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Thinning and Regeneration in Puerto Rico's Colorado Forest, With Comments About Their Effect on the Puerto Rican Parrot

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ABSTRACT.—A 50 % basal area reduction in Puerto Rico's colorado forest had little immediate impact on diameter at breast height growth for most residual stems. A slight positive response was evident for several species after 5 to 30 yrs. Instead, thinning served as a major stimulus for a massive ingrowth of two common colorado forest tree species important to the Puerto Rican Parrot: palo colorado (*Cyrilla racemiflora* L.), the major parrot nesting tree, and cupeíllo (*Clusia clusoides* (Griseb.) D'Arcy), a main source of food. Canopy opening appeared beneficial for the survival and regeneration of laurel sabino (*Magnolia splendens* Urban), an uncommon tree used by the parrot for nesting and food. Other species that showed substantial increases in stem numbers were palo de hueso (*Haenianthus salicifolius* Grised.) and camasey (*Miconia tetrandra* (L.) DC).

INTRODUCTION

The earliest forestry studies in the Luquillo Experimental Forest (LEF) involved tree species identification, forest inventories, and the determination of growth rates on permanent plots (Wadsworth 1951, 1957). From the late 1960s through the mid-1980s, the plight of the nearly extinct Puerto Rican Parrot (*Amazona vittata*) was the focus of research efforts (Snyder et al., 1987). One discovery of that program was that tree cavities used for nesting were scarce due to past cutting of mature trees for timber, to extract honey, or to remove parrot nestlings.

Among permanent plot studies established in the mid-1940s was a thinning trial in montane rain forest (hereafter, colorado forest) which indicated that residual trees did not respond to improved growing conditions (thinning) in the short term (Wadsworth, 1957). In the early 1980s, numerous permanent plots were remeasured, among them the thinned colorado stand. The purpose of this paper is to compare the response to thinning on CCU (cutover, or thinned colorado slope plot) with a nearby CS-2 (colorado slope control plot), and to indicate its potential importance to the Puerto Rican Parrot.

SETTING

The LEF has four main forest types growing from the forest border near 150 m to the 1075 m summits. The montane rain forest, locally called colorado forest, grows between 600 and 900 m. Lower montane rain forest (locally, tabonuco forest) grows below the colorado forest, while dwarf forest grows above it. Palm brake is scattered on steep windward slopes and in ravines throughout most of the LEF. Mean annual rainfall at 715 m in the LEF averages 4600 mm/yr. The soils, mainly clays or silty clay loams, are saturated most of the year. The two permanent plots in this study (CS-2 and CCU) are on slope topography; the first at 700 m and the second at 670 m (Weaver, 1983).

METHODS

On CS-2, all trees ≥4.1 cm in dbh (diameter at breast height, or 1.4 m above the ground) were identified to species using Little and Wadsworth (1964), Little et al. (1974), and Liogier (1985-97). All these trees had been measured in 1946. Sequentially numbered tags were used to permanently label each tree.

On CCU, several large overstory trees were cut in 1947 leaving the residual canopy trees with at least 2 m of crown freedom on all sides (Wadsworth, 1957). Both small and large stems remained in the stand to provide for sustained yield. Thinning reduced the initial basal area by about one-half, which was considered satisfactory to stimulate a favorable growth response. Residual trees were then measured as for CS-2. Both plots were remeasured in 1956-57, in 1975-76, and in 1981.

Mean dbh increment and standard errors were determined for eight of the largest species shared between the plots to allow general comparisons. Detailed statistical comparisons were not undertaken because of numerous factors that complicate interpretations in multi-species stands, among them: variable tree sizes, crown classes and initial densities; changing numbers of stems and basal area over time due to ingrowth and mortality; the unknown age of the trees; and the fact that many trees on long-term plots have ceased to grow, or are slowly dying.

Results

Changes in species

CCU had 22 species after thinning in 1947 and 30 when remeasured in 1981 (Table 1). Eleven new species were tallied on CCU and three were lost during the 34 yrs of monitoring. CS-2 had 46 species in 1946 and 43 in 1981 (Table 2). Three new species were tallied on the plot and six disappeared over 35 yrs.

