A CHRONOLOGY OF HURRICANE INDUCED CHANGES IN PUERTO RICO'S LOWER MONTANE RAIN FOREST

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SUMMARY

*Ridges in the lower montane rain forests of Puerto Rico and the Lesser Antilles from St. Kitts to Grenada are dominated by tabonuco (*Dacryodes excelsa *Vahl), a long-lived tree adapted to recurrent hurricanes. The oldest tabonuco trees in Puerto Rico appear to survive 500 to 600yrs in forests that periodically (perhaps every 50 to 60yrs) lose nearly one-fifth of their biomass. Post hurricane-recovery, characterized by greater rates of stem ingrowth and mortality, showed an immediate and abundant regeneration of yagrumo hembra (*Cecropia schreberiana *Mig.) along with numerous small- to medium-sized species in forest openings. Stem density, species numbers, and the rate of biomass accumulation are at a maximum 15yrs after the hurricane; about 50yrs later, most of the secondary species associated with past forest disturbance have disappeared and the rate of biomass accumulation becomes asymptotic.*

RESUMEN

*Las cimas de las colinas en las selvas pluviales intermedias de Puerto Rico y las Antillas Menores, entre St. Kitts y Granada, están dominadas por tabonuco (*Dacryodes excelsa *Vahl), un árbol de larga vida adaptado a huracanes recurrentes. Los tabonucos más antiguos en Puerto Rico parecen sobrevivir unos 500 a 600 años en bosques que periódicamente (tal vez cada 50 a 60 años) pierden casi la quinta parte de su biomasa. La recuperación poshuracán, caracterizada por tasas más altas de reclutamiento y mortalidad, demostró una regeneración de yagrumo hembra (*Cecropia schreberiana *Mig.) inmediata y abundante, junto con varias especies de tamaño pequeño a mediano, en aperturas dentro del bosque. La densidad de los tallos, número de especies, y tasa de acumulación de biomasa alcanzan un máximo cerca de unos 15 años después del huracán; alrededor de 50 años después, la mayoría de las especies secundarias asociadas con anteriores perturbaciones han desaparecid y la tasa de acumulación de biomasa se hace asintótica.*

Introduction

Puerto Rico's lower montane rain forest covered nearly one-quarter of the island at the time of discovery by Europeans. The largest trees, tabonuco (*Dacryodes excelsa* Vahl), ausubo (*Manilkara bidentata* A. DC. [Chev.]), granadillo (*Buchenavia tetraphylla* [Aublet] R. Howard), and motillo (*Sloanea berteroana* Choisey), grew to >2m in dbh (diameter at breast height, or 1.4m above the ground) and >30m in height (Wadsworth, 1950). After settlement, land clearing and agriculture removed most of Puerto Rico's timber replacing it with the farmlands and secondary forest evident today (Birdsey and Weaver, 1982; Franco *et al.*, 1997). The island's best remaining stands of primary lower montane forest are in the Luquillo Mountains below 600m. The most impressive of these are situated on ridges where tabonuco is the dominant tree (Wadsworth, 1953; Crow and Grigal, 1979; Crow, 1980; Basnet, 1992).

Hurricanes are a regular phenomenon in the Caribbean Basin between June and November; most storms affecting Puerto Rico occur in July, August, and September (Salivia, 1972; Weaver, 1998). The impact of hurricanes on Puerto Rico's forests has received much attention since the passage of Hugo in September 1989 (Walker *et al.*, 1991; 1996). Many of these observations, however, were made on plots set up after the storm.

The Forest Service established many of its permanent plots in the Luquillo Mountains during the mid-1940s (Crow, 1980; Weaver, 1998). Their long-term records show changes in structure and composition after impacts by Hurricanes San Felipe of 1928, San Nicolas of 1931, and San Cipriano of 1932, mainly the latter, which traversed the mountains. The effects of Hurricanes Hugo of 1989, and Georges of 1998, both of which impacted the mountains, are also evident. The purpose of this work is to show the major changes in stem density, species diversity, and species dominance on TR-1, the only long-term plot summarized to date for all of the major 20th century hurricanes.

