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Elfin Woodland Recovery 30 years After a Plane Wreck in Puerto Rico's Luquillo Mountains

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ABSTRACT.—Grasses and ferns characterized the recovery of elfin woodland for the first 18 years after a December 1968 airplane crash. From 1986 to 1998, ferns and woody dicots were prominent and the total aboveground dry weight biomass increased from 775 to 2210 g/m^2. Woody dicots increased 3.5 times, palms 1.3 times, and ferns 4.4 times above their 1986 levels. Grasses and herbs decreased by nearly 10 %. Recovery was patchy, with some areas dominated by trees ≥4 m in height and others by grasses and scattered ferns. Puerto Rican endemic trees are playing a critical role in the recovery of the elfin woodland and are prominent in mature elfin woodland as well. Endemics account for 88 to 94 % of the woody dicot stems 18 to 30 years after the wreck, and from 55 to 72 % of the stems in mature elfin woodland. The largest stems on the wreck site average about half of the typical heights and dbhs of mature elfin woodland trees, and biomass is about a fourth of that found in mature elfin woodland. Species composition is similar. It is estimated that complete recovery will take almost two centuries.

INTRODUCTION

Disturbances with long-term impacts such as landslides (Guariguata, 1990), road construction (Olander et al., 1998) and hurricanes (Weaver, 1999) have been recorded at high elevation in Puerto Rico's Luquillo Mountains, but perhaps the most unusual disturbance was the December 1968 crash of a C-119 aircraft at 1000 m elevation in the elfin woodland near Pico del Este. The plane severed branches and trees and exploded on impact, burning the area around the fuselage (Byer and Weaver, 1977). The soil was disturbed in several places and debris was strewn into the surrounding woodland. Tree mortality after the crash exposed a swath extending about 65 m upslope from the point of initial contact. Most of the debris, including the fuselage, came to rest in an area of about 300 m^2 above the swath and only a few meters below the ridgecrest (Fig. 1).

There is little information on the recovery of high elevation Neotropical forests following a catastrophic disturbance. Gaps created by natural causes in Mexico (Arriaga, 1988) and Costa Rica (Lawton and Putz, 1988) suggested turnover rates in elfin or cloud forests ranging from 95 to 158 years. In Costa Rica's Cordillera de Talamanca, two studies showed that post-fire recovery was slow. At 3300 m in native scrub reaching 3 m in height, shoot regeneration and colonization was incomplete, leaving large patches of bare ground 3 years after a burn (Janzen, 1973). In paramo, bamboo and ericaceous scrub up to 2 m in height resprouted vigorously after burning (with the bamboo reaching pre-fire heights in 10 years) but herbs and shrubs did not colonize for a decade or more (Horn, 1989). In Puerto Rico's Luquillo Mountains, the margins of the Pico del Este road, about 700 m distant and at the same elevation as the airplane wreck, have remained in planted grasses with little invasion of arborescent dicotyledons since 1960 (Olander et al., 1998).

Most studies of post-disturbance forest recovery at high elevations are of short duration. In contrast, forest recovery on the plane wreck site was first monitored in the early 1970s, again in 1986 (Byer and Weaver, 1977; Weaver, 1990), and now spans a 30-year period. Fortunately, surrounding elfin woodland protected regen-

FIG 1. Airplane wreck site in April, 1977 (8 years and 4 months after the crash). Looking east-northeast (down slope), small ferns and grasses are prevalent.

eration in the wreck site from most damage caused hurricanes Hugo in 1989 and Georges in 1998. This work reports on the long-term monitoring of elfin woodland recovery by recording changes in stem numbers and total aboveground dry weight biomass (hereafter, biomass) by major species and plant groups.

METHODS

Two sampling schemes, the results of which were combined on a hectare basis, were used to characterize the vegetation on the 780 m^2 wreck site. First, minor vegetation (grasses, vines, ferns, and dicotyledonous plants <15 cm tall) was cut at ground level on 20 randomly selected subplots 1 × 1m throughout the plane wreck site. The samples were oven-dried to constant weight at 75 °C and weighed. The impact of destructive sampling on future measurements should be minimal because grasses and ferns will regenerate quickly and most of the small dicoyledonous stems would most likely succumb to competition or shading by taller plants.

