# Growth Rates of Tree Height Six Years after Hurricane Damage at Four Localities in Eastern Nicaragua[1]

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## ABSTRACT

Growth rates for 44 species of trees in a posthurricane forest in Nicaragua were measured. The pattern is consistent with the interpretation of succession as a two stage process: an initial building phase after the hurricane followed by a thinning phase. Localities that were damaged less from the hurricane are now entering the thinning phase of postdisturbance succession, while those subjected to the most severe damage appear to remain in the building phase.

DISTURBANCE IS RECOGNIZED AS AN IMPORTANT ECO-LOGICAL FACTOR (Miller 1982, Sousa 1984, Pickett & White 1985, Petraitis *et al.* 1989 Caswell & Cohen 1991). In forests, windthrows are a major component of natural forest dynamics, whether in the form of a single felled tree creating a light gap (Brokaw 1987, Denslow 1987) or a large storm creating an extensive area of damage (Vandermeer et al. 1990, 1996; Brokaw & Walker 1991, Yih *et al.* 1991). Understanding the details of postdisturbance succession remains an important research goal of forest ecology. Here we present data on the rate of growth in tree height of the trees in a lower canopy of a regenerating rain forest, following the catastrophic damage of a hurricane six years ago.

Hurricane Joan struck the eastern seaboard of Nicaragua in October 1988, causing extensive damage to the lowland rain forests (Boucher 1989,Vandermeer *et al.* 1990). In the six years following the hurricane, we have witnessed the successional processes at four localities. The forest initially exhibited major physical damage with the majority of trees either coppiced, truncated or felled (Yih *et al.* 1991) with complete defoliation of all trees. How-

ever, soon there was a large amount of resprouting in almost all damaged trees (Vandermeer *et al.* 1990, Yih *et al.* 1991), followed by a large delayed mortality the following year (Boucher *et al.* 1996). The trees that remained standing resprouted high on the trunk and formed a diffuse canopy, 15–20 m high. The resprouts, surviving saplings and seedlings, and the newly arrived saplings and seedlings have grown to form a low-statured canopy that is currently very dense. The process of forming this low-lying canopy is referred to as the "building phase," while the subsequent phase of intense competition is the "thinning phase" (Vandermeer *et al.* 1996).

We now observe a diffuse upper canopy (*ca* 15–20 m high) and a dense lower canopy (*ca* 9 m high; Vandermeer *et al.* 1996). It is in this lower canopy that we expect the process of competition to be operative, eventually leading to the elimination of many of the currently competing individuals.

Tree growth in the lower dense canopy, especially extension in height, is expected to follow certain patterns, depending upon the rate and degree of succession. We expect that the average growth rates will decline as succession proceeds. This expectation can be illustrated graphically (Fig. 1), in which species are divided into pioneer, heliophyte, and primary forest species, and the post-damage time sequence is divided into building
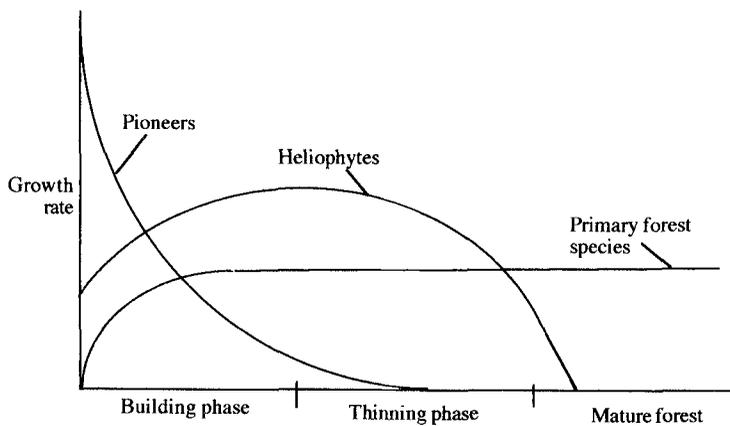
FIGURE 1.   Diagrammatic representation of expected growth rates along the successional gradient for three guilds of rain forest trees.

phase, thinning phase and mature forest. Furthermore, as the successional process proceeds from building phase to thinning phase, we expect the variability of growth rates (from individual to individual in a given species) to change from low to high, due to the shading of individuals in the lower canopy by faster-growing individuals.

Our hypothesis is that in the thinning phase, all species will have low growth rates, while in the building phase, the pioneers will be growing fastest (with the heliophytes and primary forest species having depressed growth rates) because of competition from vines and other pioneer vegetation.