Setting

The lower montane rain forest (*sensu* Beard, 1949) or tabonuco forest of the Luquillo Experimental Forest (LEF) in northeastern Puerto Rico extends from the forest border near 120m in elevation to about 600m (Wadsworth, 1951). The 0.4ha permanent plot (TR-1, or tabonuco ridge) monitored in this study is situated on a northeast-facing ridge at 350m in elevation (Weaver, 1994), about 2km

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RESUMO

*Os cumes das selvas pluviais intermediárias de Porto Rico e as Antilhas Menores, entre St. Kitts e Granada, estão dominadas por tabonuco (*Dacryodes excelsa *Vahl), uma árvore de longa vida adaptada a furacões recorrentes. Os tabonucos mais antigos em Porto Rico parecem sobreviver uns 500 a 600 anos em bosques que periodicamente (tal vez cada 50 a 60 anos) perdem quase a quinta parte de sua biomassa. A recuperação pós-furacão, caracterizada por taxas mais altas de recrutamento e mortalidade, demonstrou uma regeneração de yagrumo fêmea (*Cecropia schreberiana *Mig.) imediata e abundante, junto com várias espécies de tamanho pequeno a médio, em aberturas dentro do bosque. A densidade dos talhos, número de espécies, e taxa de acumulação de biomassa alcançam um máximo de 15 anos aproximadamente depois do furacão; mais ou menos uns 50 anos depois, a maioria das espécies secundárias associadas com anteriores perturbações desapareceram e a taxa de acumulação de biomassa se faz assintótica.*

distant from the LTER (long-term ecological research) site at Bisley (Scatena, 1989). This windward portion of the LEF has also been classified as subtropical rain forest (Ewel and Whitmore, 1973) in the Holdridge (1967) life zone system. Rainfall averages about 3800mm/yr, mean annual temperature is 22°C, and the soils are acid clays (Weaver, 1998). The dominant tree species are evergreen and normally reach 30m in height and 0.6m in diameter (Wadsworth, 1951).

Methods

TR-1, established in 1946, was remeasured in 1951, 1956, 1966, 1977, 1988, 1994, and 2000. In 1946, all trees rooted within TR-1 were tallied sequentially but not mapped (Weaver, 1983, 1998). All trees ≥4.1cm in dbh were identified to species, measured to the nearest 0.1cm in dbh, and permanently tagged with a nail 15cm below dbh to avert swelling around the nail. Most of the nail was left exposed to allow future growth. Ingrowth, or recruitment into the smallest dbh class, was not tallied until 1977. In 1988, ingrowth was measured and tagged, and for the first time, total tree heights were recorded to the nearest 0.1m with an optical range finder. Species names follow local texts (Liogier, 1985-97; see also, Little and Wadsworth, 1964; Little *et al.*, 1974).

Above-ground dry weight woody biomass (hereafter, biomass) was determined for dicotyledons using an equation derived for the tabonuco forest,

$$Y = 3.45 - 2.47\,D + 0.533\,D^2,\ r^2 = 0.89$$

where D = dbh in cm and Y = biomass in kg (Weaver and Gillespie, 1992). Total aboveground biomass for palma de sierra (*Prestoea montana* [R. Grah.] Nicholls) was estimated by

$$Y = 6.4\,x - 10.0,\ r^2 = 0.96$$

where x = height in m and Y = total aboveground biomass in kg (Frangi and Lugo, 1985). Biomass estimates were determined to elucidate the dominance of tabonuco on ridge topography.

The age of the largest tabonucos was estimated by dividing their dbh by the mean annual increment for all surviving stems. Since measurements only involved stems ≥4.1cm in dbh, the age estimates assume that seedlings and saplings grew at the mean rate until they reached 4.1cm. Moreover, the survival rates of four major canopy species, five common understory species, and two major gap species (secondary species that regenerate in openings) recorded in 1946, were considered in detail.

Results

Species

Fifty-six species were recorded at least once during the 54yrs of measurement on TR-1 (Table I; Appendix Table I). The total number of species declined from 46 in 1946 to 40 in 1977, increasing slightly to 43 in 1988. The decline continued after the hurricanes to 40 in 1994, and 37 in 2000 (Figure 1). The numbers of stems per species also declined in most instances.

Thirteen species recorded in 1946 were absent from TR-1

TABLE I
SPECIES CHANGES ON THE TR-1 STAND FROM 1946 TO 2000

Parameter (units)	Year							
	1946	1951	1956	1966	1977	1988	1994	2000
Species (no.)[1]								
Original[2]	46	44	42	40	36	36	32	28
Residual[3]	46	44	42	40	36	38	35	33
New[4]	–	–	–	–	4	5	5	4
Total	46	44	42	40	40	43	40	37
Stems per species (no.)								
1	11	11	12	11	8	10	7	6
2	3	4	1	2	3	4	7	11
3-4	8	6	6	5	9	11	10	6
5-10	8	9	8	9	7	6	7	4
11-20	5	4	5	3	5	6	4	3
21-50	8	7	7	8	6	4	2	5
≥51	3	3	3	2	2	2	3	2

[1] Fifty-six tree species were recorded at least once during the 54 yrs of measurement on TR-1. TR-1 lost 13 residual species by 2000 and gained 10 new species of which only 4 survived in 2000.

