other, if some regular disturbance event repeatedly sets population densities back to low levels, the competition process will begin anew, thus deterring the competitive exclusion (Vandermeer et al., 1996).

Most forests are mosaics of treefall gaps of various ages and it is most natural to consider such gaps as the ''disturbance'' that promotes species diversity. The study of gap phase dynamics thus has long been an important component of tropical rain forest ecology (Bauer, 1964; Poore, 1968; Vandermeer et al., 1974, 2001; Richards and Williamson, 1975; Hartshorn, 1978; Ehrenfield, 1980; Orians, 1982; Denslow, 1980, 1985, 1987; Brokaw, 1985a,b, 1987; Dalling et al., 1998; Hubbell et al., 1999; Chazdon et al., 1999; Brokaw and Busing, 2000; Schnitzer et al., 2000; Schnitzer and Carson, 2000). Recently Hubbell et al. (1999) challenged the notion that tree fall gaps could represent the disturbance that partly explains the maintenance of species diversity. Even when properly corrected for population density (number of stems per hectare), light gaps actually contained fewer species than the mature forest of a similar area (Hubbell, 1999). Analyzing data from our sites in the same manner, we found a striking difference—the forest damaged by a hurricane had significantly more species than a mature forest (after correcting for population density and area) (Vandermeer et al., 2000). The key difference seems to be the size of the disturbance.

With a large enough disturbance (e.g. a large storm), the population densities of pioneer species are significantly reduced and consequently potential seed trees are rare. This results in recruitment limitation of pioneers (pioneers are generally recruited into treefall gaps whereas primary forest species pre-exist as seedlings or saplings in the understory before the gap occurs). In a treefall gap of normal size, nearby pioneer seed trees will survive, thus providing a seed source to colonize the gap and taking up space that otherwise would be occupied by non-pioneers. The conclusion, then, must be that larger disturbances (exactly what size or intensity is not known) may function to maintain large numbers of species, whereas smaller disturbances may not (Vandermeer et al., 2000). An example of this sort of disturbance would be hurricanes.

Since hurricanes (or typhoons or cyclones) are frequent in tropical areas, it is natural to expect them sometimes to be an important disturbance event in structuring tropical forests. Given the time frame of forest demographics (hundreds or thousands of years), even rare hurricanes are common in the context of forest dynamics. When they strike, they do enormous physical damage. However, in tropical rain forests there is a great deal of resprouting, and the pattern of early post-hurricane succession is dominated by vegetative growth (Vandermeer et al., 1990, 1996; Burslem et al., 2000). In accordance with the idea that disturbance may aid in the preservation of species diversity, a disturbed area generally should have more species than an undisturbed area, which is the case in our study (Vandermeer et al., 2001). The course of development of the canopy subsequent to a large disturbance event will, to some extent, determine the pattern of accumulation and decline of species richness in a successional forest, which makes the characterization of the physical development of the canopy interesting. Such a characterization is the purpose of the present communication.

The pattern of 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-stature, but very dense canopy, followed by thinning (mortality) of individuals from that canopy through the process of competition (e.g. Vandermeer et al., 1990, 1996, 2001). After the hurricane, the damaged forest contains: (1) a few standing or

snapped-off trees that begin resprouting high above the ground; (2) felled trees that do so at 1–2 m; and (3) the saplings and seedlings that survived the hurricane. During the building phase (also called the "innovation phase" (Oldeman, 1990), or the "stand initiation stage" (Oliver and Larson, 1990)), growth is rapid for all individuals since the entire area is bathed in light. But soon these individuals form a dense canopy at a much lower height than the original canopy—the thinning canopy. In this dense canopy it is normally assumed that there is much competition for light.

As this canopy develops, it is expected that some individuals will come to dominate while others will become suppressed, due to the normal processes of competition (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 the "thinning phase" (also called the "aggradation phase" (Oldeman, 1990; Bormann and Likens, 1979), or the "stem exclusion stage" (Oliver and Larson, 1990)). As the process of thinning begins, we 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, in accordance with traditional plant competition theory (Harper, 1977; Weiner and Thomas, 1986; Yodzis, 1986). We here report on the first 14 years of the development and dynamics of the thinning canopy after the catastrophic hurricane damage occasioned by the landfall of Hurricane Joan in October 1988 in the general area of Bluefields, on the Caribbean coast of Nicaragua, in which approximately 500,000 ha of forest were severely damaged (Vandermeer, 1990; Yih et al., 1991), following up on a previous report (Vandermeer et al., 1999) where height growth in this forest was reported for 6 years after the disturbance.