Next, all ferns, palms, and dicotyledonous stems ≥0.15 m tall were sampled on 13 plots 5 × 12 m. Stems were identified to species (Liogier, 1985-97; Liogier and Martorell, 1982; Little and Wadsworth, 1964; Little et al., 1974) and tagged with flagging to avert double sampling. Height was recorded to the nearest 0.1 m. Stem diameters were measured at dbh (1.4 m above the ground) if they reached that height, or at ground level, and were recorded to the nearest 0.1 cm.

The equation for estimating tree fern biomass was determined by sampling 17 *Cyathea arborea* (L.) J.E. Smith and *C. bryophila* (R. Tryon) Proctor stems ranging from 0.15 to 11.2 m in height. The biomass equation derived for ferns was

$$Y = 3.82\,X - 3.62,\ r^2 = 0.83,\ n = 17,$$

where Y is biomass in kg and X is height in m. The remaining biomass equations were derived from published sources: for dicot stems ≥ 0.15 cm and <1.4 m tall (Weaver, 1990); for dicot stems reaching dbh (Weaver and Gillespie, 1992); and for palms (Frangi and Lugo, 1985).

The 780 m^2 plane wreck site was mapped (Fig. 2). The categories used were: tree dominated, where trees formed a canopy ≥2 m in height; grass dominated, with occasional small ferns; fern dominated, where ferns averaged about 2 m in height with grass below; mixed grasses and small ferns; and areas dominated by airplane debris.

RESULTS

Of the 3100 plants and 23 species ≥0.15 cm tallied individually, more than 75 % were dicotyledons and all but 0.2 % of the remainder were ferns (Table 1). *Henriettea squamulosa* (Cogn.) Judd., the most abundant species, and *Eugenia borinquensis* Britton, accounted for 65 % of the total stems. *Cyathea bryophila* accounted for 11 % of the total stems and nearly half of the recorded ferns. Five species totaling 31 stems attained ≥4 m in height: *Eugenia borinquensis*, *Clusia clusioides* (Grieseb.) D'Arcy, *Tabebuia rigida* Urban, and *Micropholis garciniaefolia* Pierre (Table 1).

Ten of the 17 dicotlyedonous species recorded on the site are endemic to Puerto Rico. Four tree species comprising 1.7 % of the stems entered the plot since the 1986 measurement (Weaver, 1990): *Grammadenia sintenisii* (Urban) Mez and *Miconia pachyphylla* Cogn., both endemics, and *M. tetrandra* (Sw.) D. Don ex G. Don and *Psychotria berteriana* DC. Six species accounting for about 20 % of the 1986 stems were not recorded in 1999: *Psychotria maleolens* Urban, *Heterotrichum cymosum* (Wendl.) Urban and *Wallenia yunquensis* (Urban) Mez., all endemics, and *Daphnopsis americana* (Mill.) J.R. Johnst., *Hedyosmum arborescens* Sw., and *Palicourea alpina* (Sw.) DC.

Cyathea bryophila, the most common fern, also had the greatest biomass (Table 1). Despite the numerical abundance of *Henriettea squamulosa*, it had less biomass than *Eugenia borinquensis, Tabebuia rigida*, or *Clusia clusioides*.

Biomass averaged 2.2 kg/m^2 in 1999 (Table 2), an almost three fold increase over