[2] Original species are survivors of the 1946 population of stems.

[3] Residual species are those first recorded in 1946 and also found in the year indicated. Residuals may be lost temporarily through mortality and then reappear as ingrowth.

[4] New species are those that were not present in 1946 that were recorded in the year indicated. New species may be lost temporarily through mortality and then reappear as ingrowth. New species were not tallied from 1951 through 1966.

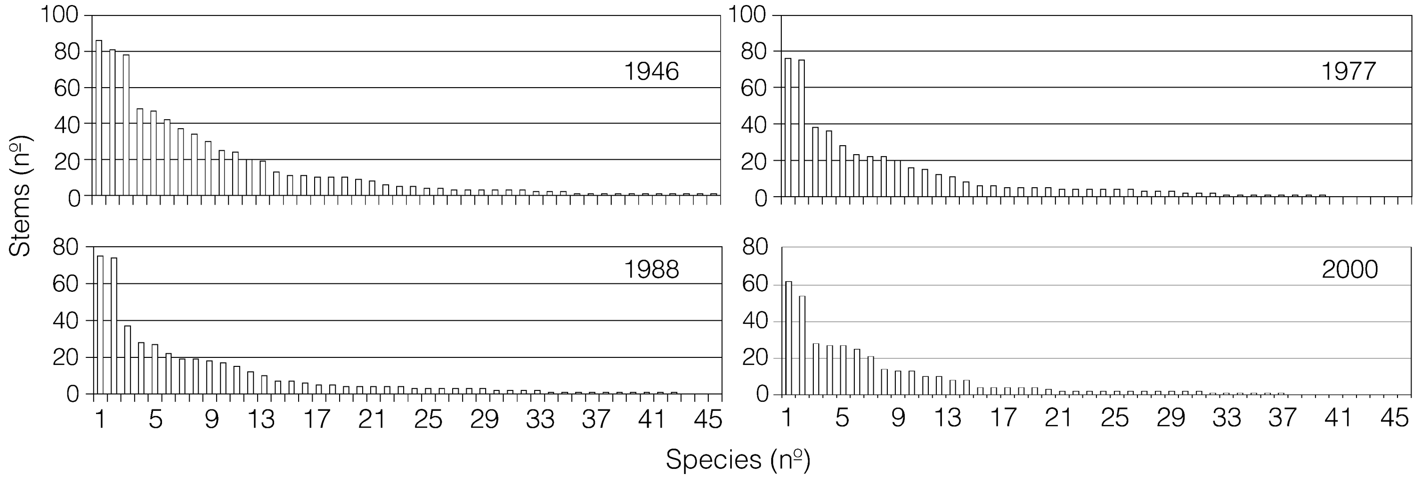

Figure 1. Numbers of species and number of stems per species for four different samples taken on TR-1 from 1946 to 2000.

in 2000: guajón (*Beilschmiedia pendula* [Sw.] Hemsl.), maricao (*Byrsonima spicata* [Cav.] HBK), cafeíllo (*Casearia sylvestris* Sw.), sabinón (*Croton poecilanthus* Urban), helecho gigante (*Cyathea arborea* [L.] J.E. Smith), majagua brava *Daphnopsis philippiana* (Krug & Urban), haya blanca (*Guatteria caribaea* Urban), azafrán (*Hedyosmum arborescens* Sw.), maricao verde (*Laplacea portoricensis* [Krug & Urban] Dyer), cieneguillo (*Myrcia deflexa* [Poir] DC.), hoja menuda (*Myrcia splendens* [Sw.] DC.), tabaiba (*Sapium laurocerasus* Desf.), and tabacón (*Solanum rugosum* Dunal) (Appendix Table I). Twelve of these species, totaling 22 stems, had ≤4 stems each in 1946; only maricao verde with 20 stems was well represented in 1946.

Ten new species entered the plot after the 1946 measurement: mameyuelo (*Ardisia obovata* Desv. ex Hamilt), ortegón (*Coccoloba swartzii* Meisner), cafeíllo (*Ixora ferrea* [Jacq.] Benth.), yaya (*Oxandra laurifolia* [Sw.] A. Rich), cachimbo (*Palicourea crocea* [Sw.] Roem. & Schultes), palo de cachimbo (*Palicourea croceoides* W. Hamilton), hueso blanco (*Chionanthus domingensis* Lam.), camasey (*Miconia prasina* [Sw.] DC.), hoja menuda (*Myrcia fallax* [A. Rich] DC.), nuez moscada (*Ocotea moschata* (Meissn.) Mez), but only the last four species were present in 2000 (Appendix Table I). Of the new species, all but nuez moscada are small to medium in size.