## METHODS

The study was conducted in the region surrounding Bluefields, on the southern Caribbean coast of Nicaragua (the core area damaged by Hurricane Joan). Data from four sites located within the damaged area (Fig. 2) are reported. Background information on the choice and details of the sites are given in Vandermeer et al. (1996). Note that Bodega is almost exactly in the center of the hurricane damage area while Fonseca is near the edge of that damage. Loma de Mico is intermediate, but closer to the edge than the center. La Unión is a unique site in that the permanent plot there is directly to the west of a large hill, thus partly protected from the major winds of the hurricane. The appearance of this forest supports the expectation that it was the least damaged of all four plots. We take the relative position of each of the plots as a rough estimate of the position we expect to find the forest on the time axis of Figure 1. At one extreme, we

expect that Bodega will still be in the building phase since it sustained considerably more damage than the others while we expect Fonseca and La Unión to be at least approaching the thinning phase, due to their having experienced less damage. All sites are on level ground and the soils are ultisols (judging from soil maps and general appearance) with apparently similar drainages. Soil analysis (Vandermeer, pers. obs.) at Bodega and Fonseca indicated no significant differences in major nutrients, soil organic matter, or pH. There is no reason to expect significant site differences in terms of physical factors.

Beginning in 1994, tree heights were measured by means of a telescoping pole. The highest leaf on the tallest branch was taken to be the height. Because of logistic difficulties, not all trees were measured in 1994 and the remaining individuals were measured in 1995. In 1996, the heights were measured for all individuals at all four sites. Growth rates (m/yr) were calculated as either the difference between the heights in 1996 and 1995, or the difference between the heights in 1996 and 1994 divided by two. Growth rates were analyzed with an analysis of variance, after first using Bartlett's test for homogeneity of group variances. Tukey's honestly significant difference (HSD) tests were used for pairwise comparisons.

Height measurements are difficult for a variety of reasons, making the accuracy of the measurements questionable. First, it is difficult to see the top of the tree under current canopy conditions, with intertangled branches from many trees obstructing vision from almost every angle. Second, judging which branch actually ascends to the high-
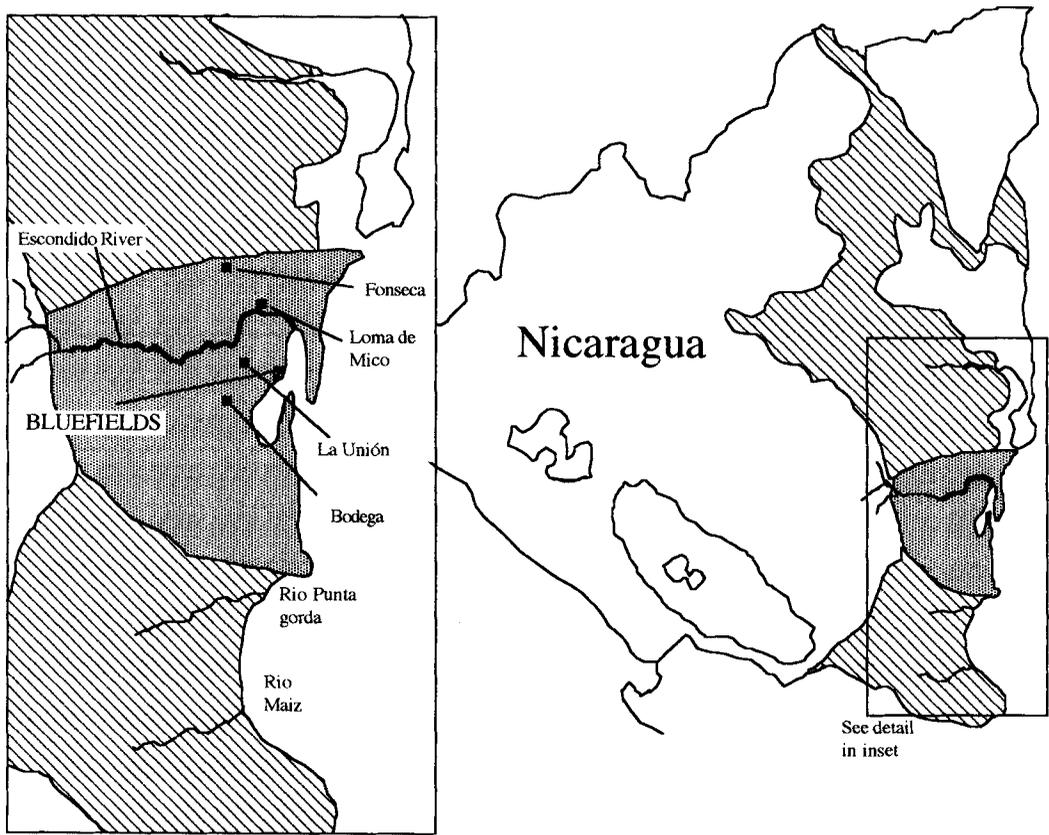
FIGURE 2.   Map of Nicaragua showing area of damage and position of the four sites in this study. Diagonal hatching indicates the approximate position of original lowland tropical rain forest, and dark shading indicates approximate extent of hurricane damage.