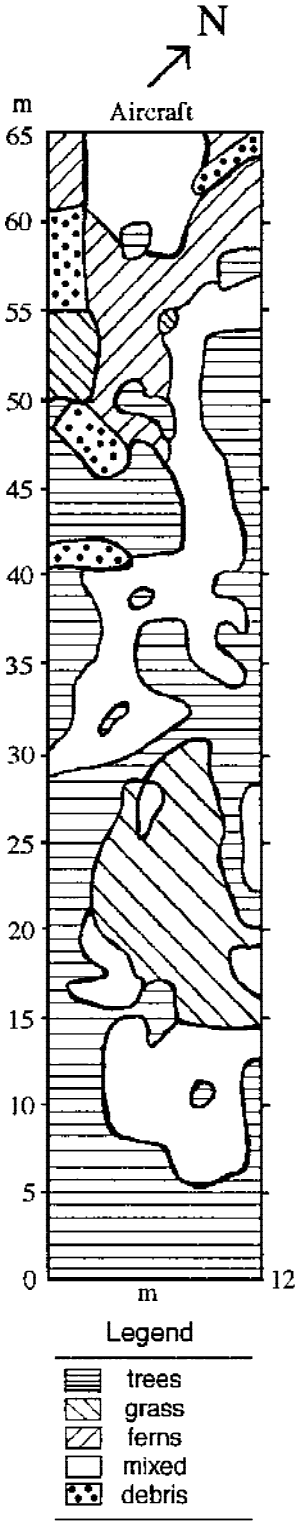

FIG 2. The 65 × 12 m airplane wreck site. The C-119 fuselage lies above the diagram. The plane cut the swath from the base of the diagram to the top.

the 1986 total: woody dicots increased 3.5 times, palms 1.3 times, and ferns 4.4 times. Grasses and herbs decreased by nearly 10 %. Proportionally, ferns and arborescent dicots increased while palms, and grasses and herbs combined, decreased. On an areal basis, 44 % of the wreck site was dominated by trees, 12 % by grasses, 10 % by ferns, 30 % by mixed grasses and ferns, and 4 % by airplane debris (Fig. 2).

DISCUSSION

Plant groups and species.—Succession on the wreck site is passing through stages dominated by different plant groups. Grasses and ferns were prominent during the first six years while seedlings of woody species were scarce (Byer and Weaver, 1977). In late 1986, ferns and arborescent dicots were nearly equal in biomass, with grasses and herbs slightly less (Table 2). By 1999, the biomass of arborescent ferns and dicots had continued to increase whereas grasses and herbs continued to decline. Throughout, palms were uncommon and accounted for the least amount of biomass, although their number per unit area was approximately equal to their number in mature elfin woodland (Table 3).

Elfin woodland on Pico del Este is dominated by woody dicots (Table 3), with ferns and scattered patches of grass concentrated mainly in openings. In a combined plot survey of 0.525 ha of elfin woodland on El Yunque, Pico del Este, Pico del Oeste, and El Toro, 80 % of the stems ≥4.1 cm in dbh were dicots, 19 % were tree ferns, and 1 % were palms (Weaver, 1999). Dicots were most abundant on ridges, palms in ravines, and tree ferns on slopes and in ravines.

Between 1986 and 1999, *Henriettea squamulosa* replaced *Eugenia borinquensis* as the most common dicot tree species but its stems were smaller (Table 1). In 1999 there were over six times the number of dicot stems ≥4 m in height than in the 1986 survey, when only five stems of four species reached that size (*Ocotea spathulata* Mez, *Alchornia latifolia* Sw., *Clusia clusioides*, and *Tababuia rigida*).

TABLE 1. Number of plants ≥15 cm in height by species and size class for the entire 780 m^2 wreck site after 30 years.