The eight selected species showed no apparent short-term response to thinning; changes in long-term dbh growth, however, may be apparent for the survivors of palo colorado (*Cyrilla racemiflora*), and possibly laurel sabino (*Magnolia splendens*) (Table 3). Jusillo (*Henriettea squamulosa*),

TABLE 1. Stem density and basal area for species with ≥15 stems/ha on the thinned Colorado slope plot (CCU) in the Luquillo Experimental Forest.[1]

	Stems (no./ha)[2]				Basal area (m^2/ha)	
Species	Stand 1947	Ingrowth 47-80	Mortality 47-80	Stand 1980	1947	1980
Byrsonima wadsworthii Little	18	2	8	12	0.09	0.09
Clusia clusoides (Griseb.) D'Arcy	10	362	7	365	0.07	5.29
Cyrilla racemiflora L.	82	755	67	770	5.63	7.03
Daphnopsis philippiana Krug & Urban	18	30	10	38	0.05	0.07
Haenianthus salicifolius Grised.	12	43	0	55	0.28	0.76
Henriettea squamulosa (Cogn.) Judd.	230	105	117	218	2.32	2.49
Magnolia splendens Urban	28	5	2	31	0.71	1.05
Miconia tetrandra (S.) D. Don	0	182	0	182	0	0.90
Micropholis garciniaefolia Pierre	1108	98	148	1058	7.82	11.51
M. guyanensis (A.DC.) Pierre	40	22	0	62	0.27	0.71
Ocotea spathulata Mez	80	5	70	15	0.50	0.11
Tabebuia rigida Urban	218	150	58	310	3.35	6.50
Torralbasia cuneifolia (C. Wright) Krug & Urban	15	2	10	7	0.07	0.03
Remaining (19 species)[3]	46	58	32	72	0.42	0.42
Total	1905	1819	529	3195	21.58	36.96

[1]Plot size = 0.4 ha.

[2]All values rounded to nearest integer

[3]Remaining species (≤14 stems): species gained through ingrowth—*Alchornea latifolia* Sw., *Cecropia schreberiana* Mig., *Cordia borinquensis* Urban, *Ficus crassinervia* Desf., *Myrcia fallax* (A. Rich) DC., *Ocotea leucoxylon* (Sw.) Mez, *Psychotria berteroana* DC., *Marliera sintinenisii* Kiaersk., *Prestoea montana* (R. Grah.) Nichols., and *Schleflerra morototoni* (Aubl.) Maguire; species lost through mortality—*Hedyosmum arborescens* Sw., *Ternstroemia luquillensis* Krug and Urban, and an unknown species; persistent uncommon species—*Hirtella rugosa* Pers., *Ilex sideroxyloides* (Sw.) Griseb., *Matayba domingensis* (DC.) Radlk., *Meliosma herbertii* Rolfe, *Miconia prasina* (Sw.) DC., *Myrcia splendens* (Sw.) DC., and *Ocotea coriacea* (Sw.) Britt.

TABLE 2. Stem density and basal area for species with ≥15 stems/ha on the undisturbed Colorado slope plot (CS-2) in the Luquillo Experimental Forest.[1]

Species	Stems (no./ha)[2]				Basal area (m^2/ha)	
	Stand 1946	Ingrowth 46-80	Mortality 46-80	Stand 1980	1946	1980
Byrsonima spicata (Cav.) HBK	18	0	16	2	0.22	0.07
B. wadsworthii Little	15	5	2	18	0.07	0.14
Cecropia schreberiana Mig.	25	2	15	12	0.67	0.42
Clusia clusoides (Griseb.) D'Arcy	15	10	2	23	0.67	1.80
Cordia borinquensis Urban	125	40	17	148	0.72	0.99
Croton poecilanthus Urban	99	55	32	122	0.94	2.68
Cyrilla racemiflora L.	108	8	48	68	13.65	10.25
Dacryodes excelsa Vahl	15	0	3	12	0.08	0.12
Daphnopsis philippiana Krug & Urban	102	20	44	78	0.31	0.22
Ditta myricoides Griseb.	18	27	0	45	0.10	0.24
Eugenia borinquensis Britt.	45	0	20	25	0.17	0.10
Haenianthus salicifolius Grised.	15	5	2	18	0.98	1.06
Hedyosmum arborescens Sw.	42	5	42	5	0.09	0.01
Henriettea squamulosa (Cogn.) Judd.	128	18	36	110	1.40	1.46
Hirtella rugosa Pers.	20	12	14	18	0.09	0.08
Ilex sideroxyloides (Sw.) Griseb.	22	0	12	10	0.08	0.05
Magnolia splendens Urban	28	0	8	20	2.60	3.04
Miconia laevigata (L.) DC.	28	0	15	13	0.14	0.24
M. tetratandra (S.) D. Don	0	42	0	42	0	0.20
Micropholis garcinifolia Pierre	15	15	13	152	4.06	4.58
M. guyanensis (A. DC.) Pierre	257	42	24	275	3.32	5.29
Myrcia splendens (Sw.) DC.	20	0	12	8	0.06	0.04
Ocotea spathulata Mez	99	28	65	62	1.52	0.54
Prestoea montana (R. Grah.) Nicholls	278	68	106	240	4.64	4.16
Psychotria berteroana DC.	35	8	35	8	0.07	0.01
Sloanea berteroana Choisy	32	0	14	18	0.37	0.58
Remaining (22 species)[3]	74	58	40	92	1.74	1.22
Total	1813	468	637	1644	38.78	39.59

