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MULTIPLE SCALE PATTERNS IN GROWTH AND
STRUCTURE OF SUBTROPICAL DRY FORESTS: SOILS,
TREES, AND HURRICANES

presented by

Skip Judson Van Bloem

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MULTIPLE SCALE PATTERNS IN GROWTH AND STRUCTURE OF SUBTROPICAL DRY FORESTS: SOILS, TREES, AND HURRICANES

by

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ABSTRACT

MULTIPLE SCALE PATTERNS IN GROWTH AND STRUCTURE OF SUBTROPICAL DRY FORESTS: SOILS, TREES, AND HURRICANES

by

Skip Judson Van Bloem

Compared to dry forests found in other tropical locations, those in the West Indies have a unique structure – with higher stem density, a larger proportion of multiple stemmed trees, and less basal area at maturity. The primary goal of this dissertation is to identify factors that lead to the unique structure of West Indian dry forest, using Guánica Forest, Puerto Rico, as a representative example. This dissertation addresses two potential mechanisms for the unique structure of West Indian dry forest: nutrient limitation and hurricane disturbance.

I assessed forest maturity by resampling trees from plots within a research site 18 years after site establishment. Basal area increased by 7.3% while stem density increased by <1%. Mortality equaled in-growth. Nutrient pools remained constant. Without the effects of the hurricane, the forest would appear to be aggrading, with increases of 11% in stem density and 26% in basal area since 1981. Species composition changed little, but putative pioneer species decreased in importance.

The size and distribution of nutrient pools were analyzed using geostatistical methods in four research sites in Guánica Forest. Nutrient limitation was assessed by comparing species distribution and tree growth rates to nutrient gradients and by manipulating nutrient concentrations in root in-growth cores. Nutrient patch size ranged from 17-25 m. Spatial distributions of nitrogen and organic matter were similar among and within sites. Although calcium binds with phosphorus at the high pH (7.8) found in Guánica soils, there were no strong correlations between pool sizes and spatial distributions for pH, Ca, and P. Soil nutrients were greatest where litter accumulated, either in small depressions or crevices between outcrops. Individuals of common tree species were present across the entire breadth of each nutrient gradient, suggesting that these species distributions were not limited by nutrient pool size. Nutrient pools influence the growth of basal sprouts, but were not associated with the growth of mature trees. Root growth in cores treated with N exceeded that in control or P treatments but was greatest in the NP-combined treatment, indicating co-limitation of root growth. Guánica Forest had higher values of soil pH and larger pools of organic matter (OM), N, and total P than reported for other dry forests.

The effects of hurricane disturbance were determined following Hurricane Georges in 1998. Over 3000 stems were assessed for damage, mortality, and sprouting in 33 different plots within Guánica Forest and nearby in 19 forest fragments. Hurricane winds damaged only 12.4% of stems but damage was biased toward larger-diameter stems. Stem mortality was only 2% and not associated with size class. Damage was greatest in exposed sites and was caused by the storm's strongest winds. Leaf litterfall was about half that of average annual levels, but nutrient return in leaf litterfall equaled or surpassed annual averages. Basal sprouting following the hurricane was tenfold greater than pre-hurricane levels (3.5%). Sprouting was not related to the severity of stem damage or defoliation.

Overall, hurricanes appear to have a greater influence on the structure of Guánica Forest than do nutrient pools. Hurricane Georges damaged large stems and caused basal area losses equaling decades of growth. Furthermore, the hurricane resulted in a widespread sprouting response that could increase stem density and the proportion of multi-stemmed trees as sprouts mature into stems. Soil nutrient content most influenced growth and survival of basal sprouts. Although other mechanisms may exist, hurricanes play a central role in determining the structure of West Indian dry forest.

ACKNOWLEDGMENTS

I would never have been able to wade through the reams of data and hours of lab work necessary to complete this project without the professional and personal assistance of many individuals.

Ariel Lugo provided cheerful advice, support and encouragement, as well as helping to identify other useful opportunities for my research and career development. He and Fred Scatena allowed me to use the facilities of the soil nutrient labs at the USDA Forest Service, International Institute of Tropical Forestry. Under a co-operative agreement with the Forest Service (IITF-98-CA-006), funding was provided to finance my field trips to Puerto Rico and to allow the lab staff of Mary Jeane Sanchez, Edwin Nuñez, and Maribelis Santiago to help analyze my nutrient samples. Their careful attention to detail and helpful advice were indispensable. Having worked with them, it is easy to understand why the IITF soils lab has such a good reputation. In addition, Carlos Rodriguez provided GPS equipment and processed data, making many of the spatial analyses performed herein possible.

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One's advisor inevitably plays a major role in one's satisfaction with their research and their motivation and desire to continue a career in science. This influence can be positive or negative. Peter G. Murphy, my advisor, has been a fine guide. I appreciate his candor, his ability to ask to the right questions to guide the research, and the excitement he shows when discussing research and reviewing results. Pete has the uncanny ability to be realistic without being discouraging. I hope that I can follow his example in my future interactions with graduate advisees.

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CHAPTER ONE

INTRODUCTION TO THE DISSERTATION

If tropical forests were human societies, dry forests would be the proletariat – overlooked despite being widespread and exploited with little return. Dry forests cover the most land area (42%) of any tropical forest type (Murphy and Lugo 1986a) and are found in nearly every tropical country (Bullock et al. 1995, Van Bloem et al. 2004). Dry forests have been extensively cleared for agriculture and human settlements because their soils are less leached than in wet zones and the climate provides seasonal respite from humidity, pests, and disease. As a result, only about 5% of dry forests worldwide are protected in parks and reserves (Van Bloem et al. 2004). While tropical rainforests have experienced rapid and recent expansions of human disturbance (Nepstad et al. 2002), human conversion of dry forests has a much longer history that may have caused these forests to be under-appreciated by the research community. For example, since 1970, only approximately 30% of scientific journal articles on tropical forests have focused on dry forests, with the balance discussing moist, wet, or rain forests (metadata analysis by Skip Van Bloem using Science Citation Index ®).

Across their geographical distribution, mature dry forests show a large range in structure and function. Stem density (minimum 2.5 cm diameter at breast height, this criteria is used throughout the dissertation) varies from about 650 to 12000 stems/ha, height ranges from 8 to 30 m, and basal area from 18 to 49 m^2/ha (Murphy and Lugo 1990, Van Bloem et al. 2004). Tree growth in diameter averages from 0.3 to 4.7 mm/y (Dunphy et al. in prep). Annual litter production varies from 1.5 to 12.6 Mg $ha^{-1}yr^{-1}$ (Martinez-Yrizar 1995), while nutrient use efficiency varies about two-fold for nitrogen (44-97 g/g) and six-fold for phosphorus (926-6056 g/g; Van Bloem et al. 2004). Among dry forests, those in the West Indies tend to exhibit the most extreme characteristics, with the greatest stem density (>10,000 stems/ha) and P-use efficiency (up to 6000 g/g), and the lowest basal area (17.8 m^2/ha), height (9 m), and tree growth rate (3 mm/yr) (Lugo and Murphy 1986, Murphy and Lugo 1986b, Dunphy et al. in prep). These characteristics lead to a unique forest physiognomy with a short, shrubby growth form, many (>40%) multiple-stemmed trees, and an even forest canopy without emergent trees. Despite the unusual physiognomy, the climate of Caribbean dry forests is not extreme in comparison to other dry forest areas (Murphy and Lugo 1986a). For example, the climate of Guánica Forest, Puerto Rico, which is considered among the best preserved tracts of Caribbean dry forest (Ewel and Whitmore 1973), consists of average annual rainfall of 860 mm, 25.1°C mean annual temperature, and temperature to precipitation ratio of 2.9. These values all fall near or slightly above median values for dry forests worldwide (Murphy and Lugo 1986a, Van Bloem et al. 2004). Thus, although Caribbean dry forests are among the densest, shortest, and have the most multi-stemmed trees, they are not the driest or hottest, suggesting that other factors interact with climate to generate the physiognomy of the region. Broadly, the overall objective of this dissertation is to identify factors and mechanisms which lead to the unique structure of West Indian dry forest, using dry forests of Puerto Rico as a representative example.

A BRIEF HISTORY OF RESEARCH IN GUÁNICA FOREST

An explanation for the unique structure of West Indian dry forests has been elusive. A single, overriding factor is unlikely to exist as the forests must respond to various climatic, biological, and human stresses. Fortunately, a long record of research in permanent plots in

Guánica Forest, Puerto Rico, has helped to identify and evaluate possible explanations. This dissertation adds to previous research efforts in Guánica Forest in an attempt to further our understanding of the uniqueness of West Indian dry forests and the structure and function of dry forests in general.

Guánica Forest was originally protected by the US government in 1917 with major additions of land area occurring in the late 1930s and from 2000-2004. The forest now includes over 4500 ha. Initial descriptions of plant communities and succession were made in the 1920s by Gleason and Cook (1927). Experiments determining the suitability of mahogany plantations in the forest and early analysis of hurricane effects on forest structure were performed from 1940-1957 (Wadsworth 1950, Wadsworth and Englerth 1959). Early succession from an experimental clearcut established in 1969 was described by Ewel (1971) and reassessed by Dunevitz (Dunevitz 1985). The abandonment of a small village within the forest boundaries in the 1930s provided the opportunity to evaluate 60-yr patterns of succession and the effects of land use (Molina Colón 1998). Studies describing physiological, functional, and structural characteristics of the forest in detail have been completed since 1978 (Lugo et al. 1978, Lugo and Murphy 1986, Murphy and Lugo 1986b, Cintron and Lugo 1990, Medina and Cuevas 1990, Murphy and Lugo 1990, Farnsworth 1993, Murphy et al. 1995, Quigley and Platt 2003). Many of these studies were conducted in a 1.44 ha permanent site established by Peter G. Murphy and Ariel E. Lugo in 1981 (Murphy and Lugo 1986b). These studies documented the unique structural and functional characteristics of Guánica Forest highlighted above and suggested potential explanations for these characteristics.

MOTIVATION FOR THIS RESEARCH

This dissertation addresses two potential explanations for the unique structure of Caribbean dry forest: nutrient limitation and disturbance. However, it should be noted at the outset that all dry forest dynamics occur within the context of seasonal drought and unpredictable rainfall patterns. Annual rainfall limits productivity, however, rainfall appears to be sufficient during the growing season because dry forest productivity at that time approaches that of rainforests (Murphy and Lugo 1986a). Tree growth and the phenology of most tree species are tied to seasonal rains (Murphy et al. 1995). Severe drought during the rainy season can lead to the death of terminal buds which could result in multiple stemmed trees if they were to resprout from the base. However, within Guánica Forest, only one species, *Gymnanthes lucida*, appears to incur top-kill and when this occurs the tree usually resprouts above 1 m height (personal observations and Dunphy 1996). Therefore it appears that water limitation does not explain the multi-stemmed growth form and, at least during the rainy season, other conditions influence forest structure.

Previous research has identified important nutrient characteristics of Guánica Forest that could influence its structure. Total soil P is relatively high (1820 kg/ha) but only 1.3% is bioavailable (Lugo and Murphy 1986). Leaf N:P ratios are high (21-38, Medina and Cuevas 1990) and phosphorus use efficiency (>6000) is the highest reported from the tropics (Vitousek 1984). The calcareous soil has a mean pH of 7.8, a level at which phosphorus binds to calcium (Lugo and Murphy 1986). Leaves have a tendency to be sclerophyllous (Murphy and Lugo 1995), which can be a sign of P limitation (Medina et al. 1990). Together, these characteristics suggest potential nutrient limitation of forest productivity and structure, primarily by P, although the short supply of P could be the result of insufficient soil moisture for P transport (Murphy et al. 1995). The possibility of P limitation motivated some of the nutrient research within this dissertation, but another compelling reason was the opportunity to compare 18 years of on-going tree-growth measurements to soil nutrient pools in the permanent plot (Murphy et al. 1995, Dunphy et al. in prep).

Another key factor that may explain mature Caribbean dry forest structure is disturbance – two types of which commonly occur. The first is anthropogenic – primarily cutting or clearing by humans. Until the 1930s, some areas within Guánica Forest were cleared for agriculture and housing while other areas were selectively cut for firewood and small-scale charcoal production (Lugo et al. 1996, Molina Colón 1998). Regrowth on cleared forest lands resulted in forests with lower stem density, more single-stemmed trees, and a species assemblage dominated by exotics (Molina Colón 1998). Conversely, high stem density and coppice clumps were common in former charcoal sites (Molina Colón 1998), which makes cutting a reasonable explanation for Caribbean forest structure. However, it now appears that a natural mechanism must exist which generates the Caribbean forest structure because other studies have shown that stumps of main stems were absent on multi-stemmed trees and that multi-stemmed trees were present in size classes that were too small to have existed during fuel-wood harvests (Dunphy et al. 2000).

Hurricanes are another major disturbance type endemic to the Caribbean. They strike Puerto Rico about once every nine or ten years (Weaver 1999), but the last major hurricane to cross over Guánica Forest was in 1928 (Miner-Solá 1996). By luck rather than by design, I arrived in Puerto Rico five days before Hurricane Georges in September, 1998, and therefore was able to assess the effects of this "natural experiment" on the structure of Caribbean dry forest.

LAY-OUT OF THE DISSERTATION

The dissertation contains five main chapters (2-6), each on a different aspect of the relationship of forest growth and structure to soil nutrient content or hurricane disturbance. Chapter Two evaluates structural changes in the permanent site (the Main site) 18 years after it was established. As I discuss in the chapter, long term reassessments of permanent sites – even if only 18 years – are rather uncommon in the dry tropics. Understanding change provides a good context by which to address the role of nutrients and hurricanes in shaping forest structure. Specific objectives of this chapter are to: 1) reassess forest structure, species composition, soil nutrient pools, and litter fall; 2) assess mortality and in-growth (recruitment into the minimum diameter class considered: 2.5 cm) during the 18-year period; 3) provide a baseline of natural variability in order to evaluate the effects of episodic disturbance by hurricanes; and 4) describe dynamics of mature Caribbean dry forest to improve our ability to compare against patterns from dry forests in other locations.

Chapters Three and Four address nutrient limitation in Guánica Forest. Chapter Three provides extensive analysis of the quantity and distribution of soil nutrient pools focusing on N, P, and Ca. Supplemental information for Chapter Three can be found in the Appendix. The primary objective of this chapter is to describe spatial patterns of soil nutrients and pH within and among four sites in Puerto Rican dry forest. Emphasis is given to relationships between phosphorus and calcium, topography and nutrient contents, and correspondence of nutrient patch size to tree crown diameter. Chapter Four compares patterns of tree growth and distribution to soil nutrient content. The objectives of this chapter are to: 1) determine whether common species in Guánica Forest were limited to certain positions along gradients in soil fertility; 2) to determine if and which soil nutrients limited growth; and 3) to evaluate whether N or P plays a greater role in nutrient limitation on forest growth.

Evaluation of hurricane effects on dry forest structure is covered in Chapters Five and Six. Chapter Five describes the immediate effects of a hurricane – damage, mortality, and defoliation. The main objectives of this chapter are to: 1) provide a detailed description of hurricane effects on Puerto Rican dry forest; 2) compare effects of hurricane winds in large tracts of forest with those in nearby forest fragments; 3) measure short-term responses of trees to hurricane winds in terms of mortality; and 4) assess the potential of hurricanes to maintain the unique forest structure of the West Indies. In addition to the data I collected in mature, south-facing forest for Chapter Five, Dr. Sandra Molina Colón and Ivelisse Ruiz Benard contributed data for forest plots with different aspects and land use histories. This chapter has been accepted by *Biotropica.* Chapter Six assesses the response of the forest by sprouting and the first two years of sprout growth following the hurricane. This chapter has already been published in *Tropical Ecology* (Van Bloem et al. 2003). The objectives of this chapter are to evaluate three predicted outcomes of hurricane disturbance: 1) sprouting frequency would be higher on damaged stems; 2) sprouting would be proportional to defoliation because sprouting response might be related to biomass loss; and 3) a majority of sprouts produced after Hurricane Georges would die after the first or second dry season due to thinning of new sprouts as they competed for resources.

SITE DESCRIPTIONS

The majority of the research presented here was performed in three sites in Guánica Forest (Figure 1-1). The Main site was the 1.44-ha permanent plot established in 1981

(Murphy and Lugo 1986b). Two 1-ha "satellite" sites were established in June, 1998: Lluberas and Ventana. Each site was >2 km from the others (Figure 1-1). Structural characteristics of the forest were measured in these sites and soils were sampled for spatial analysis in portions of each sites. In addition to the Main site and satellite sites, some additional sites were included to assess hurricane effects. These are described in Chapter Five. Also, one 25 x 25 m site (Honda) was established in 1992 for a study of plant species diversity along a latitudinal gradient of seasonal forests (Quigley and Platt 2003). I used this site as part of the analysis of spatial patterns of soil nutrients. It is described in Chapter Three. Some of the information here is repeated as needed for the context of each data chapter. Complete details of each site can be found in Appendix 1.

The Main and satellite sites were all located in mature, semi-deciduous forest (as in Lugo et al. 1978) consisting of native tree species. For stems ≥ 2.5 cm diameter at breast height (the minimum size class used for all analyses in this dissertation), 32-37 tree species were present at each site, basal area ranged from 17.9-21.3 m^2/ha and stem density from 6,400 to 10,400 stems/ha (Table 1-1). Human disturbance at each site has been minimal for the last 70 years as verified by analysis of aerial photos taken since the 1930s (Lugo et al. 1996). The topography was hilly with rocky outcrops and soils derived from limestone (calciustols). Where outcropping was prevalent, soil was only found at the surface in crevices between rocks and plants rooted in loosely consolidated humus layers. The sites were located between 23 and 150 m above sea level and elevation within each site varied from 10-20 m (Figure 1-2).

Multiple sites were used for most analyses to ensure that patterns were consistent across the forest and that results previously reported from the Main site were representative of the forest in general. In addition, multiple sites provided better opportunity to study spatial patterns of nutrient distribution and hurricane disturbance.

Table 1-1. Characteristics of the three sites used for the majority of research reported in this dissertation.

	Main	**Lluberas**	**Ventana**
Size (ha)	1.44	1.0	1.0
Sampled area (m^2)	690-1500	900	900
Mean elevation (m.a.s.l.)	129	147	25
Range of elevation (m)	20	9	14
Number of tree species*	37	33	32
Basal area (m^2/ha)*	19.1	21.3	17.9
Stem density (ha^{-1})*	10,400	9,200	6,400
Previous land use**	Mature	Mature	Mature

*minimum 2.5 cm diameter at breast height

**minor selective cutting prior to 1940 for firewood or charcoal production noted

Figure 1-1. Map of Guánica Forest showing study site locations.

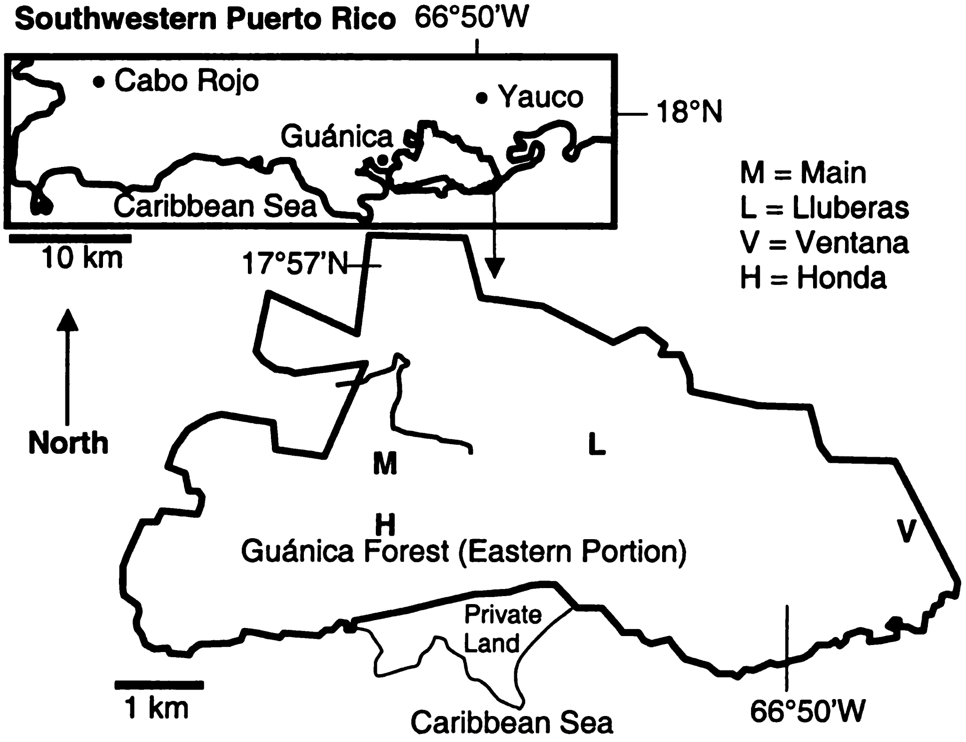
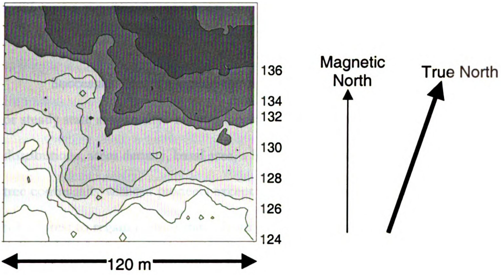
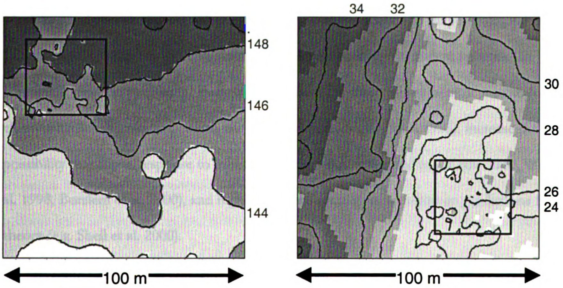


Figure 1-2. Topography of the Main and satellite study sites. Contour lines are 2 m intervals above sea level (m.a.s.l.) as labeled around maps. Boxes on Lluberas and Ventana sites indicate 30 x 30 m plots where soil sampling occurred.

Main Site





Lluberas Site

Ventana Site

CHAPTER TWO

DYNAMICS OF FOREST STRUCTURE AND NUTRIENT POOLS IN MATURE SUBTROPICAL DRY FOREST: A LONG-TERM REASSESSMENT OF GUÁNICA FOREST (1981-1999)

Succession theory suggests that a forest community will reach a dynamic equilibrium or steady state at maturity. Mature forests would be expected to maintain stable size class distributions, stem density, basal area, a balance between recruitment and mortality, and a tree community without pioneers except in canopy gaps (Richards 1996). The time required for a forest to regain mature status from a disturbance is typically greater than the time available for most research projects and grants (3-5 y). Consequently, evaluation of maturity and forest dynamics of mature forests is frequently achieved through modeling or the use of forest plots along a chronosequence of successional age instead of long term monitoring. Modeling and chronosequences have provided valuable evidence to shape ecological theory, but are unable to directly evaluate dynamics of forest structure in mature systems. In contrast, long-term permanent sampling plots allow for direct assessment of mature forests, clarify whether short-term patterns are trends or fluctuations (Sheil 1995), increase the possibility that forest response to infrequent events can be studied (e.g. Crow 1980, Waide et al. 1998, Burslem et al. 2000), and highlight information gaps or mistaken predictions from theory (e.g. Sheil et al. 2000).

Long term (≥15 y) assessment of tropical forest dynamics in permanent plots has largely confirmed the predictions of succession theory (reviewed by Swaine et al. 1987, and augmented by Burslem, et al. 2000, Taylor et al. 1996, Lwanga et al. 2000, Sheil et al. 2000, Fashing et al. 2004). These studies have all taken place in moist-to-rain forest, including sites in Puerto Rico (Crow 1980, Waide et al. 1998). Stands tend to be self-maintaining with annual mortality of 1-2%. In Malaysia, trees that maintained positive growth rates from year to year had lower mortality rates than those with negative growth rates or no growth increase over a period of years (Manokaran and Kochummen 1987), a pattern recently documented in Puerto Rican dry forest (Dunphy et al. in prep). Long term recruitment (or in-growth) into minimum size classes balanced mortality in most sites, but this balance was often not present within short periods ($\leq$ 8 y) for studies where multiple enumerations of forest populations occurred (Taylor et al. 1996, Burslem et al. 2000, Sheil et al. 2000). Distribution of stems in size classes remained steady over time, as did basal area. A few studies have also included long term measurements in plots which began in earlier successional stages due to prior logging or clearing (Okali and Olaadams 1987, Richards 1996, Sheil et al. 2000, Fashing et al. 2004). Even after 40 years, disturbed forests had yet to return to a mature forest species composition, basal area or stem density.

In addition to attaining steady state in stand dynamics, mature forests may be expected to have relatively constant nutrient pools over time (Sprugel 1985). Studies of long term soil dynamics suggest that forest fallows, after clearing and burning, require at least 15-30 years to rebuild soil nutrient pools (Maass 1995), while organic matter may take up to 60 y to return to pre-disturbance levels (Aber and Melillo 1991). In dry forests of Puerto Rico, soil nutrients in cleared sites had not returned to mature forest levels after 45 y, however soil nutrients in selectively cut sites had recovered (Molina Colón 1998). The dry forest environment responds quickly to highly variable rainfall (Lugo et al. 1978), so year-to-year variability in litter fall, standing litter, productivity, and diameter growth can be high (Lugo and Murphy 1986, Murphy and Lugo 1986b, Cintron and Lugo 1990, Murphy et al. 1995, Dunphy et al. in prep), but can only be determined with long-term observations.

The conclusions of previously published long term permanent plot studies have been successful in verifying many assumptions of mature forest dynamics and highlighting some surprises (e.g., persistence of pioneer species in forest canopy; Sheil et al. 2000). Dry forests may approach dynamic equilibrium at a different rate than wetter forests due to a longer dormant season, lower annual tree growth rates, and lower biomass. The objectives of this chapter are to: 1) assess forest structure, species composition, soil nutrient pools, and litter fall after an 18 year period in a long-term permanent dry forest plot, 2) assess mortality and in-growth during this period, 3) provide a baseline of natural variability in order to evaluate the effects of infrequent disturbance by hurricanes (which are dealt with in Chapters Five and Six), and 4) describe dynamics of mature Caribbean dry forest to improve our ability to compare against patterns from dry forests in other locations.

METHODS

Forest structure

In 1981, a permanent 1.44-ha research site was established in Guánica Forest (Murphy and Lugo 1986b), a state forest originally established in 1918 and expanded in the 1930s. The site was considered to be mature forest but there was some evidence of selective cutting for charcoal production from before the 1930s (Lugo et al. 1996). Cut areas were localized, approximately 10-20 m in diameter, and covered less than 15% of the plot. Within the site, fifteen 10 x 10 m plots were censused in November, 1981 (Figure 2-1). The diameter, height and species were recorded for all stems ≥ 5.0 cm diameter at breast height (dbh). Within the SE quarter of each plot, these same data were recorded for stems ≥ 2.5

cm dbh. These plots were remeasured in the same manner in 1999 and the fate of individual trees was determined based on precise locations recorded in 1981. Hurricane Georges passed over the site in September, 1998. Some effects of the hurricane are reported here, but details of data collection and overall effects are reported in Chapter 5. Original structural data were reported in Murphy and Lugo (1986) (Table 2-1). Mortality, in-growth, and changes in basal area, height, stem density, and species composition were determined by comparing structural data from 1999 with those from 1981. Species were determined using Little and Wadsworth (1964) and Little et al. (1974).

Because multiple-stemmed trees are the dominant growth form in the forest, data were generally analyzed using stems instead of trees. When results refer to trees, this includes single-stemmed individuals and an entire clumps of stems. When discussing individual trunks, regardless of whether growing singly or clumped, I use "stem."

Litter fall and soil nutrients

In 1982, litter fall was collected monthly in thirty 50 x 70 cm wire mesh traps (Lugo and Murphy 1986, Murphy and Lugo 1995). I collected litter fall from these same traps, in different locations, eight times between August 1998 and August 2000. Litter fall was dried to a constant weight to determine biomass. Nutrient content of litter fall was not analyzed because collection intervals were greater than one month, a period during which some labile nutrients would be lost (Cuevas and Medina 1986).

Soil nutrient content was originally analyzed from composites of 20 subsamples taken from 0-5 cm depth in five plots in the main site on seven different dates (n=35) from 1981-1983 (Lugo and Murphy 1986) and from monoliths from four soil pits. In 1999, as part of a study of spatial patterns in soil nutrient content (see Chapter 3), I collected 623 soil samples from 0-10 cm depth along 6 transects. Total soil nitrogen was analyzed on 100-mg soil subsamples using dry combustion in a LECO CNS (LECO Corp. St. Joseph, MI) analyzer. Soil samples were combusted at 1450°C. Organic matter (OM) was measured as loss on ignition by combusting samples in a muffle furnace at 490°C. At this temperature, loss on ignition does not include clay-bound water and therefore estimates OM well (Nelson and Sommers 1996). Total concentrations of other elements (Ca_{to}, K_{to}, P_{to}) were determined by digesting 100-mg subsamples in nitric acid followed by hydrogen peroxide. Using 5-g subsamples, available calcium (Ca_{av}) was extracted in 1.0 M KCl while available phosphorus (P_{av}) and potassium (K_{av}) were extracted using a modified Olsen solution (Wilde et al. 1979). Digested total and available element concentrations were determined using an atomic-emission spectrometer. Measurement accuracy was maintained for each analysis by verifying standards after every twenty samples and running duplicates of every tenth sample. Bulk density was measured using intact cores of 10 cm soil depth.

RESULTS

Changes in structural characteristics of Guánica Forest over the 18-y period were generally small, despite the occurrence of Hurricane Georges <1 y before the end of the sampling period (Table 2-2). Three new species were present in the size classes of trees measured: *Colubrina arborescens, Eugenia rhombea*, and *Reynosia uncinata*. Only *E. rhombea* has not been recorded in the understory in 1981 (P.G. Murphy, unpublished data) and therefore was assumed to be entirely new to the site. Elsewhere in Guánica Forest, this species is common. No species were lost. Basal area of stems ≥2.5 cm dbh increased 7.3% while overall stem density increased by <1%. The number of stems ≥ 5 cm dbh decreased 4.8%, while stems 2.5-4.9 cm dbh increased 1.9%. The number of multiple-stemmed trees increased by only 1%.

