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A Twelve-Year Comparison of Stand Changes in a Mahogany Plantation and a Paired Natural Forest of Similar Age[1]

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ABSTRACT

We compared forest structure over a 12 yr period (1982–1994) that included measurements before and after a severe hurricane in two forests: a 64 yr old *Swietenia macrophylla* tree plantation and a paired natural forest of similar age in a subtropical wet forest life zone at 200 m elevation in Puerto Rico. We measured trees ≥ 4 cm diameter at breast height in a 40 × 50 m plot at each forest type. The natural forest had lower total tree height (8.8 vs. 10.2 m in 1984), and greater basal area (35.7 vs. 28.5 m^2/ha in 1989) and tree density (1525 vs. 969 trees/ha in 1989) than the plantation. Rates of tree mortality and ingrowth to the ≥ 4 cm diameter class were higher in the plantation than in the natural forest. Both forest types exhibited the same rate of change in these structural parameters before and after Hurricane Hugo. However, Hurricane Hugo caused a greater reduction in the rate of change of tree density and basal area of the plantation than it did in the natural forest. After the hurricane, the plantation experienced a greater fluctuation in tree species composition and tree species abundance than did the natural forest. Tree ingrowth was lower than tree mortality in both stands. By 1994, all measured rates of change were at pre-hurricane levels. The species composition and structural changes required to make the plantation more productive in terms of stemwood biomass appear to make the plantation more vulnerable to hurricane wind effects and this in turn causes greater rates of change in species composition, tree mortality, and tree ingrowth during the initial phase following the disturbance.

RESUMEN

Comparamos la estructura del bosque sobre un período de 12 años (1982–1994) que incluía medidas antes y después del paso de un huracán sobre dos tipos de bosque: una plantación de 64 años de *Swietenia macrophylla* y un bosque natural de edad similar a una elevación de 200 m en una zona de vida subtropical muy húmeda en Puerto Rico. Se midieron árboles con diámetros a la altura del pecho ≥ 4 cm en parcelas de 40 × 50 m en cada tipo de de bosque. Comparado con la plantación, el bosque natural tenía árboles menos altos (8.8 vs. 10.2 m en el 1984) y valores más altos de área basal (35.7 vs. 28.5 m^2/ha en 1989) y densidad de árboles (1525 vs. 969 árboles/ha en el 1989). Las tasas de mortalidad y de incorporación a la clase de ≥ 4 cm fueron superiores en la plantación que en el bosque natural. Ambos tipos de bosque exhibieron las mismas tasas de cambio en sus medidas estructurales antes y después del Huracán Hugo. Sin embargo, el huracán causó una mayor reducción en la tasa de cambio de área basal y densidad de árboles en la plantación comparado con el bosque natural. Después del huracán, la plantación sufrió una mayor fluctuación en su composición y abundancia de especies arbóreas que el bosque natural. La entrada de árboles a la clase ≥ 4 cm fue menor que la mortalidad en ambos tipos de bosque. Para el 1994, todas las medidas de cambio estructural estaban en sus valores pre-huracán. La composición de especies y los cambios estructurales necesarios para hacer de la plantación un sistema productivo en términos de la producción de madera, aparentemente hacen que la plantación sea más vulnerable a los efectos de los vientos huracanados. Esto a su vez, causa que en las etapas subsiguientes al paso del huracán surjan cambios más significativos en la composición de especies, y en las tasas de mortalidad y de entrada de árboles a las clases diamétricas de ≥ 4 cm.

Key words: disturbance; Hurricane Hugo; mahogany; secondary forest; tree mortality; tropical forests; tropical tree plantations.