	Number of stems by height class (m)								Biomass	
Species	0.15-1	1-2	2-3	3-4	4-5	5-6	Totals	Percent of stems	kg	Percent of total
Ferns										
Blechnum lineatum	126	—[3]	—	—	—	—	126	4.1	15.1	1.1
Cyathea arborea	13	—	—	—	—	—	13	0.4	6.7	0.5
Cyathea bryophila[1]	204	144	6	—	—	—	354	11.4	645.9	46.7
Lonphosoria quadripinnata[2]	3	—	—	—	—	—	3	0.1	0.6	0.1
Trichipteris borinquena[1,2]	219	3	—	—	—	—	222	7.2	103.6	7.5
Subtotals	565	147	6	—	—	—	718	23.2	771.9	55.9
Palm										
Prestoea montana	2	1	1	—	—	1	5	0.2	96.4	7.0
Dicotyledons										
Alchornia latifolia	—	—	3	1	—	—	4	0.1	3.0	0.2
Henriettea squamulosa[1]	806	257	53	7	—	—	1123	36.2	38.0	2.7
Calyptranthes krugii[1,2]	—	15	7	1	—	—	23	0.7	3.7	0.3
Clusia clusioides	—	4	7	5	4	3	23	0.7	46.9	3.4
Eugenia borinquensis[1]	195	277	322	88	16	—	898	29.0	310.6	22.4
Grammadenia sintenisii[1]	—	1	—	—	—	—	1	0.1	0.1	—[4]
Ilex sintenisii[1,2]	6	19	—	—	—	—	25	0.8	0.2	—[4]
Mecranium latifolium[2]	—	2	2	—	—	—	4	0.1	0.9	0.1
Miconia foveolata[1,2]	—	3	2	—	—	—	5	0.2	1.6	0.1
Miconia pachyphylla[1]	—	2	12	—	—	—	14	0.4	5.6	0.4
Miconia sintenisii[1]	—	10	5	1	—	—	16	0.5	4.6	0.3
Miconia tetrandra	7	—	5	—	—	—	12	0.4	1.6	0.1
Micropholis garciniafolia[1]	7	4	3	4	1	—	19	0.6	16.5	1.2
Ocotea spathulata	46	6	9	4	—	—	65	2.1	6.6	0.5
Psychotria berteriana	—	8	15	4	—	—	27	0.9	12.0	0.9
Tabebuia rigida[1]	26	62	8	13	2	4	115	3.7	60.2	4.4
Trichllia pallida[2]	—	—	3	—	—	—	3	0.1	0.9	0.1
Subtotals	1,093	670	456	128	23	7	2,377	76.6	513.0	37.1
Totals (1999)	1,660	818	463	128	23	8	3100	100.0	1381.3	100.0
Totals (1986)[5]	502	539	111	15	4	1	1172	100.0	359.2	100.0

[1]Tree species endemic to Puerto Rico.
[2]Species authors not listed in text: *Lonphosoria quadripinnata* (J. F. Gremlin) C. Christensen, *Trichipteris borinquena* (Maxon) Tryon, *Calyptranthes krugii* Kiaersk, *Ilex sintenisii* (Urban) Britton, *Mecranium latifolium* (Cogn.) Skean, *Miconia foveolata* Cogn., and *Trichllia pallida* Sw.
[3]Dashed lines indicate that data are not available.
[4]Value ≤0.005.
[5]Total values from 1986 (Weaver, 1990) provided for comparative purposes. Ferns ≥15 cm in height were not tallied individually in 1986.

The number of dicot tree species recorded in 1986 and 1999 is similar to the number found in comparable areas of mature elfin woodland on Pico del Este (Table 3). However, the sampling procedures for the plane wreck site included much smaller stems than in the mature forest. Twenty-seven dicot tree species ≥4 cm were recorded in the aforementioned combined plot survey of 0.525 ha of elfin woodland (Table 3).

The prominent role of endemic dicot trees in the elfin woodland is obvious, notably during the recovery process (Table 3). Endemic dicots, losing three previously recorded species and gaining two new ones, accounted for at least 88 % of the total number of stems and 58 % of the total biomass in 1986, increasing in both categories by 1999 (Table 3). In fact, the elfin woodland, with more than half of its dicot trees as endemics in all samples (Table 3), could be

TABLE 2. Summary of biomass according to plant group on the wreck site after 18.5 and 30 years[1].

	Biomass			
	(g/m^2)		Percent of total	
Plant group	1986	1998	1986	1998
Arborescent dicots[2]	235	833	30.4	37.7
Palms	98	124	12.6	5.6
Ferns	243	1075	31.2	48.6
Grasses and herbs	200	178	25.8	8.1
Total	776	2210	100.0	100.0

[1]Source: Weaver (1990).
[2]Also includes the woody vine *Marcgravia sintenisii* Urban.

TABLE 3. Comparison of plane wreck site data in 1986 and 1998 with mature elfin woodland.