The species shown in Figure 2 accounted for 472 stems (i.e., 1171/ha), or about two-thirds of the total in 1946. Their survival rates varied during the 54yr period of measurement. The major canopy dominants had an average survival of 57%, as follows: ausubo, 80%; tabonuco, 69%; and motillo, 27% (Appendix Table I). Granadillo, also a canopy dominant, had 80% survival, but with only 5 stems is not shown. Survival of the major understory species averaged 24%, as follows: caimitillo verde (*Micropholis garciniifolia* Pierre), 50%; palma de sierra (*Prestoea montana* [R. Grah.] Nichols), 24%; jusillo (*Henriettea squamulosa* [Cogn.] Judd), 11%; and muñeco (*Cordia borinquensis* Urban), 8%. Survival of camasey (*Tetrazygia urbanii* Cogniaux), another common understory species, was only 2%. Lastly, survival of the major secondary, or gap species, averaged 10%, as follows: 17% of the yagrumo macho (*Schleflerra morototoni* [Aubl.] Maguire), and none of the yagrumo hembra.

Whereas mortality exceeded ingrowth for most species during the measurement period, yagrumo hembra gained 126 stems in 1994 of which 27 survived through 2000 (Figure 2; Appendix Table I). Palma de sierra showed a considerable flux in stems; 46 trees were recorded as ingrowth and 70 died, notably from 1988 to 2000. Ausubo and motillo also regenerated well, particularly after Hurricane Hugo (Figure 2).

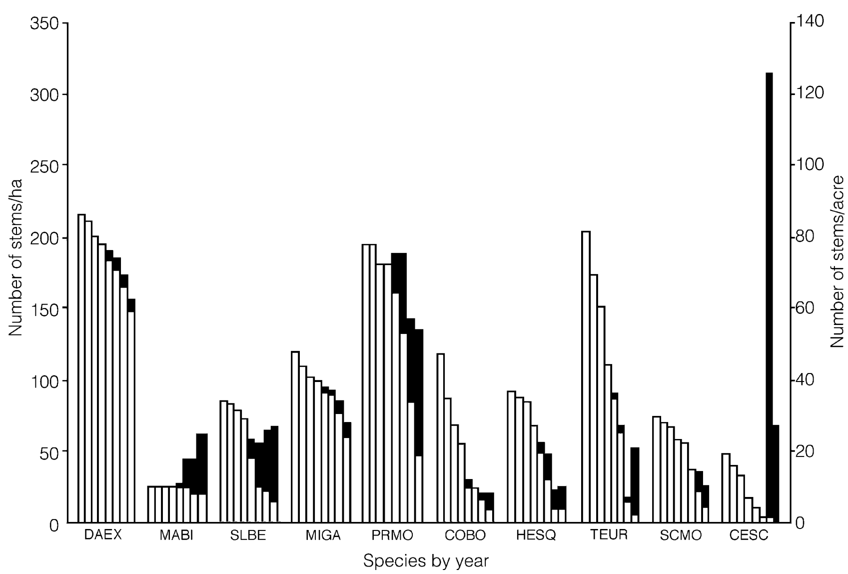

Figure 2. Changes in the number of stems by tree species on TR-1. White: surviving residual stems from 1946. Shaded: ingrowth of new stems. Species: DAEX: *Dacryodes excelsa*; MABI: *Manilka bidentata*; SLBE: *Sloanea berteroana*; MIGA: *Micropholis garciniifolia*; PRMO: *Prestoea montana*; COBO: *Cordia borinquensis*; HESQ: *Henriettea squamulosa*; TEUR *Tetrazygia urbanii*; SCMO: *Schleflerra morototoni*; CESC: *Cecropia schreberiana*. Years: 1946, 1951, 1956, 1966, 1977, 1988, 1994, and 2000.

Structure

Stand density, at 1761 stems/ha, was greatest in 1946, about 14yrs after the passage of San Cipriano (Table II).