TREE PLANTATIONS ARE AN IMPORTANT LAND USE IN THE TROPICS (Evans 1982, Shepherd 1993), particularly in degraded lands where they can be used for rehabilitation or for maximizing fiber and biomass production (Lugo *et al.* 1993, Brown & Lugo 1994). Plantation productivity also reduces pressure on the demands for wood from mature tropical forests (Evans 1982). Between 1980 and 1990, the global area in tropical tree plantations increased by 150% to 43.8 million ha (FAO 1993). How-

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ever, because plantations are artificial systems with low species richness, their establishment requires caution in terms of the potential negative effects associated with the substitution of species-rich forests with species-poor ones (*cf.* Allen *et al.* 1995, O'Loughlin 1995, Rosoman 1995). While much is written about the potential harmful effects of tropical tree plantations (*cf.* Smith 1994), very little ecological research is available to substantiate the ecological behavior of these forests (Lugo 1992).

At the Luquillo Experimental Forest (LEF), the International Institute of Tropical Forestry has been conducting experiments with tropical tree plantations for over 50 yr (Wadsworth 1995). This effort includes the ecological analysis of plantations with a focus on comparative studies of plantations and paired natural forest stands (Cuevas *et al.* 1991, Lugo 1992, Rodríguez Pedraza 1993, Sánchez Irizarry 1989). This study builds on previous studies with the objective of comparing the response to a hurricane of a mature mahogany (*Swietenia macrophylla* × *S. mahagoni*) plantation with a secondary forest of similar age. Specifically, we take advantage of a 12-yr record of observation to compare the rate of vegetative recovery after Hurricane Hugo.

METHODS

The study sites were located at 200 m elevation in the El Verde sector of the LEF. In 1995, the mahogany plantation was 64 yr old and the paired secondary forest, located within 1 km of the plantation, was of similar but unknown age. Both sites had the same aspect, general topography, and soil type (clayey, oxidic, isohyperthermic Tropeptic Haplorthox). The details of conditions at the sites, site description, and their ecology and soils are given in Lugo (1992) and Sánchez Irizarry (1989).

In 1994, we measured the diameter at breast height (DBH at 1.3 m), estimated tree height, recorded dead trees, and identified to species all trees with DBH ≥ 4 cm in one 40 × 50 m plot at each site. Trees in these plots had been previously tagged and measured in 1982 and 1984 by Lugo (1992) and in 1989 and 1990 by Rodríguez Pedraza (1993). We also identified, measured, and tagged new trees that entered the ≥ 4 cm diameter size class as ingrowth. With these data, we estimated stand basal area (sum of the basal area of each tree divided by the area of the plot) and tree density (number of trees divided by the area of the plot); species richness (tree species per plot and tree species per thousand individuals (from a log-log relationship between number of tree species per number of tree individuals counted), species importance values (sum of relative density and relative basal area expressed in percent); absolute tree mortality (number of trees dying per hectare per year), relative tree mortality (ln initial number of stems − ln remaining live stems at end of measurement interval divided by the time interval), annual change in basal area and stem density (difference in basal area or tree density between two time intervals divided by the time between intervals), and ingrowth rates (number of trees entering the ≥ 4 cm diameter class divided by the time interval between measurements). These indices were examined over time (1982 to 1994) to assess forest response to the passage of Hurricane Hugo on September 18, 1989 (Scatena & Larsen 1991). Tree mortality estimates were based on tagged trees.

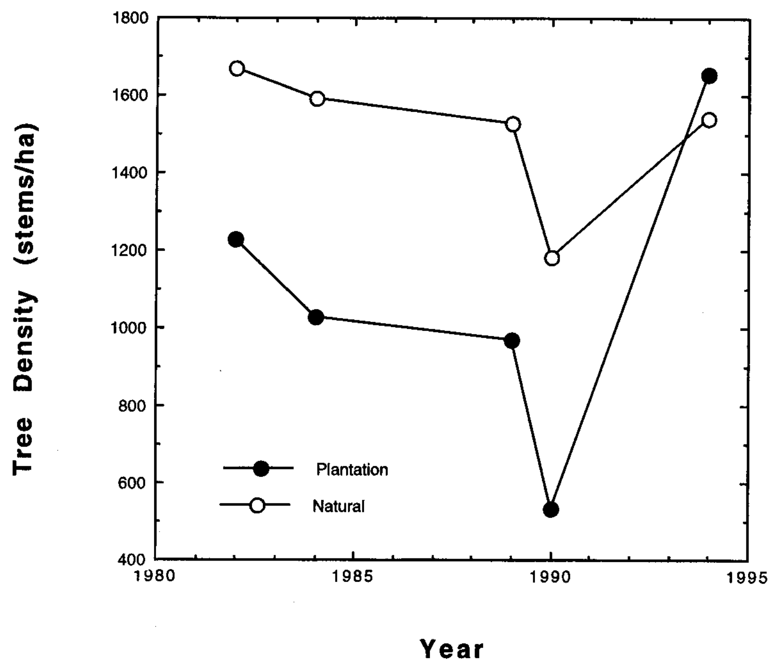
TABLE 1. *Rate of tree ingrowth into the ≥4-cm diameter at breast height diameter class in a 64 yr old* Swietenia macrophylla × S. mahagoni *plantation and a paired secondary forest of similar age in the Luquillo Experimental Forest, Puerto Rico. All values are in trees/ha/yr. Hurricane Hugo passed over the forest on 18 September 1989.*