New stems added by in-growth totaled 26% of the stems present in 1981 and accounted for 3.0 m^2/ha basal area. Annual in-growth rates were 1.4%, 149 stem/ha, or 0.16 m^2/ha basal area. In-growth was most common in the smallest size classes measured (2.5-4.0 cm) since larger trees would have been present in 1981 (Figure 2-2). Only 34% of new stems were in clumps that had existed in 1981. Most new stems were from entirely new trees, of these, 18% were multiple-stemmed. New stems came from 28 species (Figure 2-3). *Gymnanthes lucida* and *Coccoloba microstachya* accounted for the greatest influx of stems and increase in basal area, however, the two largest diameter stems added were 9-cm *Pisonia albida*.

Of the stems present in 1981, 25% died over the 18-y period, accounting for 4.3 m^2/ha of basal area. Thus the annual mortality rate was 1.4%, 144 stems/ha, or 0.24 m^2/ha. Dead stems spanned all size classes from 2.5-17 cm dbh (Figure 2-2) and included 27 of the original 34 species (Figure 2-3). Mortality was highest for *Exostema caribaeum* and *Gymnanthes lucida* when measured by number of stems or basal area. The seven largest dead stems came from *Pisonia albida, Hypelate trifoliata, Bursera simaruba*, and the cactus *Pilosocereus royenii.* Of the dead stems, 43% belonged to clumps that had living stems in 1999. The remaining dead stems were primarily single-stemmed individuals – only 7% of dead trees were multiple-stemmed. Of the species in the 1981 tally, five had neither mortality nor in-growth. These species were among the six lowest in importance in 1981 (Table 2-1).

Hurricane Georges removed 9.4% of stems below breast height and 3.3 m^2/ha basal area present in 1998 (Table 2-2). Subtracting these values from mortality data, mortality would have accounted for losses of approximately 13% of stems and 1.0 m^2/ha basal area without the hurricane. Including both mortality and in-growth there would have been an 11% increase in stem density and a 26% increase in basal area.

Among stems that carried over from 1981 to 1999, average height increased about 30 cm while average basal area increased 9.1 cm^2. Most species showed an increase in both height and basal area (Figure 2-4), despite the effects of the hurricane. The loss in basal area for *P. royenii* was primarily due to Hurricane Georges breaking off large branches that arose below breast height on trunks. Decreased basal area for the one individual of the palm *Thrinax morrisii* was probably the result of petiole loss from the trunk resulting in a narrower stem.

Community structure in terms of importance values changed little overall from 1981 to 1999, although some species' ranks changed (Table 2-3). Comparing species populations over time yielded a selection of response patterns. Some species declined, with lower frequency, density, and basal area, including *E. caribaeum, Erithalis fruticosa, P. royenii,* and *Cassine xylocarpa. Thouinia portoricensis* stem density and basal area decreased, but frequency remained the same, a result of clump thinning. Three species increased in basal area while losing stems, indicating thinning of the population but continued growth of established trees (*Pisonia albida, Antirrhea acutata* and *Krugiodendron ferreum*). Population growth was indicated by increasing population density and basal area in *Hypelate trifoliata, Pictetia aculeata,* and *Leptocereus quadricostatus. Guettarda elliptica, Coccoloba microstachya,* and *Bourreria succulenta* were increasing both population size and frequency in the site while maintaining basal area. A final group of 20 species maintained their position in the community, keeping relatively constant frequency, density, and basal area (e.g. *Gymanthes lucida, Coccoloba diversifolia, Bursera simaruba, Amyris elemifera,* and *Guettarda krugii*).

Total annual litter fall during the 2-y time period was 254 g/m^2, of which 220 g/m^2 (87%) consisted of leaves and reproductive parts. Non-hurricane leaf litter production fluctuated around the levels reported by Murphy et al. (1995) (Figure 2-5). Notable deviations were found in November 1998 when leaf litter fall was twice the 1982 rate, May 1999 when it was reduced by nearly 400%, and February 2000 when it was reduced by about 300%. Wood litter production remained >0.3 g m^{-2} day^{-1} from 1998-2000.

Soil nutrient pools in 1999 remained similar to those reported from 1981 (Table 2-4). Organic matter, available P, and available cations were higher in 1999 while Total P and N were lower, but none of these differences were statistically significant.

DISCUSSION

Forest Structure

When Murphy and Lugo (1986) first described the permanent research site in Guánica Forest, they concluded that it had reached maturity. The results of this reassessment of forest structure largely support their conclusion. In-growth equaled mortality – a pattern typical for mature forest (Swaine et al. 1987) – and nutrient pools and litter production appear to have reached a steady state. The nearly 5% decrease in larger trees can be explained by Hurricane Georges preferentially removing larger stems (Chapter Five). Hurricane disturbance appears to stimulate basal sprouting (Chapter Six), but sprouts would not have had enough time (only 2 years) to grow into the size classes measured here. Biomass and height were both increasing, despite disturbance by the hurricane, suggesting that the forest may not yet have come to steady state in terms of biomass.

A notable structural feature of Guánica Forest in 1981 was the high proportion of multiple-stemmed trees (Murphy and Lugo 1986b). This proportion was unchanged in 1999.

The survival of a tree was aided by having multiple stems, as only 7% of multistemmed trees died. The origin of this growth habit has been a subject of speculation. Dunphy et al. (2000) concluded that it was a natural occurrence for 7 of 10 common species, based on the absence of cut trunks, the presence of original, intact stems on 20% of multistemmed trees, and 23.3% of the smallest sized trees (<3.0 cm diameter at ground level) having multiple stems. Of the ten species, *Coccoloba krugi, Gymnanthes lucida,* and *Pictetia aculeata* had new multi-stemmed trees in 1999. Dunphy et al. (2000) noted that 61% and 33% of small trees of the first two species were multi-stemmed, but found no small multi-stemmed individuals for *P. aculeata.* Since 1981, 18% of the ingrown trees were multiple stemmed, further supporting the conclusion that neither cutting nor anthropogenic disturbance were needed to generate the multi-stemmed growth form. These numbers, however, fall short of explaining the overall proportion of multi-stemmed trees (43%) and the increasing proportion of multi-stemmed trees with stem size (Dunphy et al. 2000), suggesting that there is some mechanism which elicits growth of additional stems without removing the main stem. In Chapter Six I propose that development of new stems is spurred by gravitational displacement due to hurricane winds' causing sprouting – a thigmomorphogenetic response.

Guánica Forest contains 12 endemic and 14 endangered or threatened tree species (Little et al. 1974, Quevedo et al. 1990). Of these, six were found in the main site: *Pictetia aculeata, Thouinia portoricensis, Eugenia xerophytica, Reynosia guama, Linociera holdridgii,* and the cactus *Leptocereus quadricostatus. Pictetia* and *Thouinia* were common (and remained so) while only *R. guama* declined in population.

To the north of the main site, Molina Colón (1998) conducted a 5-y study on forest development 45 years after the cessation of human disturbance. The disturbances included stands which had been selectively cut and stands cleared for agriculture and housing. A mature forest stand in a north-facing valley was included for comparison. Forest structure, species composition, and soil nutrient content in the selectively cut sites had recovered to mature forest levels – unlike the cleared sites. Stem density in Molina Colón's mature forest was lower than in my site, about 7000 stems/ha, while selectively cut sites had 7800 stems/ha due to coppice growth, and the cleared sites 4000-6000 stems/ha. My site faced south and was more exposed, which led to a shorter canopy and a relative abundance of species common to drier, exposed areas (e.g. *Gymnanthes, Pictetia, Cassine, Crossopetalum*) compared to Molina Colón's north-facing stands. Basal area (19 m^2/ha) and frequency of multi-stemmed trees (43%) in Molina Colón's mature stands matched that found here (Table 2-2). Both values were lower for younger forests (8-13 m^2/ha and 23-38%, respectively). The results demonstrate that structural features and nutrient pools for mature forest are largely comparable from place to place.

Litter fall and soil nutrients

Annual litter fall in 1998-2000 was only 53% of that in 1982, but was 88% of litter fall measured in another nearby mature forest stand in 1974-76 (Lugo et al. 1978, Cintron and Lugo 1990). Leaf litter fall rates from 1998-2000 fluctuated around levels measured in the early 1980s (Lugo and Murphy 1986, Murphy et al. 1995). Some of the fluctuation, at least for 1998-99, can be explained by Hurricane Georges, which caused about 50% defoliation (see Chapter 5) on September 21-22, 1998 (Figure 2-5). Following the hurricane, trees continued to lose some damaged leaves at above-normal rates for about two months, but subsequent leaf litter fall in the dry season was lower than measured in the 1980s. Lower litter fall rates could be explained by fewer leaves in the canopy because of incomplete recovery following the hurricane, or lower inputs due to a large new flush of leaves on evergreen species, which typically remain on the trees for ≥ 1 yr before senescence (Olivares and Medina 1992, Reich et al. 1992). The low litterfall in February 2000 was probably the result of an unusually wet January (84 mm) delaying senescence. Leaf litterfall in Guánica Forest during 1998-2000 was 30% lower than the median value in other dry forests (315 g/m^2: Martinez-Yrizar 1995), but 33% higher than in 1982 (Lugo and Murphy 1986).

Constant levels of nutrient pools through time are another indication of forest maturity. Conversion of dry forest to pasture or agricultural land is frequently accomplished by clearing followed by burning (Maass 1995). In this process, a significant nutrient pulse is provided to forest soils, but these nutrients are lost rapidly due to leaching and erosion (Adedeji 1984, Maass 1995). In Mexico and India, nutrient pools in dry forest soils had not returned to original forest levels 10-15 years after clearing and burning (Maass 1995). Soil nutrient pools in cleared sites from another study in Guánica Forest were still lower than in mature sites after 60 years of succession (Molina Colón 1998). Soil chemistry reported here fell within the range of values from the same site in 1981-83 (Table 2-4). The ratio of N to P_{av} was much lower in 1999, a result of both higher P_{av} and lower N concentrations, but the 1981 value was close to that determined elsewhere in the forest (Ventana site; see Chapter Three). Although N was lower and available nutrients were higher in 1999, the differences were not statistically significant, supporting the conclusion that nutrient pools have remained stable. The slight differences measured between sampling periods may result from both methodological or environmental causes. The 1981-83 values were means from samples taken quarterly over a two-year period while 1999 was sampled in July during the short dry season, when plants and microbes would be less active and available nutrients would accumulate in the soil (Davidson et al. 1993, Srivastava 1997, Campo et al. 1998). Meanwhile, N supplies from through-fall would be lower (Campo et al. 2001). Available nutrients may also have been elevated from the nutrient pulse created by fresh, mature leaves being blown to the forest floor by Hurricane Georges in September 1998 (Lodge et al. 1994b). These leaves added relatively more phosphorus and potassium than nitrogen (Chapter 5), because retranslocation was unable to occur and N is not conserved in Guánica Forest trees (Lugo and Murphy 1986).

Guánica Forest soils generally were richer in organic matter and nutrients than soils in other dry forests (Table 2-5). Guánica Forest had the highest amounts of N and organic matter reported, as well as the most alkaline soils. Only dry forests in Belize had levels of organic matter which approached those found in Guánica Forest. The high organic matter in Guánica soils results from the forest having the highest litter turnover time reported (~3 y) for dry forests (median 1.2 y, Martinez-Yrizar 1995) despite an annual aboveground NPP of less than half that of other dry forests (Murphy and Lugo 1990). The calcareous origin of Guánica soil resulted in its high pH, however, exchangeable Ca was nearly the lowest reported. Only Ghanaian dry forests have soil N as high as the lowest values found in Guánica Forest. P_{av} levels were equal or somewhat higher than found elsewhere, with the exception of very P-rich soils in Brazil. C:N ratios were similar for all forests, but C:P and N:P ratios were higher in Guánica Forest, reflecting high C and N concentrations found there. With average amounts of phosphorus and high amounts of carbon and nitrogen in the system (Table 2-4), P supplies could limit productivity in the system as suggested by the high phosphorus use efficiency for the forest (Vitousek 1984, Lugo and Murphy 1986).

Maturity in forests with episodic disturbance

Stability or dynamic equilibrium in most of the structural and functional traits measured within the permanent research site indicated the forest had reached maturity.

Structurally, ingrowth balanced mortality and population and community structure showed little change over the 18-y period (Table 2-2). Functionally, soil nutrient pools remained constant and litter fall, while highly variable, oscillated within the range of previously reported values. Only basal area and height increased over the 18-y period, despite losses following Hurricane Georges (Table 2-2). Absent the hurricane, the forest would appear to be aggrading. However, hurricanes are a regular part of the ecosystem, occurring multiple times over the lifetime of mature trees, and thus would be expected to cause intermittent losses. Hurricane Georges followed a 70-year period free of strong hurricanes, greater than the average return interval of 43 y for Category 3 hurricanes (see Chapter 5). Potential increases in basal area and stem density would therefore be lower between more frequent hurricanes. Episodic disturbance by hurricanes may also help maintain individual occurrences of pioneer species in mature forest. Despite the similarity of characteristics from 1981 to 1999, the nature of the equilibrium in the forest was clearly dynamic, as evidenced by a 25% turnover in stems, highly variable amounts of annual litter fall, and episodic effects of hurricane winds on stem density and basal area.

Compared to mature tropical dry forests in areas less influenced by large, infrequent disturbances such as hurricanes, the structure of Guánica Forest is shorter, with less basal area and more multiple-stemmed trees. Even with this difference in appearance, Guánica Forest, as a representative of Caribbean dry forest, exhibits many functional characteristics similar to those found in other mature tropical forests (dry or wet), including: 1) annual mortality ranging from 1-2%, 2) in-growth equaling mortality, 3) slowly increasing basal area, 4) low species turnover (in Guánica Forest species were maintained by sprouting), and 5) relatively constant soil nutrient pools.

Table 2-1. Importance values (IV) of species with dbh ≥ 2.5 cm in the main site in 1981, adapted from Murphy & Lugo (1986b).[a] I.V. is the sum of relative frequency (RF), relative density (RD), and relative dominance (RBA; basal area).

Species	IV	% of Total IV	RF	RD	RBA
Gymnanthes lucida	43.58	14.53	8.09	21.69	13.80
Exostema caribeaum	25.38	8.46	8.67	7.59	9.11
Thouinia portoricensis	21.10	7.03	4.62	11.52	4.96
Pisonia albida	20.89	6.96	5.20	3.67	12.02
Pictetia aculeata	20.60	6.87	5.20	9.52	5.87
Coccoloba microstachya & *krugii*[b]	20.07	6.69	5.78	8.43	5.86
Pilosocereus royenii	11.84	3.95	2.89	0.90	8.05
Bursera simaruba	11.57	3.86	5.20	1.09	5.27
Tabebuia heterophylla	10.29	3.43	4.05	3.35	2.90
Erithalis fruticosa	10.07	3.36	3.47	3.99	2.61
Coccoloba diversifolia	9.55	3.18	4.62	1.35	3.57
Cassine xylocarpa	8.94	2.98	3.47	2.90	2.58
Hypelate trifoliata	7.78	2.59	2.89	1.35	3.54
Krugiodendron ferreum	7.53	2.51	4.05	1.35	2.13
Bourreria succulenta	7.48	2.49	4.05	1.74	1.69
Crossopetalum rhacoma	6.60	2.20	2.89	2.12	1.59
Jacquinia berterii	6.30	2.10	2.89	1.29	2.12
Antirhea acutata	6.19	2.06	1.73	2.90	1.56
Guettarda krugii	6.19	2.06	2.31	2.64	1.24
Amyris elemifera	5.63	1.88	2.89	0.97	1.77
Guettarda elliptica	4.37	1.46	1.16	2.32	0.90
Erithroxylum rotundifolium	4.26	1.42	2.31	1.03	0.92
Eugenia foetida	3.51	1.17	2.31	0.64	0.55
Forestiera segregata	3.41	1.14	1.16	1.22	1.04
Eugenia xerophytica	3.04	1.01	1.16	0.71	1.18
Leptocereus quadricostatus	2.81	0.94	1.16	0.71	0.94
Comocladia dodonaea	2.70	0.90	1.73	0.64	0.33
Linociera holdridgii	2.33	0.78	0.58	1.03	0.72
Reynosia guama	2.14	0.71	1.16	0.64	0.34
Plumeria alba	1.11	0.37	0.58	0.32	0.21
Thrinax morrisii	1.00	0.33	0.58	0.06	0.36
Zanthoxylum flavum	0.98	0.33	0.58	0.26	0.14
Rochefortia acanthophora	0.75	0.25	0.58	0.06	0.11

a. The original data were modified slightly to correct for a few misidentified trees and an addition error that had increased the IV for *G. krugii* by 4.23.

b. Most of these stems were *Coccoloba microstachya* – subtracting *C. krugii* would not change the order of importance.

Table 2-2. Comparison of structural features of Guánica Forest in 1981 and 1999 using trees with minimum dbh of 2.5 cm.

Attribute	**1981**[a]	**1999**	**1999 pre-Hurricane Georges**
Tree species richness (0.15 ha)	34	37	37
Basal Area of trees (m^2/ha)	17.8	19.1	22.4
Stem Density: Total (n/ha)	10,360[b]	10,427	11,509
2.5 – 5.0 cm dbh	8,347[b]	8,507	9,359
≥ 5.0 cm dbh	2,013[b]	1,920	2,150
Multiple stemmed trees (%)	43[b]	42	42
Average height (m)	4.2	4.5	
Mortality (stems/ha)	2,593		1,511
In-growth (stems/ha)	2,680		3,762

a. data from (Murphy and Lugo 1986b)

b. data refigured from that originally reported to match methods used in 1999.

Table 2-3. Importance values for stems ≥2.5 cm in Guánica Forest in 1999. See Table 2-1 for abbreviations.

1981 Order	1999 Order	Species	IV	% of Total IV	RF	RD	RC
1	1	*Gymnanthes lucida*	48.45	16.15	8.38	25.38	14.68
6	2	*Coccoloba microstachya*	23.38	7.79	7.26	8.57	7.55
5	3	*Pictetia aculeata*	23.38	7.79	5.59	11.19	6.60
4	4	*Pisonia albida*	21.56	7.19	5.03	2.75	13.78
3	5	*Thouinia portoricensis*	17.76	5.92	5.03	8.95	3.78
2	6	*Exostema caribeaum*	15.88	5.29	7.26	3.77	4.84
8	7	*Bursera simaruba*	10.83	3.61	5.03	1.02	4.78
15	8	*Bourreria succulenta*	9.32	3.11	5.03	2.11	2.18
11	9	*Coccoloba diversifolia*	9.21	3.07	4.47	1.34	3.39
9	10	*Tabebuia heterophylla*	8.82	2.94	3.91	2.37	2.54
13	11	*Hypelate trifoliata*	8.29	2.76	2.23	1.79	4.26
21	12	*Guettarda elliptica*	7.53	2.51	2.23	3.58	1.72
7	13	*Pilosocereus royenii*	7.30	2.43	1.68	0.64	4.99
10	14	*Erithalis fruticosa*	7.26	2.42	2.79	2.75	1.72
12	15	*Cassine xylocarpa*	7.20	2.40	2.79	2.37	2.04
26	16	*Leptocereus quadricostatus*	7.12	2.37	1.12	2.17	3.83
14	17	*Krugiodendron ferreum*	7.10	2.37	3.91	0.83	2.35
17	18	*Jacquinia berterii*	6.76	2.25	3.35	1.28	2.13
18	19	*Antirhea acutata*	6.15	2.05	1.68	2.56	1.92
19	20	*Guettarda krugii*	5.53	1.84	2.23	2.17	1.12
20	21	*Amyris elemifera*	5.48	1.83	2.79	0.96	1.73
16	22	*Crossopetalum rhacoma*	5.31	1.77	2.23	1.85	1.22
22	23	*Erithroxylum rotundifolium*	4.62	1.54	2.23	0.90	1.49
29?	24	*Coccoloba krugii*[a]	3.88	1.29	1.12	1.85	0.91
24	25	*Forestiera segregata*	3.76	1.25	1.12	1.85	0.79
25	26	*Eugenia xerophytica*	3.70	1.23	1.68	0.96	1.07
28	27	*Linociera holdridgii*	2.43	0.81	0.56	1.02	0.85
27	28	*Comocladia dodonaea*	1.95	0.65	1.12	0.58	0.26
29	29	*Reynosia guama*	1.73	0.58	1.12	0.38	0.23
30	30	*Plumeria alba*	1.64	0.55	1.12	0.32	0.21
	31	*Colubrina arborescens*	1.54	0.51	0.56	0.77	0.21
32	32	*Zanthoxylum flavum*	1.01	0.34	0.56	0.26	0.19
23	33	*Eugenia foetida*	0.93	0.31	0.56	0.26	0.12
	34	*Eugenia rhombea*	0.89	0.30	0.56	0.26	0.07
31	35	*Thrinax morrisii*	0.83	0.28	0.56	0.06	0.21
33	36	*Rochefortia acanthophora*	0.75	0.25	0.56	0.06	0.13
	37	*Reynosia uncinata*	0.71	0.24	0.56	0.06	0.09

a. originally reported with *Coccoloba microstachya* in 1981 (Table 2-1). 1981 order is estimated from 1999 data.

Table 2-4. Comparison of soil chemistry in the Main site in 1981-83 and 1999.

	1999			**1981-1983**[a]		
	mean	**SD**	**n**	**mean**	**SD**	**n**
pH	7.91	0.16	614	7.8	0.1	33
OM (%)	29.08	13.32	623	23.2	10.65	38
N (%)	0.88	0.22	623	1.13	0.41	14
P_{to} (mg/g)	0.48	0.14	622	0.57	0.06	38
P_{av} (mg/g)	0.014	0.006	622	0.0074	NR	NR
K_{av} (mg/g)	0.69	0.22	623	0.41	0.23	14
Ca_{av} (mg/g)	8.27	2.52	623	4.71	2.98	14
% P_{av}	2.9			1.3		
% K_{av}	6.9			25		
N/P_{to}	28.3	6.5		19.8[b]		
N/P_{av}	670	317		1525[b]		
Bulk density	0.60	0.25	570	0.77	NR	NR

No differences between means using t-tests at $\alpha=0.05$.

NR = Not reported.

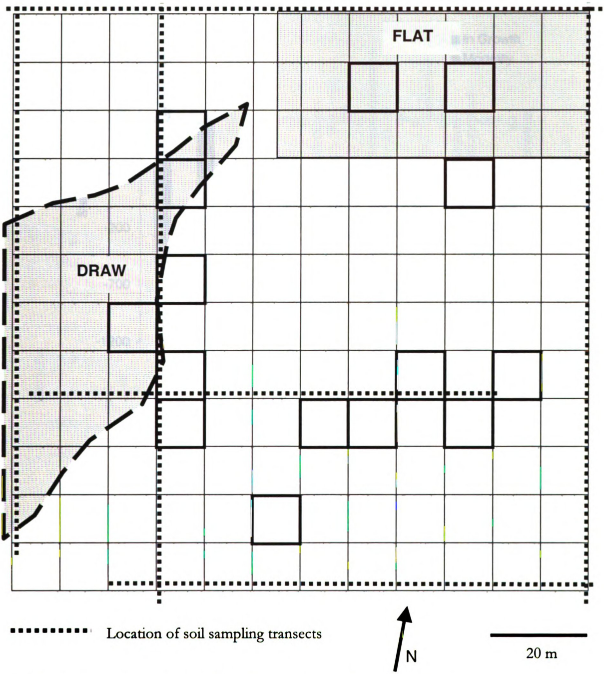
[a] Data collected from the top 5 cm of soil (Lugo and Murphy 1986).

[b] Computed from means above, not reported in Lugo and Murphy (1986).

Table 2-5. Comparison of soil nutrient content and pH from various dry forests. Ranges reported below reflect values from multiple sites in a study.

Soil Property	Guánica, Puerto Rico	Chamela, Mexico	Yucatan, Mexico	Brazil	Belize	St. Lucia	Ghana	Chandra-prabha, India	Vindhyan Hills, India	Kotwa, India
pH	7.72-8.02	6.2-6.9	6.0-7.3	5.9-6.3		6.32	6.1-6.9	6.6-7.2	6.2-6.6	
P_{to} (mg/g)	0.48-0.96	0.12-0.32	2.17						0.35-0.37	0.24-0.33
P_{av} (mg/kg)	9-14	3.21	9.21	22-73		1.23	2.0-10.1	32	8.6-10.1	
Total N (mg/g)	4.8-17.7	1.84-2.57	3.81		0.31-0.46		2.8-4.7	0.6-0.9	2.36-2.95	0.76-1.73
Ca_{av} (mg/g)	5.19-12.08	1.7		2.36-4.88			5.0-9.2			3.3-3.6 (Ca_{to})
K_{av} (mg/g)	0.49-0.70	0.16		0.22-0.26			0.11-0.19	0.10		
Carbon										
Total (%)	13.5-26.4	3.1-3.4					3.3-5.3			
Organic (%)						3.3	3.6-4.7		2.04-2.32	1.14-2.45
Organic matter (%)	16.6-48.9	2.9	35	5.4-7.2	14.1-20.2			1.6-2.1		
C:N	12.4-28.2	12-19			19.8-20.3		10.3-11.8			14.2-15.0
$C:P_{to}$	196-309	99-160								47.3-74.2
$N:P_{to}$	7.0-28.3	5.8-10.8	1.8							3.2-5.2
Reference	This study	(Garcia-Oliva et al. 2003)	Solis and Campo pers. comm.	(Oliveira-Filho et al. 1998)	(Arnason and Lambert 1982)	(Gonzalez and Zak 1996)	(Swaine et al. 1990, Baker et al. 2003)	(Singh 1989)	(Srivastava 1997)	(Roy and Singh 1994)

Figure 2-1. Map of Main site in Guánica Forest. Areas that are not designated Draw or Flat are rocky slopes.



Bolded boxes are the 15 original plots used to describe forest structure.

Figure 2-2. Mortality and in-growth of stems ≥2.5 cm in the Main site of Guánica Forest from 1981 to 1999.

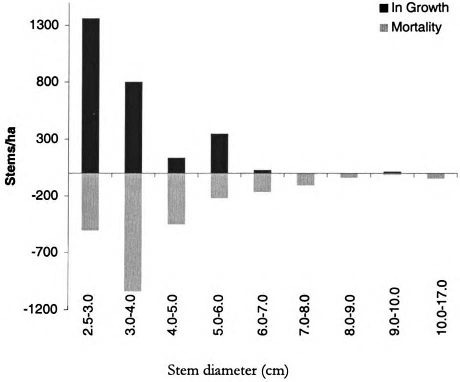


Figure 2-3. Mortality and in-growth as basal area (top) and stem density (bottom) of stems ≥2.5 cm by species in the Main site of Guánica Forest from 1981 to 1999.

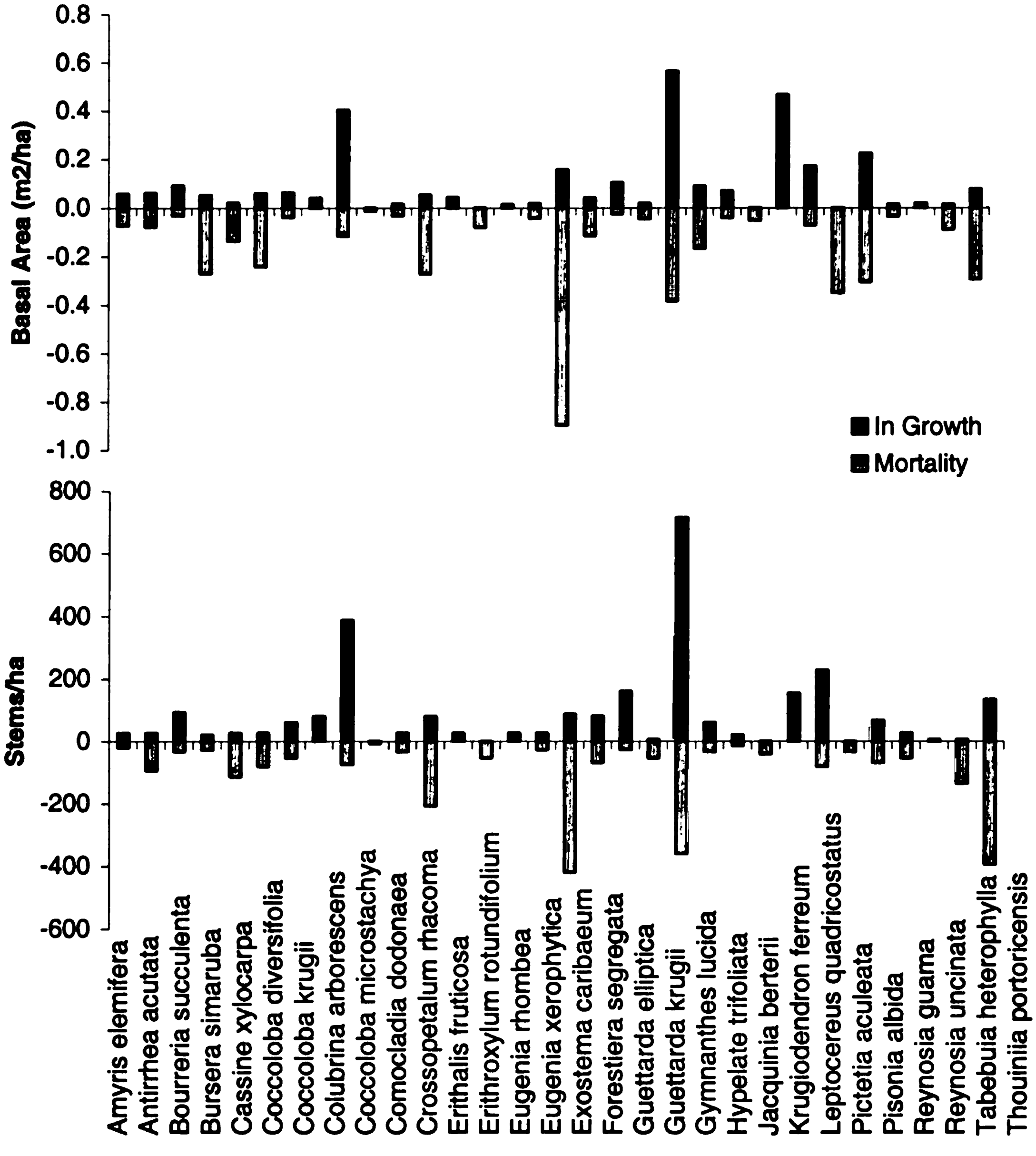


Figure 2-4. Average change in height and basal area (top) and average percent change (bottom) by species for stems ≥2.5 cm dbh that carried over from 1981 to 1999 in the Main site in Guánica Forest.