2. Methods

Subsequent to the landfall of Hurricane Joan in 1988 we established two permanent sites that today contain approximately 4000 trees (in approximately 200 species) which are permanently marked. The complete history of all the sites, past and present, can be found elsewhere (Vandermeer et al., 1995, 1997, 2001). Currently the study is focused on two sites within the main region directly affected by Hurricane Joan. The sites are named for local features—Bodega, almost at the center of the damaged area and La Unión, approximately 30 km north of Bodega, still well within the damaged area. Currently we have a total of seven plots established at these two sites, with all trees >3.2 cm diameter (10 cm circumference) tagged. Two of the plots have been censused yearly since 1989, one has been measured yearly since 1994, two were established in 2000, and two in 2001. The two oldest plots (located at Bodega) are 100 m × 10 m, established originally as transects since the recently hurricane-damaged forest was difficult to penetrate and precluded rectangular plots. All other plots are 30 m × 50 m. Other plots reported in our earlier studies had to be abandoned for various reasons, mainly fires associated with the 1997/1998 ENSO. However, the plots of concern in the present manuscript are all within the matrix of the same forest that was affected by the 1988 hurricane and represent a continual record of forest succession, along with our data from other plots, for the past 14 years. Previous work on this forest emphasized the development of the thinning canopy (summarized in Vandermeer et al., 2001). That process has now been completed and evidence suggests that the forest is now in the thinning phase. Changes in density and basal area over time reached asymptotes some time ago (Vandermeer et al., 2001). The accumulation of species has also stabilized (Vandermeer et al., 2000).

The floristic composition of the forest is similar in both sites, but with distinct differences in dominance. In Table 1 we present those species that attain a density of at least 30 stems per hectare at one or both of the sites (note that we do not report numbers for the case where the species occurs at a density of less than 30 ha, even though most all of the species occur at both sites). Both the differences and similarities in species composition are interesting. Note that the abundance of pioneers is mainly in the two species *Cecropia obtusifolia* Bertol. and *Croton smithianus* Croiz, both of which arrived after the hurricane of 1988, but not in especially numerous quantities (Vandermeer et al., 2001), one of which is characteristic of each of the sites. Those that remain are large trees and

Table 1

Tree species, densities (stems/ha), and approximate ecological "niche" for those species that occur with a density equal to or greater than 30 stems per hectare in one or both sites (no record indicates a density less than 30 stems per hectare, but only rarely absolute absence)

Species	Bodega	La Unión	Ecological "Niche"
Guatteria diospyroides Baill.		218	Subcanopy heliophyte
Casearia sylvestris Sw.		178	Subcanopy heliophyte
Pourouma bicolor Mart.		138	Canopy heliophyte
Cryosophila warscewiczii (H. Wendl.) Bartlett		110	Understory primary forest
Pentaclethra macroloba (Willd.) Kuntze		98	Canopy primary forest (swamp)
Cecropia obtusifolia Bertol.		85	Pioneer
Croton schiedeanus Schlecht.		78	Canopy primary forest
Hyeronima alchorneoides Allemao		55	Canopy primary forest
Anaxagorea crassipetala Hemsl.		52	Subcanopy primary forest
Xylopia sericophylla Standl. & L.O. Williams		50	Canopy heliophyte
Piper auritum H.B.K.		45	Pioneer
Synechanthus warscewiczianus H. Wendl.		42	Subcanopy primary forest
Virola koschnyi Warb.		38	Canopy primary forest
Dendropanax arboreus (L.) Dec. & Planch.	50	398	Canopy primary forest
Lacistema aggregatum (Berg) Rusby	48	150	Subcanopy heliophyte
Mabea occidentalis Benth.	38	120	Canopy primary forest
Casearia arborea (Rich.) Urb.	58	105	Subcanopy heliophyte
Cordia bicolor A. DC.	36	75	Canopy primary forest
Pseudolmedia spuria (Sw.) Griseb.	60	60	Subcanopy primary forest
Guatteria recurvisepala R.E. Fries	68	55	Subcanopy heliophyte
Protium schippii Lundell	96	40	Canopy primary forest
Bactris porchiana	154	37	Subcanopy primary forest
Vochysia ferruginea Mart.	346		Canopy heliophyte
Croton smithianus Croiz.	178		Pioneer
Cupania glabra Sw.	140		Subcanopy primary forest
Miconia prasina (Sw.) DC.	134		Subcanopy heliophyte
Rinorea squamata Blake	100		Subcanopy primary forest
Inga cocleensis Pitt.	100		Canopy primary forest
Qualea paraensis Ducke	82		Canopy primary forest
Terminalia amazonia (J.F. Gmel.) Exell	58		Canopy primary forest
Byrsonima crassifolia (L.) H.B.K.	58		Subcanopy heliophyte
Amaioua corymbosa Kunth	54		Canopy primary forest
Simarouba amara Aubl.	48		Canopy heliophyte
Brosimum guianense (Aubl.) Huber	48		Canopy primary forest
Cespedesia macrophylla Seem.	44		Subcanopy primary forest
Unonopsis pittieri Saff.	38		Subcanopy heliophyte
Prestoea decurrens (H. Wendl. ex Burret) H.E. Moore	38		Subcanopy primary forest
Myrcia sp.	38		Subcanopy primary forest
Henriettea seemannii (Naudin) L.O. Williams	34		Subcanopy heliophyte
Miconia elata (Sw.) DC.	32		Subcanopy primary forest
Miconia stevensiana Almeda	30		Subcanopy heliophyte