est point may be influenced by the particular position the observer takes in the forest; and thus the branch measured may change from one year to the next. However, these biases are not likely to be systematic. We thus have confidence in average figures but do not put much emphasis on the growth of individual trees in this paper.

TABLE 1.   *Basic statistics for rate of growth in height at the four sites. Different lower case letters signify statistically significant differences at the 95 percent level.*

|  | $\bar{x}$ | SD | N | CV |
|---|---|---|---|---|
| Bodega | 0.858 a | 0.990 | 934 | 115 |
| Loma de Mico | 0.643 b | 0.663 | 575 | 151 |
| Fonseca | 0.486 c | 1.324 | 847 | 272 |
| La Union | 0.332 c | 0.902 | 409 | 271 |

## RESULTS

All growth rates were pooled at each of the four sites (Table 1). As expected, the average growth rate for Bodega was largest, since the most severe hurricane damage had been at this site and growth into the lower canopy was still proceeding. The other three sites had smaller average growth rates since damage had been less severe. An analysis of variance indicated that there were significant differences among the average growth rates at the different sites ($F = 31.3$, $P < 0.001$; Bartlett's test for homogeneity of group variances yielded a chi-square of 311.4, $P < 0.001$). Pairwise comparisons indicated strong differences between Bodega and all other three sites and weaker differences among Loma de Mico, Fonseca, and La Unión (Table 1). Variability, as measured by the coefficient of variation ($CV$), was as expected with the lowest vari-

TABLE 2.  *Summary of height growth rates (m/yr) at all four sites.*

| Scientific name | Bodega | Loma de Mico | Fonseca | La Unión |
|---|---|---|---|---|
| *Acidoton nicaraguense* | 0.3093 | | | |
| *Amaioua corymbosa* | | 0.3271 | | |
| *Ardisia* sp. | −0.0127 | | 0.48 | |
| *Astrocaryum alatum* | | 0.3088 | | |
| *Byrsonima crassifolia* | 0.9725 | | 1.005 | |
| *Casearia arborea* | 1.181 | | | 0.5121 |
| *Casearia sylvestris* | | | | 0.2348 |
| *Cecropia obtusifolia* | | | 0.5272 | 0.4528 |
| *Cordia bicolor* | 1.153 | | | |
| *Croton schiedeanus* | | | −0.4582 | |
| *Croton smithianus* | 1.2356 | 0.8571 | 0.5593 | |
| *Cupania glabra* | 0.808 | 0.6743 | 0.7051 | |
| *Dendropanax arboreus* | 0.748 | | −0.0954 | 0.2274 |
| *Galipea granulosa* | | | 0.8233 | |
| *Goethalsia meiantha* | | | 0.3974 | |
| *Guatteria diospyroides* | | | | 0.2455 |
| *Guatteria recurvisepala* | 1.349 | 0.9352 | −0.0656 | |
| *Guettarda combsii* | | 0.6024 | | |
| *Guettarda deamii* | | 0.8262 | 1.0942 | |
| *Henrietea seemannii* | 0.931 | | | |
| *Hirtella americana* | 0.62 | | 0.4028 | |
| *Hirtella guatemalensis* | | 0.4854 | | |
| *Hyeronima alchorneoides* | | | | 0.3822 |
| *Inga cocleensis* | 0.933 | 0.8871 | 0.9678 | |
| *Inga thibaudiana* | 1.148 | | | |
| *Isertia haenkeana* | 0.513 | 0.0947 | 0.44 | |
| *Lacistema aggregatum* | 0.718 | | | 0.6284 |
| *Mabea occidentalis* | 1.089 | 0.6359 | | |
| *Manilkara zapota* | | | 0.8618 | |
| *Miconia prasina* | 1.049 | 0.7471 | 0.6986 | |
| *Myrcia* sp. | 0.97 | | | |
| *Piper auritum* | | | | 0.053 |
| *Protium schippii* | 0.956 | | | |
| *Pseudolmedia spuria* | 0.789 | | 0.1221 | |
| *Qualea paraensis* | 0.809 | | | |
| *Rinorea squamata* | 0.132 | | −0.0707 | |
| *Simarouba amara* | 1.533 | | | |
| *Spachea correae* | | 0.721 | | |
| *Terminalia amazonia* | 2.177 | | | |
| *Tetragastris panamensis* | | 0.477 | 0.3538 | |
| *Unonopsis pittieri* | 0.723 | | | |
| *Virola koschnyi* | | | | 0.5608 |
| *Vismia macrophylla* | 1.44 | | | |
| *Vochysia ferruginea* | 1.281 | 1.154 | 0.5586 | |
| $\bar{x}$ | 0.9465 | 0.6489 | 0.4653 | 0.3663 |