TABLE II
Dbh CLASS DISTRIBUTIONS FOR TR-1 BETWEEN 1946 AND 2000[1]

Parameter (units)	1946	1951	1956	1966	1977	1988	1994	2000
1946 stems/ha	1761	1578	1420	1267	1045	877	613	450
	Percentage of 1946 stems in each class by year							
Dbh (cm)								
4.1-9.9	58.4	50.3	45.4	38.5	32.0	27.5	20.2	16.4
10.0-19.9	28.0	32.6	35.3	36.7	38.4	38.3	40.1	38.1
20.0-29.9	6.3	8.8	9.9	2.5	14.8	15.7	16.3	17.5
530.0-39.9	2.2	2.5	3.0	4.9	5.4	7.2	7.9	7.9
≥40.0	5.1	5.8	6.4	7.4	9.4	11.3	15.5	20.1
total stems/ha	1761	–	–	–	1190	1136	1193	916
	Percentage of total stems in each class by year							
Dbh (cm)								
4.1-9.9	58.4	——	——	——	37.9	38.8	52.5	45.3
10.0-19.9	28.0	——	——	——	36.1	34.3	26.6	31.8
20.0-29.9	6.3	——	——	——	12.9	12.4	8.7	8.9
30.0-39.9	2.2	——	——	——	4.8	5.6	4.1	3.8
≥40.0	5.1	——	——	——	8.3	8.9	8.1	10.2

[1]Per hectare values rounded to nearest unit.

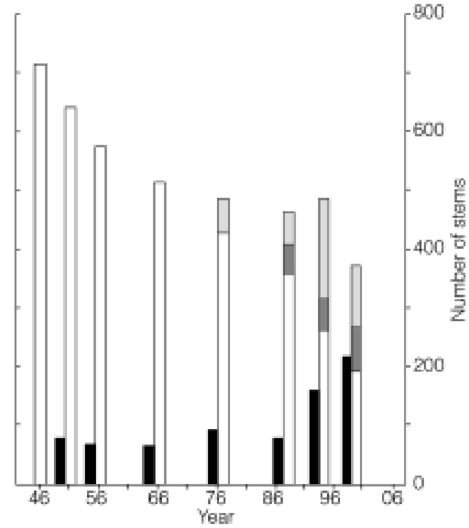

Figure 3. Changes in stem numbers on TR-1. Complete stand measurements are presented for 1946, 1977, 1988, 1994, and 2000. Ingrowth was not available for 1951, 1956, and 1966. Ingrowth in 1977 represents cumulative data from the first measurement in 1946. White, number of residual stems from 1946; black, mortality since last measurement; light gray, most recent ingrowth; dark gray, surviving ingrowth previous to last measurement.

Thereafter, the residual stems (those surviving from 1946) steadily declined to 450/ha in 2000, a loss of 75% of the trees originally tallied. Total stems (including ingrowth) declined continuously to 1136/ha in 1988 (Figure 3). After Hurricane Hugo, total stems increased slightly in 1994, and declined again in 2000 after Georges.

Fluxes in stem numbers, both ingrowth and mortality, were greatest immediately after the hurricanes. Ingrowth totaled 111 stems ($6ha^{-1}yr^{-1}$) and 276 stems ($57ha^{-1}yr^{-1}$) before and after Hugo, respectively (Appendix Table I). Comparable values for mortality were 363 stems (21 $ha^{-1}yr^{-1}$) and 365 stems ($75ha^{-1}yr^{-1}$).

Stand biomass, about 235t/ha in 1946, gradually increased to about 290t/ha in 1988, and then declined after both hurricanes to 240t/ha, virtually the same value as in 1946. The biomass accumulation rate after San Cipriano decreased from 3.6 $t\cdot ha^{-1}yr^{-1}$ between 1946 and 1951, to 1.3 $t\cdot ha^{-1}yr^{-1}$ between 1951 and 1977, becoming asymptotic between 1977 and 1988. During the last 12yrs, after Hugo and Georges, biomass change was negative, averaging -4.3 $t\cdot ha^{-1}yr^{-1}$. Tabonuco comprised from 51 to 55% of the biomass from 1946 through 1994, increasing to 59% in 2000.

The distribution of stems by dbh class in 1946, 14 years after San Cipriano, shows nearly 60% in the smallest class and only 5% in the largest class (Table II). The proportion of stems present in 1946 subsequently declined in the smallest class, and increased in the remaining classes through 2000. For total stems which include ingrowth, there was more variability. In general, there was a proportional increase in the largest dbh class after San Cipriano. In contrast, the smallest class initially declined after 1946, then fluctuated after Hugo, reflecting the ingrowth and competition for survival of yagrumo hembra.

Age of tabonuco

The mean annual dbh increment for the 59 tabonuco trees that survived the 54yr period of measurement was 0.19 ±0.02cm/yr. Although growth by class varied, no trends were apparent. Mean dbh growth rates by class, in cm (and sample size), were

4.1-9.9:	0.12 ± 0.02	(20)
10.2-19.9:	0.26 ± 0.03	(11)
20.0-29.9:	0.16 ± 0.07	(6)
30.0-39.9:	0.14 ± 0.03	(6)
40.0-49.9:	0.22 ± 0.05	(7)
50.0-59.9:	0.30 ± 0.04	(6)
≥60.0:	0.17 ± 0.02	(5)

Of the 27 tabonuco trees that died during measurement, only 2 grew at 0.19cm/yr or faster. The remaining trees averaged only 0.06cm/yr while they were alive.