seeming at the maximum of their potential growth, many emerging from the canopy. Especially noteworthy is *Vochysia ferruginea* Mart. a large fast-growing heliophytic tree (Vandermeer et al., 1996; Boucher et al., 1994) that is especially common at Bodega but does not enter the plots at La Unión (although an individual adult tree can be found nearby, along with a significant sapling shadow, suggesting its relative absence at La Unión is a result of dispersal limitation). Several palm species are abundant: *Cryosophils warscewiczii* (H. Wendl.) Bartlett and *Syunechanthus warscewiczianus* H. Wendl. at La Unión, *Prestoea decurrens* (H. Wendl. ex Burret) H.E. Moore at Bodega, and *Bactris porschiana* Burret at both sites.

Also common at both sites is *Welfia regia*, but mainly as stemless juveniles, thus not entering into the formal tabulations of Table 1. Two large canopy species are common at the La Unión site—*Pourouma bicolor* Mart. and *Hyeronima alchorneoides* Allemao, the later as standing survivors of the hurricane and the former as a fast-growing heliophyte similar to *V. ferruginea*. Thus, it seems that the forests are similar enough to be thought of as replicates of the same forest, yet different enough to sample a substantial variability in its regional diversity.

In all established plots, the heights of all trees in the census has been measured yearly since 1996. Height was defined as the highest green leaf on the tree. Measurements were taken either with a telescoping pole, for individuals less than 15 m high, or with a hypsometer for all individuals greater or equal to 15 m high. High accuracy of height measurements is notoriously difficult to attain, and this study is no exception. Errors resulted from two sources—the worker making the measurement fails to locate the actual highest branch, or the worker using the hypsometer fails to adjust for apparent height of the branch. The latter usually results in an overestimation of height. This difficulty in measurement was partly controlled by having the prior year's data available to the workers making the measurements. When there was a significant deviation from the previous year's data the recorder queried the person taking the measurement so as to be sure that the highest branch had been located. If significant deviation from the previous year's measurement was verified, observations were made as to what may have caused the deviation. Frequently it was possible to observe either a doubling over of the stem due to vine growth, or the death of the principal trunk, leaving a shorter branch as the highest point.