[1]Plot size = 0.4 ha.
[2]All values rounded to nearest integer.
[3]Remaining species (≤14 stems): species gained through ingrowth—*Clibadeum erosum* (Sw.) DC. and *Tabebuia heterophylla* (DC.) Britt.; species lost through mortality—*Ardisia glauciflora* Urban, *Citharexylum caudatum* L., *Cyathea arborea* (L.) J. E. Smith, *Eugenia stahlii* (Kiaersk.) Krug & Urban, *Guarea guidonia* (L.) Sleumer, and *Ocotea coriacea* (Sw.) Britt.; species persistent in low numbers—*Alchornea latifolia* Sw., *Ardisia obovata* Desv. ex Hamilt., *Cleyera albopunctata* (Griseb.) Krug & Urban, *Drypetes glauca* Vahl, *Ficus sintenisii* Warb., *Guarea glabra* Vahl, *Ilex nitida* (Vahl) Maxim, *Marliera sintinenisii* Kiaersk., *Miconia prasina* (Sw.) DC., *Myrcia fallax* (A. Rich) DC., *Ocotea leucoxylon* (Sw.) Mez, *O. moschata* (Meissn.) Mez, *Tabebuia rigida* Urban, *Ternstroemia heptasephala* Krug & Urban, and *T. luquillensis* Krug & Urban.

caimitillo verde (*Micropholis garcinifolia*), and caimitillo (*Micropholis guyanensis*) showed slight long-term increases in growth. The data sets for cupeíllo (*Clusia clusoides*) and roble de sierra (*Tabebuia rigida*) are too small to evaluate.

Density and basal area

Although similar in total number of stems after thinning (Tables 1 and 2), the dbh class distributions on CS-2 and CCU were different (Table 4). CCU contained no stems ≥50 cm; moreover, it had a greater proportion of stems ≤10 cm than did CS-2. On CCU, with massive regeneration (new stems from seeds), the proportion of stems in the smallest two dbh classes remained virtually the same in 1947 and 1981. In contrast, on CS-2, the proportion of stems in the smallest dbh class declined during the

TABLE 3. Comparison of short- and long-term growth rates after thinning for select tree species in Colorado forest in the Luquillo Experimental Forest.[1]

Species	Measurement interval 1947-52	1952-75	1947-81
	dbh growth in cm/yr ± SE[1] (no. stems)		
Thinned plot (CCU)			
Clusia clusoides	0.27 ± 0.12 (2)	0.81 ± 0.45 (2)	—
Cyrilla racemiflora	0.08 ± 0.02 (30)	0.17 ± 0.06 (20)	0.17 ± 0.04 (12)
Henriettea squamulosa	0.06 ± 0.01 (79)	0.10 ± 0.01 (49)	0.09 ± 0.01 (44)
Magnolia splendens	0.16 ± 0.04 (10)	0.14 ± 0.04 (10)	0.14 ± 0.03 (10)
Micropholis garcinifolia	0.09 ± 0.01 (444)	0.06 ± 0.00 (412)	0.07 ± 0.00 (380)
M. guyanensis	0.13 ± 0.04 (16)	0.13 ± 0.02 (16)	0.14 ± 0.03 (16)
Ocotea spathulata	0.03 ± 0.01 (28)	0.01 ± 0.00 (11)	0.02 ± 0.01 (6)
Tabebuia rigida	0.19 ± 0.02 (82)	0.21 ± 0.02 (69)	0.19 ± 0.01 (65)
Eight species[1]	0.098 (691)	0.089 (589)	0.091 (533)
Control plot (CS-2)			
Clusia clusoides	0.40 ± 0.09 (6)	0.32 ± 0.11 (5)	0.39 ± 0.16 (5)
Cyrilla racemiflora	0.07 ± 0.01 (41)	0.07 ± 0.02 (28)	0.09 ± 0.02 (23)
Henriettea squamulosa	0.07 ± 0.01 (49)	0.06 ± 0.01 (41)	0.06 ± 0.01 (38)
Magnolia splendens	0.12 ± 0.03 (10)	0.06 ± 0.02 (9)	0.11 ± 0.03 (8)
Micropholis garcinifolia	0.11 ± 0.02 (59)	0.04 ± 0.01 (56)	0.06 ± 0.01 (55)
M. guyanensis	0.12 ± 0.01 (103)	0.09 ± 0.01 (96)	0.10 ± 0.01 (93)
Ocotea spathulata	0.06 ± 0.02 (37)	0.03 ± 0.01 (19)	0.01 ± 0.00 (13)
Tabebuia rigida	0.25 ± 0.13 (3)	0.14 ± 0.01 (2)	0.18 ± 0.02 (2)
Eight species[1]	0.103 (308)	0.071 (256)	0.086 (237)