	Ingrowth	
Time interval	Plantation	Natural forest
1984 to 1989 (pre-hurricane)	32	28
1989 to 1994 (post hurricane)	135	18

This comparison follows the case study approach discussed by Lugo (1992). We realize that there are no replicate ecosystems or replicate plots to verify the observed tendencies. This means that no statistical inference can be made to draw general conclusions. However, this particular set of stands is part of a larger research program at the LEF (see above) and, as such, provides useful site-specific comparative information that builds on models of ecosystem function under different land uses (*cf.* Waide & Lugo 1992).

RESULTS AND DISCUSSION

TREE DENSITY, BASAL AREA, AND HEIGHT.—During the period of study, the natural forest had a higher tree density and basal area than the mahogany plantation except in 1994 when post-hurricane ingrowth (Table 1) increased the tree density of the plantation above that of the natural forest (Fig. 1). This difference in structure is probably the result of the management history of the plantation; the



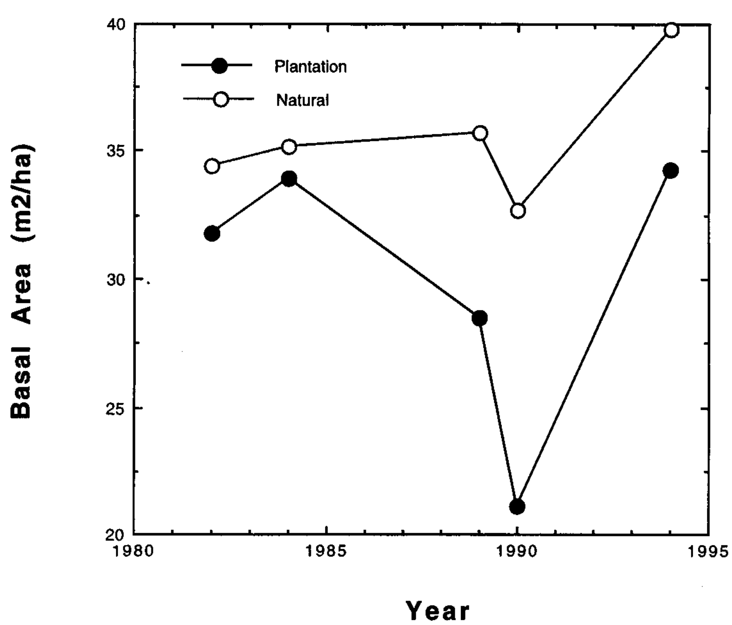


FIGURE 1. Pattern of tree density (a) and basal area (b) from 1982 to 1994 in a tree plantation and a natural forest in the Luquillo Experimental Forest. Hurricane Hugo passed over the area on 18 September 1989. Data are for trees with dbh ≥ 4 cm.