Assuming the mean growth rate, the largest surviving tabonuco on TR-1, with a dbh of 94.5cm, should be about 500yrs old. The largest previously measured tree, 111cm in dbh, was blown over during Hurricane Hugo. It may have been about 600yrs old.

Discussion

Species and structure

The most notable phenomena of TR-1's history are the persistent dominance of tabonuco, both in numbers and biomass, in the pre- and post-hurricane stand, and the sudden and abundant regeneration of yagrumo hembra a few years after Hugo (Figure 2). Past inventories of 4ha of lower montane rain forest on several sites showed that tabonuco comprised 10% of the stems ≥10cm in dbh (Wadsworth 1951). Ausubo, granadillo, and motillo in the same inventories accounted for another 6% of the stems. On ridge topography in mature lower montane rain forest, tabonuco attains large size and may account for 50 to 60% of the total basal area (Wadsworth, 1953; Weaver, 1983).

The decline in the total number of species on TR-1 from a high 14 years after hurricane San Cipriano in 1946 to a low in 2000 immediately after Hurricane Georges reflects two main trends (Figure 1). The first, from 1946 to 1988, is the gradual loss of several species that regenerated in openings caused by San Cipriano as well as the loss of uncommon species (Appendix Table I). These losses were tempered by the occasional ingrowth of new species as the stand matured (Crow, 1980; Weaver, 1989). The second, from 1989 to 2000, is the sudden loss of some uncommon species due to the impact of Hurricane Hugo. The immediate ingrowth and rapid decline of yagrumo hembra is associated with its life history strategy (Brokaw, 1998). Yagrumo hembra is a typical pioneer (gap) species with frequent and abundant flowering and seed production, wide seed dispersal, and a seed bank in the soil whose germination is tied to canopy opening. After canopy disturbance, seeds in the seed bank germinate. Initial height growth is rapid, but competition for growing space results in high mortality.

Similar species changes were evident after San Cipriano in the lower montane rain forest at El Verde, also in the LEF (Crow, 1980): tabonuco and ausubo declined by about 20% from 1946 to 1976 whereas yagrumo hembra virtually disappeared from the stand. Moreover, between 1943 and 1976, 12 new species were recruited into the stand while 19 were lost.

Long-term recovery, as witnessed on TR-1, has different stages. The first is the growth stage lasting about 10 or 15yrs. It is characterized by rapid ingrowth of many stems, particularly secondary species (Crow, 1980; Weaver, 1998). Biomass accumulation, however, is slow because the new stems are small, most being light in weight (i.e., low specific gravity). Much of the initial growth on residual stems, in turn, is largely confined to recuperation of branches and foliage.

Next is the building stage lasting about 35yrs. It involves competition among both the survivors of the growth stage and new ingrowth, as all stems increase in size. Mortality, at first rapid, decreases over time as the total number of stems decline. Biomass accumulation, initially rapid, also decreases over time. Species richness peaks early in the building stage 15 to 20yrs after the storm (Table I), when stem numbers are greatest, and both secondary and primary species are interspersed. Gradually, short-lived secondary species succumb, and long-lived, shade-tolerant species dominate the stand.

In the last, or mature stage, about 50yrs after the storm, the stand reaches its greatest standing biomass. Short-lived secondary species have largely disappeared, their numbers being maintained at low levels through gap dynamics. Stem ingrowth and mortality remain low and consistent compared to earlier stages.

Some differences will likely be seen during the post-Hugo recovery pattern, however. TR-1's peak in stem density observed 15 to 20yrs after San Cipriano, a phenomenon also noted on the El Verde plot (Crow, 1980), will most likely be delayed due to the impact of Georges during the post-Hugo growth stage. The combined destructive effect of both hurricanes, without further disturbance on TR-1, could result in stem densities around 2012 similar to those of 1946. Moreover, the comparatively high biomass accumulation rate similar to that witnessed 15 to 20yrs after San Cipriano will most likely occur at this time.

The loss of three-quarters of the original stems during 54yrs, especially understory and gap species, provides some insights to tree turnover on the TR-1 stand. A simple extrapolation based on tree survival would be about 72yr. Ratios of biomass to production (Odum, 1971), or possibly the annual proportion of canopy openings to total area under study (Lawton and Putz, 1988) could also be used to approximate turn-over. However, as is evident from this study, an estimate of turn-over may vary with the starting point used to characterize stand conditions as well as climatic events, regardless of the criterion used to determine it. Although turn-over on portions of plots similar to TR-1 may occur several times in one-half of a millennium, other parts will remain covered for much or all of that period by long-lived tabonuco trees and other canopy dominants.