3. Results

Not surprisingly, the canopy has been growing in the past 8 years. Examining only those trees that entered the census in 1996, the pattern of growth is clear, where larger trees have been growing and smaller ones more-or-less stagnant, although with a great deal of variability (see Fig. 1). As mentioned in Section 2, frequently the height of an individual tree
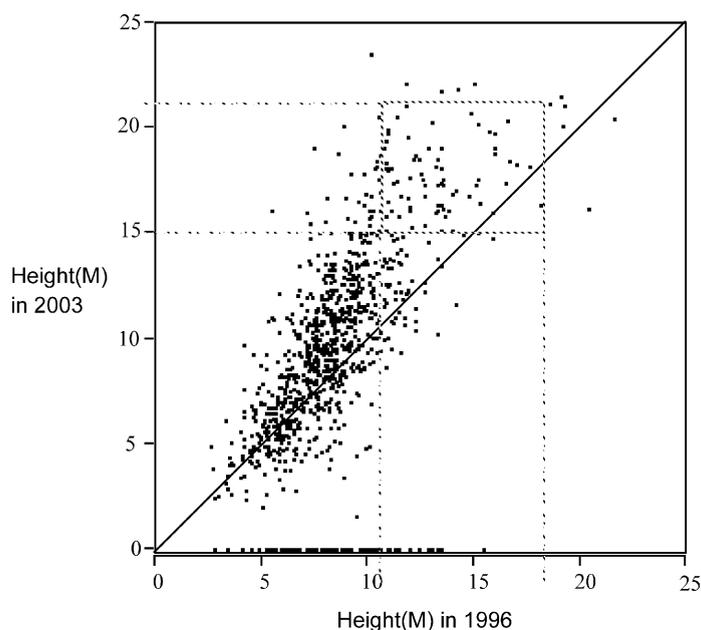
Fig. 1. Eight years of height increase for those individuals encountered in the census of 1996. Dotted lines indicate a rough estimate of the position of the upper canopy. Expired individuals are indicated with a height of zero. Note the concentration of expired individuals at the lower height classes, a picture that is more exaggerated when looking at the original data since in this graph many points are on top of one another.
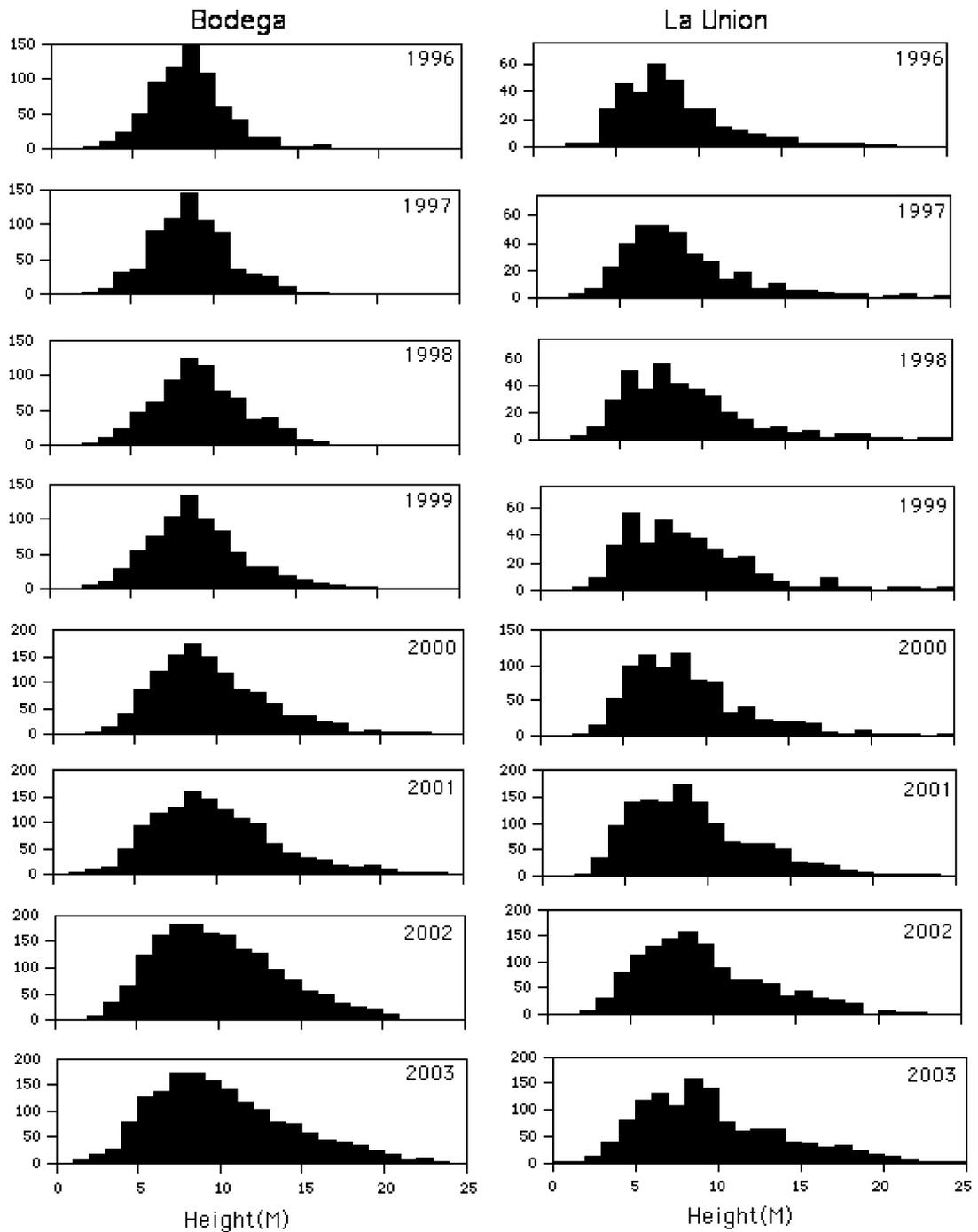
Fig. 2. Frequency diagrams of the heights of all trees in each year.