TABLE 2. *Median and maximum tree height in a 64 yr old* Swietenia macrophylla × mahagoni *plantation and paired secondary forest of similar age in the Luquillo Experimental Forest, Puerto Rico. Data for the dominant species I each stand are also given. Only trees with d.b.h. ≥4 cm were considered.*

Year	Plantation				Paired secondary forest			
	Median height (m)	95% CL	Maximum height (m)	*N*	Median height (m)	95% CL	Maximum height (m)	*N*
1982								
All species	4.6	1.0	44.8	177	2.5	0.6	23.7	191
S. macrophylla × *S. mahagoni*	5.3	2.1	44.8	74				
Dacryodes excelsa					5.5	4.5	23.7	12
1984								
All species	7.6	1.1	36.0	144	7.3	0.8	25.6	139
S. macrophylla × *S. mahagoni*	7.3	1.7	36.0	74				
Dacryodes excelsa					9.6	4.6	23.5	12
1989								
All species	8.3	1.4	35.0	128	8.0	0.9	27.0	194
S. macrophylla × *S. mahagoni*	8.0	2.1	35.0	65				
Dacryodes excelsa					18.0	3.3	23.0	12
1994								
All species	8.5	0.7	32.0	250	10.0	0.8	25.5	188
S. macrophylla × *S. mahagoni*	8.0	1.2	32.0	126				
Dacryodes excelsa					18.8	2.7	23.0	12

plantation was thinned three times (1945, 1958, and 1964), causing reduced tree density and basal area. In 1989, Hurricane Hugo decreased the basal area and tree density of both forest stands (Fig. 1).

Prior to Hurricane Hugo, tree height was higher in the plantation than in the natural forest (Table 2). After the hurricane, the average tree height in the plantation was similar to that of the natural forest. The tallest tree was still in the plantation but its absolute value was lower than in 1982. *Swietenia* trees in the plantation had the same height after 1984, but trees of the dominant *Dacryodes excelsa* appeared to increase in height during the same interval in the natural forest.

The rate of change in basal area and stem density (Fig. 2) shows a different ranking in the behavior of the two stands relative to that shown in Fig 1. In Fig. 1, the absolute values of these parameters were different between stands. However, both the plantation and the natural forest show similar rates of basal area and tree density change before Hurricane Hugo in 1989 (Fig. 2). The plantation suffered a greater reduction in rates due to the hurricane, and its recovery rate was similar to that of the natural forest.

Rodríguez Pedraza (1993) found that the plantation transferred more biomass and a higher fraction of its aboveground biomass from the aboveground tree compartment to the forest floor than did the secondary forest. This observation is consistent with the rates of change in Fig. 2. Greater openness of the canopy, taller trees, the spatial distribution of trees (planted in lines in the plantation), and the lower species richness of the plantation were suggested as the reasons for the greater susceptibility of the plantation to hurricane damage (Rodríguez Pedraza 1993).

Differences in wood density (at species or stand level) do not explain the differences in response to hurricane winds between stands. The stand level weighted wood density in g/cm^3 (estimated using tree importance values in Lugo [1992] and wood density data in Reyes *et al.* [1992]), was almost identical in both stands (0.54 in plantation vs. 0.58 in the natural stand). At the species-level, species such as *Swietenia* and *Dacryodes* had dissimilar response to wind despite similar wood densities. Zimmerman *et al.* (1994) found a significant relationship between wood density and wind damage to trees in a natural forest stand near our study area. We suggest that changes in stand structure, such as those introduced by artificial plantations, introduce vulnerability to winds that do not occur in the natural stands. However, our study cannot be conclusive on either of the two levels of explanation for our results, *i.e.*, the species or stand level.