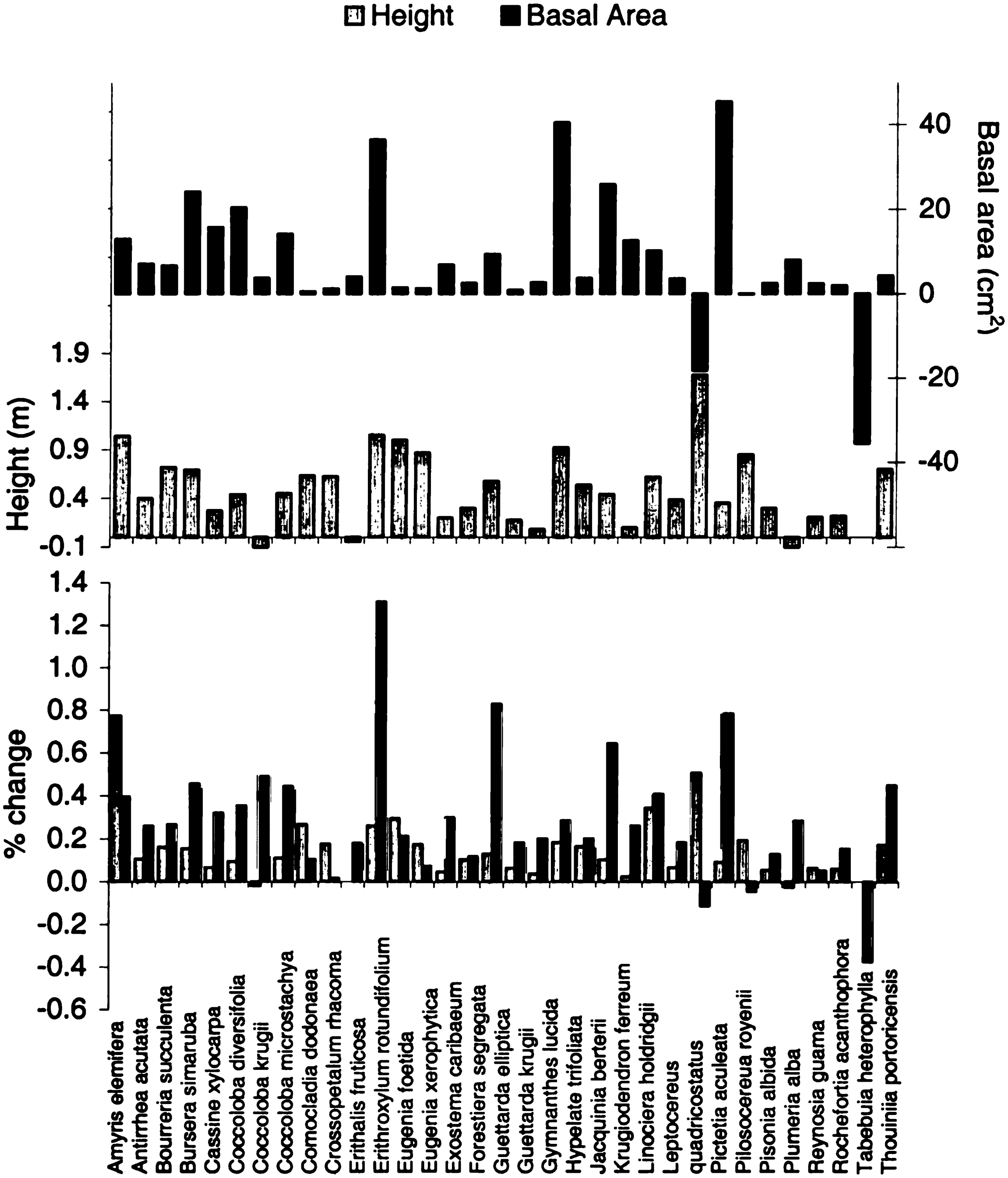
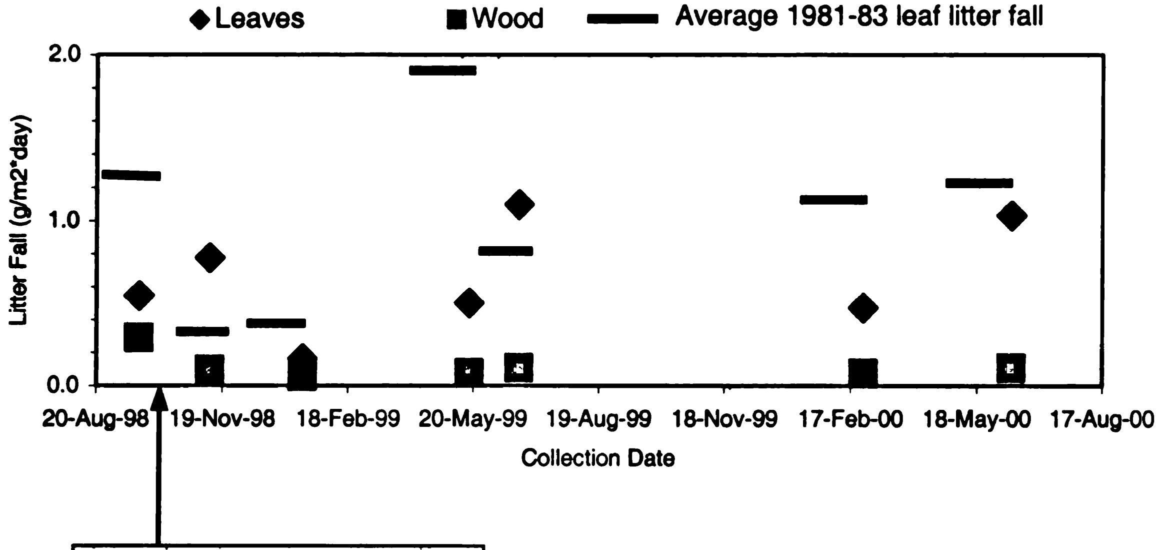


Figure 2-5. Leaf and wood litter production from thirty 0.35-m^2 litter baskets in Guánica Forest. Daily rates are from the previous collection period. Traps were placed on August 20, 1998. Black bars are average leaf-litter-fall values for the time period between collections, based on 3 years of monthly sampling from 1981-83 (Murphy et al. 1995). Hurricane Georges occurred one day after the initial sample was taken. Hurricane litter production was not included in the data for the second collection period.



Hurricane Georges:
Leaf litter fall = 239 g/m^2
Wood litter fall = 510 g/m^2

CHAPTER THREE

SPATIAL PATTERNS OF SOIL NUTRIENTS IN SUBTROPICAL DRY FOREST

Tropical dry forests hold the potential to evaluate questions about spatial patterns of soil nutrients and carbon cycling. These forests have higher alpha diversity than seasonal temperate forests (Bullock et al. 1995), providing the opportunity to evaluate tree species effects on soil nutrient pools in systems with more complex species assemblage. In the dry neotropics, litter turns over more slowly (1-3 y, Martinez-Yrizar 1995) than in other tropical forest systems or deciduous temperate forest systems (<1 y, Schlesinger 1997). The accumulation of litter on the forest floor may subsequently increase the importance of microbes, or lack of microbial activity, in determining spatial patterns of soil nutrients (Binkley and Giardina 1998, Burghouts et al. 1998).

Spatial heterogeneity of soil resources can be influenced by plant growth (Day et al. 2003a, Day et al. 2003b), the strength and outcome of competition among plant species (Reynolds et al. 1997, Fransen et al. 2001, Hodge 2003, Hutchings et al. 2003) and plant-microbe interactions (Kinzig and Harte 1998, Ettema and Wardle 2002). Plants can strongly affect nutrient content of underlying soil by nutrient uptake and nutrient return through litter fall (Binkley and Giardina 1998). One trait common to plants growing in low-nutrient environments is the retranslocation of the majority of a limiting nutrient from senescing leaves, resulting in low-nutrient leaf litter (Boerner 1984, Vitousek 1984, Schlesinger 1997). This creates a positive feedback where soil nutrients decrease as plants take up more nutrients from the soil than they return via litterfall. Conversely, plants that retranslocate fewer nutrients produce higher quality litter that can lead to comparatively nutrient-rich soil patches (Schlesinger 1997). Plant-soil feedback can result in heterogeneous soil nutrient pools with rich or poor patches roughly equal to the size of mature plants. Plant or plant-population-sized patches of soil nutrients have been measured in desert (Schlesinger et al. 1996), grassland (Gallardo et al. 2000), old-field (Robertson et al. 1988), temperate forest (Boettcher and Kalisz 1990, Gross et al. 1995) and tropical forest locations (Døckersmith et al. 1999). However, larger scale processes can also influence nutrient patch size. For example, spatial heterogeneity has been shown to differ among forest stands within a successional sequence (Gross et al. 1995) or with different disturbance histories (Hirobe et al. 2003).

Spatial patterns of soil and litter nutrients interact with the activity and diversity of soil microbial communities. Microbes decompose litter at lower rates as C:N ratios increase, resulting in slow turnover of soil carbon and immobilization of soil nutrients. Spatial patterns of microbial activity can therefore be influenced by the amount and quality of litter produced by different tree species (Saetre 1999, Saetre and Baath 2000). Spatial patterns of decomposition depend on particle size and distribution. Uniform distributions of same-quality litter tend to decompose faster than patchy distributions and decomposition progresses more quickly in smaller particles than larger ones because there is greater soil-particle contact (Sorensen et al. 1996, Henriksen and Breland 2002). Smaller particles can result in greater immobilization of nutrients as microbes are able to take advantage of larger surface-area-to-volume ratios (Sorensen et al. 1996, Corbeels et al. 2003). However, decomposition rates depend on initial litter quality and the amount of nitrogen available in the soil for microbial uptake (Angers and Recous 1997). The diversity of microbial communities decreases in low-carbon environments due to competition, but sites with high organic matter maintain uniform microbial distributions and high diversity in space, possibly because competition is reduced in an environment with a high diversity of carbon resources (Zhou et al. 2002).

Parent material also influences patterns of nutrient availability. Soils developing from limestone substrates will have higher pH and cation exchange capacity than those from igneous substrates, which produce very acid soils in the tropics. Rainfall interacts with parent material to increase weathering and leaching of nutrients. Tropical soils beneath dry forests tend to be more fertile than those for wet forests when developed from similar parent material, due to lower rates of leaching and lower decomposition rates. While the high calcium content of calcareous soils maintains favorable cation exchange for plant growth, it can decrease phosphorus availability by forming calcium phosphates at $pH > 7.6$ (Aber and Melillo 1991).

The amount of soil heterogeneity and correspondence of soil nutrient pools to plant size has been assessed using geostatistics (Robertson 1987, Goovaerts 1998). Spatial heterogeneity can be evaluated by the amount of variability that can be explained by spatial autocorrelation, known as spatial structure. Patch size can be inferred from the range, or distance, over which spatial autocorrelation exists. While most geostatistical studies focus on a single plot or single plots within a series of treatments, this study uses four sites separated by distances of at least 2 km in an effort to evaluate spatial heterogeneity not only within a site, but among sites.

The primary objective of this research is to describe spatial patterns of soil nutrients and pH within and among four sites in Puerto Rican dry forest. Within this objective, special attention will be given to: 1) the association between soil Ca and available P, 2) the potential for trees to determine spatial patterns of soil nutrients, and 3) the effects of local topography on soil nutrient pools. Within these objectives, the following hypotheses were considered:

i. Available phosphorus will be inversely related to calcium and pH. Soils in Guánica Forest are calcareous in origin and have average pH > 7.6 (Lugo and Murphy 1986). Under these conditions, P is bound into calcium orthophosphates and becomes unavailable for plant use.

ii. If individual trees have a strong effect on soil nutrient pools, then the range of spatial autocorrelation will be similar to crown diameter. In temperate and tropical wet forests, litter fall and tree productivity have been shown to have a greater influence on spatial patterns of soil nutrients than did microbial activity, at least on scales > 1 m (Burghouts et al. 1998). If similar patterns hold for dry forests, then spatial autocorrelation should decline at distances of 3-5 m.

iii. Soil organic matter, total N, and available P content will be lower in draws than on slopes and ridges. The combined effects of deeper soils and greater soil moisture would decrease soil carbon and nutrient levels due to greater leaching, decomposition by microbes, and nutrient uptake by plants. Low soil nutrient pools in draws may occur despite higher litter biomass or depth. Studies of topographic effects on soil nutrient pools in other dry forests have generated conflicting results on this question. Raghubanshi (1992) measured lower organic matter and nutrients on "hillbases" in Indian dry forests. In Mexico, organic matter and total N content were lower in lowlands than adjacent uplands, but there were no differences identified in N concentration (Jaramillo et al. 2003). Finally, in another Indian dry forest, troughs were found to have higher organic matter and nutrient concentrations than flats (Roy and Singh 1994). In this last case, low drainage from troughs appeared to have concentrated leaf litter and nutrients.

METHODS

Site description

This study was conducted in Guánica Forest which is located in subtropical dry forest in SW Puerto Rico on calcareous soils with limestone parent material. The soils are classified as mollisols and have organic soil over clay extending to 70 cm depth. The topography is hilly with rocky outcrops. Sampling occurred in a 1.4-ha Main site and in three smaller satellite sites (Lluberas, Ventana, and Honda) located 1-5 km from the Main site. Elevation of the sites ranged from 25-147 m above sea level (Figure 3-1). See the Appendix for complete site descriptions.

The 1.4-ha Main site has been the subject of scientific study for over 20 years, beginning in 1981 by Peter Murphy and Ariel Lugo (Murphy and Lugo 1986b). The northeastern portion of the site is flat with shallow litter layers and few outcrops. The northwestern, center, and southern portions of the site are sloping and rocky with deep (>10 cm) litter layers. Frequently, soil was only found at the surface in crevices between rocks and plants would root in loosely consolidated humus layers. The western side of the site consists of a shallow draw which drains the northeast corner and most of the western half of the site (Figure 3-1). Surface rocks are absent in the draw and the litter layer varies in thickness, presumably accumulating in the bottom from transport from the sides and direct deposition from trees overhead. The site had previously been used (before 1930) for non-commercial charcoal production, where pits of 3-5 m diameter were dug, filled with wood cut from nearby, lit on fire, and covered with soil. The surfaces of the pits are now flat. At least three pits were located in the flat, northeastern portion of the site and one in the draw. There was no evidence of charcoal pits in sloped areas.

The Lluberas site is located in the original portion of the Commonwealth Forest, set aside in 1919. The western third of the site follows the side of a very shallow draw located further to the west (Figure 3-1) and has few outcrops. The eastern two-thirds of the site were rocky with little surface soil. There were no signs of human use since 1930.

The Ventana site straddles a valley which runs from NW to SE. The soil surface is rocky, resulting in rooting in the lower layers of litter. Of all the sites, Ventana is the most open, having about 60% of the stem density found elsewhere. There have been no signs of human use since 1930, but before 1920 there had been extensive ranching to the west of this site and in the 1600s there was a Spanish outpost about 1.5 km west (M. Canals, personal communication), so it is likely that the site has incurred some human disturbance in the past.

The Honda site is located just up the slope from a valley bottom. Outcrops are absent. Mahogany (*Swietenia mahagani*) had been planted in the area in the 1930s. The mahogany was abandoned after planting and the area allowed to regrow without intervention. Most of the mahogany trees were dead when the soil was sampled in March 2000.

Soil collection

Soil samples were collected for three objectives: 1) to determine spatial autocorrelation among soil characteristics, 2) to map patterns of soil nutrients and pH across the landscape, and 3) to relate nutrient content to growth of specific trees (Chapter 4). Sampling locations were therefore established to optimize these objectives and differed between the satellite sites and the Main site. To obtain an initial estimate of spatial autocorrelation of soil properties, pH and soil moisture were determined from samples collected at 1-m intervals along a 100-m transect on the west side of the Main site two days after a soaking rainfall in June 1998. In July 1999, soil samples were collected around the base of each of 475 trees that had been measured for 2-20 years previously for growth and phenology. These trees were located 1-10 m from 6 transects which criss-cross the 1.44-ha site (Figure 3-2A). For most locations, samples consisted of three bulked subsamples collected in roughly equiangular locations 1 m from the trunk (Figure 3-2B). To improve spatial analysis at short distances, some subsamples were analyzed separately instead of bulked. Twenty additional samples were added at approximately 10 m intervals in areas between transects to improve mapping. In total, there were 623 soil samples.

At the satellite sites, soils were collected to assess spatial distribution of nutrient pools. The amount and placement of samples were determined in advance using GS+ 5.0 (Robertson 1998) to ensure sufficient comparison pairs for geostatistical analyses. At the Ventana and Lluberas satellite sites, 76 soil samples were collected from within a 30 x 30 m block. Of these, 25 samples were uniformly spaced in a 7.5 m grid (Figure 3-2C). The remainder were placed in a stratified random design, dividing the block into four quarters. The Honda site was established by Martin Quigley (Quigley and Platt 2003) and measured 25 x 25 m, therefore only requiring 69 samples (25 in a 5 m grid, 44 random).

At each sampling point, the top 10 cm of soil (a volume of ~200 cm^3) was collected using a hammer corer or bulb planter. In approximately 10% of samples, where the rocky soil or outcrops prevented collection to 10 cm depth, shallower depths or alternate sites were used within 50 cm of the target location. As a coarse estimate of litter mass and productivity, litter depth was measured to the nearest 0.5 cm at each soil sampling point except at Ventana. Fresh soil samples were placed in clean cloth bags, kneaded to break up clumps, and air dried at 40°C. (Cloth bags facilitate air drying and kneading without tearing.) Dry soils were sieved with a #18 mesh for lab analysis. All sample locations were recorded using a 12-channel Trimble Pro GPS system. The GPS data were differentially corrected using the US State Plane 1927 coordinate system, PR&VI 5201 coordinate zone, and NAD 1927 (Puerto Rico) datum. Horizontal positions were precise to within 1 m (Table 3-1) and elevation to 2 m. Sampling occurred in June 1999 for Lluberas and in March 2000 for Ventana and Honda.

Laboratory analysis

Total soil nitrogen was analyzed on 100-mg soil subsamples using dry combustion in a LECO CNS analyzer with a thermal conductivity detector. Soil samples were combusted at 1450°C. Organic matter (OM) was measured as loss on ignition by combusting samples in a muffle furnace at 490°C. At this temperature, loss on ignition does not include clay-bound water and therefore estimates OM well (Nelson and Sommers 1996). Organic C was estimated as 50% of OM. Total concentrations of calcium and total phosphorus (TP) were determined by digesting 100-mg subsamples in nitric acid followed by hydrogen peroxide. Using 5-g subsamples, available phosphorus (P_{av}) was extracted using a modified Olsen solution (Wilde et al. 1979). Digested total and available element concentrations were determined using an atomic-emission spectrometer. Measurement accuracy was maintained for each analysis by verifying standards after every twenty samples and running duplicates of every tenth sample.

Statistical analysis

Differences in soil characteristics among sites were assessed using ANOVA with Tukey tests for multiple comparisons. Trends in nutrient contents were compared using multiple correlation with Bonferroni adjustments for p values. Strong correlation between factors was indicated by $|r| > 0.8$, moderate correlation by $0.8 > |r| > 0.5$, and weak correlation by $0.5 > |r| > 0.3$. Significance levels were set at $\alpha=0.05$. Parametric analyses were completed using SYSTAT 8. The amount of variability of soil properties within sites was evaluated using coefficients of variability (CV).

Patchiness of soil properties was determined by analysis of spatical autocorrelation using semivariance. Semivariance models are developed by determining the amount of dissimilarity of measured values (e.g. nutrient content) for each pair of data points sampled within a given range of distances (lag interval). At greater distances, the similarity between sampling points decreases and semivariance increases. Semivariance analysis provides four statistics that are useful in describing spatial autocorrelation of a given property (Figure 3-3A). The range (*a*) estimates the maximum distance between two samples that exhibits spatial autocorrelation. Range therefore can estimate patch size for a soil property. Structure (*C*) is the variance in a property (i.e., a soil nutrient) that can be explained by spatial autocorrelation. Nugget variance (*Co*) is the variance that cannot be explained by spatial autocorrelation. The sill (*C* + *Co*) is the amount of semivariance at its asymptote, which is reached at the range. Theoretically, the nugget should be zero, but measurement error or processes which occur at scales finer than the smallest sampling interval result in nugget variance. When structure accounts for a large proportion of sample variance (PSV), spatial autocorrelation of the measured property is high. Theoretically, the sill equals the population variance (s^2) of the sample. If the sill is lower than population variance, spatial structure exists at a distance greater than that modeled. Sometimes this is the result of larger scale processes (e.g. land use or topography) influencing patterns at distances greater than the maximum interval sampled. These influences can lead to nested structure (Figure 3-3B).

Semivariance models were subsequently used to interpolate (krig) surface maps of each soil characteristic. All geostatistical procedures were performed using GS+ 5.3a software (Robertson 1998). A minimum of 30 pairs of data points were present in each lag interval in order to assure valid estimates of semivariance. When necessary, raw values were transformed prior to analysis because geostatistical methods require normally distributed data. Data were back-transformed after kriging.

At all sites, the closest spacing of samples was 1 m, while the maximum spacing varied from 35-168 m (Table 3-1). I used a minimum lag interval of 2 m for the main site, corresponding to the measurement error of the GPS data, even though sufficient pairs existed for comparison at 1 m intervals. Wider intervals were used in the satellite sites to satisfy minimum pair requirements. The maximum separation distance with sufficient pairs was 32 m for Ventana and Lluberas, 27 m for Honda, and 150 m for the Main site. Analyses at the main site were also performed using a maximum separation distance of 32 m for comparison to the satellite sites. At the main site, some soil nutrients exhibited different levels of autocorrelation depending on spatial scale. In these cases, nested models were fit by analyzing spatial structure at varying lag distances.

RESULTS

Most soil properties differed among sites, indicating high variability across the landscape (Table 3-2), including: pH (range 7.7-8.0), N (0.48-1.77%), Ca (53-260 mg/g), and N:P_{av} (400-1490). Average TP differed among three sites (range 0.48-0.96 mg/g). The proportion of TP that was in available forms ranged from 1.3-2.9%. On the other hand, three soil properties showed few differences among sites. Three sites shared similar values of P_{av} (13-14 mg/kg) and N:TP (18-20). C:N was the same for Main and Honda (17-18) but differed from Lluberas and Ventana (14).

Within sites, CVs for soil nutrient content and ratios were usually greatest at the Main site, ranging from 29-61%, and lowest at Honda (9-38%). Ca and N were among the more variable soil properties within each site (range of CVs for Ca: 40-73% excluding Honda; and N: 21-53%) while pH, C:N, and TP varied little within sites (range of CV: 2-3%, 11-28%, 15-29%, respectively). Litter depth showed high variability among and within sites (averages: 3.5-9.3 cm; CV 32-54%).

At the satellite sites spatial autocorrelation of soil nutrient content existed to a range of 17-25 m (Table 3-3) with two exceptions at Lluberas, where TP was structured to only 7 m and P_{av} to 28 m. In addition, the limit of spatial structure was greater than the maximum lag interval (27 m) for Ca at Honda, as indicated by a linear model. Despite these exceptions, the similarity among ranges across nutrients and sites is noteworthy. Spatial structure described at least 74% of sample variability, indicating strong autocorrelation for all nutrient contents at each satellite site except for P_{av} at Lluberas (PSV 56%). Ranges of spatial autocorrelation for nutrient ratios, pH, and litter depth were either <16 m or >25 m (Table 3-4). Limits to spatial autocorrelation were greater than maximum lag intervals for N:TP at Ventana and litter depth at Honda and Lluberas. Spatial structure described 53-100% of variability in nutrient ratios, litter depth, and pH at the satellite sites.

Ranges of spatial structure when analyzed over short distances at the Main site were similar to those found at the satellite sites, with few exceptions (Tables 3-4). When measured over short distances (32 m), pH, OM, N, P_{av}, and TP were spatially autocorrelated to a range of 18-21 m. Spatial autocorrelation was indicated at ranges greater than 32 m for Ca, greater than the ranges found for other soil nutrients or for Ca at the satellite sites. PSV was only 66% for TP at Main, nearly 20% lower than at the next lowest site. Spatial structure accounted for 77-100% of variability for all other soil nutrients and pH. Nutrient ratios also showed a high degree of spatial structure (71-85%) with ranges from 10 to 27 m. Litter depth and soil moisture were autocorrelated to a range of about 30 m but with only 50-58% of variability explained by structure.

In the Main site, all soil parameters with the exception of Ca exhibited nested spatial structure when analyzed over 100 m (Figure 3-4) with a second level of structure developing at 45-82 m (Table 3-3). Ca was structured to a range of 73 m, without nesting. Litter depth was also nested, with the largest range of spatial structure at 112 m. The nested pattern of nutrients is illustrated by the soil nutrient maps at the Main site (Figure 3-5). Within the areas of higher N or OM (the second darkest color band), for example, exist smaller patches containing the highest N or OM contents, indicating smaller-scale variability. Larger scale trends are shown by higher N or OM near the center and east of the site grading to lower contents in the north and west sides.

Soil N was strongly correlated with organic matter ($r>0.8$) at all sites, but relationships between other combinations of soil properties were less consistent (Table 3-5). Total and available forms of P showed no forest-wide patterns of association. P_{av} increased with TP only at the Main and Ventana sites ($r = 0.43, 0.67$). At the main site Ca was negatively correlated with the other nutrients, while TP and P_{av} increased with OM and N ($r = 0.60\text{-}0.72$). Ca content increased with pH at Main and Ventana. No consistent patterns of association existed among combinations of nutrients aside from OM and N at the satellite sites. N and OM decreased with pH, but correlations were moderate to weak ($r < 0.6$). Association between soil nutrients and litter depth were only apparent at the Main site. Elevation had no effect on phosphorus or Ca, but weak positive correlations were present for N and OM in two satellite sites ($r < 0.4$). Soil nutrient contents decreased as C:N increased. N:P ratios were positively correlated with OM and N. N:P_{av} decreased as P availability increased in soils.

Strong correlation between nutrients was evident by their similar spatial distributions. At the Main site, high levels of OM, N, P_{av}, and N:TP were found on the slope forming the east side of the draw and on the east side of the site, while low levels were found in the draw and on the north side (Figure 3-5). These soil properties had the opposite pattern of Ca, reflecting their negative correlations with Ca. With the exception of C:N, N:P_{av}, and litter depth, soil characteristics appeared to track the draw on the west side. Locations of high N, OM, and P_{av} also correspond to areas where rock outcrops were common as organic matter was trapped in crevices.

At Lluberas, the general lack of correlation between soil properties was evident in the dissimilarity among their spatial distributions (Figure 3-6). However, the strong correlation between N, OM, and N:TP was reflected by all three properties having high values in a patch in the NE quarter of the site, with decreasing values to the south and west. This patch corresponds with the highest elevation at the site and the area with the most open canopy. Properties with low range of structure (e.g., litter depth and TP) were illustrated by the presence of many small patches and patches of high levels located near low level patches (note high TP patches on west side of site within 10 m of low TP in the NE).

Soil nutrient contents at the Ventana site were greatest in the NE corner, which had the highest elevation (Figure 3-7). Nutrient-poor areas were found in the NW and SE corners. C:N ratios were highest in the area with both low OM and N. The similarity in nutrient distributions reflected both the positive correlations and the consistent range structure among all nutrients.

High OM, N, and TP were present in the north-central portion of the Honda site (Figure 3-8). Low values of these nutrients were found at or near the lowest elevation of the site, but high values were also found at intermediate elevations. The small range of spatial autocorrelation (5 m; Table 3-4) indicated by the patchiness of pH contrasted with the 18-19 m ranges for OM, N, and P_{av} and the linear trends of Ca and litter depth across the site.

DISCUSSION

Among-site patterns of soil nutrients

Soil nutrient pools varied significantly across the landscape, even though each site had similar soil types and forest cover. The advantage of using multiple plots is that the repeatability of patterns across the landscape can be assessed. For example, total soil nutrient pools and pH differed among sites, while P_{av} remained constant. Some properties maintained patch size from site to site (e.g., OM and N), while patch size varied among sites for others (e.g. pH or C:N). In some locations, combinations of soil properties were correlated while the same patterns were absent elsewhere (e.g. contrasts for soil nutrients in Ventana and Lluberas, Table 3-5). The high degree of variability among sites separated by only a few kilometers indicates that extra care must be taken when interpreting results from single plot studies. Using plots of different sizes also help to address issues of scale and identify patterns that would otherwise be overlooked in smaller plots.

Despite the high variability of soil nutrients from site to site, some trends emerged. Soil OM and N were always closely correlated in space and content. In addition, N generally increased with TP and with decreasing pH. Thus, although each site varied from the other in fertility, soil factors that contribute to fertility tended to vary in tandem within sites. The association between OM, N, and TP may be the result of higher productivity. At the Main site, litter depth increased at higher concentrations of TP, P_{av}, OM, and N and distributions of OM, N, and P_{av} were also similar spatially. Considering previous indications that the forest may be P-limited (e.g., PUE, high leaf and soil N:P ratios; Lugo and Murphy 1986), one might expect P pools to be strongly correlated to OM and N pools, as higher P supplies would result in greater productivity. However, the strength of correlation between P and OM or N was always less than between OM and N alone. The weaker relationships between P and OM than between OM and N probably result from two factors. First, trees in Guánica Forest retranslocate a greater proportion of P than N from senescing leaves (Lugo and Murphy 1986), so litter P would not be as closely tied to litter mass than litter N. Second, while higher levels of soil P may alleviate some nutrient limitation, these P-rich locations may not be in areas with favorable soil moisture. In addition, average C:N ratios for each site were below 20 (Table 3-2), suggesting that N was in sufficient supply for microbial activity and unlikely to be immobilized (Paul and Clark 1996). As such, N would be free to cycle through the system with OM. To adequately evaluate whether plant uptake or microbial activity has the greatest effect on soil nutrient pools, nutrient flux measurements would need to be performed.