ability at Bodega and the highest at Fonseca and La Union (Table 1).

For 44 species, a minimum of 9 individuals occurred at least once at each site, enabling the calculation of growth rates for these individual species (Table 2). Values ranged from 2.2 m/yr (*Terminalia amazonia* at Bodega) to negative 0.5 m/yr (*Croton schiedeanus* at Fonseca). This general pattern reflected the same as for the pooled growth rates, with the means of these 44 species ordered in the same way (*i.e.*, Bodega highest, followed by Loma de Mico, Fonseca, and La Unión). While no individual species occurred abundantly enough at all four localities to have growth rates computed, several species occurred at three of the localities. For example, *Croton smithianus,* a classic pioneer species (Vandermeer *et al.* 1997), had a pattern of a fast growth rate at Bodega (1.2 m/yr), a slower rate at Loma de Mico (0.9 m/yr), and a yet slower rate at Fonseca (0.6 m/yr). *Guatteria recurvisepala* and *Miconia prasina,* both heliophytes (Vandermeer *et al.* 1997), showed similar patterns, with *G. re-*
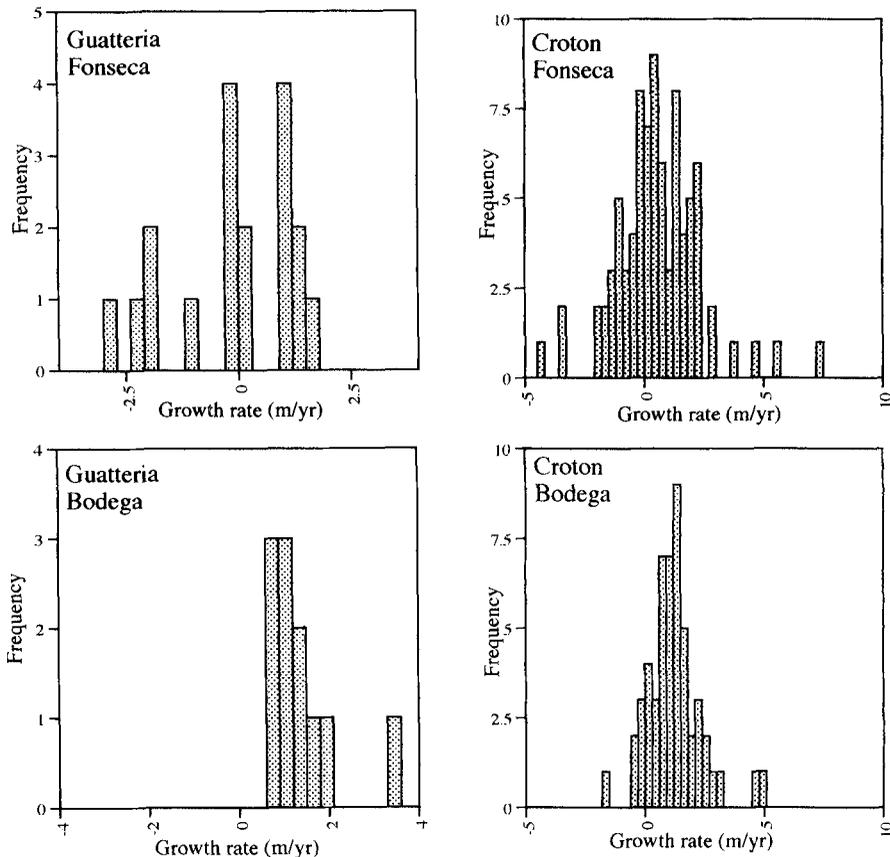
# Pioneers/heliophytes



FIGURE 3.    Histograms of growth rates for four illustrative species at two of the sites.