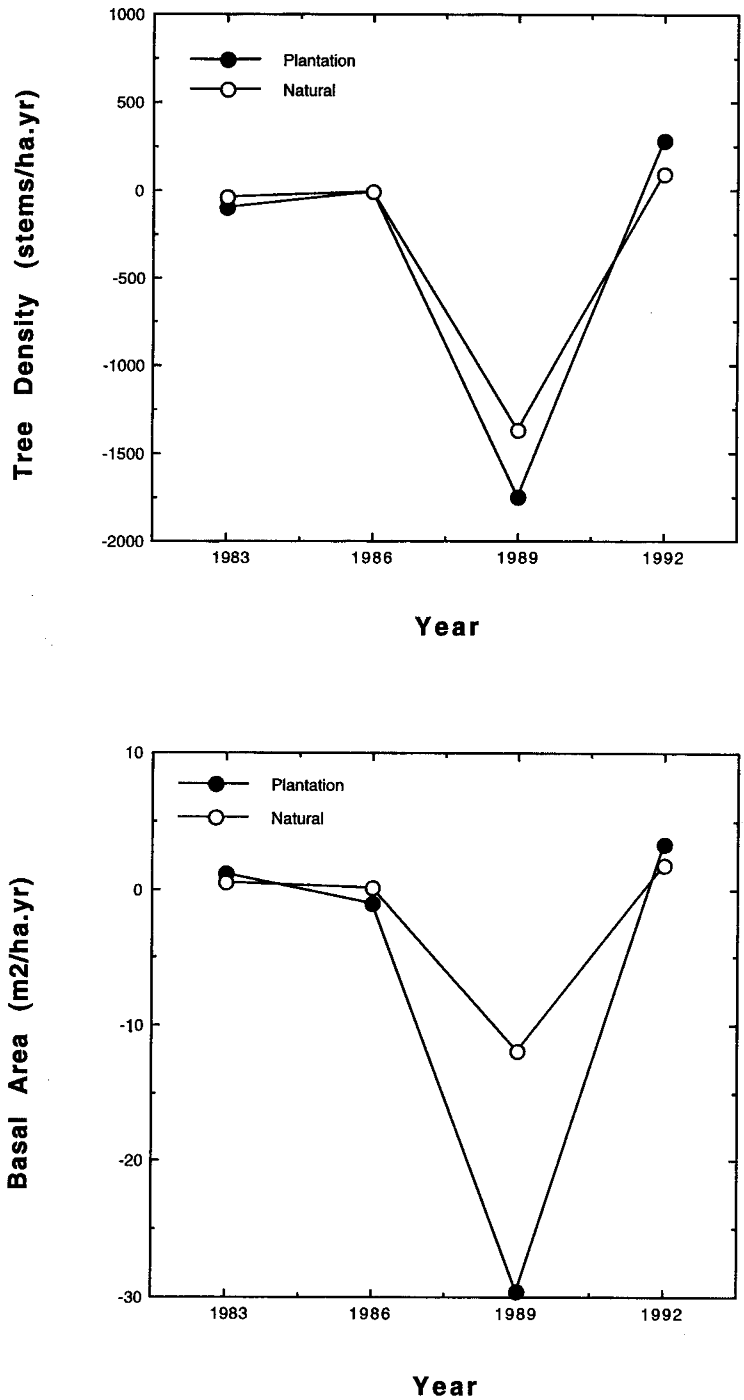


FIGURE 2. Rate of change of tree density (a) and basal area (b) from 1982 to 1994 in a tree plantation and a natural forest, in the Luquillo Experimental Forest. Data are for trees with dbh ≥ 4 cm and are plotted at the mid point of the measurement time interval.