Age of tabonuco

The largest living tabonuco tree on TR-1 appears to have regenerated about the time Columbus discovered Puerto Rico, and the largest tree recorded on the plot, about 100yrs earlier. Most arithmetic estimates of age for tropical trees without annual rings rely on the assumption that the particular tree under consideration is growing at the average rate for all trees measured in the sample, a condition that is questionable since most survivors should grow at a more rapid pace. When procedures for estimating tree ages were first devised (Foggie, 1945; Osmaston, 1956), many tree growth records were of short duration and field samples included some trees that would succumb within a few years.

The mean growth estimate for tabonuco trees on TR-1, however, is based on long-term survivors. For the largest trees, that covers about 10% of their life cycle. Moreover, the oldest trees have suffered at least five hurricanes since the mid-1700s (Weaver, 1989; this paper). Assuming that the record before 1750 contained a similar number of storms, the largest trees should have experienced about 10 hurricanes during the last 500yrs, or about one every 50 to 60yrs (Scatena and Larsen, 1991). Given that each storm causes a loss of foliage, breakage of numerous branches, and occasionally the loss of tree tops, the mean growth rate for the survivors seems to be a plausible value to estimate age.

Tabonuco growth rates spanning 18yrs (1957-1975) are available for LEF sites with different disturbance regimes (Crow and Weaver, 1977). Tabonuco's average dbh increment at Sabana 8, Río Grande 3, and Sabana 4, was 0.74, 0.46, and 0.25cm/yr, respectively. The first two sites had been disturbed. Sabana 8, in 1947, was covered with heavy brush, saplings, and pole-size trees. Río Grande 3, in 1934, had pasture at lower elevations and cutover forest at mid-elevations. The dbh growth on both of these secondary sites was more rapid than at Sabana 4, which, like TR-1, remained undistubed by human activities.

The arithmetic approach, used to estimate the age of other major species in the LEF, indicated that the oldest trees of two other species most likely survived at least 5 centuries. Palo colorado (*Cyrilla racemiflora* L.) at 100cm in dbh, and laurel sabino (*Magnolia splendens* Urban) at 65cm in dbh, were estimated to be about 650 and 500yrs old, respectively (Weaver, 1986, 1987).

Implications

TR-1 is but one small, very exposed ridge in the middle of a montane rain forest. Although hurricane damage varied consideraby by site (aspect, topography, slope, and exposure) within the LEF (Boose *et al.*, 1994), the TR-1 stand appears representative of ridge topography in the forest's northeastern sector. The LEF's largest tabonuco trees grow on ridges suggesting that root anchorage among rocks or possibly root grafts that occur among clustered tree groups help them survive storms (Wadsworth, 1953; Basnet, 1992; Basnet *et al.*, 1993). In addition, ridges are better drained and more stable, with fewer landslides and treefall gaps, than other topographic positions (Scatena and Lugo, 1995). The relatively high 54yr survival of other major dominants on TR-1, ausubo and granadillo, also lends some support to this hypothesis.

Tabonuco is a dominant tree species in the lower montane rain forests of Puerto Rico and the Lesser Antilles from St. Kitts to Grenada (Beard, 1949; Little and Wadsworth, 1964; Lugo and Wadsworth, 1990). Hurricane damage in Dominica after David of 1979 was considerable; tabonuco associations, however, suffered the least damage whereas palm brakes were most affected (Lugo *et al.*, 1982). The combination of longevity and the capacity to survive numerous storms during its life cycle are what account for the abundance of tabonuco on ridges in the Caribbean hurricane belt. Interestingly, tabonuco is also very abundant in the montane rain forests of Grand Etang, Grenada, an area described as physiognomically mature but floristically impoverished (Beard, 1949). Grenada lies south of the Caribbean hurricane belt and has suffered only one recorded hurricane, Janet of 1955.