Of note are the high concentrations of OM found in Guánica Forest that tend to be greater than those found in other dry forest locations (Chapter 2). High OM may minimize microbial competition for carbon, thereby maintaining high diversity and size of microbial populations (Zhou et al. 2002). Large, diverse communities may be more able to maintain functionality during periods of stress and more efficiently cycle nutrients.

Patterns of calcium, pH, and available phosphorus

As expected based on previous studies (Lugo and Murphy 1986), levels of Ca and pH were high at all sites in Guánica Forest while the percentage and quantity of P_{av} was low. However, in contrast to expectations, there were no consistent spatial patterns or correlative trends supporting direct control of P_{av} by Ca or pH. Nor were there consistent patterns between TP and P_{av}. For example, at Ventana, Ca was strongly positively correlated with P_{av}, while at Main there was a weak negative correlation. Spatial patterns of P_{av} and pH differed at all sites, as did P_{av} from Ca and TP (except at Ventana). While it is apparent that much of the TP was bound to Ca in the soil based on low $\%P_{av}$, the difference in spatial patterns of P_{av} from TP, Ca, and pH would be influenced by a variety factors. Geologic sources of P_{av} include weathering of P-rich minerals and dissolution of clay- or calcium-bound phosphates by carbonic or organic acids. Mycorrhizae and other fungi release organic P for plant uptake (Allen 1991) and plants can acidify the rhizosphere to increase P availability (Aber and Melillo 1991). Once available, P, as the potentially limiting nutrient in the system, would be rapidly taken up by plants as long as sufficient water was present to transport P through the soil. Thus, multiple sources and sinks of P_{av} control its unique distribution across the landscape and its lack of consistent association with other nutrients from site to site.

Local spatial patterns of soil nutrients

Patch sizes of soil nutrients (as inferred from the range of spatial autocorrelation) measured 17-25 m, with few exceptions. Soil nutrient patches were at least threefold greater in size than average crown diameter, contradicting the hypothesis that nutrient patch size would equal tree crown diameter. Therefore there is no evidence of the tight tree-soil nutrient feedbacks that have resulted in crown-sized patches of soil nutrient content noted in other forested systems (Boettcher and Kalisz 1990, Gross et al. 1995, Døckersmith et al. 1999, Gallardo et al. 2000). In addition to being small in diameter, tree crowns and root systems in Guánica Forest intermingle and leaf area index is low (~3, Murphy et al. 1995). Tree species diversity is high and analysis of leaves in litter traps (personal observation) shows that constant trade winds are able to transport leaves away from directly beneath their trees. Therefore leaf litter is well mixed on the forest floor and the ability of single trees to control patterns of soil nutrients is diminished.

At the Main site, nested spatial distribution of soil nutrients reflected multiple influences operating at different scales (Figure 3-4). Larger scale trends were only measurable at the Main site because more samples were taken over greater distances. The northeast and a section of the west side of the site were used for charcoal production until 70 years ago. The southeast quarter of the site has numerous rock outcrops. It is probable that both land use and topography have influenced soil properties in Guánica Forest at scales >25 m, leading to nested spatial structure. Spatial patterns at scales < 25 m were probably driven by the effects of litter on soil nutrients as mediated by plant production and uptake, microbial decomposition, and transport by wind and water.

The large patch size of soil nutrient pools has several implications for carbon and nutrient cycling. A well-mixed forest floor and large patches of nutrient pools may lower the potential for hotspots of cycling to occur (Hutchings et al. 2003). Conversely, if hotspots did develop, they could be larger than found in other forest systems, at least when water is plentiful. At a centimeter scale, the mixing of leaf litter on the forest floor will bring substrates of different qualities closer together, potentially increasing decomposition compared to systems where nutrient patches are more discrete. More homogenous collections of leaf litter or nutrient pools tend to result in faster decomposition and nutrient turnover (Sorensen et al. 1996, Henriksen and Breland 2002). On the landscape level, the intermingling of more nutrient-rich leaves with nutrient-poor leaves on the forest floor may partially counteract the potential for dry forests to sequester carbon. However, the overriding control of decomposition in these systems is water availability which has been interpreted to result in long turnover times for leaf litter (Lugo and Murphy 1986, Martinez-Yrizar 1995). The effects of water on nutrient cycling in dry forests is a question that remains to be addressed, particularly as rainfall is highly variable within rainy seasons.

Effects of topography

Large scale (i.e., 50 m) differences in elevation in Guánica Forest did not appear to be related to soil properties (Table 3-2). While the highest site, Lluberas, had the greatest amounts of OM, N, and TP, the second highest amounts of these nutrients were found at the lowest elevation site, Ventana. This finding contrasts with results from Mexican dry forests, where less OM was consistently found in sites at lower elevations (Jaramillo et al. 2003) due to loss by erosion and soil turnover.

In each of the four Guánica Forest sites, but particularly evident in the Main site, microtopography affected soil properties. Higher concentrations of soil OM and N were found at locally higher elevations. These locations were frequently covered by limestone outcrops which trapped litter in crevices, retained less rainfall, and dried quickly, resulting in slower decomposition and greater litter build up. OM accumulated in the crevices between outcrops, increasing N and C concentrations, creating a thick humus layer, and resulting in root development above the mineral soil, which was observed during sample collection. Conversely, organic matter in areas with deeper soil and less outcropping (such as Honda and the draw in the Main site) could decompose faster as a consequence of greater contact with mineral soil (as opposed to rocks) and higher soil moisture. Honda had the lowest average values of soil OM and N (Table 3-2), despite being the most productive site, suggesting that decomposition rates are relatively fast. Ca was highest in deeper soils as a consequence of being a major constituent of the mineral soil – as opposed to areas with deeper humus between outcrops of limestone.

In an Indian dry forest, higher OM at higher elevations was associated with microtopography, where small depressions in the terrain caught litter (Raghubanshi 1992), similar to patterns found at the Main site. At another Indian forest, small troughs concentrated litter, resulting in more OM and nutrients (Roy and Singh 1994). The patterns in Indian dry forests complement the pattern found in Guánica Forest – where microtopography is able to concentrate or trap litter, soil OM and nutrients increase, regardless of elevation.

Spatial structure in Guánica Forest compared to other forests

Spatial patterns of soil properties have been analyzed with geostatistics in two other tropical dry forests. On volcanic soils in St. Lucia, Gonzalez and Zak (1994) analyzed a 56 x 56 m plot with 4-m spacing between samples. They found spatial structure for pH, P_{av}, and organic C at distances of 58 m, 48 m, and 71 m, respectively, indicating that spatial structure was not related to crown diameter. Forest floor biomass and soil texture were structured to ranges of 20-24 m. Their patterns for P_{av} and organic C appeared nested, with the first plateau occurring at about 24 m. Overall, the range of spatial structure on St. Lucia corresponded well to Guánica Forest (Tables 3-3, 3-4), especially when comparing the nested values for P_{av} and organic C. Conversely, the spatial structure explained less variation in St. Lucia where PSVs (pH=58%, P_{av}=45%, organic C=26%, forest floor biomass=29%) were either at or below the lowest PSV for any site in Guánica Forest. The 4-m sampling interval used in St. Lucia would have missed a notable amount of spatial structure, as demonstrated for Guánica soils (Tables 3-3, 3-4, Figure 3-4). In a Thai dry forest (Hirobe et al. 2003), the range of soil moisture and inorganic forms of nitrogen decreased from ≥ 9.0 m to 1-3 m as forests recovered from fire. The smallest ranges were for forests fire-free for 35 y, but model fits were low ($r^2 < 0.5$). The small scale at which this study was conducted (9 m) makes it difficult to compare to patterns at Guánica Forest but does suggest that individual trees may affect N mineralization and denitrification as the forest recovers from fire.

In other ecosystems, Gross et al. (1995) found spatial structure in soil moisture to ≥ 16 m in a mature temperate forest in Michigan and at ranges of 4-6 m (PSV 50-80%) in a soy bean field and an old field. In these same sites, the range of soil N was greatest in the old field (15.6 m; PSV 63%) and less in the soy bean field (2.5 m; PSV 33%) and forest (8.4 m; PSV 35%). Compared to these locations, spatial patterns are stronger and exist over longer distances in Guánica Forest. In an agricultural field in Michigan, soil moisture, pH, C:N, organic C, and inorganic P exhibited spatial structure from 45-63 m (Robertson et al. 1997). Spatial variability explained most of the sample variability (PSV 76-93%) and a nested model was computed for pH. Nesting was attributed to plant-soil interactions, soil development, topography, and land use history as spatial scales increased. These results were very similar to patterns found in the Main site at Guánica Forest, except that the smallest range of nesting at ~20 m was absent, probably due to the homogenizing effects of cultivation.

CONCLUSIONS

Analysis of spatial patterns of soil properties in Guánica Forest reveals a landscape with high variability among and within sites, but relatively large patch sizes when compared to other forest types. Soil nutrient contents varied as much among sites as within sites. Throughout the forest, levels of Ca, OM, and pH were high, and P_{av} was low. C:N ratios were <20, suggesting that microbial immobilization of N was unlikely. OM and N were greater in locations where microtopography tended to collect litter. Clear associations between P_{av} and pH or Ca were absent, despite the potential for Ca to bind P at high pH, suggesting that the distribution of P_{av} was controlled by both physical and biological activity, rather than by soil chemistry alone. Patch sizes for most soil properties measured 17-25 m with another level of spatial structure at 45-112 m. Pools of OM and N were strongly correlated in space and size and, to a lesser degree, with P. The range of spatial structure for most soil properties in Guánica Forest was comparable to dry forests in St. Lucia, but greater than in other forest types where ranges tended to track average crown diameter. Crown-sized patches of soil nutrients in Guánica Forest were absent – likely the result of the forest's thin canopy and high stem density, which would intermingle crowns and roots and diminish the localized influence of individual trees on soil nutrient pools. Thus, the diversity of trees above ground was not translated below ground, because crown diameter did not correspond to soil nutrient patch size.

Although this research identifies clear trends in patch sizes of soil nutrient pools, further research will be necessary to identify mechanisms that determine patch size. One issue to be resolved would be whether patch sizes of soil nutrients are controlled more by microbial decomposition of litter or the possibility of P limitation of plant productivity indirectly influencing litter biomass. Some studies have suggested that plants will have a greater influence on soil nutrient content via litterfall than microbes will by decomposition (Burghouts et al. 1998). However, both productivity and decomposition appear to be resource limited, possibly by P and certainly by water. A more direct method to measure resource limitation of productivity would be to compare growth rates against soil nutrient content. This is undertaken in Chapter Four. The information presented here on patch size and spatial distribution of nutrient pools across the landscape should be a useful guide in developing future projects to measure nutrient fluxes in relation to decomposition or P limitation of plant productivity.

Table 3-1. Sampling points, lag classes, and intervals used for geostatistical analysis of soil data. Horizontal precision is the measurement error for XY locations measured by the GPS unit.

Site	**Main**	**Lluberas**	**Ventana**	**Honda**
Sample points	623	76	76	69
Horizontal precision (m)	0.90	0.98	0.84	1.06
Uniform lag interval (m)	2	4	4	3
Maximum interval (m)	32 or 100	32	32	27
Pairs, 1st interval	1207	101	106	63
Pairs, 2nd interval	1496	336	310	219

Table 3-2. Means of elevation (m above sea level) and soil properties of four sites in Guánica Forest. Means across sites were different unless indicated with the same letter. ND: Not determined

	Main			**Lluberas**			**Ventana**			**Honda**		
	mean	SD	CV	**mean**	SD	CV	**mean**	SD	CV	**mean**	SD	CV
Elevation[1] (m.a.s.l.)	**129**	5	4	**147**	2	1	**25**	2	8	**100**	3	3
[range] (m)	**[20]**			**[9]**			**[14]**			**[14]**		
pH	**7.91**	0.16	2	**7.72**	0.23	3	**7.84**	0.22	3	**8.02**	0.12	2
OM (%)	**29.1**	13.3	45	**48.9**	12.8	26	**38.9**	11.3	29	**16.6**	2.5	15
N (%)	**0.88**	0.22	53	**1.77**	0.48	27	**1.41**	0.55	39	**0.48**	0.10	21
Ca (mg/g)	**181**	88	50	**88**	34	40	**53**	39	73	**260**	24	9
TP (mg/g)	**0.48**	0.14	29	**0.96**	0.14	15	**0.70a**	0.17	24	**0.69a**	0.12	17
P_{av} (mg/kg)	**14a**	6	43	**14a**	4	26	**9**	4	39	**13a**	3	38
% P_{av}	**2.9**			**1.5**			**1.3**			**1.9**		
C/N	**17a**	5	28	**14b**	2	12	**14b**	2	12	**18a**	2	11
N/TP	**18a**	11	61	**19a**	5	30	**20a**	6	28	**7**	1	15
N/P_{av}	**688**	317	46	**1330**	390	29	**1493**	432	28	**402**	82	21
Litter depth (cm)	**9.3**	4.8	50	**5.0a**	1.6	32	ND			**3.5a**	1.9	54
Soil moisture (%)	**10.9**	2.5		ND			ND			ND		

Table 3-3. Parameters for variogram models of soil nutrient concentrations. PSV is the proportion of structural variance (*C*/(*C*+*Co*)) where *C* is structure and *Co* is nugget variance.

Site	Max lag	Model	Effective Range (m)	r^2	PSV %
Organic Matter					
Honda	27	spherical	18.9	0.92	83
Lluberas	32	spherical	24.0	0.97	74
Ventana	32	spherical	18.6	0.90	97
Main	32	spherical	21.4	0.95	100
Main	100	spherical	55.5	0.69	94
Nitrogen					
Honda	27	spherical	19.3	0.94	82
Lluberas	32	spherical	25.0	0.96	82
Ventana	32	spherical	19.6	0.94	100
Main	32	spherical	19.1	0.94	100
Main	100	spherical	69.2	0.75	88
Available P					
Honda	27	spherical	17.8	0.88	78
Lluberas	32	spherical	27.7	0.91	56
Ventana	32	spherical	17.4	0.68	98
Main	32	spherical	18.7	0.85	77
Main	100	spherical	62.2	0.72	67
Total P					
Honda	27	spherical	22.9	0.95	100
Lluberas	32	exponential	7.0	0.63	85
Ventana	32	spherical	20.5	0.97	93
Main	32	spherical	20.7	0.77	66
Main	100	spherical	45.2	0.59	83
Total Ca					
Honda	27	linear	*	0.91	
Lluberas	32	spherical	17.8	0.96	74
Ventana	32	spherical	18.8	0.78	100
Main	32	linear	*	0.97	
Main	100	spherical	72.6	0.96	91

* greater than maximum lag interval

Table 3-4. Parameters for variogram models for litter depth, pH, elevation, and nutrient ratios. PSV is the proportion of structural variance (*C*/(*C*+*Co*)).

Site	Max lag	Model	Effective Range (m)	r^2	PSV %
C:N					
Honda	27	exponential	11.8	0.80	82
Lluberas	32	exponential	28.7	0.97	51
Ventana	32	spherical	15.1	0.88	95
Main	32	spherical	10.3	0.79	85
Main	100	spherical	81.5	0.80	57
N:TP					
Honda	27	exponential	15.7	0.78	54
Lluberas	32	exponential	15.2	0.93	88
Ventana	32	linear	*	0.96	
Main	32	spherical	17.3	0.80	65
Main	100	spherical	61.7	0.89	70
N:P$_{av}$					
Honda	27	spherical	8.5	0.82	84
Lluberas	32	exponential	48.5	0.92	53
Ventana	32	spherical	14.6	0.83	59
Main	32	spherical	19.5	0.96	72
Main	100	spherical	54.7	0.70	77
Litter Depth					
Honda	27	linear	*	0.91	
Lluberas	32	exponential	4.4	0.43	96
Main	32	exponential	30.1	0.85	58
Main	100	linear	*	0.83	87
pH					
Honda	27	spherical	5.0	0.31	100
Lluberas	32	spherical	15.1	0.75	80
Ventana	32	spherical	21.6	0.59	58
Main	32	spherical	18.1	0.90	78
Main	100	spherical	64.6	0.75	68
Soil Moisture					
Main	32[1]	spherical	28.8	0.95	50

* greater than maximum lag interval

[1] Estimated from a 100 m transect 2 d after a soaking rain.

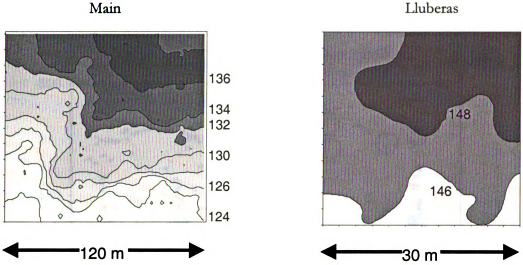
Table 3-5. Pearson correlation coefficients among soil nutrients and between soil nutrient concentrations and elevation, litter depth, and acidity at the Main and satellite sites in Guánica Forest. Elevation was not correlated with either pH or litter depth at any site. Litter depth and pH were weakly correlated at the Main site ($r = -0.35$, $p < 0.0005$).

	N	OM	Ca	TP	C:N	N:TP	N:P_{av}	Elevation	pH	Litter Depth
Main										
N					-0.53	0.52	0.58	ns	-0.58	0.57
OM	0.97				-0.34	0.52	0.55	ns	-0.60	0.56
Ca	-0.62	-0.68			ns	-0.35	-0.46	<	0.48	-0.38
TP	0.72	0.67	-0.45		-0.48	ns	0.44	ns	-0.44	0.43
P_{av}	0.60	0.60	-0.31	0.43	-0.36	0.36	<	ns	<	0.48
Lluberas										
N					ns	0.87	0.61	0.40	-0.46	ns
OM	0.97				ns	0.88	0.60	0.38	-0.44	ns
Ca	ns	ns			ns	ns	-0.49	ns	ns	ns
TP	ns	ns	ns		ns	ns	ns	ns	ns	ns
P_{av}	ns	ns	0.41	ns	ns	ns	-0.55	ns	ns	ns
Ventana										
N					-0.81	0.77	ns	0.37	ns	ND
OM	0.98				-0.71	0.79	ns	0.38	ns	ND
Ca	0.60	0.60			-0.48	ns	ns	ns	0.57	ND
TP	0.64	0.60	0.70		-0.70	ns	ns	ns	0.40	ND
P_{av}	0.70	0.71	0.81	0.67	-0.60	0.39	-0.51	ns	0.50	ND
Honda										
N					-0.69	0.57	ns	ns	-0.48	ns
OM	0.87				ns	0.49	ns	ns	-0.40	ns
Ca	ns	ns			ns	-0.47	ns	ns	ns	ns
TP	0.67	0.59	ns		-0.47	ns	ns	0.38	ns	ns
P_{av}	0.37	ns	ns	ns	ns	ns	-0.68	ns	-0.37	ns

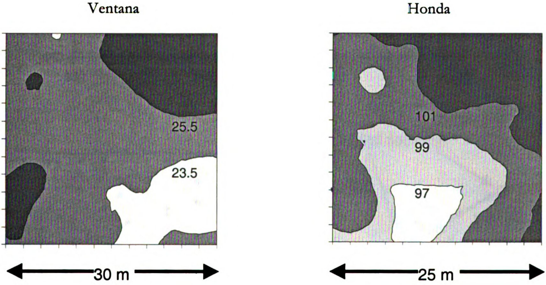
ns = non-significant at α=0.05, < indicates significant but small correlation ($r < 0.3$)

ND: Litter depth not measured at Ventana.

Figure 3-1. Elevation maps of experimental sites in Guánica Forest, Puerto Rico. Contour bands are at 2 m intervals.


Main

Lluberas


Ventana

Honda

Figure 3-2. Soil sampling and mapping locations in Guánica Forest: (A) Main site, (B) at the base of trees in the Main site and (C) general scheme for satellite sites using Lluberas as an example. The higher density of soil samples along six transects in the main site reflect locations of trees measured for growth and phenology for the last 4-20 years.

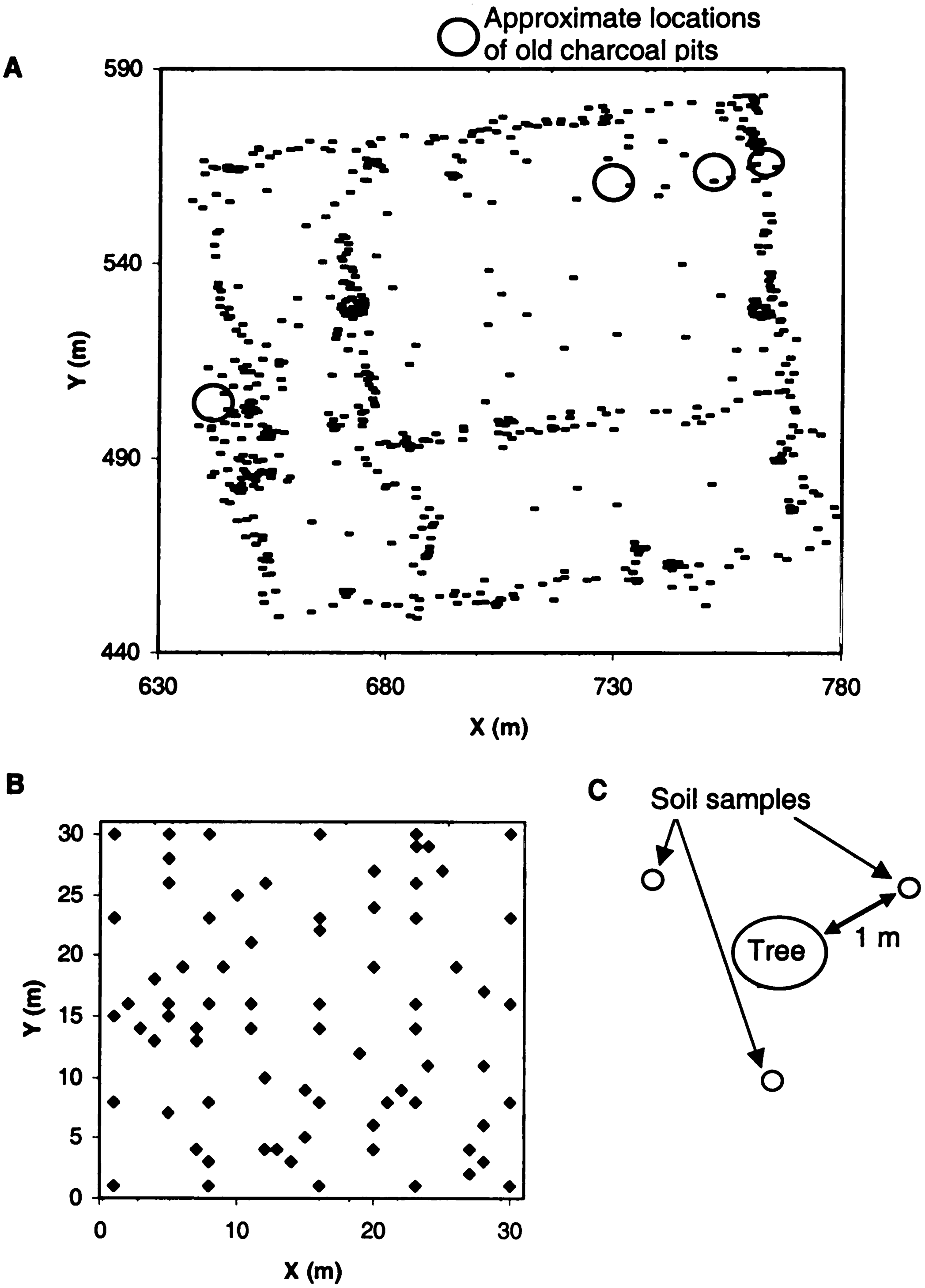


Figure 3-3. A) A generalized semivariogram, showing nugget variance. The sill is the total amount of variability within the sample. Structure is the amount of variability explained by spatial autocorrelation. Random variability, sampling or measurement error, and variability attributable to spatial scales smaller than the smallest lag interval make up nugget variance. The range is the distance where the values measured at two points are completely independent – the distance where spatial structure ceases. When no spatial structure is present, the nugget equals the sill. As the distance between sampling points increases, structure decreases. B) Nested structure in spatial autocorrelation caused by three hypothetical influences operating at different spatial scales.

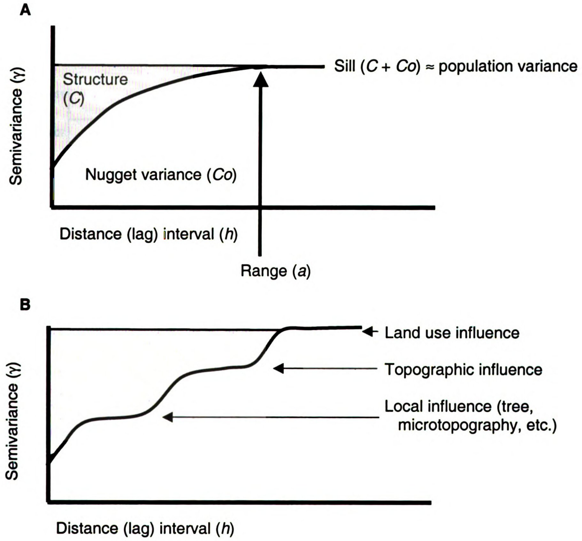


Figure 3-4. Variograms for soil nutrient concentrations at the Main site. Dotted lines are sample variance (s^2). Parameters for each model are listed in Table 3. Left panel in each case is at 150 m interval, right panel is 32 m interval.