*curvisepala* having a negative growth rate in Fonseca. On the other hand, two primary forest species (*i.e.*, *Cupania glabra, Inga cocleensis*) did not show that general pattern, while *Vochysia ferruginea,* another primary forest species, had high levels of growth in all three sites where it occurred abundantly.

A more detailed comparison was made between the two geographically extreme sites, Bodega and Fonseca. Twelve species were common enough in both sites to be evaluated: 4 pioneers/heliophytes (*Croton smithianus, Guatteria recurvisepala, Isertia haenkeana, Miconia prasina*) and 8 primary forest species (*Vochysia ferruginea, Cupania glabra, Inga cocleensis, Hirtella americana, Dendropanax arboreus, Byrsonima crassifolia, Pseudolmedia spuria,* and *Rinorea squamata*). Mean growth rates were calculated for each of these 12 species at the two sites.

A paired *t*-test was performed on each and the *CV* was calculated (Table 3). As expected, 3 of 4 pioneers/heliophytes showed a difference between the two sites in their growth rates, still growing quite rapidly in Bodega but with significantly reduced growth rates in the more successionally advanced Fonseca. In contrast, the primary forest species (Table 3) did not show a difference in growth rates between the two sites, again as expected.

In 11 of the 12 species in this comparison (Table 3), the *CV* was greater in Fonseca than in Bodega. The one exception was *Byrsonima crassifolia,* which had almost the same *CV* for both sites. A paired *t*-test showed the *CV*s to be significant between Fonseca and Bodega; applied directly to *CV*s and after logrithmic transformation, Wilcoxon signed rank test gave a significance of 0.002). This was as expected from the basic theory of plant
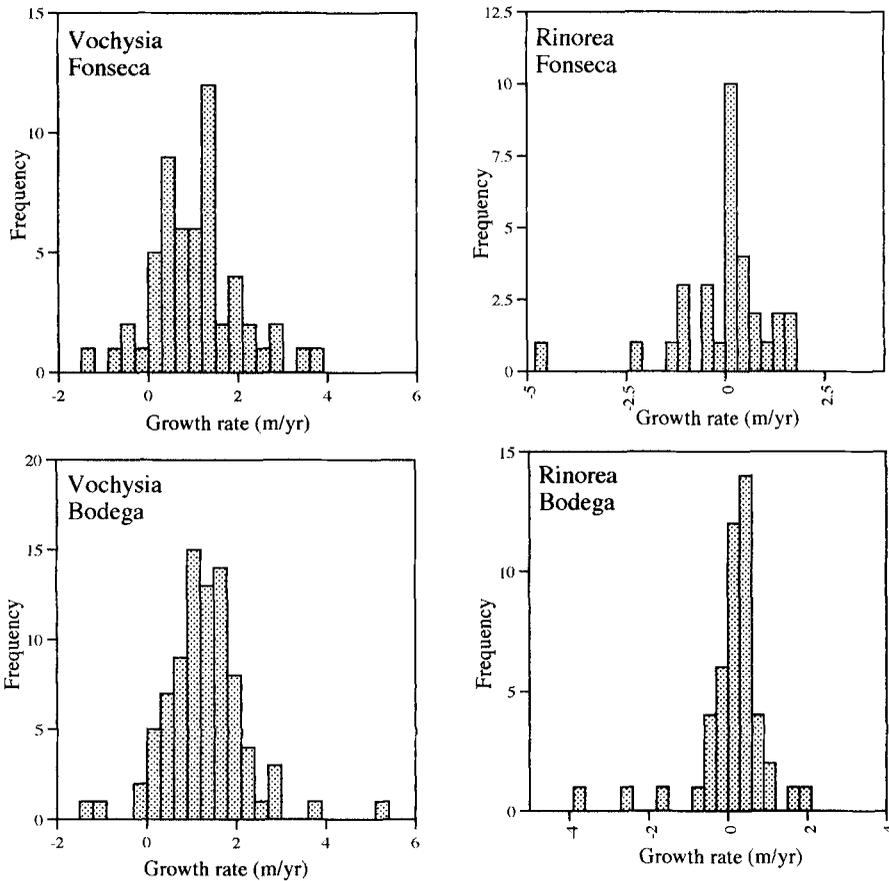
## Primary forest species



Figure 3.   Continued.

competition, according to the hypothesis that Fonseca is further along in the successional process such that some individuals are now being suppressed while others are growing well. In Figure 3 we illustrate typical distributions for both the pioneer/heliophyte category and the primary forest category. In both cases it is apparent that the variability at Fonseca is greater than the variability at Bodega with different means for the pioneer/heliopytes but not for the primary forest species.