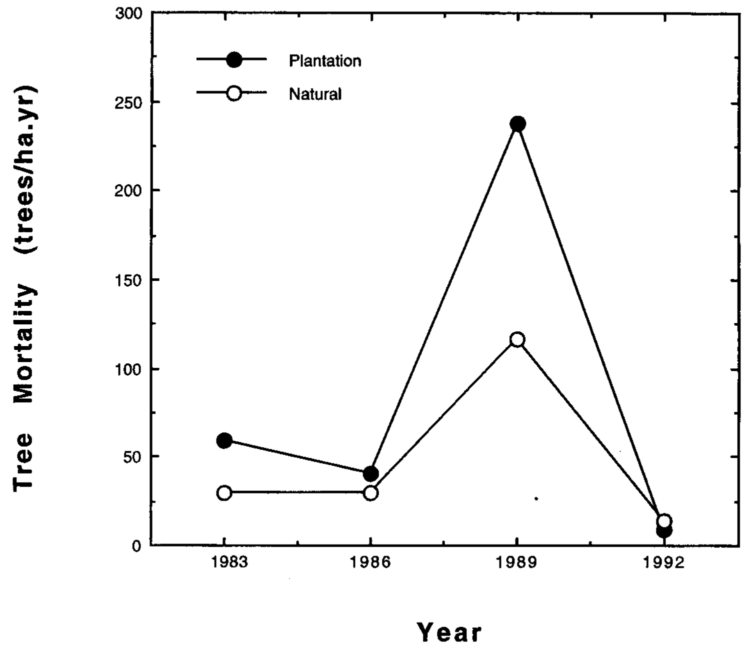


FIGURE 3. Pattern of tree mortality from 1982 to 1994 in a tree plantation and a natural forest, in the Luquillo Experimental Forest. Data are for trees with dbh ≥ 4 cm and are plotted at the mid point of the measurement time interval.

Tree mortality and ingrowth.—The absolute rate of tree mortality was either higher or the same in the plantation than in the natural forest (Fig. 3). The plantation had a higher relative rate of tree mortality (4 to 5%/yr before the hurricane) that the secondary forest (2%/yr). Hurricane Hugo greatly increased the absolute (Fig. 3) and relative rate of tree mortality in the plantation (up to 31%), but not as much in the natural forest (up to 7%). By 1994, absolute and relative tree mortality rates had returned to values similar to those measured before the hurricane (1 and 2%/yr in plantation and natural forest, respectively). The lower increase in hurricane-induced tree mortality in the natural forest (almost a four-fold increase) was barely sufficient to be termed catastrophic, *i.e.*, it was equivalent to 7 percent of the stems compared to the normal background mortality of 2 percent per year. Tree mortality in the plantation was clearly catastrophic, *i.e.*, equivalent to 31 percent of the stems.

Rates of tree ingrowth were also higher in the plantation than in the natural forest (Table 1). In either stand, these rates were not sufficient to compensate for tree mortality, resulting in decreased tree densities. Tree ingrowth after the hurricane was lower than pre-hurricane ingrowth in the natural stand while it increased four-fold during the same time interval in the plantation. We attribute this difference to the greater opening of the canopy in the plantation relative to the natural forest (below). *Swietenia* accounted for half of the ingrowth in the plantation, and had a high abundance of seedlings regenerating copiously both before and after the hurricane.

Species dynamics.—The pattern of tree species change before and after the hurricane was identical in both stands (Fig. 4). The number of tree species decreased after the hurricane with a clear recovery 5 yr later. The reduction in the number of tree species as well as the recovery of species was slightly higher in the plantation (−8 and + 6 species) than in the natural forest (−6 and +2 species). The greater effect of the hurricane on the plantation is reinforced if the same data are expressed according to number of species per thousand individuals (to correct for stem density changes). The greater number of tree ingrowth into the plantation causes a greater reduction in the species richness index when expressed per thousand individuals (from 20 in 1984, to 17 in 1989, and 11 in 1994, a 45% reduction). For the natural forest the changes were from 55 in 1984, to 46 in 1989 and 1994, a 16 percent reduction.