declines, mainly due to doubling over from the weight of vines, or death of the main stem and survival of subsidiary branches. The majority of decline in height was with smaller individuals, reflecting the basic process of thinning of the canopy. Furthermore, the death rate (discussed further below) is concentrated among the smaller individuals as reflected in the concentration of points at zero in the ordinate of Fig. 1.

Taking a mean height figure is not reflective of the apparent size of the canopy in that the upper canopy is formed mainly by the larger trees. But examining the range of values as presented in Fig. 1, it is apparent that the upper canopy was somewhere on the order of 11–18 m in 1996 and is currently somewhere between about 15 and 22 m in 2003, as indicated by the dotted box in Fig. 1. Thus a rough estimate of the growth of the upper canopy would suggest a growth rate of slightly more than half a meter per year (about 4 m in 7 years) during this period.

The pattern of change in height is reflected in the histograms of Fig. 2. In 1996 the distribution of heights was centered on approximately 8 m, with the vast majority of individuals smaller than 10 m high. If we focus on those individuals greater than 10 m separately from those smaller than 10 m, we see a general pattern of the larger individuals (greater than 10 m) increasing in size through 2003, while those less than 10 m remain stagnant with a mean of approximately 8 m during the entire time period. To be sure, the canopy is dynamic, with some individuals growing above the canopy (and thus leaving the less than 10 m category), other individuals dying and others recruited into the smallest size classes from smaller sapling and seedling stages. The pattern reflects the basic story of growth into the thinning canopy followed by intense competition where some individuals overtop others, thus creating a platykurtic distribution with a skewed bias towards smaller individuals, because of the few individuals overtopping the others. Calculations of skewness and kurtosis reflect this pattern, as can be seen in Fig. 3.

Substantial mortality rates were observed during the last 3 years of the study (rates prior to 2000 were small): rates for Bodega were (for the years 2000–2001, 2001–2002, and 2002–2003, respectively) 33.0, 6.6, and 18.1 per thousand stems, while, in the same order, for La Unión they were 26.5, 6.4 and 13.3. More interesting than the rates themselves were the
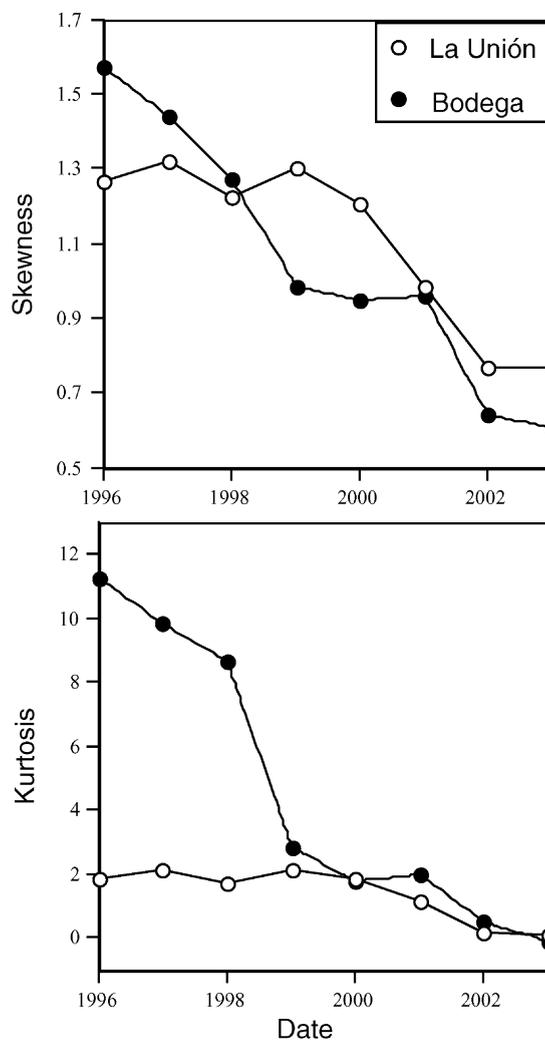
Fig. 3. Skewness and kurtosis calculations for the period of 1996–2003 for both sites.