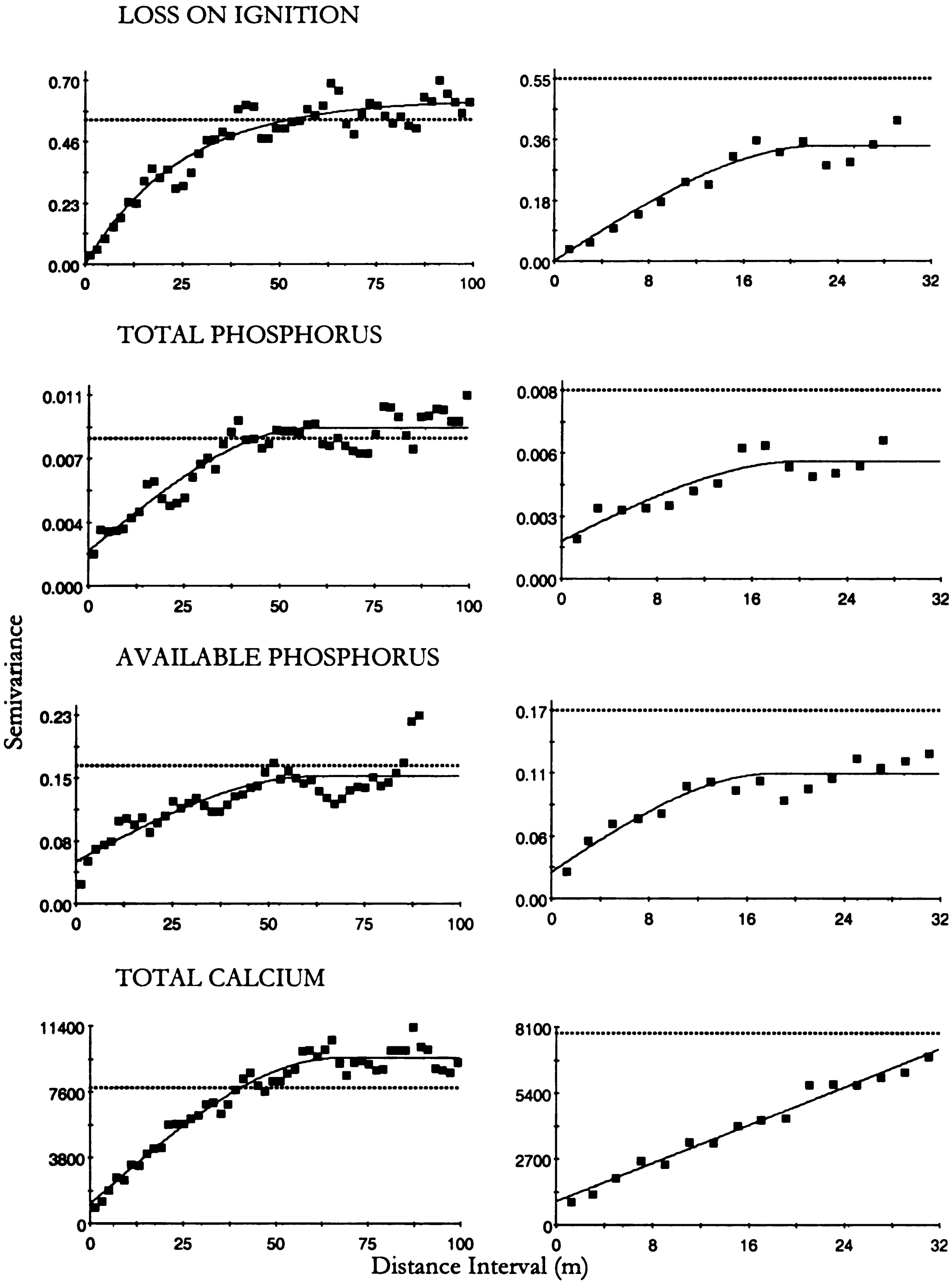


Figure 3-4. Continued

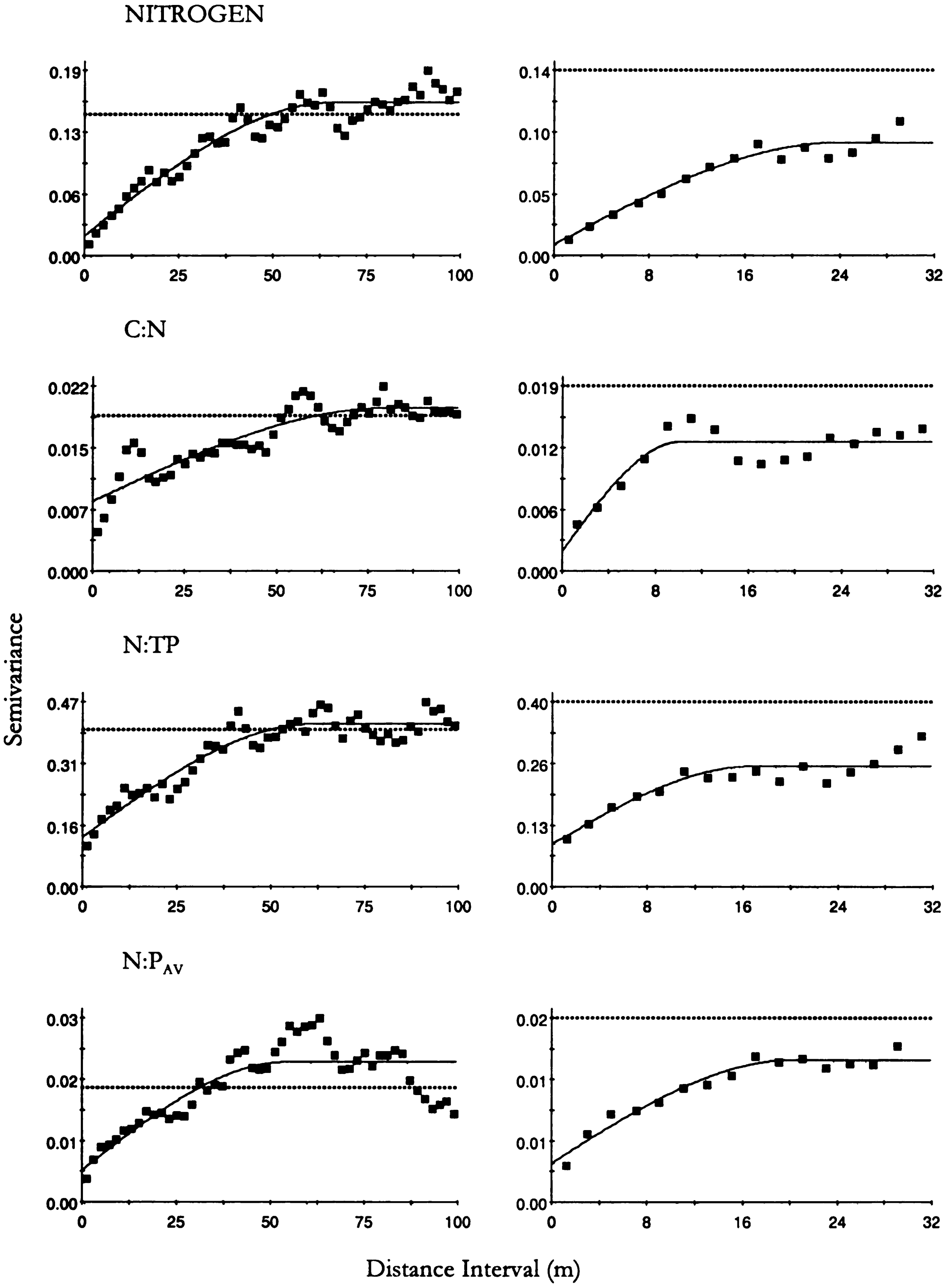


Figure 3-4. Continued

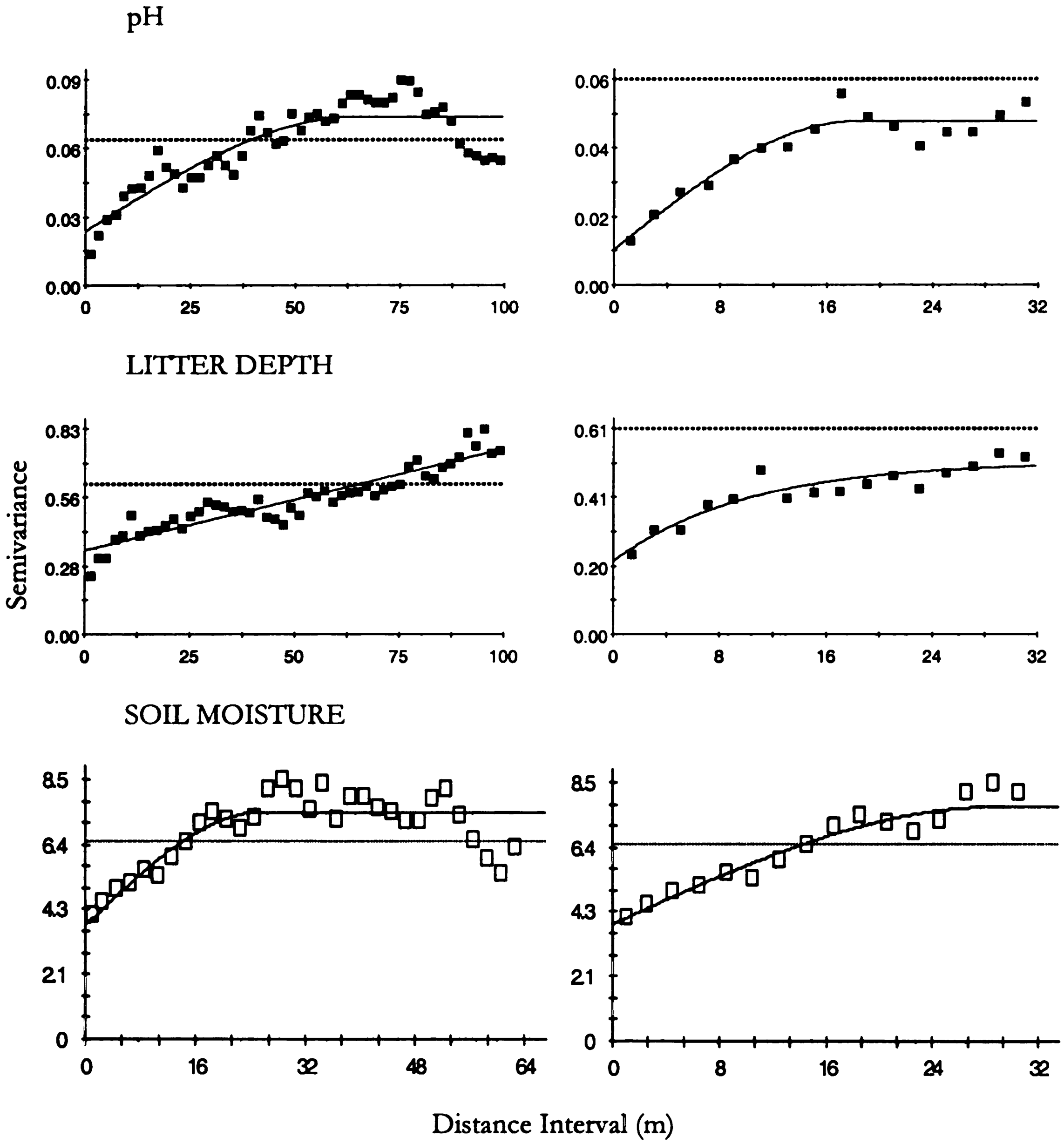
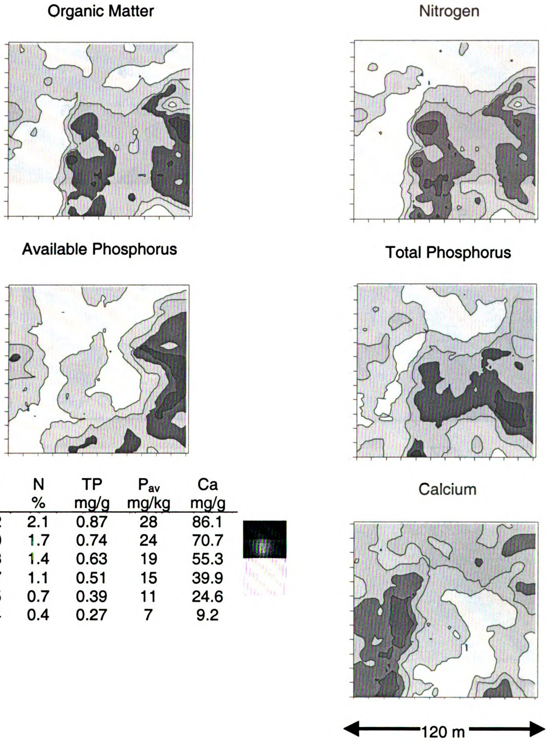
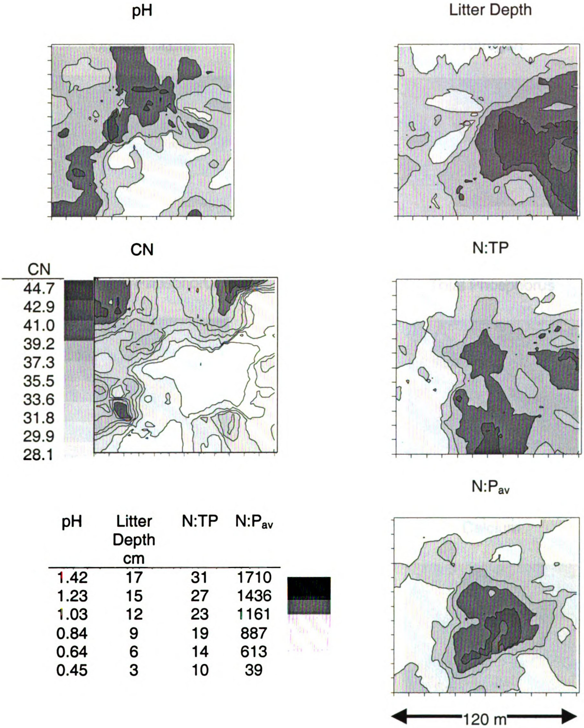


Figure 3-5. Isopleths of soil chemical properties at the Main site derived by 2x2 m block kriging. The site measures 120 m on each side. Table with legend gives levels for each color band.



OM %	N %	TP mg/g	P_{av} mg/kg	Ca mg/g
63.2	2.1	0.87	28	86.1
53.0	1.7	0.74	24	70.7
42.8	1.4	0.63	19	55.3
32.7	1.1	0.51	15	39.9
22.5	0.7	0.39	11	24.6
12.4	0.4	0.27	7	9.2

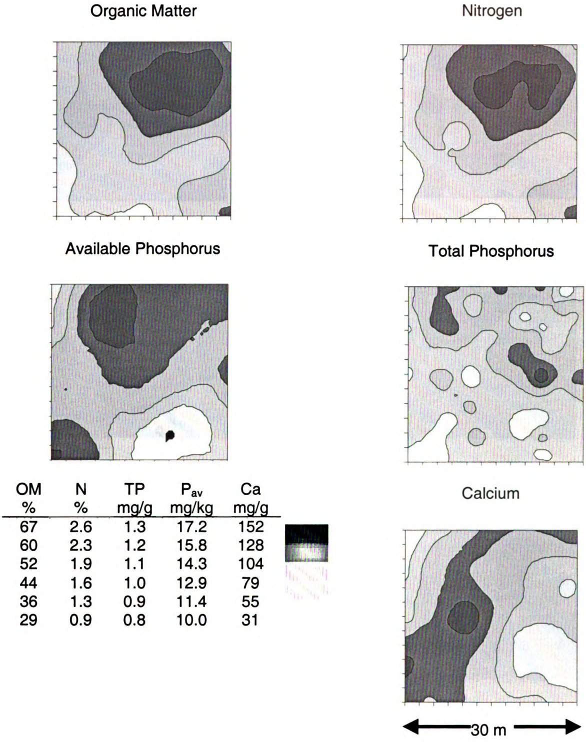
Figure 3-5. continued



CN
44.7
42.9
41.0
39.2
37.3
35.5
33.6
31.8
29.9
28.1

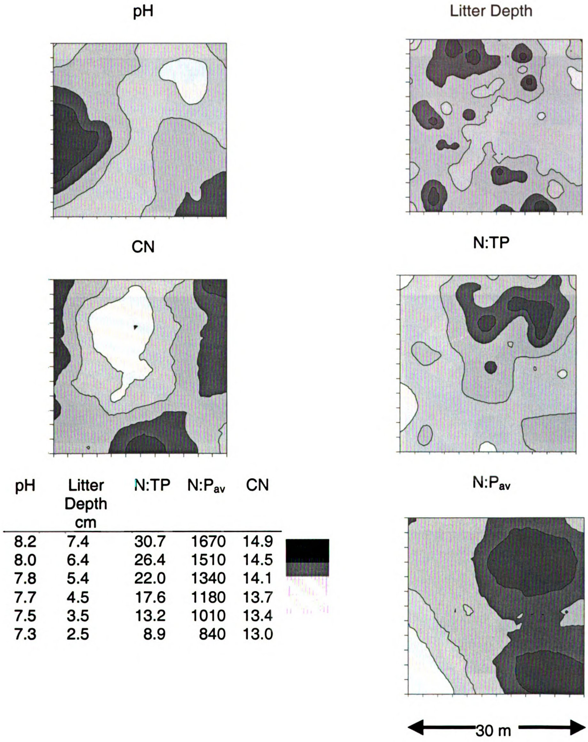
pH	Litter Depth cm	N:TP	N:P_{av}
1.42	17	31	1710
1.23	15	27	1436
1.03	12	23	1161
0.84	9	19	887
0.64	6	14	613
0.45	3	10	39

Figure 3-6. Isopleths of soil chemical properties at the Lluberas site derived by 2x2 m block kriging. The site measures 30 m on each side. Table with legend gives levels for each color band.



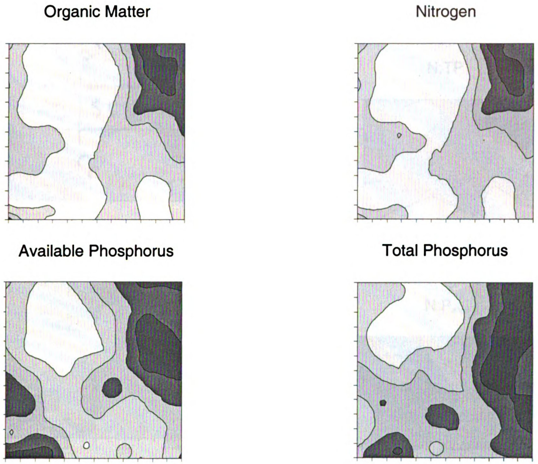
OM %	N %	TP mg/g	P_{av} mg/kg	Ca mg/g
67	2.6	1.3	17.2	152
60	2.3	1.2	15.8	128
52	1.9	1.1	14.3	104
44	1.6	1.0	12.9	79
36	1.3	0.9	11.4	55
29	0.9	0.8	10.0	31

Figure 3-6 continued



pH	Litter Depth cm	N:TP	$N:P_{av}$	CN
8.2	7.4	30.7	1670	14.9
8.0	6.4	26.4	1510	14.5
7.8	5.4	22.0	1340	14.1
7.7	4.5	17.6	1180	13.7
7.5	3.5	13.2	1010	13.4
7.3	2.5	8.9	840	13.0

Figure 3-7. Isopleths of soil chemical properties at the Ventana site derived by 2x2 m block kriging. The site measures 30 m on each side. Table with legend gives levels for each color band.


Organic Matter

Nitrogen

Available Phosphorus

Total Phosphorus

OM %	N %	TP mg/g	P_{av} mg/g	Ca mg/g
67	2.9	0.98	15.9	153
59	2.4	0.87	13.5	125
51	2.0	0.76	11.2	96
42	1.6	0.65	8.8	68
34	1.2	0.54	6.4	39
26	0.8	0.44	4.0	11

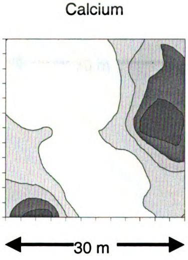
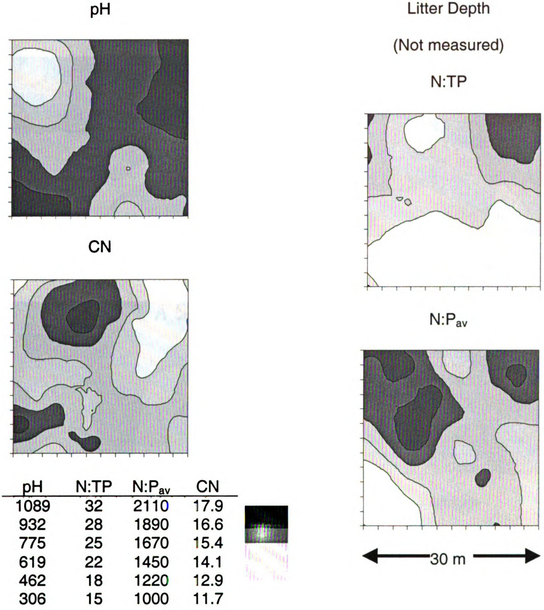
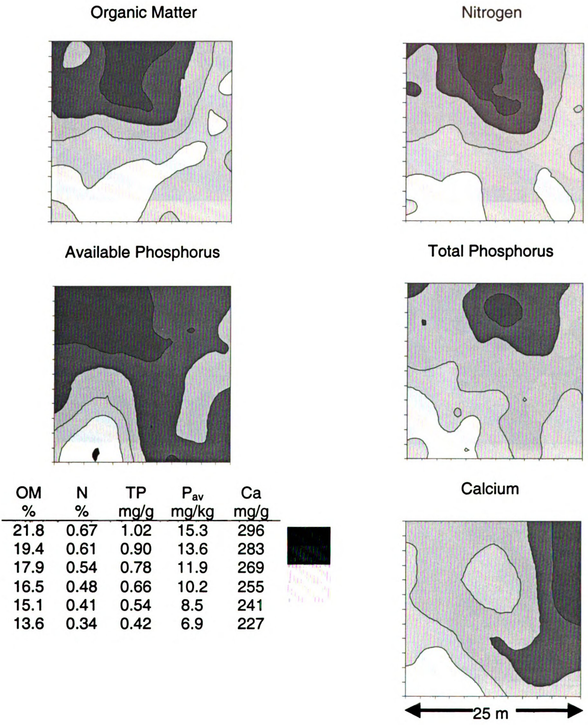

Calcium

Figure 3-7 continued



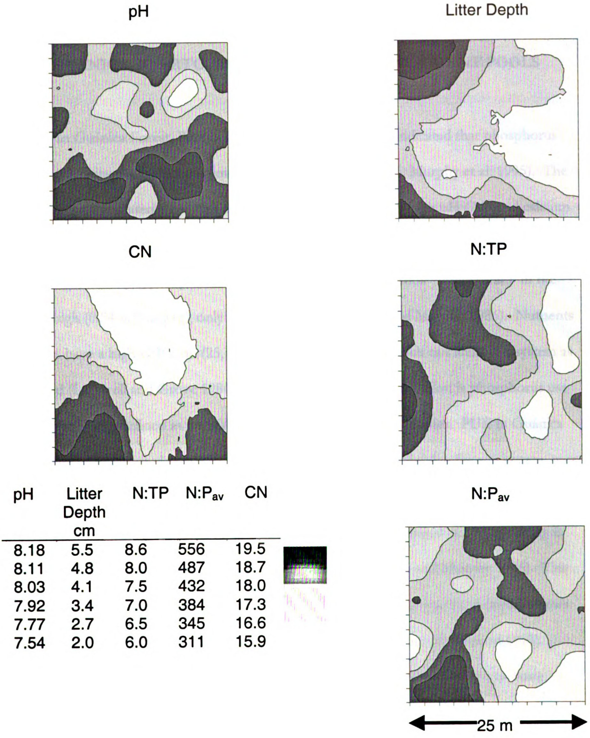
pH	N:TP	N:P_{av}	CN
1089	32	2110	17.9
932	28	1890	16.6
775	25	1670	15.4
619	22	1450	14.1
462	18	1220	12.9
306	15	1000	11.7

Figure 3-8. Isopleths of soil chemical properties at the Honda site derived by 2x2 m block kriging. The site measures 25 m on each side. Table with legend gives levels for each color band.



OM %	N %	TP mg/g	P_{av} mg/kg	Ca mg/g
21.8	0.67	1.02	15.3	296
19.4	0.61	0.90	13.6	283
17.9	0.54	0.78	11.9	269
16.5	0.48	0.66	10.2	255
15.1	0.41	0.54	8.5	241
13.6	0.34	0.42	6.9	227

Figure 3-8 continued



pH	Litter Depth cm	N:TP	N:P_{av}	CN
8.18	5.5	8.6	556	19.5
8.11	4.8	8.0	487	18.7
8.03	4.1	7.5	432	18.0
7.92	3.4	7.0	384	17.3
7.77	2.7	6.5	345	16.6
7.54	2.0	6.0	311	15.9

CHAPTER FOUR

TREE GROWTH PATTERNS IN THE SUBTROPICAL DRY FOREST OF GUÁNICA, PUERTO RICO: INFLUENCE OF NUTRIENT POOLS

In Guánica Forest, Puerto Rico, previous studies have indicated that phosphorus may be a limiting factor to tree growth (Lugo and Murphy 1986, Murphy et al. 1995). The limestone parent material beneath the forest produces soils with high pH (7.8) and calcium content (52 - 260 mg/g). Phosphorus and calcium bind together to form insoluble calcium phosphates, removing phosphorus from the available nutrient pool. While total P in the soils is high (0.54-0.57 mg/g), only 1.3% is extractable (Lugo and Murphy 1986). Nutrients in leaves have a high N:P ratio (25, Lugo and Murphy 1986), which can identify a system as P limited (Lathwell and Grove 1986). Another indicator of P-limitation is phosphorus use efficiency (PUE), defined as litterfall mass divided by P content in litter. PUE in Guánica Forest has been reported at 6057g/g, among the highest reported value for any system, most of which range from 800 to 4000 (Vitousek 1984). Nitrogen use efficiency was only 98, a median value. Retranslocation of P before leaf fall has been estimated at 65% resulting in only 0.71 kg P/ha returned to the forest floor in leaf litter (Lugo and Murphy 1986). This amount is lower than any value reported for mature forests of any type in multiple reviews on the topic (Vitousek 1984, Vitousek and Sanford 1986, Jaramillo and Sanford 1995).

In spite of the evidence suggesting P-limitation, Guánica Forest soils also have attributes that could result in limitation by nitrogen. The soils are classified as mollisols, which tend to support large microbial communities due to high carbon content (18-23%). Total nitrogen in Guánica Forest averages 1.0-1.1% (Lugo and Murphy 1986). Microbes generally out-compete plants for nitrogen, at least in the short term (Hodge et al. 2000). Despite having high total nitrogen in the soils, a large proportion of the N could be sequestered in the microbial community, rendering it unavailable for plants.

Nutrient limitation in forests is typically addressed by using indirect indicators (e.g., leaf N:P ratios or nutrient use efficiency). Some lack of attention to the topic in dry forests can be explained by the fact that water is the factor most obviously limiting forest growth. However, most dry forests have a season when water is not limiting and soils are saturated to field capacity. During these times, other factors including nutrients could become limiting to forest growth as trees experience multiple resource limitations (Chapin 1980, Chapin et al. 1986). In addition, deciduous tree species may be dormant in the dry season, requiring little or no nutrient inputs. The goal of this study is to assess nutrient limitation in Guánica Forest using multiple techniques – including root in-growth cores and evaluation of correlations between tree growth and soil nutrient content.

Nutrient cycling studies have demonstrated positive feedbacks between trees and soils. Strong feedback suggests that soil nutrient pools should be correlated with tree growth. Low-nutrient environments are maintained by trees with slow growth, high retranslocation of nutrients, and low litter quality, while the opposite is true for more fertile sites (Hobbie 1992). Cuevas and Lugo (1998) documented this pattern in moist forests of Puerto Rico. Correlative studies have implicated nutrients as controls for the distribution of tropical plant communities. For example, Australian rain forest species were shown to be more tolerant of aridity than low soil P (Beadle 1966). Wet areas with low fertility were dominated by sclerophyllous and xeromorphic species more typically found in drier, nutrient-poor zones. Also in Australia, Adam (1989) found greater species diversity at lower P concentrations in soils. Within wet forest, Gunatilleke (1997) found that different species of *Shorea* grew differently across gradients of N, P, and Mg. Species which grew the most when given extra nutrients tended to be found in more fertile locations in the field, while species with the smallest growth response were found on the poorest soils. In Mexico, dry forest pioneer species require higher amounts of P and light for growth and survival than mature forest species (Huante et al. 1995b). All species grew faster with increased P, but pioneer growth was greater than that of mature species. Seedlings showed similar responses to N, with pioneers increasing relative growth rate more than mature species (Huante et al. 1995a). In dry montane systems in Mexico, deciduous species were found on richer soils and evergreen species on more acidic soils, but the evergreens were able to grow on richer sites (Goldberg 1982).

Some studies have attempted to identify limiting nutrients by adding fertilizer to large plots of forest (at least 100m^2, but often larger). (See Tanner et al. 1998, for review.) In this way, Vitousek and Farrington (1997) reported P limitation in wet forests on old soils in Hawaii, N limitation on young soils, and co-limitation of N and P on middle aged soils. Similarly, N limitation was demonstrated in lower montane moist forests in Jamaica and Venezuela (Tanner et al. 1990, Tanner et al. 1992). Large-plot fertilization additions have not been attempted in dry forests where it is impractical for a number of reasons. The response time to fertilization amendments can be quite long. In Venezuela, moist forests took 2.6 years to respond to fertilizer treatments in diameter growth (Tanner et al. 1992). Response in dry forests would be slower because the lack of water results in shorter growing seasons and slower cycling of nutrients through the system. Dry forests can be very dense (e.g., 10,000 stems/ha in Guánica Forest) and therefore the fate of added nutrients would be difficult to follow. Fertilizing large plots permanently alters the characteristics and history of the site.

Root in-growth cores have been shown to be an effective substitute for fertilization plots in a variety of ecosystems, at least for evaluating treatment effects. In a series of soil types within Venezuelan wet forest, Cuevas and Medina (1988) used root in-growth cores to demonstrate that caatinga and bana forests were N limited and tierra firme were Ca limited. Raich et al. (1994) used in-growth cores in Hawaii and reported the same results as the large scale fertilization experiments (Vitousek and Farrington 1997). More recently, Stewart (2000) has used root in-growth cores to repeat N limitation findings from Jamaica (Tanner et al. 1990). Root in-growth cores are good substitutes for large scale fertilization experiments because roots are responsible for nutrient uptake, and thus are responsive to variations in nutrient pools in soils. In addition, in-growth cores are simple to establish and add a minimum of artificial nutrient to the system.

The objectives of this study were to: 1) determine whether common species in Guánica Forest were limited to certain positions along gradients in soil fertility, 2) to determine if and which soil nutrients limited growth, and 3) to evaluate whether N or P plays a greater role in nutrient limitation of forest growth.

METHODS

Associations of tree and sprout growth with soil nutrients

Tree growth was assessed for 481 trees in the Main site. Of these trees, 270 had been measured beginning as early as 1981 in previous studies (Murphy and Lugo 1986b, 1990, Murphy et al. 1995) and included 27 species. In 1998, I added 205 more trees to attain sample sizes of ≥ 30 individuals for six species: *Amyris elemifera, Bursera simaruba, Eugenia foetida, Gymnanthes lucida, Pictetia aculeata,* and *Exostema caribaeum.* Of these species, *Bursera, Exostema,* and *Pictetia* are considered pioneers (Molina Colón 1998), *Amyris* and *Gymnanthes* are mid- to late successional species occupying canopy positions while *Eugenia foetida* is a mid-successional subcanopy species. The added trees were single-stemmed with few exceptions. Diameter measurements were taken at breast height (1.4 m; dbh) using a diameter tape. To ensure consistency of measurement location, a chain was suspended from a nail placed ≥ 30 cm above breast height. The chain was marked at 5 cm intervals bracketing breast height, so that five diameters were measured on each stem. Growth was determined by comparing averaged diameters from each time interval. This technique has proven able to assess small differences in growth (Murphy and Lugo 1995, Dunphy et al. in prep). Trees were divided into size classes for analysis based on diameter: <2.5 cm, 2.5-4.9 cm, 5.0-7.4 cm, and ≥7.5 cm. Diameters were converted to basal area. Growth rate analyses were based on two-year averages, from May 1998 to May 2000.

In September, 1998, Hurricane Georges passed over Guánica Forest and was followed by a flush of sprouts (see Chapter Six). The number of sprouts that developed below breast height on the 481 trees were counted immediately after the hurricane, at the end of the rainy season in January 1999, and in July 2000. Sprout initiation was assessed using January 1999 data. Sprout mortality was determined by comparing data from 2000 with that from January 1999. The length of the longest sprout on each tree was measured to the nearest cm in July 2000 to assess growth. More details on these measurements can be found in Chapter Six. Analysis of sprout data only included those from defoliated or undamaged stems. Sprouts from broken stems were excluded because broken stems would be more likely to coppice, coppice sprouts would receive a greater proportion of nutrients taken up by roots, and broken stems were a small percentage (<10%) of the total sample.

Growth rates were compared to levels of soil organic matter, total N, total and available Ca (Ca_{to} and Ca_{av}), total and available P (P_{to} and P_{av}), and pH. Soil was collected from the top 10 cm of the rooting zone at the base of each of the trees measured for growth. Three subsamples were collected at 1-m from the trunk, approximately evenly spaced around the tree. Samples were air-dried, sieved using 1 mm mesh, and analyzed as described in Chapter Three. Some subsamples were not bulked prior to analysis to facilitate geostatistical analysis of nutrient pools (Chapter Three) but their values were averaged for analyses here.

Root In-growth Cores

Three 15-meter transects were installed running east-west off of the west edge of the Main site in Guánica Forest (Murphy and Lugo 1986b). The transects were approximately 5 m apart and ran across a gentle slope on well-drained, relatively rock-free soils near a small draw. Sixteen root in-growth cores (four from each of three treatments and control) were placed at 1-m intervals along each of the transects.

Baskets used for root in-growth cores were based on those used in Cuevas and Medina (1988) and constructed from cylindrical high density polyethylene mesh tubing with 4 mm^2 holes. Baskets were 7 cm in diameter, 10 cm high, and enclosed with nylon mesh on the bottom. About 33% of the area on the sides of the baskets was open.

Baskets were filled with soil taken from near the beginning of each transect. Soil was pooled, mixed thoroughly, and sieved to remove existing fine roots. In previous studies (Cuevas and Medina 1988, Raich et al. 1994), an inert medium was used to fill the baskets (e.g., vermiculite or calcined clay). In this study, native soil was used in this experiment to maintain the microbial community, mycorrhizal innocula, and the natural geochemistry of the ecosystem. After preparation, the soil was divided into four equal amounts for treatment. The four treatments were N, P, NP combined, and a control of pooled, sieved soil that received no nutrient amendment. N was added as NH_4NO_3 and P as P_2O_5 in granular form. Nutrients were added at a rate of 40 g/m^2 of N or P. Baskets were filled with treated soil and placed into 10-cm-deep cylindrical holes so that the top of the basket was level with the top of the mineral soil surface. Gaps between the sides of the baskets and the sides of the holes were filled with excess treated soil. Cores were covered with forest floor litter which was set aside while making the holes.