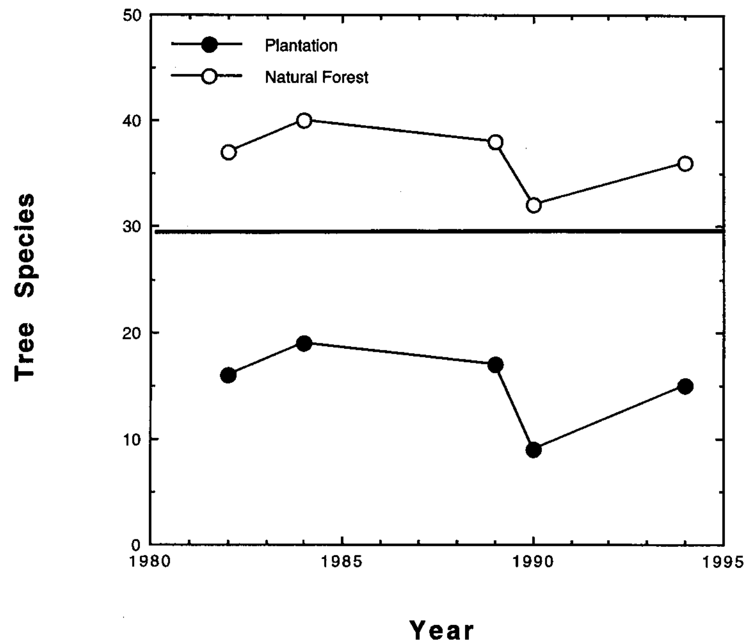


FIGURE 4. Pattern of tree species richness from 1982 to 1994 in a tree plantation and a natural forest, in the Luquillo Experimental Forest. The number of species correspond to an area of 0.2 ha. Data are for trees with dbh ≥ 4 cm.

Figure 5 compares the changes in importance value by species for the six most important species in each stand. The following trends are apparent:

- the plantation had greater dominance by fewer species, *i.e., Swietenia* and *Tabebuia* contributed to over 60 percent of the importance value, more than the sum of the six species shown for the natural forest
- there was more year to year variation in species importance value in the plantation than in the paired natural forest (*Swietenia* is a notable exception)
- the hurricane had a differential effect on the importance value of tree species in both forests, but the magnitude of change was higher for species in the plantation.

The two-most important species of the natural forest (*Dacryodes* and *Manilkara bidentata*) increased their importance value after the hurricane, and so did *Buchenavia capitata,* a shade-adapted late successional species (Sastre de Jesus 1979, McCormick 1995). *Casearia arborea* decreased in importance value after the hurricane, *Drypetes glauca* had begun to decrease before the hurricane, while *Tabebuia heterophylla* maintained the same importance value through the whole study period. These changes in importance value integrate the effects of mortality and ingrowth in the stem density and basal area of tree populations at the time of the estimate. The index is useful for assessing how a particular species compares with others at different times before and after a disturbance event.

In the plantation stand, *Swietenia, Casearia sylvestris,* and *Cecropia peltata* (synonymous with *C. Schreberiana*) increased their importance value after the hurricane. Both *Casearia* and *Cecropia* were in declining modes before the hurricane, while *Swietenia* was slowly increasing in importance. We observed extensive regeneration of *Swietenia* in the plantation stand. *Cecropia* invaded the plantation after the hurricane, but failed to invade the natural forest where canopy opening was less pronounced. *Myrcia splendens* and *Tabebuia* both declined in importance value after the hurricane. The decrease in importance value for *Tabebuia* was particularly notable given that it increased in importance value immediately after the event. After the hurricane this species behaved differently in the plantation compared to the natural stand. In the natural stand it held its position of importance, but in the plantation its ingrowth rate was low and it could not compete with faster growing species such as *Cecropia.*