## DISCUSSION

What one expects to find in the growth rate of tree heights depends on where the forest is located on the time axis of Figure 1. If the successional process is very slow, we might expect all pioneers to grow very rapidly while the primary forest species remain growth limited by these pioneers and other non-arborescent vegetation such as vines. Our expectation was that Bodega would be nearer to the origin of the time axis (Fig. 1) while the other sites would be farther to the right of that axis. This is the pattern we find. Comparing growth rates of pioneers/heliophytes from Bodega to those from Fonseca, we find a clear pattern of reduced growth rate at the latter site. The only exception to this pattern is *Isertia haenkeana*, a small subcanopy tree that we suspect has reached its maximum growth capacity at all sites.

This result is consistent with our interpretation of the successional process (Vandermeer *et al.* 1996) as a two stage process involving an initial building phase after the hurricane followed by a

TABLE 3.    *Basic statistics for the species found commonly at both Fonseca and Bodega (t and p refer to growth rate).*

| | Mean growth rate Fon | Mean growth rate Bod | CV Fon | CV Bod | df | t | P |
|---|---|---|---|---|---|---|---|
| Pioneers/heliophytes | | | | | | | |
| *Croton smithianus* | 0.559 | 1.236 | 316 | 94 | 134 | 2.44 | 0.016 |
| *Guatteria recurvisepala* | −0.07 | 1.349 | 2030 | 60 | 27 | 3.168 | 0.004 |
| *Isertia haenkeana* | 0.440 | 0.518 | 256 | 116 | 61 | 0.314 | 0.754 |
| *Miconia prasina* | 0.698 | 1.049 | 127 | 49 | 108 | 2.574 | 0.011 |
| Primary forest species | | | | | | | |
| *Vochysia ferruginea* | 1.057 | 1.281 | 90 | 70 | 139 | 1.417 | 0.159 |
| *Cupania glabra* | 0.705 | 0.823 | 181 | 92 | 102 | 0.578 | 0.564 |
| *Inga cocleensis* | 0.968 | 0.933 | 126 | 69 | 21 | 0.090 | 0.929 |
| *Hirtella americana* | 0.403 | 0.620 | 273 | 123 | 36 | 0.711 | 0.482 |
| *Dendropanax arboreus* | −0.10 | 0.748 | 900 | 114 | 34 | 1.912 | 0.064 |
| *Byrsonima crassifolia* | 0.943 | 1.048 | 50 | 70 | 32 | 0.444 | 0.660 |
| *Pseudolmedia spuria* | 0.122 | 0.789 | 1179 | 96 | 38 | 1.861 | 0.070 |
| *Rinorea squamata* | −0.07 | 0.132 | 1770 | 686 | 77 | −0.84 | 0.403 |

thinning phase. During the building phase, a low canopy is formed from resprouted saplings and previously existing seedlings. This low canopy is currently very dense and is where intense crown competition among the individual trees that form it occurs. From this intense competition we expect a thinning process to follow (Vandermeer *et al.* 1996). The less damaged sites are more likely to be entering this thinning phase and those trees do show slower average growth rates.

Further evidence that we have entered the thinning phase at Loma de Mico, Fonseca and La Unión comes from the distribution of growth rates at all four sites. The *CV* at Bodega is 1.15 whereas at the other three sites it is 1.51, 2.72, and 2.72, as we move to Loma de Mico, Fonseca, and La Unión. The high *CV* for La Unión is probably due to that plot being protected from the high winds

by the large hill to its east, as noted earlier. Furthermore, by comparing a variety of species from Bodega to those same species from Fonseca, we find a significant trend toward increased *CV*s in almost all species.

Taking the evidence of average growth rates along with that from differences in *CV*s from site to site, we conclude that the forests that were damaged less from the hurricane are now entering the thinning phase of postdisturbance succession, while those subjected to the most severe damage appear to remain in the building phase.

## ACKNOWLEDGMENTS

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