[1]Standard error not determined among species.

TABLE 4. Percent of stems by diameter class on undisturbed and cutover Colorado slope plots in the Luquillo Experimental Forest.

Diameter class (cm)	Percent of total stems: Undisturbed[1] 1946	Undisturbed[1] 1981	Cut-over[2] 1946	Cut-over[2] 1981
≤9.9	53.2	47.9	64.6	63.6
10.0-19.9	34.1	38.3	28.8	27.8
20.0-29.0	6.4	7.4	4.0	6.7
30.0-39.9	3.4	3.9	2.1	1.5
40.0-49.9	1.9	1.3	0.5	0.4
50.0-59.9	0.6	0.9	—	—
60.0-69.9	—	—	—	—
≥70.0	0.4	0.3	—	—
Totals	100.0	100.0	100.0	100.0

[1]Total stems in 1946, 1813/ha; in 1981, 1644/ha.
[2]Total stems in 1947, 1905/ha; in 1981, 3195/ha.

35-yr measurement period, whereas the proportion in the second smallest class increased.

The basal area after thinning on CCU was 21.6 m^2/ha, while the basal area at first measurement on CS-2 was 38.8 m^2/ha. Basal area increment over the measurement period averaged 0.45 m^2/ha/yr on CCU and only 0.02 m^2/ha/yr on CS-2. Ingrowth averaged 54 stems/ha/yr on CCU and 13 stems/ha/yr on CS-2; comparative values for mortality were 16 and 18 stems/ha/yr, respectively.

Three species increased significantly in density on the CCU plot during the 34-yr period of measurement (Table 1): palo colorado (from 82 to 770/ha), cupeíllo (10 to 365/ha), and palo de hueso (12 to 55/ha). These same species decreased in numbers or increased slightly on CS-2 (Table 2). Camasey regenerated well on both plots, with 4.3 times as many new stems on CCU as on CS-2. Laurel sabino increased slightly in density on CCU and declined on CS-2.

DISCUSSION

Response to thinning

The 5-yr dbh growth rates for select species after thinning on CCU remained similar to those on CS-2, and are comparable to other permanent plots in mature, undisturbed colorado forest (Anonymous 1950, 1953, 1957; Weaver, 1983). An earlier assessment of the thinned stand revealed that "partial cuttings have not materially accelerated the diameter growth of the remaining trees" (Anonymous, 1957). The apparent lack of response to thinning was attributed to the advanced age of the released trees, despite their small sizes. Several years are required before residual trees in slow-growing colorado forest respond, even slightly, to thinning.

Previous thinning studies in tabonuco forest revealed that the greatest response to canopy opening was for species that characterize climax forest, and the least for species commonly recognized as gap opportunists (Weaver, 1983). In colorado forest, where growth rates are slower, common species with regeneration tied mainly to openings (for example, cupeíllo, palo colorado, and laurel sabino) appear to show the greatest potential for accelerated growth after disturbance.

The slow response of most residual stems to thinning on CCU provided an opportunity for the major influx of new stems. During 34 yrs, stem density increased to nearly double that of mature colorado forest, and basal area to nearly 37 m^2/ha, a value typical of mature colorado forest (Table 1). Mean annual aboveground biomass increment from the mid-1940s to 1981 averaged 2.5 t/ha/yr on CCU and only 1.33 t/ha/yr on CS-2 (Weaver, 1989).