Root in-growth cores were installed on June 30, 2000, which corresponds to a short, but unpredictable, dry season in Puerto Rico. After 30 days, during which no rain fell, the cores were inspected and no roots had grown into them. The cores were subsequently harvested on Jan 15, 2001, after the primary rainy season. One core each from the N and NP treatments was lost.

Cores were sieved though 0.5 mm mesh to remove roots from the majority of the soil particles. Visual inspection revealed very little root loss into the <0.5 mm fraction, which was subsequently analyzed to determine whether fertilization affected pH. The remaining soil particles and roots were separated using elutriation (Smucker et al. 1982). Root length was determined using a line-intercept method (Tennant 1975), with the root mixture stirred into a sucrose solution (density 1.3) to separate roots from large sand particles that were not completely separated during elutriation. Root length is considered a better functional estimate of plant nutrient uptake than biomass because uptake is positively associated with length and surface area, whereas biomass increases rapidly with root diameter, but wider roots are less active in uptake.

Statistics

Species distributions across nutrient gradients were compared using Kolmogorov-Smirnov (KS) two-sample tests, which compare similarity of distributions between samples. Correlation was used for all comparisons between soil properties and growth rates. Correlations by species or size class were only performed if sample sizes were ≥20. Correlations between nutrient content and sprout initiation were performed on species with ≥10 individuals, and for sprout mortality and growth ≥10 sprouting individuals were required. Root length data were analyzed using general linear models in Systat 8.0. Each transect was treated as a block for statistical analysis. Tukey tests were used to make multiple comparisons of treatment means. Significance levels for all tests were set at $\alpha=0.05$.

RESULTS

Species presence across nutrient gradients

The whiskers of each soil factor's box plot (the grey boxes in Figure 4-1) included approximately 90% of the values defining the gradient for a particular factor. The ability of a species to establish and survive to maturity across a soil nutrient gradient was indicated when the species' entire box plot overlapped the whiskers of the pooled data for each factor. Using this criterion, each of the six species' were distributed across the majority of each soil nutrient and pH gradient (Figure 4-1). For example, although the majority of *Exostema* individuals were found growing in areas of low P_{av}, at least four were found at the upper end of the gradient at high P_{av}, suggesting that *Exostema* was not limited from growing at either high or low nutrient levels.

Differences in species distributions were apparent across all soil gradients except for Ca_{to}. *Gymnanthes* was usually the species occurring at the highest median level of available soil nutrients, while *Exostema* had the lowest median values. These two species were involved in 26 of 28 significantly different distributions among species within soil gradients (Figure 4-1). The three pioneer species (*Bursera, Exostema*, and *Pictetia*) sorted out together only along the P_{av} gradient, although *Exostema* and *Pictetia* also occupied the two lowest positions for N and Ca_{av} and the two highest median pH values.

Effects of nutrient pools on tree and sprout growth

No significant correlations were found between soil nutrients or pH for the entire sample of trees or for size classes of mature trees. The growth of one species, *Bursera simaruba*, responded to soil nutrients when divided by size class. The 5.0-7.4-cm *Bursera* stems showed increased basal area growth with higher amounts of organic matter and N ($r = 0.74$ and 0.76 respectively, each $p < 0.001$), while 2.5-4.9-cm stems showed the same trend ($r = 0.76$ and 0.70, $p = 0.001$ and 0.003) and also responded positively to Ca_{av} ($r = 0.79$, $p < 0.001$) and negatively to Ca_{to} ($r = -0.80$, $p < 0.001$). The largest size class of *Bursera* stems showed no correlation between growth rates and soil nutrients.

Soil nutrient pools were related to the initiation, growth, and survival of five species' sprouts that developed after Hurricane Georges (Table 4-1). Sprouting in *Bourreria succulenta, Crossopetalum rhacoma, Eugenia foetida*, and *Pictetia aculeata* was facilitated by higher amounts of P, alone or in relation to N or C. Sprout initiation and mortality of *Exostema caribeaum* responded to C:N ratios.

Root growth

Root length varied among transects and was affected by a significant interaction between N and P (Table 4-2). Added N always produced greater root length (Figure 4-2). P increased this effect in conjunction with N, but not when added alone. Treatment did not affect the pH of the cores after harvest. Mean specific root length (total root length/core volume) was 4.3 cm/cm^3 for P-treated cores, 6.7 cm/cm^3 for the N treatment, 7.8 cm/cm^3 for the NP treatment, and 5.7 cm/cm^3 for the control in-growth cores. Root lengths were higher than reported for temperate tree species (0.2-0.4 cm/cm^3, Crookshanks et al. 1998), coffee trees (2.1 cm/cm^3, Nutman 1934), or tropical wet forests (0.4-0.7 cm/cm^3, Ostertag 1998), but less than reported for grasslands (6.6-54.8 cm/cm^3, Dittmer 1938). The values reported here appear realistic considering higher root:shoot ratios of Guánica Forest compared to other tropical forests (Murphy and Lugo 1986a).

DISCUSSION

Despite the indirect evidence (e.g. PUE and leaf N:P) suggesting that phosphorus supplies could be limiting to tree growth, only a few weak relationships were found between growth and P pool sizes (Table 4-1). More species' sprouts responded to P than other nutrients, basal area growth of small *Bursera* trees responded to N, while root growth was most stimulated by combined NP additions. Differential response to nutrients among tropical tree species in the same community has been shown elsewhere (Huante et al. 1995a, Huante et al. 1995b, Fetcher et al. 1996, Cuevas and Lugo 1998, Lawrence 2001, 2003). *Bursera* is the fastest growing tree species in the sample (Dunphy, unpublished data). That it would have greater growth at higher soil N reflects the feedback between fast-growing species and soil nutrient pools discussed by Hobbie (1992). The response to soil N pools ceased in the largest size class of *Bursera*, perhaps as a result of increased internal stores or the attainment of equilibrium between large trees and soil nutrients. The lack of strong patterns in relation to nutrient gradients may also reflect interspecific niche partitioning among species based on root characteristics. Although the majority of fine root biomass was present in the top 10 cm of soil (Murphy et al. 1995), dry forest species elsewhere have different patterns of root distribution in time and depth (Huante et al. 1995b). At this time, little is known about rooting characteristics of individual species in Puerto Rican dry forest. The soil sampling methods used here would not be able to resolve differences in temporal or spatial responses among species' roots within the in-growth cores. The ability of each species to differentially respond to various resources, to acquire nutrients at different times and locations in the soil, and potentially to maintain different relationships with microbes, would seem to be a prerequisite to maintain the diversity of tree communities of Guánica Forest.

Both ecological and methodological factors may explain the lack of a forest-wide P response by trees. Lugo and Murphy (1986) found that retranslocation of P accounted for 65% of the annual P demand in Guánica Forest. With such a large proportion of P budget accounted for internally, mature trees may not respond to soil P content. On the other hand, sprouting trees would have a higher demand for external sources of P because defoliation, decapitation, or root breakage would reduce internal P supplies – particularly because defoliation during the hurricane would have occurred without retranslocation (Waide et al. 1998). In addition, apparent P limitation may reflect the lack of water moving P through the soil to roots, a frequent bottleneck for nutrient transport through the soil. While soil nutrient content may appear high, if it is not reaching the rhizosphere then plants will be unable to take up nutrients. Thus, soil nutrient content, as opposed to flux, is at best a coarse way to estimate availability for plants, even when available forms of nutrients are measured.

Competition between plants and microbes may also reduce the sensitivity of plant growth to P pools. Microbes tend to be limited by N supplies when C:N ratios are 20-25 (Paul and Clark 1996) but soil bacteria can immobilize N at C:N ratios as low as 12.5 (Hodge et al. 2000). The average C:N ratio in Guánica Forest ranges from 19-29 (Chapter 3 and Lugo and Murphy 1986). During the rainy season, when the root in-growth cores were in the field and microbes would have been most active, they may have sequestered a sufficient amount of N to limit root growth. Roots therefore responded to N and NP additions, which would have lowered C:N ratios and then provided additional P for growth. Assuming that the high PUE and N:P ratios represent a real P deficit, the N limitation may only be a seasonal phenomenon relieved when pulses of N enter the system after drying and initial wetting of soils (Davidson et al. 1993, Srivastava 1997) at a time when fine root production is at its highest (Kummerow et al. 1990, Kavanagh and Kellman 1992). Thus, the mature trees may be integrating long term P limitation while the in-growth cores were only measuring short-term response. On the other hand, the root response to added N and the high PUE and leaf N:P ratios may signify multiple resource limitation.

Mycorrhizae undoubtedly play an important role in nutrient acquisition, but little is known about their relationships to Guánica Forest trees. Vescicular-arbuscular (VA) types are present in the forest and are known to infect at least five tree species, including *Gymnanthes* and *Exostema* (Dunevitz 1985). Plants and fungi respond to different environmental factors (Allen 1991), so it may be that nutrient limitation is indirectly regulated in trees by the needs of mycorrhizae. Considering that the fungi are typically limited by carbon, production of sufficient carbon by photosynthesis in host trees for use by the fungi may be limited by N supply in the rainy season. Since mycorrhizae are able to help diminish the effects of drought, they may be able to stretch the amount of time that a tree can acquire P during the year (Allen 1991). Finally, an interesting phenomenon has been noted in alkaline soils where bacteria are responsible for solubilizing P which is then taken up by mycorrhizae for plant use (Azcon et al. 1976). Bacteria growing with limited N supplies would thereby limit P supplies for the plant. In this case, increasing N supplies in the in-growth cores would result in more P released to plants and greater root growth in N and NP treatments.

CONCLUSIONS

All common tree species appeared to be able to grow across the entire portion of each nutrient gradient measured in Guánica Forest. The presence of some mature individuals of each common species, even at the lowest end of a nutrient gradient, suggested that all species were able to survive the most extreme nutrient conditions in the forest.

Nutrient limitation of tree growth appeared to result from both N and P, either alone or in combination, and depended on the size and species of the tree and the time of year. Despite measurements of potential long-term responses to nutrient supplies (e.g., nutrient use efficiencies, retranslocation estimates, and N:P ratios) indicating that P might limit tree growth, nutrient limitation affected only smaller stems and sprouts. Growth or survival of sprouts and smaller trees responded to nutrient pool sizes, most frequently to P, but often in relation to OM or N. Root in-growth cores indicated the growth may be co-limited by both N and P, but there was no strong evidence for nutrient limitation on the diameter growth of mature trees based on nutrient pool size.

Table 4-1. Correlation between sprout development and soil nutrient pools or nutrient pool ratios for five more commonly sprouting species. No correlations were found between nutrient pools and other common species (see Chapter Two for species composition) or between these five species and other nutrients, pH, or organic matter.

Species	**Sprout stage**	**Nutrient**	**r**	**p**
Bourreria succulenta Jacq.	growth	C:P	.790	.039
Crossopetalum rhacoma Crantz	initiation	Total P	.889	.045
	mortality	Total P	.919	.014
Eugenia foetida Pers	initiation	C:P	.498	.041
		% Available P	.625	.001
	mortality	C:P	.455	.046
		% Available P	.570	.004
		N:P	.473	.033
Exostema caribaeum (Jacq.) Roem. & Schult.	initiation	C:N	.495	.037
	mortality	C:N	.457	.039
Pictetia aculeata (Vahl) Urb.	initiation	% Available P	.826	.037
	growth	% Available P	.939	.022

Table 4-2: Results of ANOVA for root growth. Root length was normally distributed.

Dependent variable: Root Length
N: 46 Multiple R: 0.668 Squared multiple R: 0.446

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
BLOCK	4980000	2	2490000	5.000	0.012
N	9070000	1	9070000	18.199	0.000
P	29700	1	29700	0.060	0.808
N*P	2610000	1	2610000	5.241	0.027
Error	9920000	40	498000		

Figure 4-1. Occurrence of tree species along gradients of soil nutrient pools and pH. Box plots immediately above axes (bottom, in grey) represent distributions of the entire gradient for a given nutrient or pH from soil samples at the Main site (n = 623). Box plots in black represent soil nutrient values for samples taken beneath the 6 most numerous species in the sample (n = 37 to 72). Boxes are the middle 50% of values, whiskers (lines) extending from the boxes include ≈ 90% of the data, and lines dividing boxes are sample medians. *Bursera, Exostema,* and *Pictetia* are pioneer species. Differences in species distributions across a gradient are signified using the *same* letter.

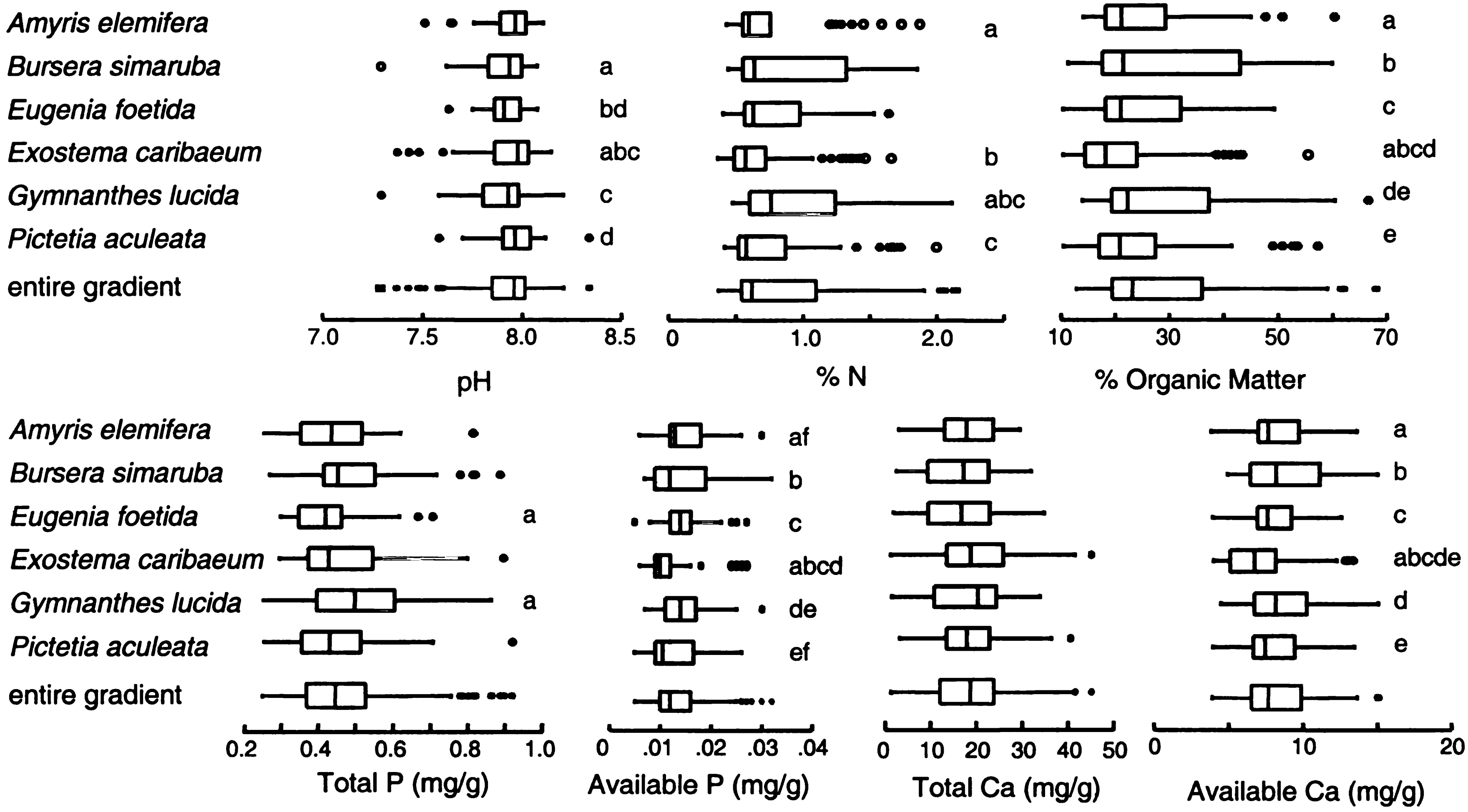
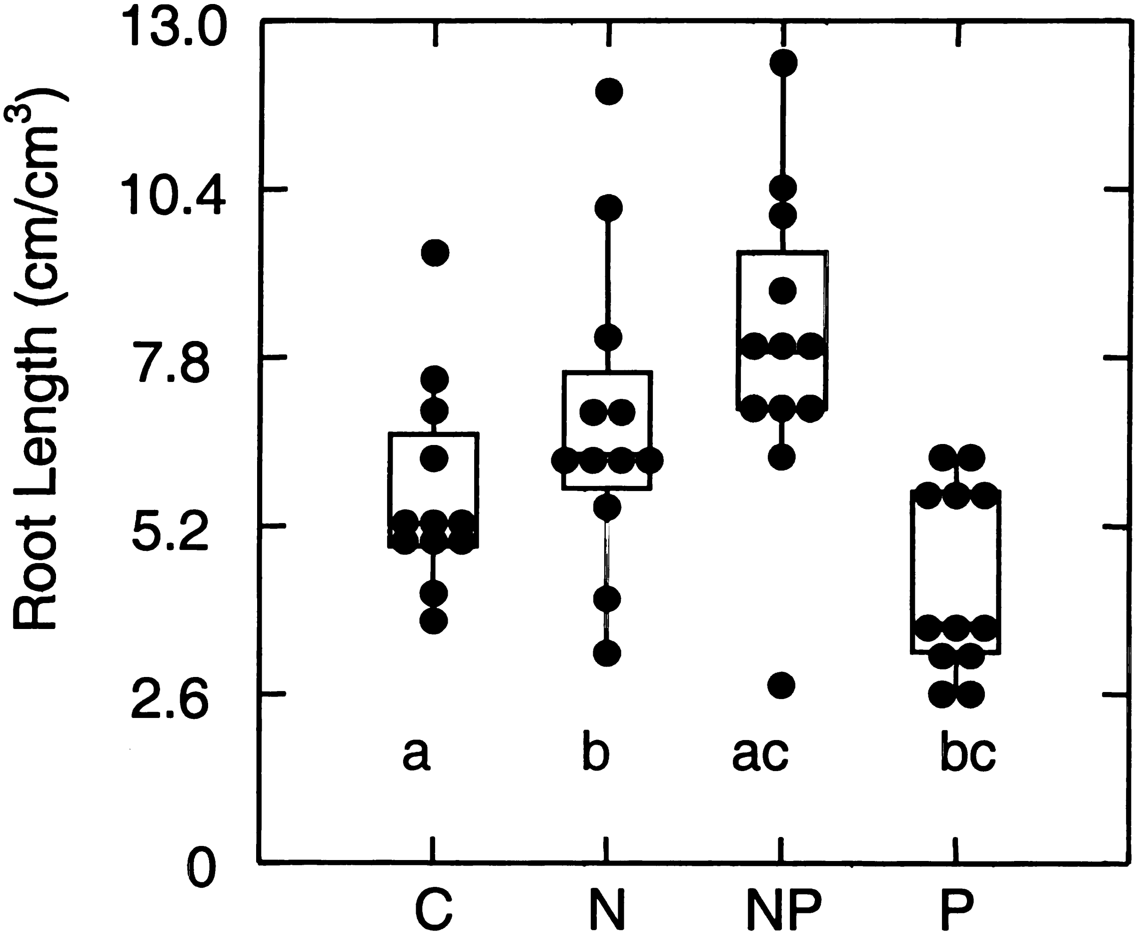


Figure 4-2. Box plots of treatment means for root length from in-growth cores. Dots represent individual cores. Nitrogen increased root length (F=18.199, p<0.0005, see Table 4-2) and there was a significant interaction with P (F=5.241, p=0.027). Treatments with the *same* letters are significantly different based on post-hoc Tukey tests for multiple comparisons. Although phosphorus cores had two groups of similar values, neither group was concentrated along a particular transect.



CHAPTER FIVE

THE INFLUENCE OF HURRICANE WINDS ON CARIBBEAN DRY FOREST STRUCTURE AND NUTRIENT POOLS

Abstract: The influence of hurricanes on the structure of seasonal tropical forests is poorly understood because there have been few opportunities to address this issue. In 1998, we measured the effects of Hurricane Georges after it passed over long-term research sites in Puerto Rican dry forest. Our primary objectives were to quantify hurricane effects on forest structure, to compare effects in a large tract of forest versus a series of nearby forest fragments, to evaluate short-term response to hurricane disturbance in terms of mortality and sprouting, and to assess the ability of hurricanes to maintain forest structure. For stems with 2.5 cm minimum diameter, 1004 stems/ha (12.4%) suffered structural damage, while 69% of the undamaged stems were at least 50% defoliated. Basal area lost to structural damage equaled 4.0 m^2/ha (22%) in south-facing native forests. Structural damage and defoliation increased with stem diameter and were more common in certain dry forest species. South-facing forests and those on ridgetops incurred more damage than north-facing forests or those comprised primarily of introduced species. Stem mortality was only 2% of all stems after 9 mo. Structural damage did not necessarily result in stem mortality. Hurricane-induced mortality was not associated with stem height or diameter, but was ten times greater than background mortality. Basal sprouting was proportional to the amount of structural damage incurred in a stand. Forest fragments experienced the same patterns of hurricane effects as the reference forest. The low, dense structure of Caribbean dry forest

can be maintained by hurricanes damaging larger stems and inducing basal sprouting to generate multi-stemmed trees.

INTRODUCTION

The structure of West Indian dry forests differs markedly from those elsewhere in the neo-tropics. Compared to tropical dry forests or seasonal forests in temperate zones, subtropical dry forests (sensu Holdridge 1967) have fewer canopy layers, no emergent trees, and, especially in the West Indies, have high stem densities resulting from numerous multi-stemmed trees (Murphy and Lugo 1986b, Dunphy et al. 2000, Quigley and Platt 2003). Differences in structure among dry forests have been attributed to climatic factors such as low annual rainfall and high potential evapotranspiration, as well as a suite of disturbances – including human impacts such as grazing and cutting (Murphy and Lugo 1986b, Kelly et al. 1988, Murphy et al. 1995, Gonzalez and Zak 1996, Molina Colón 1998), and natural disturbances such as salt spray (Smith and Vankat 1992), trade winds (Lawton 1982), and hurricanes (Lugo et al. 1983, Kelly et al. 1988, Reilly 1991). However, the difficulty in teasing apart causal factors of forest structure after the fact is illustrated by studies in the Solomon Islands, where species composition was initially attributed to hurricane disturbance but, after further analysis, to logging by humans (Burslem et al. 2000). Although hurricanes are common in the subtropics and widely studied in moist and wet forests (cf. Biotropica 23(4a) 1991 and recent reviews: Everham and Brokaw 1996, Whigham et al. 1999), their effects have been less completely studied in dry forests. In this study, we report the effects of Hurricane Georges on dry forests in southwestern Puerto Rico.

If climate alone determined forest structure, the driest forests (based on potential evapotranspiration) would be expected to have the least basal area and biomass. Stem density may also be higher in the driest forests if basal sprouting is caused by droughts killing terminal buds. However, in independent projects, both Murphy and Lugo (1986b) and Quigley and Platt (2003) found that Guánica Forest, Puerto Rico, had structural characteristics that could not be explained by climate alone. Murphy and Lugo (1990) reviewed the structure of 12 mature tropical and subtropical dry forests across a rainfall gradient from 603–1800 mm/yr. Of the 12 forests, Guánica Forest had the only fifth highest temperature to precipitation ratio (2.9; T:P ratio acts as a surrogate for potential evapotranspiration, which is seldom reported), yet it was the shortest (9 m canopy height), with the least aboveground biomass (53 Mg/ha), and the second lowest basal area (17.8 m^2/ha). In Guánica Forest, 42% of all trees were multi-stemmed, leading to a stem density of 12,000 stems/ha (Murphy & Lugo 1986). Quigley and Platt (2003) compared structural characteristics of seasonal forests from the equator to 40°N in the Western Hemisphere and found that forests at 20-30°N, including those in Puerto Rico, had greater stem densities and lower basal areas than those found elsewhere. These results suggest that other factors such as hurricane disturbance supplement the effects of drought stress in structuring dry forest.

Aside from damaging stems, hurricanes can rapidly redistribute resources and alter community composition and function. Hurricane winds lead to canopy thinning through the loss of leaves – transferring substantial biomass and nutrients to the forest floor. In Hawaii, hurricane litterfall was 1.4 times greater than normal annual levels (Herbert et al. 1999). In two wet forests and a cloud forest in Puerto Rico, hurricane litterfall ranged from 1.2–1.9 times greater than normal annual litterfall (Lodge et al. 1991). In Mexican dry forests, hurricane litterfall was about 1.3–2.0 times as much as the average of the previous four years (Whigham et al. 1991). These large inputs of litter change spatial and temporal resources availability and serve as important nutrient pulses (Lodge et al. 1994a).

Another poorly understood aspect of hurricane disturbance is its interaction with forest fragmentation. Fragmented forests have more edge to face hurricane winds than do larger tracts of continuous forest and might therefore be more vulnerable to damage. Only 23.2% of the dry forest area of SW PR remains forested, contained in a collection of over 600 fragments (Ramjohn 2004). Therefore, the region provides a good location to evaluate the effects of hurricanes on forest fragments.

The main objectives of this study were to: 1) provide a description of hurricane effects on Puerto Rican dry forest, 2) compare effects of hurricane winds in a large tract of forest with those in nearby forest fragments, 3) measure short-term responses of trees to hurricane winds in terms of sprouting and mortality, and 4) assess the potential of hurricanes to maintain the unique dry forest structure of the West Indies.

MATERIALS AND METHODS

THE SITE AND THE EVENT.—Guánica Forest is located in SW Puerto Rico (17°58'N, 65°30'W). Rainfall averages 860 mm/yr and mean annual temperature is 25.1°C (Murphy and Lugo 1986b). The rainy season is bimodal, split between spring rains in March-April and fall rains from August to December corresponding to the hurricane season. The amount and distribution of rains within years and seasons is highly variable (Murphy et al. 1995). The forest canopy reaches 5 m height on south-facing slopes and ridgetops (Murphy and Lugo 1986b), and 9 m in valleys (Molina Colón 1998). Emergents are absent and taller trees are always found in valley areas, leading to a more uniform canopy. Considered one of the best preserved examples of Caribbean dry forest (Ewel and Whitmore 1973), Guánica

Forest has been extensively studied over the last 25 years (Lugo et al. 1978, Lugo and Murphy 1986, Murphy and Lugo 1986b, 1990, Murphy et al. 1995, Lugo et al. 1996, Molina Colón 1998, Dunphy et al. 2000, Genet et al. 2002a, Genet et al. 2002b, Quigley and Platt 2003, Ramjohn 2004). The forest was set aside for protection in 1917 and its boundaries expanded in the 1930's to include all the plots within this study. Forest structure before Hurricane Georges had been shaped by multiple factors, including human activity (Molina Colón 1998, Lugo et al. 2002). Surrounding Guánica Forest are a collection of dry-forest fragments that vary in land use history, size, age, and dominant tree cover (Lugo et al. 1996, Genet et al. 2002a, Ramjohn 2004). Most fragments exist in a matrix of agriculture or pasture but some are surrounded by residential areas.

The flora of Guánica Forest provides a good basis to study regional effects of hurricane disturbance. Of the 18 species for which we had at least 10 trees in our plots, only one (*Pictetia aculeata* (Vahl) Urban) is endemic to Puerto Rico, 17 are found elsewhere in the Caribbean, 10 in Florida, 10 in Central America, and 5 in South America.

The eye of Hurricane Georges passed over Guánica Forest on September 21-22, 1998. Sustained winds blew at 176–184 km/h and gusted up to 240 km/h (Bennett and Mojica 1998), making this a Category 3 hurricane. It took about 18 hr to cross over the forest and maximum winds lasted about 4 hr. Georges was a relatively dry hurricane (Bennett and Mojica 1998), depositing 151 mm of rainfall, about equal to the September average (Murphy et al. 1995).

Between 1700 and 2004, the eyes of 37 hurricanes traversed some portion of PR, a return interval of one hurricane every 8 yr (Quiñones 1992). Only 15 approached the dry forest area (Figure 1), including the last two – Hortense in 1996 and Georges in 1998 – an average return interval of 20 yr. Not all of the 15 hurricanes affected the forest equally.

Historical records report that seven of the 15 hurricanes were at least category 3 in the Guánica area, therefore most likely to influence forest structure. Thus, strong hurricanes have an average return interval of 43 yr. Hortense was a category 1 hurricane (Saffir-Simpson Index) with less than 100 mm of rainfall in the Guánica area (Bennett 1996) and resulted in very little damage to the forest (AE Lugo & M Canals Mora, pers. obs.). Prior to Georges, the structure of Guánica Forest was probably last affected by Hurricane San Felipe in 1928.

PLOTS AND TERMINOLOGY USED IN THIS STUDY.—We compiled data for this study from a variety of different plots established prior to September 1998 for other research projects. Following the hurricane, we pooled all available data to provide a more comprehensive explanation of hurricane effects than would have been possible otherwise. We measured hurricane effects in 33 experimental plots in Guánica Forest (Figure 2). These plots were located in semi-deciduous forest (Murphy and Lugo 1986b, Molina Colón 1998) but differed in size, time studied, and land-use history (Table 1). Twenty-eight of the plots were established before the hurricane to study long-term forest growth, structure, and regeneration (Lugo and Murphy 1986, Murphy and Lugo 1986b, Murphy et al. 1995, Molina Colón 1998). Following the hurricane, we established one plot in each of three old *Swietenia mahagoni* Jacq. plantations and two new plots on ridges after extensive field surveys revealed that ridges received the greatest damage. Total area sampled was 1.3 ha spread across an area of 3162 ha in the eastern portion of Guánica Forest. However, much more of the forest was inspected as we conducted field surveys, leading us to conclude that our results were representative of the forest as a whole.