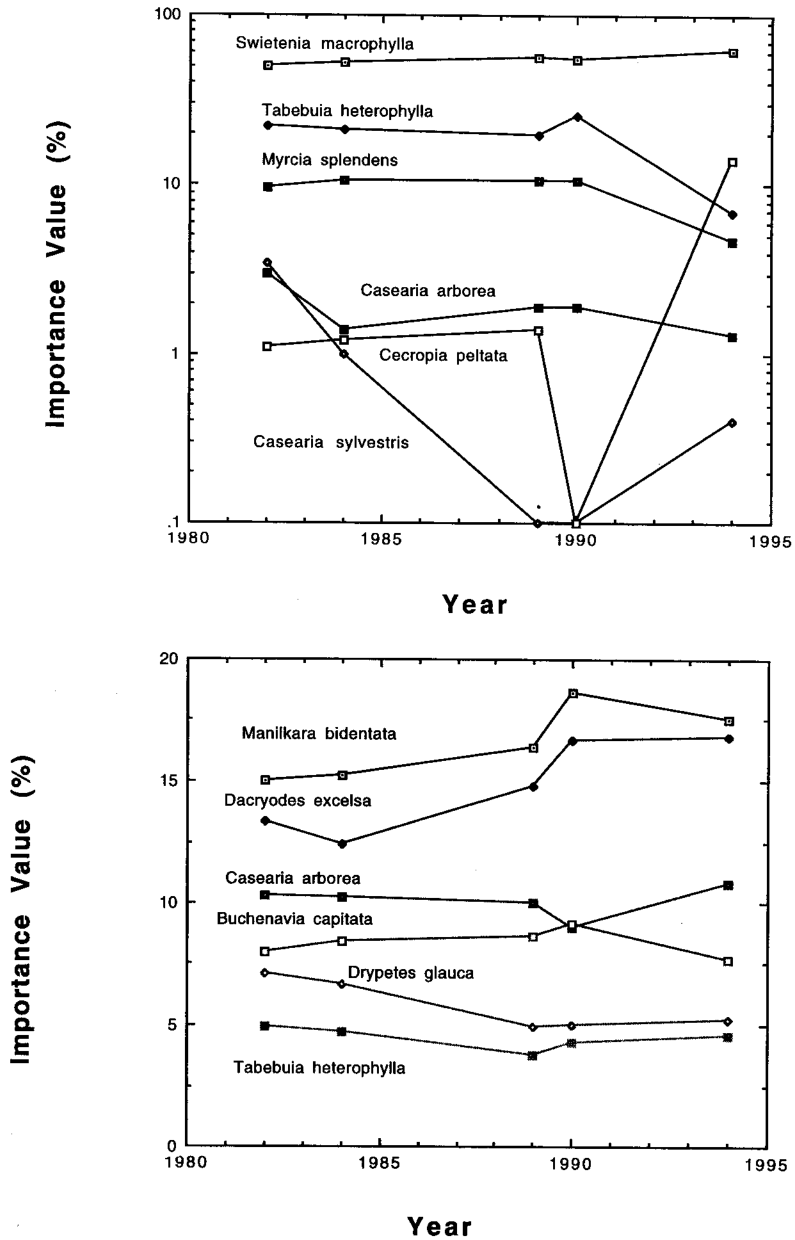


FIGURE 5. Changes in the importance value of the six most important species in a plantation (a) and paired natural forest (b) for the period of 1982 to 1994. The log scale for the plantation data (a) is to accommodate rare species that became common after the hurricane. The forest stands were located in the Luquillo Experimental Forest. Data are for trees with dbh ≥ 4 cm.

Conclusion

Our results underscore important similarities and differences in the response of the plantation and paired natural forest to Hurricane Hugo. Before the hurricane, both forest types had similar rates of ecosystem-level functions (Cuevas *et al.* 1991, Lugo 1992) and after the hurricane they increased in tree density and basal area at similar rates (Fig. 2). But, there were differences in pre-hurricane stand structure in terms of basal area, tree density, and tree height (Fig. 1, Table 2). The pre-hurricane difference in structure and composition was a result of management activities that gave the plantation an advantage over the natural forest in the production of stemwood and commercial volume (*cf.* Lugo 1992). The result was a differential effect on the plantation forest after the hurricane (measured in the amount of biomass transferred to the forest floor [Rodríguez Pedraza 1993], basal area and tree density changes [Figs. 1 and 2), and the rates of tree mortality [Fig. 3] and ingrowth [Table 1]).

These events had consequences for the success of tree species within both forest stands. In the natural forest, the reduced structural damage resulted in fewer species either leaving or invading the site after the hurricane (Fig. 4). As a result, the most important species maintained their dominance although species like *Buchenavia* and *Casearia arborea* exchanged their position of relative importance (Fig. 5). The canopy of the plantation opened to a greater degree and allowed early successional species like *Cecropia* to become abundant (*cf.* McCormick 1995, Silander 1979), reversing a long-term trend of reduction of importance as the plantation aged. By holding its high dominance through vigorous ingrowth and regeneration, *Swietenia* left little space for the rest of the native tree species that had invaded the plantation. The result is that these species oscillated widely in terms of their importance after Hurricane Hugo.

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