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APPENDIX TABLE I
NUMBER OF STEMS ON TR-1 FROM 1946 TO 2000

	Number of stems/acre[1]						
	Stand	Ingrowth		Mortality		Res.[2]	Stand
	1946	46-88	88-00	46-88	88-00	1946	2000
Species							
Alchornea latifolia Sw.	11	0	0	5	4	2	2
Alchorneopsis portoricensis Urban	3	0	1	0	1	3	3
Andira inermis (W. Wr.) DC.	3	0	0	1	0	2	2
Antirhea obtusifolia Urban	1	1	0	0	0	1	2
Beilschmiedia pendula (Sw.) Hemsl.	1	0	0	0	1	0	0
Buchenavia tetraphylla (Aublet) R. Howard	5	0	0	1	0	4	4
Byrsonima spicata (Cav.) HBK	2	0	0	1	1	0	0
Byrsonima wadsworthii Little	3	0	0	0	2	1	1
Casearia sylvestris Sw.	2	0	0	2	0	0	0
Cassipourea guianensis Aubl.	1	2	3	0	4	0	2
Cecropia schreberiana Mig.	19	0	131	18	105	0	27
Cordia borinquensis Urban	49	3	4	40	6	4	10
Croton poecilanthus Urban	1	0	0	0	1	0	0
Cyathea arborea (L.) J.E. Smith	4	0	0	4	0	0	0
Cyrilla racemiflora L.	6	0	0	2	0	4	4
Dacryodes excelsa Vahl	86	2	1	14	13	59	62
Daphnopsis philippiana Krug & Urban	2	2	0	2	2	0	0
Eugenia borinquensis Britt.	3	0	0	0	1	2	2
Garcinia portoricensis (Urban) Alain	10	12	8	3	14	3	13
Guarea glabra Vahl.	1	1	0	0	0	1	2
Guatteria caribaea Urban	1	0	0	0	1	0	0
Hedyosmum arborescens Sw.	3	0	0	3	0	0	0
Henriettea squamulosa (Cogn.) Judd.	37	6	3	24	12	4	10
Hirtella rugosa Pers.	25	9	2	6	17	8	13
Homalium racemosum Jacq.	5	0	0	0	3	3	2
Inga laurina (Sw.) Willd.	11	0	0	5	4	2	2
Laplacea portoricensis (Krug & Urban) Dyer	20	0	0	17	3	0	0
Magnolia splendens Urban	10	0	0	6	2	2	2
Manilkara bidentata (A. DC.) Chev	10	8	17	0	10	8	25
Margaritaria nobilis L.f.	1	0	0	0	0	1	1
Matayba domingensis (DC.) Radlk.	8	0	0	1	3	4	4
Meliosma herbertii Rolfe	13	5	2	6	6	5	8
Micropholis garciniifolia Pierre	48	1	2	12	11	24	28
Myrcia deflexa (Poir) DC.	1	0	0	1	0	0	0
Myrcia splendens (Sw.) DC.	3	0	0	3	0	0	0
Ocotea leucoxylon (Sw.) Mez	1	0	1	1	0	0	1
Ocotea spathulata Mez	42	2	1	27	16	2	2
Prestoea montana (R. Grah.) Nichols.	78	22	24	25	45	19	54
Psychotria berteriana DC.	24	1	17	24	4	0	14
Sapium laurocerasus Desf.	1	0	0	1	0	0	0
Schleflerra morototoni (Aubl.) Maguire	30	0	6	15	11	5	10
Sloanea berteroana Choisy	34	11	20	23	15	6	27
Solanum rugosum Dunal	1	0	0	1	0	0	0
Tabebuia heterophylla (DC.) Britt.	9	2	3	7	3	0	4
Tetragastris balsamifera (Sw.) Kuntze	3	0	0	0	1	2	2
Tetrazygia urbanii Cogniaux	81	2	18	56	24	2	21
Subtotals	713	92	264	357	346	183	366
New species from 1977-2000							
Ardisia obovata Desv. ex Hamilt.	0	1	0	0	1	0	0
Chionanthus domingensis Lam.	0	0	3	0	0	0	3
Coccoloba swartzii Meisner	0	0	1	0	1	0	0
Ixora ferrea (Jacq.) Benth.	0	5	0	2	3	0	0
Miconia prasina (Sw.) DC.	0	0	1	0	0	0	1
Myrcia fallax (A. Rich) DC.	0	1	1	0	1	0	1
Ocotea moschata (Meissn.) Mez	0	4	0	3	0	0	1
Oxandra laurifolia (Sw.) A. Rich.	0	1	0	1	0	0	0
Palicourea crocea (Sw.) Roem. & Schultes	0	0	2	0	2	0	0
Palicourea croceoides W. Hamilton	0	7	4	0	11	0	0
Totals	713	111	276	363	365	183	372

[1]Multiply by 2.47 to convert to hectare basis.
[2]Res. = residuals, or survivors from 1946.

consequences of root grafting in tabonuco (*Dacryodes excelsa*) trees in the Luquillo Experimental Forest, Puerto Rico. *Biotropica 25*: 28-35.

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