We also sampled hurricane effects in 19 forest fragments within 31 km of Guánica Forest (Figure 2) (Genet et al. 2002a, Genet et al. 2002b, Ramjohn 2004). Fragments ranged in size from 0.01–75.6 ha and had species assemblages comparable to the native forest plots. The fragments faced various directions and occurred over the same elevation range as Guánica Forest. Hurricane effects were measured along 2-m wide transects, the lengths of which varied by fragment size. Transects started on the north and south edges of fragments and ran toward the center. Total area sampled in the 19 fragments was 0.68 ha.

Land-use history of Guánica Forest resulted in two types of forest: 1) those dominated by native species, and 2) those that consisted primarily of naturalized species (*i.e.*, *Leucaena leucocephala* (Lam.) deWitt and *Prosopis juliflora* (SW.) DC.). We refer to these types of forest as "native forest" and "Leucaena forest" (Table 1). Leucaena forest plots had been used for a baseball field, agriculture, and housing sites until about 65 years ago (Molina Colón 1998). Native forest plots either had no signs of human disturbance or some selective cutting prior to the 1930s for subsistence charcoal production (Murphy and Lugo 1986b, Molina Colón 1998). The native forest plots on the north side of Guánica Forest occurred in the lee of hurricane winds, while those on the south side faced Georges' strongest winds (Bennett and Mojica 1998). Thus, we use "native-north" and "native-south" to highlight the influence of aspect on hurricane effects.

Since many trees were multi-stemmed, we use "tree" to refer to single-trunked individuals *and* entire clumps. When discussing individual trunks, regardless of whether growing singly or clumped, we use "stem." Thus, there will be more stems than trees at each site. Effects were seldom uniform among stems in a clump.

STEM MEASUREMENTS FOR FOREST STRUCTURE.—Within each plot, we tagged all stems ≥2.5 cm diameter at breast height (DBH). Species identifications were based on Little and Wadsworth (1964) and Little *et al.* (1974). Stem height and DBH were measured on all trees between June and September 1998. Height was measured to the nearest 0.25 m using a telescoping pole. DBH was measured at 1.3 or 1.4 m depending on who established the plot (Murphy & Lugo 1986, Molina Colón 1998). In the fragments, we measured the height and DBH of damaged (but living) and hurricane-killed stems only.

ASSESSMENT OF EFFECTS.—We assessed effects on each tagged stem in the native-south forest plots and in two of the three mahogany plots within 10 days of the storm. Assessment of other plots and fragments was completed by February, 1999. Hurricane impacts on stems were divided into six categories: uprooted, snapped, large branches broken, leaning, defoliated only, and no visible effect. The first four categories result in severe structural damage to a stem and are collectively referred to as such. "Large branches broken" indicates that ≥25% of the secondary or tertiary branches were snapped off. For our purposes, secondary branches had diameters ≥ 50% of DBH and tertiary branches had a diameters 25–50% of DBH. Branch loss was not evaluated for the native-north or Leucaena plots, precluding their inclusion in some of our analyses. Leaning stems were bent to an angle >30° from vertical at some point along the trunk, but lacked signs of uprooting or breakage. We compared the direction of fall for snapped, uprooted and leaning stems to the direction of the strongest winds based on meteorological reports (Bennett and Mojica 1998).

We estimated defoliation visually for each tree using six classes: 100% (no leaves at all), 95% (one to a few leaves remaining), 75%, 50%, 25% and 0% (all leaves present). New leaf growth prevented assessment of defoliation in plots sampled after late-November 1998 and in all fragments. Thus, analyses of defoliation patterns were restricted to the native-south plots and two mahogany plots.

LITTERFALL.—We collected litterfall in thirty 50 x 70 cm wire baskets haphazardly placed in the 1.44 ha native-south forest plot. We emptied the baskets the day before the hurricane and on September 26, 1998 – four days after the hurricane. We checked baskets again in early October, but <1 g of new litterfall was present in any basket, suggesting that all litter had fallen out of the canopy by Sept. 26. Thus, we considered the litterfall samples to have been created during the 18 hours it took the hurricane to traverse the site.

We also collected standing litter on the forest floor 12 d after the hurricane in the 1.44-ha native-south plot. A 15 x 15 cm template was randomly located in the vicinity of the litter baskets (*N* = 26). All material within this area was collected and sorted into four categories: leaves, brown wood, green wood, and miscellaneous. We distinguished brown wood from green wood based on flexibility. By the twelfth day, green and brown leaves could not be distinguished. Leaves included all leaf parts, and wood included stems, branches and woody vines. The miscellaneous category included any material that did not fit into other categories, including reproductive parts and small fragments of leaves or wood.

Nutrient stocks in standing litter and litterfall are expressed here on a content basis (kg/ha). Tissues were dried at 65°C to a constant weight and ground in a Wiley mill (18 mesh) before analysis. Ground samples were digested with H_2O_2 and concentrated HNO_3 (Luh Huang and Schulte 1985), and concentrations of P, K, Ca, and Mg were determined on a Beckman Spectra Span V plasma emission spectrometer. Because forest floor samples often harbor soil particles, we express all standing litter mass values on an ash-free basis. Forest floor nutrients were analyzed using bulked samples (*N* = 6), except for green wood, which was not present in all samples (*N* = 4). Forest floor N was determined using duplicate samples in a CE Instruments NC2100 analyzer. Litterfall N was determined on duplicate samples using a LECO CNS 2000 analyzer.

SHORT-TERM RESPONSE.—We determined mortality for stems with DBH ≥2.5 cm. Stems were considered dead if they had no leaves, no sprouts, and dried bark as of June 1999 (9 months post-hurricane) when the plots were resampled. Multi-stemmed trees were considered dead only if all stems were dead. Mortality was not assigned to mode of damage in the native-north or Leucaena forests. Mahogany plots were not revisited, so mortality was not assessed there.

We recorded sprouting from roots and trunks below breast height to evaluate the potential for hurricanes to generate multi-stemmed trees. We counted sprouts on each of the living, tagged stems in the native-south and ridgetop plots in September or November 1998 to determine the number of sprouts existing before the hurricane. In June 1999, we counted new sprouts and noted their point of origin on the stem. New sprouts were distinguished from old sprouts by bark coloration and lignification. Summary data are presented here. Patterns of sprout survival after two years were reported elsewhere (Van Bloem et al. 2003).

STATISTICAL ANALYSES.—Plots were pooled by forest type. Categorical data (height, DBH, damage type) were analyzed using χ^2 statistics. Categories were pooled when sample sizes were too small to produce valid χ^2s – these instances are noted in the results. For analysis of species effects, we only included species that had ≥25 individuals in our samples. We used a null hypothesis of equal damage or mortality across all categories (locations, stands, or stem size).

We used regression to compare snap heights to stem diameter, sprouting rates to structural damage rates, and rate of structural damage to wood density (reported for species we examined in Molina Colón 1998). For all tests, $\alpha = 0.05$ and we verified normal distribution of data sets with Kolmogorov-Smirnov tests.

RESULTS

FOREST-WIDE EFFECTS.—In Guánica Forest as a whole, structural damage was present on 12.4% of stems (1004 stems/ha) as a result of Hurricane Georges. Both hurricane winds and falling limbs or stems caused structural damage to stems. Details of stem damage are below. The median rate of defoliation was 50%. Overall, 74.6% of stems were at least 25% defoliated and 69% were at least 50% defoliated. New leaves began to appear within two weeks for many species, particularly *Coccoloba diversifolia* Jacq., *Bourreria succulenta* Jacq., *Pisonia albida* (Heimerl) Britton, *Guettarda krugii* Urban, and *Pictetia aculeata.*

EFFECTS BY FOREST TYPE.—Severity of defoliation and stem damage varied by forest type and topographic setting (Figure 3). Structural damage was greatest on ridgetops (20%). Native-north forest, in the lee of the strongest winds, had the highest percentage of stems without visible hurricane effects and the lowest amount of structural damage (Figure 3). The basal area of stems suffering structural damage was 4.0 m^2/ha in native-south plots and 3.5 m^2/ha in ridgetops, 22% and 19%, respectively, of total live pre-hurricane basal area. Ridgetops lost less basal area than native-south forests because the average stem diameter in ridgetops was lower before the storm. The mode of structural damage varied by forest type and topography (Figure 4). Ridgetops generally had higher rates of each mode of structural damage than other forest stands, with the exception of snapping, which affected the greatest number of stems in native-south forests. Although having low damage overall, Leucaena forest had the highest proportion of snapped stems.

HURRICANE EFFECTS BY STEM SIZE.—Throughout the dry forest region of Puerto Rico, stems in all height and DBH classes sustained structural damage and the size classes with the most stems (3 to 6 m in height and 2.50 to 4.99 cm in DBH, Murphy and Lugo 1986b) had the greatest number of stems damaged. Proportionally, stem damage increased with stem diameter in native-south forest ($\chi^2 = 26.60$; 4 df; $P < 0.0005$; diameter classes >12.5 cm pooled), but not in native-north or Leucaena forests (Figure 5a). Native-north forests had the least damage of all forest types in all diameter classes. In plots where all modes of damage were measured (*i.e.*, native-south, ridgetops, and mahogany plantations), stems ≥7.5 cm DBH incurred proportionally more damage than smaller stems (Figure 5b), but damage was not related to stem height (Figure 5b). Unlike other studies (Putz et al. 1983), no relationship existed between damage and height:diameter ratios.

The type of damage was related to stem size (Figure 5b). Both taller and wider stems were more likely to have broken branches while shorter, thinner stems more often leaned. Snap height was not related to stem diameter ($r^2 = 0.03$). Stems that were poorly rooted or damaged at or near root level before the hurricane were nearly always snapped or uprooted after the hurricane. Taller, wider stems were also more likely than short, narrow stems to be defoliated (χ^2 for height = 70.432; 5 df; $P < 0.0001$; height classes ≥7 m pooled; χ^2 for DBH = 31.475; 3 df; $P = 0.0076$; ≥ 10 cm DBH classes pooled). The strongest hurricane winds came from the southeast (Bennett and Mojica 1998) resulting in northwesterly fall directions of stems in Guánica Forest and fragments (Figure 6).

Surveys in fragments included only damaged stems along a transect, so proportional damage could not be assessed among size classes. However, patterns of stem damage in fragments and Guánica Forest were similar. Total density of damage was 703 stems/ha in fragments and 1004 stems/ha in Guánica Forest. The proportion of damaged stems in the 2.5 to 4.9 cm DBH class differed by only 8% between the fragments and Guánica Forest (52-60%, respectively) and by ≤5% in all other size classes.

SPECIES EFFECTS.—Rates of both defoliation and structural damage differed by tree species. However, defoliation rates were not related to functional traits such as successional status or leaf phenology (Table 2). Pioneers accounted for 80% of species with above-average stem damage rates (Table 2). As in other studies of hurricane effects (Putz et al. 1983, Zimmerman et al. 1994, Asner and Goldstein 1997), no relationship existed between wood density and structural damage.

LITTER AND NUTRIENTS.—Total litterfall averaged 7.5 Mg/ha during the 18 h period of Hurricane Georges or 1.6 times the annual rate reported by Lugo and Murphy (1986). Compared to non-hurricane years, the litterfall pulse was 499 times average daily September litterfall and 17 times the average September monthly rate (Murphy et al. 1995). Leaf litterfall totaled 55% of annual estimates for the semi-deciduous Guánica Forest, corresponding to the median 50% defoliation estimate. Wood litterfall from Hurricane Georges was >11 times than measured for the year 1981. In October 1998, leaves comprised 46%, and wood 33%, of the total standing litter mass (Table 3). Post hurricane wood litter stocks more than doubled those found in 1981, a non-hurricane year (Lugo and Murphy 1986).

Nutrient content (kg/ha) of standing litter and litterfall immediately after Hurricane Georges exceeded that measured in 1981, primarily due to wood (Table 3). Hurricane leaf litterfall deposited 100% of annual N and 170% P, despite equaling only 55% of annual leaf litterfall. Wood litterfall contained 9.6 times the amount of N and 13.8 times the amount of P deposited in a non-hurricane year (Table 3). Total N, P, and K stocks on the forest floor after the hurricane were 71%–320% higher than in 1981 (Table 3). The total standing stocks of Ca (930 kg/ha) and Mg (37.7 kg/ha) after the hurricane were each 5 times greater than hurricane litterfall inputs. Ca and Mg stocks in 1998 were 47% and 8% of stocks found in the top 5 cm of soil in 1981 (forest floor Ca and Mg were not measured at that time, Lugo and Murphy 1986).

SHORT-TERM RESPONSE.—After nine months, mortality ranged from 1.3–2.2% for trees, and 0.7–7.4% for stems (Table 4). Total tree and stem mortality averaged 1.7% and 2.0%, respectively. There were no species effects, nor was mortality related to stem DBH or height classes (Table 5). The dead stems in ridgetop and native-south plots included 40% of the snapped stems, 21% of uprooted stems, 4.5% with large branches broken, 8.5% that were at least 95% defoliated, and 1.5% of stems incurring less defoliation. No stems that leaned or lacked visible effects died. Thus, the severity of damage increased the odds of mortality, but not all damaged stems died because many of them resprouted from stumps or roots.

New sprouts appeared below breast height on 29–63% of stems across Guánica Forest (Figure 7), far outnumbering the pre-hurricane sprouting rate of 3.5%. Stems on ridgetops sprouted most. The proportion of stems sprouting correlated with the proportion having structural damage ($r = 0.94$; $P = 0.017$), but even undamaged stems without signs of defoliation sprouted at eight times the pre-hurricane rate (Van Bloem et al. 2003). In addition to the sprouts measured, many stems also sprouted above breast height. These higher sprouts would not contribute to increased stem density, basal area, or multi-stemmed growth forms common to Guanica Forest, but would fill in the small canopy gaps opened by the hurricane.

DISCUSSION

The effects of Hurricane Georges suggest that hurricane disturbance can be an important force in creating and maintaining the structure of West Indian dry forests. The hurricane reduced the number of large-diameter stems in windward sites by snapping or uprooting but without necessarily causing mortality of these trees due to subsequent resprouting. Low mortality and abundant sprouting would, over time, lead to increased stem density and multi-stemmed trees without changing species composition (Van Bloem 2004).

HURRICANE EFFECTS ON GUÁNICA FOREST IN CONTEXT OF PREVIOUS STUDIES.— Hurricane effects have been studied in nine tropical and subtropical dry forests, including this study, but comparing hurricane effects from different storms or forests is difficult because the combined effects of storm intensity and duration cannot be easily standardized. However, Everham and Brokaw (1996) and Whigham *et al.* (1999) reviewed the effects of catastrophic winds on various temperate and tropical forests, providing a context into which our results can be placed.

In general, mortality and damage were low in dry forests (Table 6). Guánica Forest (12.4%) was near the middle of the range (7–32%) in stem damage, but lost the most basal area (21%). As suggested by Whigham *et al.* (1999), mortality and basal area loss were lower in dry forests than in wet forests, as was structural damage, with the exception of the S. Florida site (Table 6).

Guánica Forest incurred disproportionate damage to larger-diameter stems – a general trend for dry forests hit by category 3 or stronger hurricanes. Hurricanes affected larger diameter trees in Jamaica (Wunderle et al. 1992), St. John (Reilly 1991), and Sri Lanka (Dittus 1985). In Guadalupe, stems of 7.5–15 cm DBH (compared to average stand DBH of 7 cm) were most affected while those >15 cm were less affected. Everham and Brokaw (1996) proposed a unimodal pattern of damage relative to stem diameter with the most damage in intermediate-size stems. This was not the trend in dry forests but large-diameter stems can be quite rare in these forests. For example, our samples included only 86 stems larger than 15 cm DBH, and only 26 stems >20 cm. Therefore, dry forests may represent only the increasing part of the curve.

In Guánica Forest, stem size influenced the mode of damage incurred (Figure 5b). Tall, wide-diameter stems would be most exposed to hurricane winds, but potentially the best anchored. Branch loss on these stems would reduce wind resistance before snapping or uprooting occurred (Vogel 1994). Uprooting was absent in larger stems, suggesting that their root systems were strong enough to withstand winds. Leaning stems were most common in small size classes because thin, flexible stems bent without breaking. Only the distribution of snapped stems across diameter classes followed the unimodal pattern predicted by Everham and Brokaw (1996). Fall-direction patterns indicated that the strongest hurricane winds created the most damage (Figure 6), a commonly observed pattern

(Boose et al. 1994). The greater variability of fall directions in the forest fragments reflects their position in relation to the trajectory of the storm and the mitigating effects of topography.

As in other forests, aspect and forest type influenced damage severity (Everham and Brokaw 1996). Native-north forest incurred substantially less damage than native-south stands. The low damage rates in mahogany plantations and Leucaena forests can be attributed to a combination of factors. First, dominance by trees of a single species and age leads to a continuous canopy resistant to wind. Second, the mahogany plantations were in valleys and the Leucaena forests were on flat land and therefore relatively sheltered. Neither introduced forest type was found on ridges or south facing slopes and it was therefore impossible to determine whether their lower damage rates were due to topography or forest type.

RESISTANCE, RESILIENCE AND THE POTENTIAL EFFECTS OF NUTRIENTS.—Guánica Forest contained species that exhibited either resistance (displayed by low rates of damage) or resilience (low mortality and high sprouting) to hurricane winds, which resulted in only minor changes in species composition. Resistance was increased by the prevalence of multi-stemmed trees because the likelihood of mortality was lower and wind-speed effects on any one stem in a clump were reduced (Vogel 1994). Resistance may also be related to nutrient supply (DeAngelis et al. 1989). Following a hurricane in Hawaii, trees in nutrient-limited moist forests resisted damage, breaking less than those in fertilized plots. Conversely, fertilized trees responded with higher post-hurricane growth rates and productivity (Herbert et al. 1999). Similarly, Guánica Forest's structural resistance may be related to water or phosphorus limitation, both of which are in short supply (Lugo and Murphy 1986). Trees in resource-limited environments tend to invest high amounts of carbon into physical structure built for strength and longevity (Chapin 1980).

Unable to undergo retranslocation, hurricane leaf litter provided a nutrient pulse to the forest floor equal to average annual inputs with two-thirds of the rainy season remaining. Studies in wet forests have shown that pulses of dead wood resulted in short-term (< 5 yr) immobilization of nutrients in microbial pools and decreased forest productivity (Zimmerman et al. 1994, Scatena et al. 1996). However, dry forest soils rarely remain wet throughout the entire rainy season and wet-dry cycles can release a significant portion of immobilized nutrients by plasmoptysis of microbes (Kieft et al. 1987, Lodge et al. 1994a, Jaramillo and Sanford 1995, Campo et al. 1998). Some portion of the hurricane nutrient pulse may therefore have been available for plant uptake, aiding sprout development and refoliation (Lugo and Murphy 1986, Cornejo et al. 1994, Cuevas and Lugo 1998).

EFFECTS OF FRAGMENTATION.—Overall damage rates in forest fragments of the region were similar to Guánica Forest. Throughout the dry forest zone, larger-diameter stems incurred proportionally higher structural damage than smaller stems. Most fragments were located on sites that are highly marginal for cultivation or grazing due to slope or thin, rocky soils (Lugo et al. 1996). These sites, like ridgetops in Guánica Forest and slopes in Luquillo Forest (Wadsworth and Englerth 1959, Basnet et al. 1992, Basnet et al. 1993, Scatena and Lugo 1995), provided poor anchorage for trees and resulted in uprooting being the most common type of structural damage in fragments.

SHORT-TERM RESPONSE.—Whereas hurricane disturbance resulted in >20% stem mortality in moist or wet tropical forests (Everham and Brokaw 1996), mortality was low in

Guánica and other dry forests (Table 6). Catastrophic stem mortality (CSM: mortality resulting directly from a disturbance) was only 2% after 9 months for stems of ≥2.5 cm DBH. Mortality was unrelated to stem size, but this was not surprising considering that larger stems have root systems able to support a flush of new sprouts. The 2% mortality rate would lead to an average loss of 240 stems/ha and 0.4 m^2/ha basal area (Murphy and Lugo 1986b). We estimated CSM because delayed mortality can continue for at least 4 yr after a hurricane (Dittus 1985, Lugo and Scatena 1996) as heavily damaged or defoliated stems may die as a result of subsequent stresses such as seasonal or more prolonged droughts (Lugo and Waide 1993, Walker 1995). Although hurricane mortality in stems did not show an association with size class, if delayed mortality caused by CSM is related to structural damage or to degree of defoliation, then larger stems may eventually die in higher proportions.

Over time, however, it is unlikely that CSM will impact as many total stems as background stem mortality (BSM: mortality due to senescence or competition). BSM in Guánica Forest has been calculated at 0.3% yr^{-1} (PG Murphy unpub data). Although CSM from Hurricane Georges was nearly seven times greater than BSM, a hurricane as strong as Georges would have to cross the forest once every ten years to kill the same the number of stems, or twice as often as has historically occurred (Salivia 1972, Quiñones 1992, Miner-Solá 1996).

Whigham *et al.* (1999) predicted that sprouting would be an important response in dry forests, particularly when mortality and damage rates were low. Furthermore, they predicted that sprouting would be greater on damaged stems and that the sprouting response would result in minimal changes in species composition of the forest. The prevalence of sprouting following Hurricane Georges (Figure 7) largely followed these predictions except that sprouting occurred regardless of mode or severity of structural damage, even on undamaged stems (Van Bloem et al. 2003). Survival of sprouts would generate multi-stemmed trees and result in the dense, clumped growth form of West Indian dry forest. Although the cohort of new sprouts experienced some mortality, 88% survived two years after the hurricane (Van Bloem et al. 2003) and, in some cases, sprout growth exceeded 2 m in height. With a forest-wide sprouting rate of 33%, it would take only two hurricanes per tree generation to achieve the current proportion of multi-stemmed trees (42%), assuming sprouting effects were roughly additive, or a single hurricane in heavily impacted areas, such as the ridgetops (Figure 7). Based on typical growth rates (Murphy *et al.* 1995), and the size of some stems in multi-stemmed trees, it appears that many stems could have arisen as a response to a hurricane in 1928 (Figure 1). Although we recognize that alternative explanations exist (*e.g.* cutting and drought), our observations support hurricane disturbance as a plausible explanation for the maintenance of high stem densities seen in Guánica Forest and throughout dry forests of the West Indies.

Whigham *et al.* (1999) noted that "there are few examples where it has been shown that the structure and dynamics of the forest are strongly influenced by periodic hurricane events as much or more than by background canopy gaps." Dry forests of the West Indies may be an exception. As demonstrated in Guánica Forest, hurricanes disproportionately damaged larger stems and promoted sprouting at or near the base of trees, even on undamaged stems. Damage rates were primarily determined by stem diameter and topographic exposure to wind. Damaged stems did not necessarily die. Sprouting minimized mortality and changes in species composition, and increased the potential to add new stems to the forest. Post-hurricane mortality rates were elevated over background mortality, but would affect fewer stems over time. A collection of forest fragments incurred the same rate and type of structural damage as Guánica Forest, suggesting that the spatial extent of a forest stand did not influence hurricane effects. The effects of Hurricane Georges on the structure of Guánica Forest were comparable to other cases of hurricane disturbance in dry forests, but were less than those reported for most wet tropical forests. Climate characteristics alone fail to explain dry forest structure in the West Indies and, as hurricanes are common in the region (Neumann et al. 1993), we conclude that the unique West Indian dry forest structure arises at least in part from recurring hurricane disturbance.

Table 5-1. Description of sites in SW Puerto Rico used to assess hurricane effects. All sites except the fragments were in Guánica Forest.

Forest Type	**# of plots**	**Sampled Area (m^2)**	**Aspect**	**Elevation (m)**	**# of stems ≥ 2.5 cm**	**Date established**	**Prior land use**
Leucaena[a]	5	2000	Flat	175	359	1996	Baseball Field
Leucaena[a]	5	2000	All	100	390	1996	Houses
Leucaena[a]	5	2000	All	100–175	455	1996	Agriculture
Native-North[a]	5	2000	North	100	667	1996	Charcoal Pits
Native-North[a]	5	2000	North	100	591	1996	Mature[e]
Native-South[b]	1	690	South	175	456	1981	Charcoal Pits/ Mature
Native-South[c]	2	1800	South	55–185	1430	June 1998	Mature[e]
Ridgetop[c]	2	200	None	175–200	162	Nov. 1998	Mature[e]
Mahogany[c]	3	300	South	100–150	126	Oct/Nov 1998	Mahogany Plantation
Fragments[d]	19	6790	All	5–175	f	Jan. 1999	Forest fragments

[a] Molina Colón 1998 [b] Murphy & Lugo 1986 [c] this study [d] Ramjohn 2004 [e] Mature forest stands did not show signs of major or recent human disturbance. f: Only dead or damaged stems in transects were measured in fragments.

Table 5-2. Hurricane effects on representative tree species in Guánica Forest. Defoliation was assessed in native-south forests and mahogany plantations within two weeks for species with ≥25 total trees. Median defoliation rate was 50%. Damage was assessed in all forest types for species with ≥25 total stems. Average damage rate was 12.4%. Designation of species as evergreen, deciduous, and pioneer from Little and Wadsworth (1964), Little *et al.* (1974), and Molina Colón (1998).

Species	Successional status	Total trees	Percent ≥50% defoliated	Leaf habit
Defoliated trees				
Guettarda krugii		42	91	deciduous
Bursera simaruba	pioneer	65	86	deciduous
Krugiodendron ferreum		25	84	evergreen
Coccoloba diversifolia		83	83	evergreen
Exostema caribaeum	pioneer	90	78	deciduous
Pictetia aculeata	pioneer	97	75	deciduous
Amyris elemifera		115	73	evergreen
Eugenia foetida		94	73	evergreen
Swietenia mahagani		37	51	deciduous
Gymnanthes lucida		257	43	evergreen
Damaged stems		**Total stems**	**Percent damaged**	
Pilosocereus royenii	pioneer	47	63.8	
Erythroxylum rotundifolium		35	37.1	
Bursera simaruba	pioneer	113	30.1	
Pisonia albida	pioneer	52	25.0	
Erithalis fruticosa	pioneer	37	21.6	
Eugenia foetida		184	12.5	
Exostema caribaeum	pioneer	130	12.3	
Krugiodendron ferreum		39	10.2	
Amyris elemifera		204	10.1	
Bourreria succulenta	pioneer	54	9.3	
Bucida bucerus		65	9.2	
Swietenia mahagani		54	7.4	
Thouinia portoricensis		148	7.4	
Gymnanthes lucida		452	7.1	
Crossopetalum rhacoma		30	6.7	
Coccoloba diversifolia		320	6.3	
Coccoloba microstachya		190	5.8	
Guettarda krugii		187	5.3	
Pictetia aculeata		218	2.8	
Pithecellobium unguis-cati	pioneer	44	2.3	
Tabebuia heterophylla		138	1.1	
Eugenia xerophytica		55	0.0	

Table 5-3. Biomass and nutrient content of litterfall and standing litter in the 1.44-ha native-south forest plot. Mass values of standing litter are expressed as means (standard errors) and are corrected for ash-free dry mass.

Component	Dry mass	N	Ca	P	K	Mg
	g/m^2	------------	kg/ha	-----------		
October 1998 Standing Litter [a]						
Leaves	845 (126)	160	370	3.8	39.5	19.6
Brown wood	573 (65)	69	195	1.4	18.8	5.0
Green wood	30 (16)	3	7	0.1	1.5	0.4
Misc.[b]	356 (38)	92	358	2.3	21.7	12.7
Total	1833 (148)	324	930	7.6	81.5	37.7
July 1981 Standing Litter [a, c]						
Leaves	1033 (56)	165		3.7	17.0	
Wood	244 (1) [d]	24		0.5	2.3	
Total	1277 (56)	189		4.2	19.3	
September 1998 Litterfall						
Leaves	238.7	43.8	44.4	1.2	17.5	4.5
Wood	509.5	40.3	140.7	1.1	21.0	3.1
1981-82 Annual Litterfall[c]						
Leaves	433.7	44.3		0.7	35	
Wood	45.6	4.2		0.08	1.0	

[a] *N*=26. [b]Miscellaneous category includes small leaf fragments, fruits, and flowers. [c]July 1981 standing litter and 1981-82 leaf litter values from Lugo and Murphy 1986; *N* = 30, missing nutrient values were not reported therein. [d]Calculated from data reported in Murphy and Lugo (1986) and Lugo and Murphy (1986).

Table 5-4. Hurricane-related mortality of trees and stems ≥2.5 cm DBH in four types of forest in Guánica Forest 9 mo after Hurricane Georges.

Site	**Mortality %**[a]		**Total Trees live and dead**	**Total Stems live and dead**	**Area sampled (m^2)**
	Trees[a]	**Stems**[a]			
Native-South	1.6[b]	2.7	850	1886	2490
Native-North	2.2	1.6	836	1223	4000
Ridgetops	2.0	7.4	102	162	200
Leucaena	1.3	0.7	853	1172	6000
Total	1.7	2.0	2641	4443	12690

[a] There were no significant differences in tree mortality among sites ($\chi^2 = 2.262$; $P = 0.45$; 3 df). Stem mortality differed among sites ($\chi^2 = 36.664$; $P < 0.0005$; 3 df).

[b] Tree mortality reported here is only for the two 1.0-ha sites in native-south stands (sampled area was 1800 m^2) because multi-stemmed trees in the 1.44-ha native-south site were not assessed for mortality. Stem mortality includes all native south stands.

Table 5-5. Percent stem mortality by size class for height and DBH for all stems in native-north, native-south, ridgetop, and Leucaena plots. Mortality was not assessed in mahogany plantations.

Height (m)	**3-3.9**	**4-4.9**	**5-5.9**	**6-6.9**	**7-7.9**	**8-8.9**	**≥9.0**	**Total**
Total stems	447	865	843	738	364	196	213	3690[a]
% Mortality	2.7	2.5	3.2	2.0	1.4	1.0	1.9	2.0

DBH (cm)	**2.5-4.9**	**5.0-7.4**	**7.5-9.9**	**10.0-12.4**	**12.5-14.9**	**≥15.0**	**Total**
Total stems	2192	1482	464	153	64	86	4441[a]
% Mortality	2.4	1.8	1.3	1.3	1.6	1.2	2.0

[a] Totals for height and DBH are not equal because heights were not measured on all live stems. Mortality was not associated with size class. For height: $\chi^2 = 6.165$; $P = 0.19$; $\alpha = 0.05$; 4 df; 7 to 9 m height classes pooled. For DBH: $\chi^2 = 4.021$; $P = 0.13$; $\alpha = 0.05$; 2 df; 7.5 to 15 cm DBH classes pooled.