	Values[1]			
	Plane wreck		Elfin woodland	
Factor	1986[2]	1999	Mature[2]	Survey[3]
Plot size (m^2)	1,080	780	1500	5,250
Dicot trees				
species (number)	19	17	16	27
total (stems/ha)	10,778	30,474	2,950	4,440
≥3 m (stems/ha)	185	2,025	2,360	—[4]
≥4 m (stems/ha)	46	384	~1,725	—
Endemic dicot species (number)	11	10	6	12
% of total dicot stems	88	94	55	72
% of total dicot biomass	58	86	—	—
Total palms (stems/ha)	74	64	66	63
Tree ferns ≥2 m (stems/ha)	—	77	940	836

[1]Values rounded to nearest integer.
[2]Source: Weaver (1990) for mature elfin woodland within 500 m of the airplane wreck site.
[3]Stems measured in mature elfin woodland in the combined plot survey of elfin woodland plots on El Yunque, El Toro, Pico del Este and Pico del Oeste were ≥4.1 cm in dbh. For ferns, this included all stems ≥1.4 m above the ground (Weaver, 1999).
[4]Dashed lines indicate that data are not available.

called Puerto Rico's "endemic forest." Moreover, of the 85 species that characterize the entire vascular flora of nearby Pico del Oeste, one-third are endemic (Howard, 1968). High endemism is also common in Panama's cloud forests (Lewis, 1971) which occur at elevations similar to those in Puerto Rico.

Forest structure.—The tallest trees on the plane wreck site (Table 1) have reached about half of the maximum height of the tallest elfin woodland trees on Pico del Este. Typical heights recorded in the surrounding forest are: ≤2.9 m, 20 % of the stems; 3.0-6.9 m, 70 % of the stems; and ≥7 m, 10 % of the stems (Weaver, 1999). Tree height varies considerably by topography at high elevations in the elfin woodland with the tallest stems on lower slopes and in ravines.

The maximum dbh attained on the plane wreck site was about 10 cm, or about half of the maximum dbh values commonly found in the elfin woodland. Typical dbh values in the surrounding forest are: 4.1-9.9 cm, 65 % of the stems, 10.0-19.9 cm, 30 %; and ≥20 cm, 5 % of the stems (Weaver, 1999). The largest and oldest tree species in the elfin woodland, *Magnolia splendens* Urban, may attain 0.5 m or more in dbh (Weaver, 1987). Although not yet recorded on the wreck site, Puerto Rico's endemic magnolia

is present only a few meters from the wreck.

Of the 2377 woody dicot stems tallied (Table 1), equivalent to 30,474/ha (Table 3), only 40 (512/ha), attained a dbh ≥4.1 cm. The number of stems ≥4.1 cm in mature elfin woodland typically ranges from 3000 to 4500/ha (Table 3), varying condiderably with topography and exposure. Stem numbers usually increase during the recovery process and decline with competition. Post-hurricane examples of this phenomenon in the Luquillo Mountains were shown for the tabonuco (lower montane) forest (Crow, 1980), and the colorado (montane) forest (Weaver, 1989).

The current biomass on the plane wreck site is about 22 t/ha (Table 2). Previous estimates of biomass for mature elfin woodland on Pico del Este ranged from 48 to 110 t/ha for ridge and ravine plots, respectively (Weaver et al., 1986). If a mean of 80 t/ha is assumed as characteristic of elfin woodland (Weaver and Murphy, 1990), then the current biomass on the wreck site is slightly greater than one-quarter of that in mature elfin woodland.

Patchy recovery.—Although structural and biomass data are presented on a unit area basis for the entire wreck site (Tables 1-3), notable microsite variation exists. Several square meters of the site are covered by trees ≥4 m in height whereas adjacent patches are dominated by grass. The tallest trees grow along the plot boundaries, as reported earlier (Weaver, 1990). A patch of grass with scattered ferns, first described as "soil disturbance in varying degrees" (Byer and Weaver, 1977), remains visible, possibly reflecting a gouging by the aircraft wing. The fact that this small patch has persisted for 30 years suggests that small alpine meadows or grassy balds evident elsewhere within elfin woodland may have been caused by major soil disturbance, such as landslides, or the stripping of forest cover during hurricanes (Odum, 1970).