characteristics of the individual trees that died. The average height in the year prior to death was 7.1 m at La Unión and 8.2 m at Bodega. The average height of individuals that survived through that same time period was 9.2 m at La Unión and 9.9 m at Bodega. Independent t-tests at each site verified a highly significant difference between heights of surviving individuals and heights of those that had died ($t = 5.28$, d.f. $= 53.8$, $P < 0.001$ at La Unión: $t = 4.17$, d.f. $= 87.5$, $P < 0.001$ at Bodega). Thus, the unsurprising fact is that smaller individuals die at greater frequency than larger individuals, corroborating what
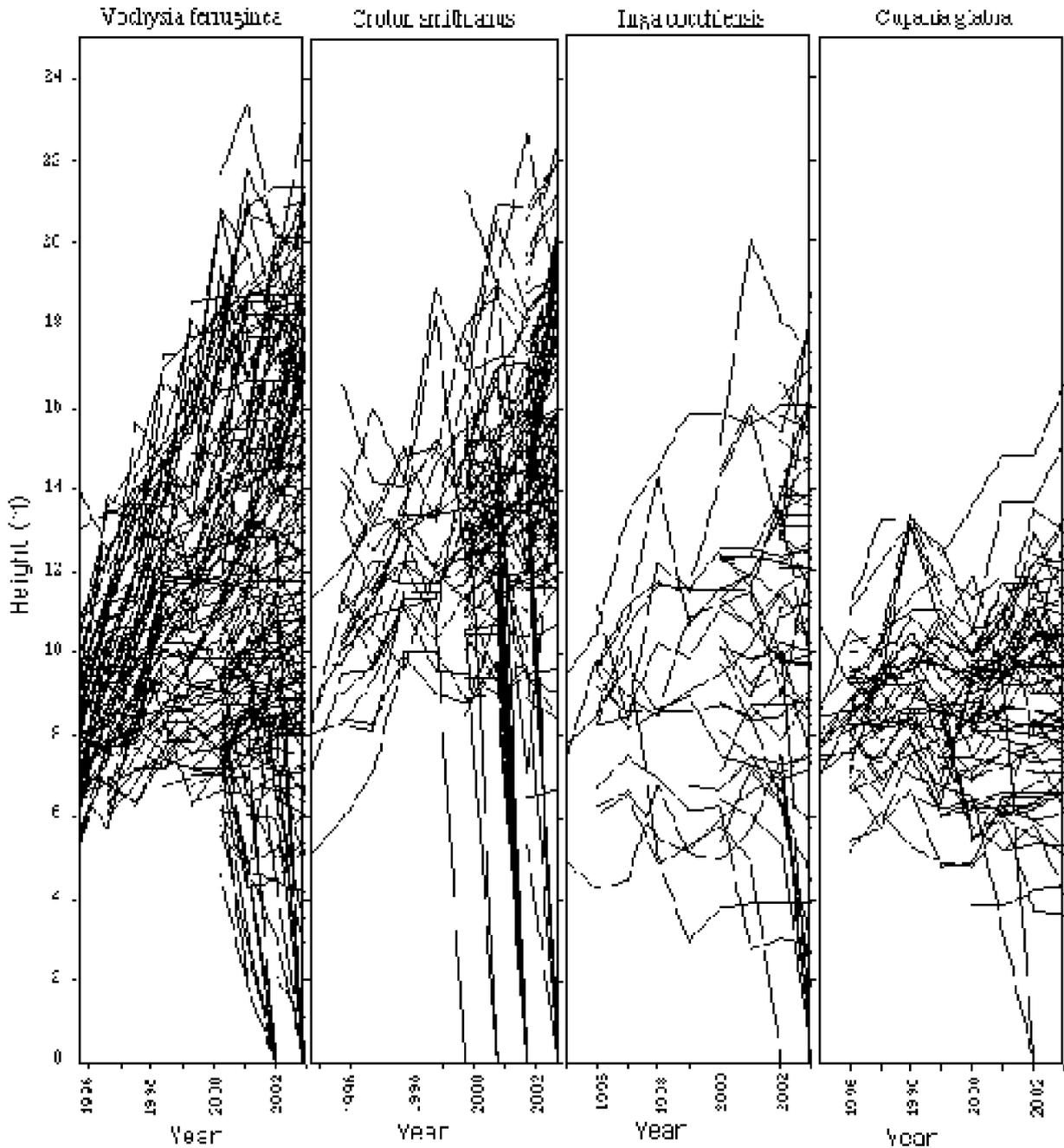
Fig. 4. Heights of individual trees of four typical species, a primary forest heliophyte (*V. ferruginea*), a pioneer (*Croton smithianus*), a primary forest canopy tree (*I. cochleensis*), and a primary forest subcanopy tree (*Cupania glabra*).