Tree species

Two tree species critical to the Puerto Rican Parrot, palo colorado and cupeíllo, regenerated abundantly after the thinning. Parrots depend on palo colorado for nesting sites and feed on cupeíllo fruits and leaves (Snyder et al., 1987). Laurel sabino, another potential nesting tree whose fleshy seeds, leaves, and twigs are eaten (Snyder et al., 1987), appears to have regenerated in reponse to canopy opening.

The above three species were classed as "secondary" from among the 20 species that reach the canopy on different sites within mature colorado forest (Weaver, 1992). Palo colorado is a long-lived tree, slow-growing during most of its life cycle, possibly attaining 1 m in dbh in about 650 yrs (Weaver. 1986). Young palo colorado responds to small openings in the colorado canopy, often growing at an angle to reach the light (Snyder et al., 1987). It's phototropic response and capacity for initial rapid growth allows the species to benefit from natural openings and thinnings.

Cupeíllo grows rapidly in open conditions at high elevations in the LEF. Typically, it regenerates in forest openings, on boulders, on the root masses of fallen trees, and occasionally within the major branches of other trees (in this instance aerial roots descend to the ground). Patches of forest dominated by cupeíllo grow at high elevations along the East Peak Road (pers. obs.), presumably due to hurricane disturbance.

Although the increase of laurel sabino on CCU is minor (Table 1), it contrasts with losses on CS-2 (Table 2). Moreover, there was a 35 % decline in laurel sabino on all unthinned LEF colorado and tabonuco permanent plots between the mid-1940s and 1981 (Weaver, 1987). During this period, the forests of the LEF were recovering from Hurricane San Cipriano of 1932 (Weaver, 1989). Laurel sabino, formerly a prized furniture wood, was harvested in the LEF through the early 1950s, when large trees in prime reproductive condition were still being cut. The decline of this species is apparently due to the reduction of mature trees by harvest and to its incapacity to regenerate in closed forest conditions (a situation that prevailed in the LEF from the mid-1940s, about 15 years after the passage of Hurricane San Cipriano, until major disturbance caused by Hurricane Hugo in 1989).

Roble de sierra is one of the most common species in the upper reaches of colorado forest and in the dwarf forest (Wadsworth, 1951; Weaver, 1983). In dwarf forest, it regenerates in forest openings and grows more rapidly than most other species (Weaver, 2000). Being adapted to open conditions, it appears to respond positively to thinning in the colorado forest.

Management implications for the LEF

Hurricanes are likely to pass over the LEF every 50 to 60 years (Scatena and

Larsen, 1991) and cause severe defoliation, uprooting, and snapping of tree crowns. The thinning on CCU-a 50 % basal area reduction including the removal of competing canopy trees-simulated damage caused by the most severe hurricanes. Forest recovery from such events spans decades and is characterized by several stages: ingrowth for several years after the storm, competition among stems, building or accumulation of biomass on survivors, and maturity (Weaver 1989, 1998).

The thinning on CCU also has implications for the long-term recovery of the Puerto Rican Parrot. The lack of parrot nest cavities in colorado forest was resolved in the short-term by mounting nest boxes in appropriate areas (Snyder et al., 1987). Selective thinning of small patches of colorado forest, leaving residual trees of palo colorado and other species useful to the parrot such as cupeíllo and laurel sabino, could contribute to favorable long-term changes in species composition and forest structure. In a sense, deliberate intervention favoring laurel sabino might partially compensate for its past heavy exploitation throughout the LEF.

The Puerto Rican Parrot, once widespread in Puerto Rico, has been largely confined for the past three-quarters of a century to the LEF's colorado forest. As Puerto Rico's population continues to grow, and urban infrastructure expands throughout the northeast, the LEF begins to look more like a central park than a national forest. With increased disturbance outside the forest boundaries, the forest functions of the LEF (wildlife habitat, water supply, and recreational opportunities) become more critical to the rest of the island.

Hurricanes have always impacted the forests of the LEF and its animal populations. Human disturbance in the tabonuco forest, however, was the likely reason that the Puerto Rican Parrot abandoned the lower slopes of the LEF where tabonuco (*Dacryodes excelsa* Vahl) and other large trees once provied nesting sites (Thompson Baranello, 2000). The recent recording of two nests in tabonuco may indicate that these forest areas are again becoming satisfactory for nesting. Given the precarious situation of the island's forests in general, and the parrots in particular, some traditional uses of the national forest system of which the LEF is a part (for example, timber supply and related forest industry) should be excluded from management planning in the forseeable future. Development on private holdings surrounding the LEF should be controlled by zoning and continual surveillance so that much of the land remains in forest cover.

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