Roadside soils in the elfin woodland, disturbed by construction activities in the early 1960s and planted with an exotic grass, are dominated today by non-woody vegetation (Olander et al., 1998). The average biomass along the roadside after 35 years is only 1050 g/m^2, nearly 80 % of which is non-woody. A detailed study of landslides in the colorado forest, just below the elfin woodland, showed that weathered bedrock or mineral soil were often exposed in the upper zone of the slides whereas the lower zones had an accumulation of plant material, carbon and nutrients (Guariguata, 1990; Walker, 1994). Ferns are more competitive in the mineral soils while herbaceous plants and trees compete better in nutrient-rich organic soils. Most major disturbances such as hurricanes or landslides do not leave uniform conditions for regeneration of residual stems or colonization by new ones.

The degree of recovery of the wreck site can be considered from three standpoints: biomass, forest structure, or species composition. A linear projection of biomass accumulation on the site after 18 years suggested that 170 years would be required for biomass recovery (Weaver, 1990). However, that linear function interpolated for only 30 years, underestimates the site's current biomass by 40 %. After a slow initial accumulation of biomass, mainly of ferns and grasses during the first couple of decades, the rate of recovery increased with the regeneration and growth of trees.

The tallest trees with the largest dbhs on the plane wreck site are about half of the maximum commonly recorded in the elfin woodland. The 40 fastest growing trees on the wreck site range between 4.1 and 10.5 cm, suggesting minimal dbh growth rates between 0.14 and 0.35 cm/yr if the trees regenerated shortly after the wreck. Estimates of mean annual dbh increment for mature elfin woodland trees ≥4.1 cm in dbh in pre- and post-hurricane conditions are 0.03 and 0.024 cm/yr, respectively, over 5 year periods (Weaver, 1983, 1999). The contrast in rates is evident and indicates that dbh growth slows considerably once the forest begins to close.

The current species composition of the site includes most of the major elfin woodland dominants. Missing are *Haenianthus salicifolius* Griseb, *Cyrilla racemiflora* L., and *Magnolia splendens*. If the pre-wreck site included either a *Cyrilla racemiflora* or *Magnolia splendens* 50 cm in dbh, recovery of the

original composition and size classes could take from 200 to 400 years, as estimated by the average diameter growth of these species (Weaver, 1986, 1987).

Complete recovery of the wreck site means that an observer would not know that a plane had crashed except for the pile of debris. If so, recovery in slightly less than two centuries is an appropriate estimate. Although trees grow slowly in the elfin woodland, the total amount of biomass per hectare to be replaced is only 40 to 60 % of that in the lower forest types of the Luquillo Mountains; moreover, the maxima of typical dbhs are a third to half of those commonly found in the lower forests (Weaver and Murphy, 1990). The number of tree species in the elfin woodland ranges from 30 to 40 % of that in the lower forests (Weaver and Murphy, 1990) and secondary colonizers are sparse (Byer and Weaver, 1977). Succession in the elfin woodland, passing through a relatively brief stage of grasses and ferns, is a more direct process than at lower elevations, where large secondary tree species such as *Cecropia schreberiana Miq.* and *Schefflera morototoni* (Aubl.) Maguire may persist for nearly half a century in openings created by hurricanes (Brokaw, 1998; Weaver, 1983).

Since the wreck observations are confined to a single, small site in the easternmost portion of the Luquillo Forest's 400-ha elfin woodland, extrapolation to other high elevation disturbed sites should be done with caution. Most natural disturbances in the elfin woodland are due to high winds associated with hurricanes or tropical storms. In many instances, soil disturbance is only partial and is limited to scattered snapped or uprooted trees. Recovery is characterized by the release of understory seedlings and the arrival of a variety of propagules from the surrounding vegetation. In contrast, road building or landslides expose large areas of subsoil which create conditions favoring long-term dominance by ferns and grasses. Site factors such as the origin and size of disturbances, their elevation, topographic position, aspect, and exposure, also influence the recovery process.

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