was expected for trees undergoing strong competition (Vandermeer et al., 2001).

In Fig. 4 we present the heights of individual trees for four common species at the La Bodega site, illustrating the typical patterns of growth and mortality for four "guilds", subcanopy primary forest (*Cupania glabra* Sw.), the canopy primary forest (*Inga cochlensis* Pitt.), pioneer (*Croton smithianus*), and

heliophyte (*V. ferruginea*) (a figure of zero is recorded in these graphs for individuals that died). A general indication of canopy development can be seen from these four examples, where growth is highest among larger individuals, lowest among smaller individuals, and mortality tends to be concentrated in the smaller individuals.

4. Discussion

Subsequent to the extensive damage done by the hurricane in October 1988, the canopy of the forest has undergone a development that is characterized by initial rapid growth to a point where the bulk of the canopy stood at about 7–8 m (in 1996). At that point the canopy appeared to be quite dense, and a casual observer might even suggest it was more dense than an older growth forest in a comparable habitat. Competition for light appeared to be intense at this point (Vandermeer et al., 2001). From 1996 through the present, there has been a very slow growth of the upper canopy, and currently it appears to be approximately 15–20 m high (see Figs. 1 and 2). However, there remains a lower canopy, perhaps less well defined than in 1996, that retains a relatively dense appearance and is now positioned at approximately 10–11 m (see Fig. 1). While a very large number of individuals are in the approximately 7–8 m category (see Fig. 2), in the field most of these individuals seem to be below the bulk of the canopy cover, and many exhibit a pattern of slow decline in height. This pattern is reflected in the individual growth curves for *I. cochleensis* and *Cupania glabra* (Fig. 4), where smaller individuals are generally declining while larger individuals are generally growing. Thus, the gradual generation of a platykurtic distribution (Fig. 3) is evident. Mortality events, still relatively rare in this forest, are mainly of those individuals situated below the main canopy (examples of which are evident in Fig. 4). However, there is a statistically significant difference in the heights of surviving versus expired individuals, demonstrating that position in the canopy determines, to some extent survivorship.

The basic dynamics of the thinning canopy is precisely as expected (Vandermeer et al., 2001). The low-statured thinning canopy (at about 7–8 m) found in 1996 has been (1) growing at its upper end, (2) stagnant at an intermediate height, (3) declining at the lower heights, and (4) generating mortality mainly of the individuals located in the subcanopy. Furthermore, it is our impression that the death rates are uncorrelated with species identity as one would expect from the so-called non-niche models (Zagt and Werger, 1998; Vandermeer et al., 2001). However, this casual observation deserves a more nuanced analysis since some species are, by nature, subcanopy or canopy, heliophyte or not, etc. A more complete analysis of this particular question will be presented elsewhere. The present communication is intended to report on the physical details of the dynamics of the late thinning canopy, verifying the general qualitative dynamics suggested earlier (Vandermeer et al., 2001; Oldeman, 1990; Bormann and Likens, 1979; Oliver and Larson, 1990).

Acknowledgements

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