Table 5-6. Comparison of mortality and structural damage caused by hurricanes in various tropical forests.

Forest life zone	Location	Hurricane (Category^a) Year	% Stem mortality (mo after)	% Structural damage (min stem size cm)	% Loss of basal area	Stem size with most structural damage	Reference
subtropical dry	Guánica, PR	Georges (3) 1998	2.0 (9)	12.4 (2.5)	21	> 7.5 cm DBH	1
subtropical dry	St John, US Virgin Is.	Hugo (4) 1989		25 (5)		taller and wider	2
subtropical dry	Sri Lanka	na (3) 1978	14 (42)	32 (na)		taller	3
subtropical dry	Yucatan, Mexico	Gilbert (5) 1988	11.2 (17)	27.6 (10)			4
subtropical dry	Jamaica	Gilbert (3) 1988		5 (3)			5
subtropical dry^b	Dominica	David (4) 1979		4 (10)	7	no trend	6
subtropical dry	Florida	Andrew (4) 1992	11.5 (4)	85 (2)		intermediate width	7
tropical dry	Guadalupe	Hugo (4) 1989	15.8 (16)	21 (3.8)	14	7.5-15 cm DBH	8
tropical wet	various	Category 3-5	1-58 (na)	4.5-80 (4-5)^c	10-58		9

[a] Category based on the Saffir Simpson Index. [b] These sites sheltered from hurricane winds. plantations and palm brakes excluded. [c] For limits defining range, other wet forest studies used 10 cm minimum diameters. Missing data were not reported or calculated in original sources. References: 1-this study; 2-Reilly 1991; 3-Dittus 1985; 4-Whigham *et al.* 1991 ; 5-Wunderle *et al.* 1992; 6-Lugo *et al.* 1983;7-Slater *et al.* 1995; 8-Imbert *et al.* 1996; 9-from Everham and Brokaw 1996. Reports of hurricane effects on dry forests of Tonga (Woodroffe 1983), Guam (Kerr 2000), Mauritius (King 1945, Sauer 1962), and Belize (Stoddart 1962), did not quantify damage rates or mortality

Figure 5-1. Hurricane tracks with year of occurrence of the 15 storms most likely to have affected Guánica Forest. Hurricane Georges is the thickest line across the center. Bolded years are hurricanes likely to have had the strongest effects on Guánica Forest. Solid lines are known hurricane tracks. Dashed lines are best-estimate trajectories based on Salivia (1972), Neuman *et al.* (1993), and Miner-Solá (1996). Hortense was a low-level storm that, according to local reports, had little impact on the forest. Luquillo Forest and Hurricane Hugo included for reference.

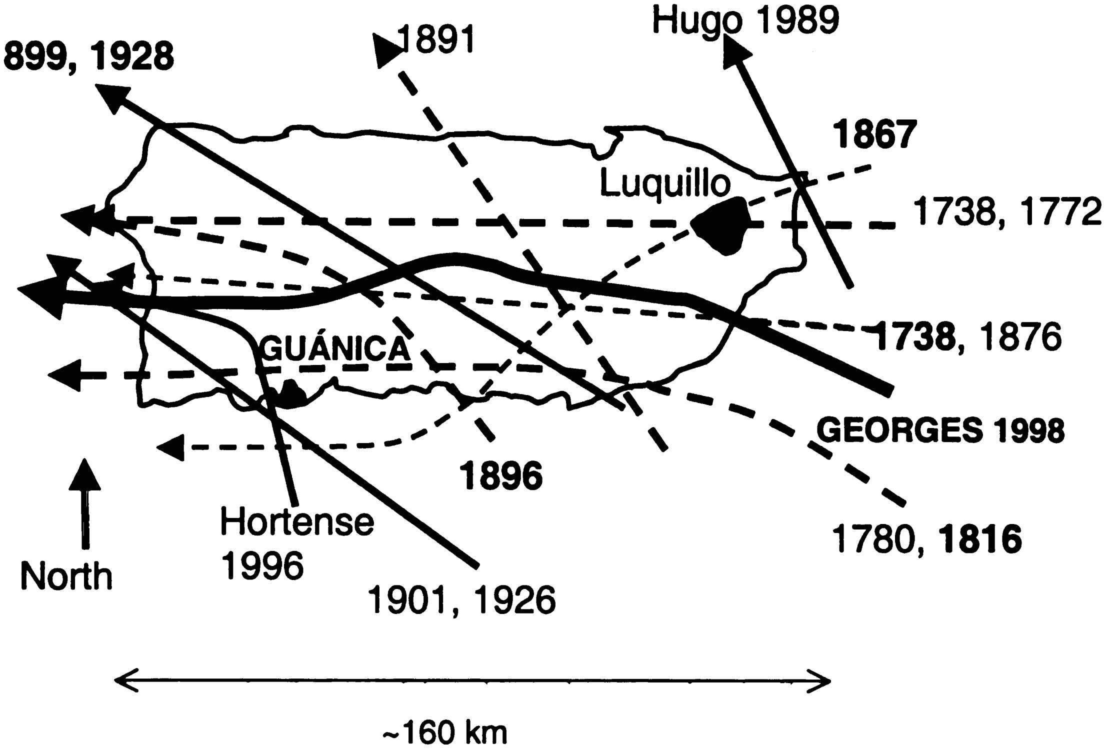


FIGURE 5-2. Locations of study plots in Guánica Forest and nearby fragments (inset) in southwestern Puerto Rico. Forest types indicated by symbols in legend. Numbers next to symbols denote multiple plots of a type in the area.

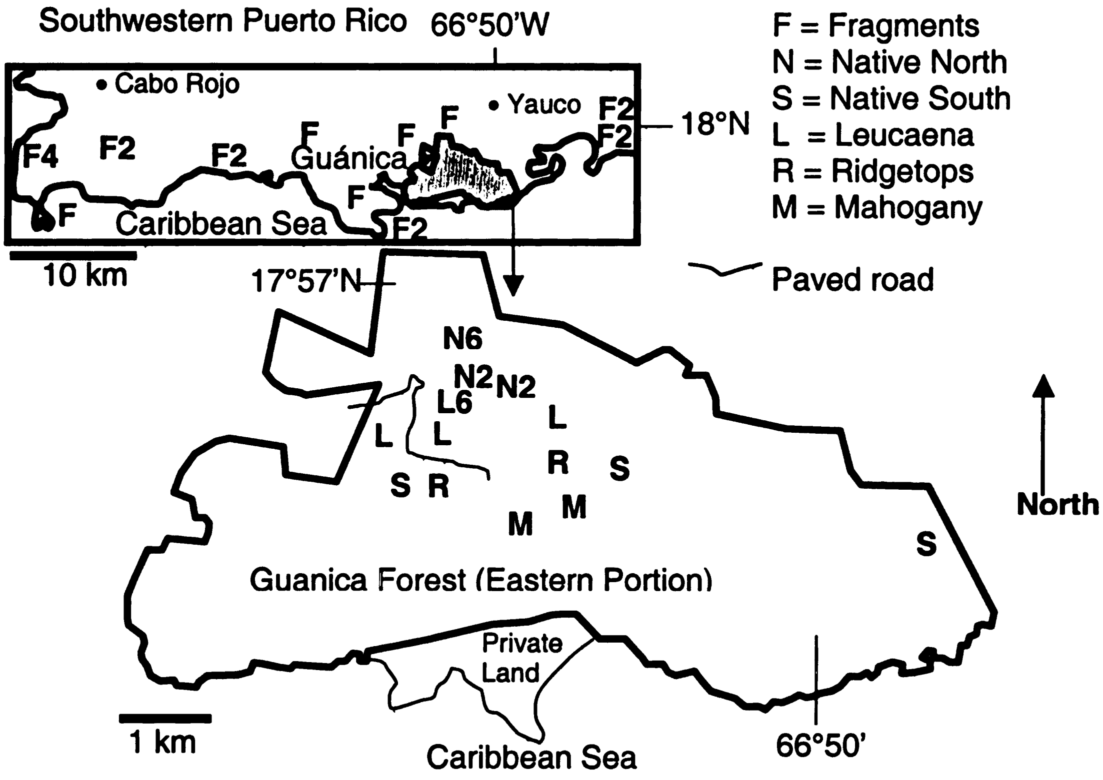


FIGURE 5-3. Hurricane effects on stems for different forest types within Guánica Forest, Puerto Rico. Structural damage includes uprooting, snapping, breakage of large branches, or leaning. "Undetermined" refers to stems that lacked structural damage but were sampled after significant refoliation had occurred. Most of the stems in this category probably had been defoliated. Numbers below forest type labels indicate the total number of stems sampled in each forest type. "All forests" is pooled data for the five forest types.

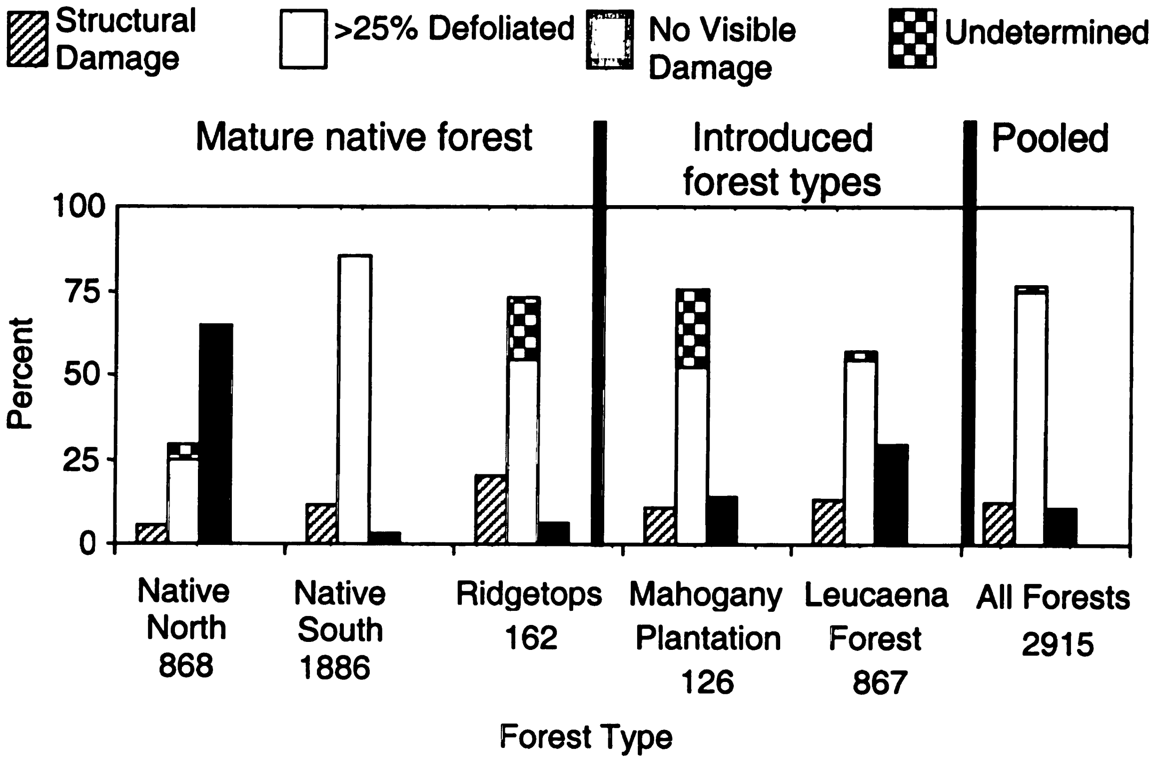


FIGURE 5-4. Stem density of various modes of structural damage in different stands of Puerto Rico dry forest. Sample included all stems ≥ 2.5 cm DBH. Numbers below forest type labels indicate total stem density of each forest type. *Branch loss not estimated for native-north or Leucaena sites, structural damage densities are therefore underestimated.

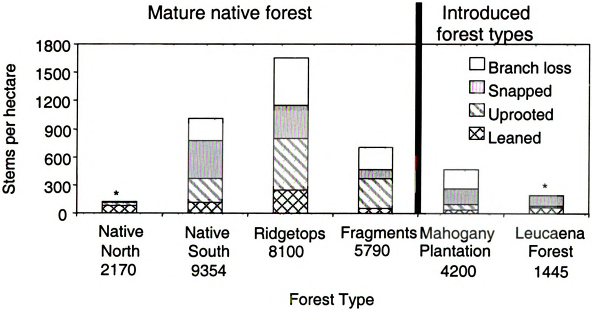


FIGURE 5-5. (A) Proportion of structural damage incurred by stems within diameter classes for three forest types in Guánica Forest. Broken branches not assessed in native-north or Leucaena forests. (B) Stems incurring various modes of structural damage as a proportion of all stems in each diameter or height class. Data included stems only from native-south, mahogany, and ridgetop sites because broken branches were not assessed for native-north or Leucaena forest.

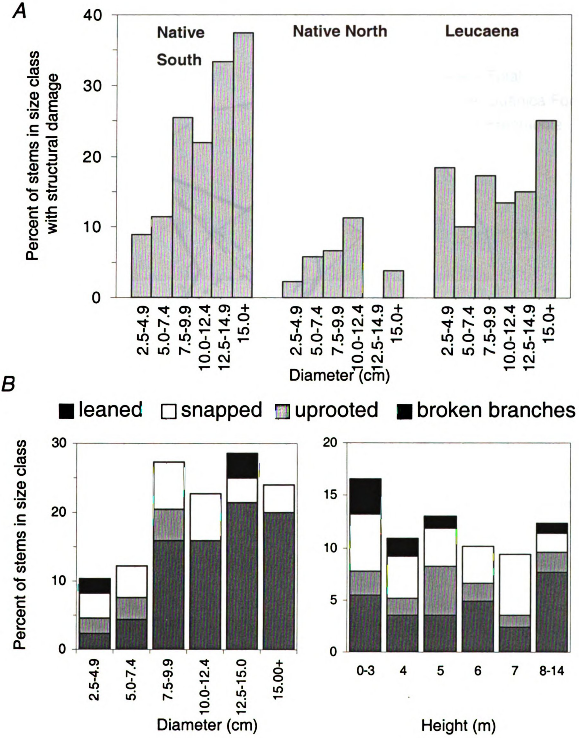


FIGURE 5-6. Stem-fall directions of snapped, uprooted, and leaning stems in Guánica Forest and nearby forest fragments. Totals are pooled from both Guánica Forest and the fragments. Strongest winds from Hurricane Georges came from the southeast. The radial scale is number of stems. The direction of fall was measured for 259 fallen stems in total; 119 from Guánica Forest and 140 from fragments.

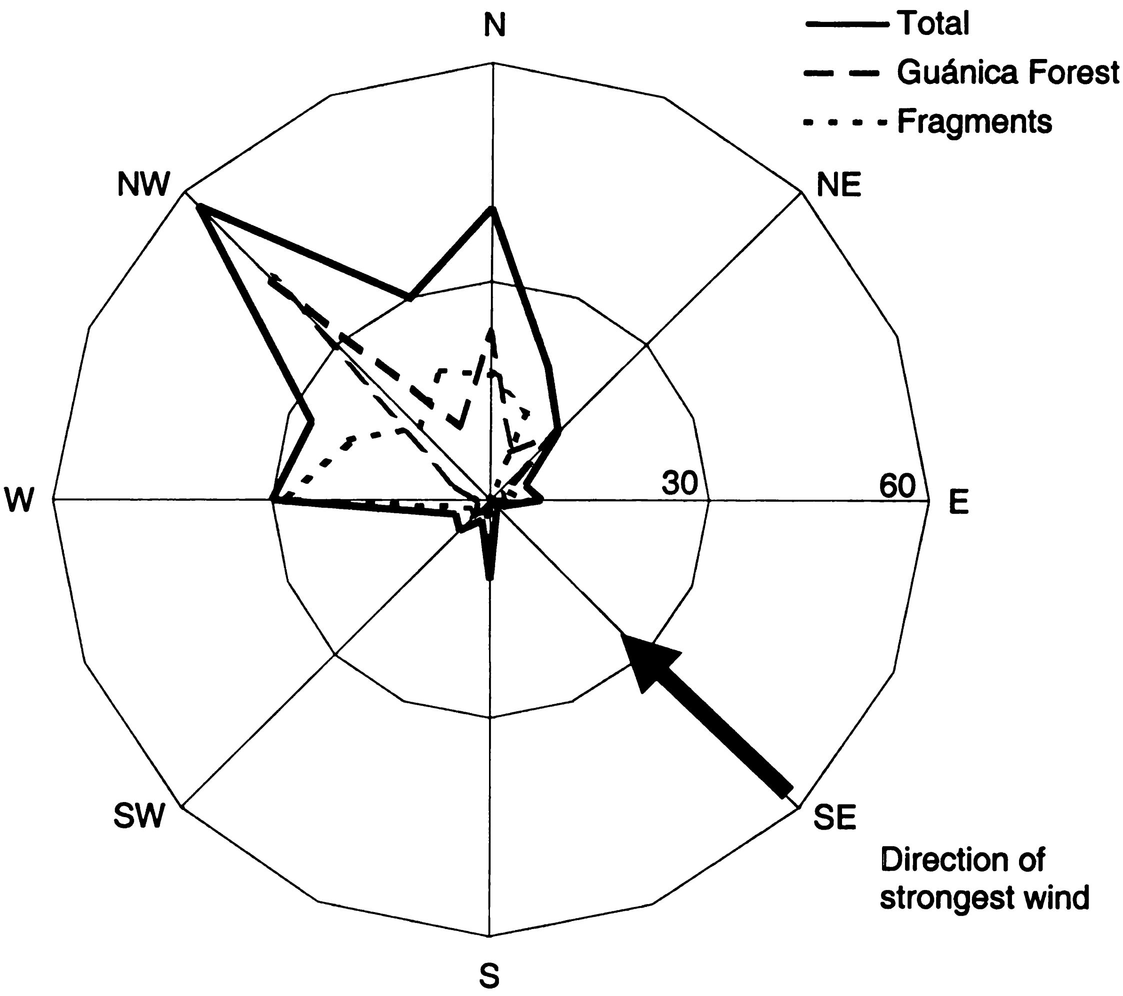
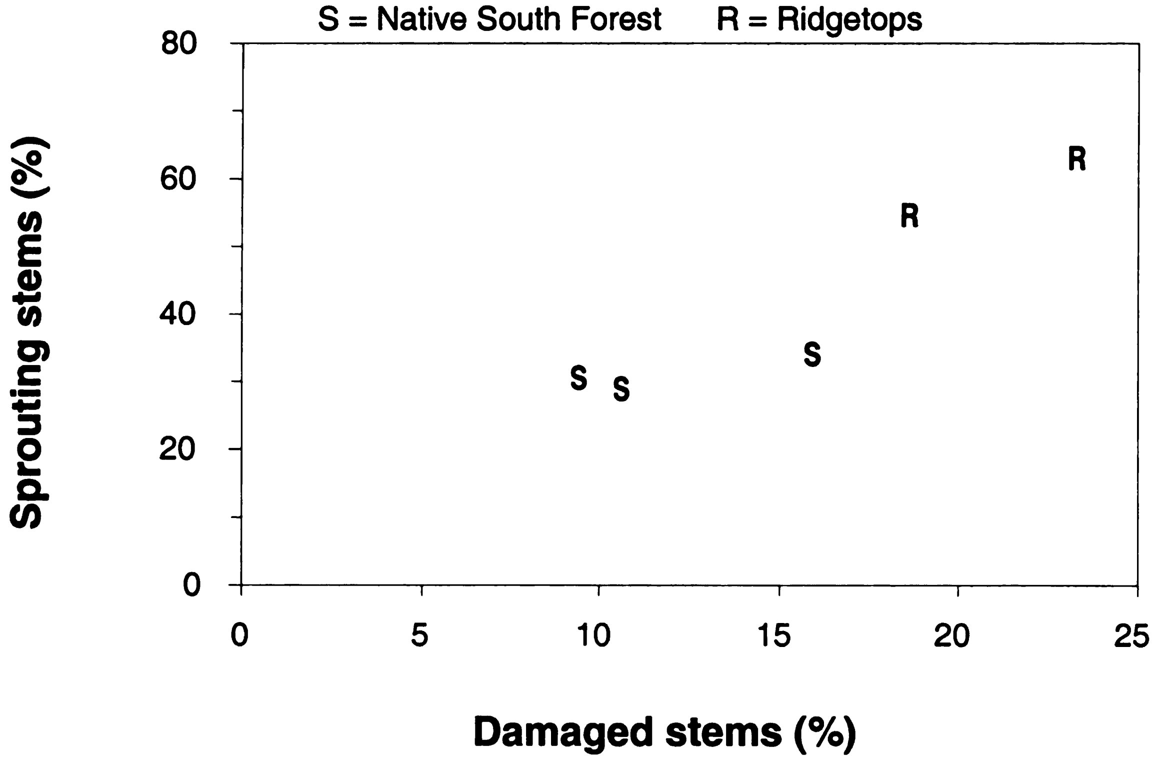


FIGURE 5-7. The relationship between sprouting and structural damage to stems in Guánica Forest as a result of hurricane winds. Structural damage includes uprooting, snapped stems, breakage of large branches, and leaning. Only living tagged stems were surveyed for sprouting. Each point represents a site. All sites are located in mature native south (S) or ridgetop (R) forests. Note that in all sites, the percentage of stems with new sprouts exceeds the percentage of stems with structural damage reflecting sprouting on defoliated and unaffected stems. Sprouting rates and structural damage rates are correlated (r = 0.94; *P* = 0.017). Pre-hurricane sprouting rates were 3.5%.



CHAPTER SIX

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Subtropical dry forest trees with no apparent damage sprout following a hurricane

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Abstract: Hurricane Georges passed over mature dry forest near Guánica, Puerto Rico in September, 1998. The trees of the dense, short-statured Guánica Forest have a multi-stemmed structure unique to the West Indies in the neo-tropics, a characteristic that has been difficult to explain. Following the hurricane, we measured sprout development below breast height on 1407 stems to assess how response to hurricane disturbance may influence dry forest structure. Basal sprouting increased 8-14 fold after Hurricane Georges. Basal sprouting was found on almost 68% of damaged stems and, notably, on about 32% of undamaged stems. Basal sprouting was found in all common species surveyed. The rate of defoliation was not related to sprout production. After two years, sprout mortality was only about 13%. We conclude that continued growth of basal sprouts will contribute to high stem densities and multi-stemmed growth forms commonly found in Guánica Forest and in the hurricane-prone West Indies.

Resumen: El huracán Georges pasó sobre el bosque maduro cerca de Guánica, Puerto Rico, en septiembre de 1998. Los árboles del Bosque Guánica, que es denso y de baja estatura, poseen numerosos tallos, característica que es única de las Indias Occidentales en el Neotrópico y que ha sido difícil de explicar. Después del huracán, nosotros medimos el desarrollo de rebrotes por debajo de la altura del pecho en 1407 tallos con el fin de evaluar de qué manera la respuesta al disturbio del huracán puede influir sobre la estructura del bosque seco. El rebrote basal incrementó entre 8 y 14 veces después del huracán Georges. Se encontró rebrote basal en casi 68% de los tallos dañados y, de manera notable, en cerca de 32% de los tallos no dañados. El rebrote basal fue observado en todas las especies comunes examinadas. La tasa de defoliación no estuvo relacionada con la producción de rebrotes. Al cabo de dos años, la mortalidad de los rebrotes fue tan sólo de alrededor de 13%. Concluimos que el crecimiento continuo de rebrotes basales contribuye a tener altas densidades de tallos y formas de crecimiento con múltiples troncos, comúnmente encontradas en el Bosque Guánica y en general en las Indias Occidentales, susceptibles a los huracanes.

Resumo: O furacão Georges passou sobre uma floresta seca adulta perto de Guánica, Porto Rico em Setembro, 1998. As árvores da floresta densa de Guánica, de baixo porte têm uma estrutura de troncos múltiplos, única nos neo-trópicos das Índias Ocidentais, característica esta que tem sido difícil de explicar. Depois do furacão, foi medido o desenvolvimento dos rebentos abaixo da altura do peito numa amostra de 1407 troncos para avaliar a resposta às perturbações e à forma como influência a estrutura da floresta seca. A rebentação basal aumentou entre 8 – 14 vezes depois do furacão George. Encontrou-se rebentação basal em quase 68% dos troncos afectados e, normalmente, em cerca de 32% dos troncos não afectados. A rebentação basal ocorreu em todas as espécies comuns

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comuns amostradas. A taxa de desfoliação não estava relacionada com a produção de rebentos. Após dois anos, a mortalidade dos rebentos só atingiu cerca de 13%. Conclui-se que o crescimento continuado dos rebentos basais contribuiu para a elevada densidade de troncos e as formas de crescimento de múltiplos troncos encontrados na floresta de Guánica e na zona das Índias Ocidentais propensa aos furacões.

Key words: Forest structure, Guánica Forest, hurricane disturbance, Hurricane Georges, multiple stems, multiple-stemmed, sprouting, subtropical dry forest.

Introduction

Among the environmental factors that influence the structure of tropical and subtropical dry forests are low annual rainfall and seasonal drought. However, comparisons among dry forests with similar climate regimes show that there are major differences in stem density (Murphy & Lugo 1986b, 1990). Generally, stem densities are higher in coastal or Caribbean forests. High densities can result from a multiple-stemmed growth habit of trees which is prevalent in Guánica Forest, Puerto Rico (at least 42% of trees) (Murphy & Lugo 1986b; Ramjohn 2003) and North Andros Island, Bahmas (Smith & Vankat 1992). Drought may be a factor involved in generating multi-stemed trees, but stem densities in Guánica Forest are at least twice that found in continental dry forests (e.g., Chamela and Ecuador) (Josse & Balslev 1994; Lott *et al.* 1987). Considering the similar climates of dry forests throughout the tropics, it seems that the high stem density found in Guánica Forest must be influenced by some other factor. Multistemmed trees have been documented as a response to cutting by humans, grazing or browsing by animals, fire damage, or stem breakage by storms (Gonzalez & Zak 1996; Kelly *et al.* 1988; Molina Colón 1998; Murphy *et al.* 1995). Each of these disturbance types would result in the loss of terminal buds and wounding near the base of tree, leading to internal changes in hormone balances which could affect sprouting. Recent discussions of sprouting response to disturbance suggest that sprouting should occur on trees immediately below the point where biomass has been lost (Bellingham & Sparrow 2000; Bond & Midgley 2001). Thus, defoliated trees should sprout from leaf axils while cut trees should sprout from roots or stumps. Our observations in Guánica Forest after Hurricane Georges suggest that strong winds can elicit basal sprout development without breaking stems – thus providing a new explanation for the multistemmed growth habit of Caribbean Forests.

Wind stress results in different responses by forests depending on the severity of the wind. Trees in chronically wind-stressed environments are often shorter with larger diameters than individuals of the same species in sheltered environments (Telewski 1995), develop buttresses (Ennos 1995), or produce reaction wood (reviewed in Timell 1986). Compared to chronic low-level stress from the trade winds, hurricanes impact a forest with extreme, but relatively brief, wind stress. However, the effects of a single acute wind event can drastically change the developmental trajectory of a forest (Brokaw & Grear 1991; Foster & Boose 1995; Steudler *et al.* 1991). Hurricane-force winds can inflict plastic damage (i.e., irreversible, as opposed to elastic, or reversible, damage) on stems including defoliation, snapping, uprooting, and branch loss (Foster & Boose 1995). In such cases, trees frequently respond by sprouting, as seen after Hurricane Joan in Nicaraguan wet forest (Vandermeer *et al.* 1990; Yih *et al.* 1991), after Hurricane Hugo in dry forests of Guadaloupe (Imbert *et al.* 1998) and wet forests of Puerto Rico (Walker 1991; Zimmerman *et al.* 1994) and after Hurricane Gilbert in Yucatan dry forest (Whigham *et al.* 1991) and Jamaican montane wet forest (Bellingham *et al.* 1994).

There is some evidence for sprouting in apparently undamaged trees exposed to wind stress. Sprouting has been noted below 2.5 m height on about 47% of "undamaged or lightly damaged" stems following hurricanes in Jamaica (Bellingham *et al.* 1994). In Puerto Rican rainforest about 57% of "undamaged" stems sprouted after Hurricane Hugo in one study (Zimmerman *et al.* 1994), but the location of sprouts on stems was not noted. Sprouts developing within 40-50 cm of the ground may lead to multi-stemmed trees if the sprouts grow and survive. Walker (1991) reported 6% of "upright" (not snapped or uprooted) stems in subtropical wet forest sprouted below 50 cm on the trunk. Imbert *et al.* (1998) and Vandermeer *et al.* (1995) mention sprouting below 50 cm on trunks, but neither specifically state whether undamaged stems sprouted at that height.

To date, no satisfactory explanation for the high stem density of mature dry forest (>12,000 stems ha^{-1}) nor the prevalence of multi-stemmed trees (42%) in study plots near Guánica, Puerto Rico, has been proposed. Because of the governmentally protected status of Guánica Forest, cutting and grazing in the vicinity of our plots has been light or absent in the last 70 years and fire has never been an influential factor. Where cutting has taken place in Guánica Forest, sprouting is common (Molina Colón 1998; Murphy *et al.* 1995), but sprouting is also common in areas which were not subject to cutting. Dunphy *et al.* (2000) analyzed multi-stemmed trees in Guánica Forest and concluded that for a majority of species the growth form was natural – not the result of cutting. The last few hurricanes that have passed over the forest have broken few stems (<13%) (Van Bloem *et al.* 2001). Sprout development following Hurricane Georges has provided new insight into tropical dry forest structure. Following the hurricane, we expected that: (1) sprouting frequency would be higher on damaged stems, (2) sprouting would be proportional to defoliation because sprouting response might be related to biomass loss, and (3) a majority of sprouts produced after Hurricane Georges would die after the first or second dry season due to thinning of new sprouts as they competed for resources. The objectives of this paper are to evaluate these expectations; to report patterns in post-hurricane sprouting, and to assess the potential role of hurricanes in creating multi-stemmed trees and short-statured, dense forests.

Methods

Guánica Forest is comprised primarily of semi-deciduous dry forest and is located along the southwestern coast of Puerto Rico (17° 58′ N, 65° 30′ W). The forest was originally protected in 1917 and its boundaries expanded in the 1930's to include all the plots within this study. Canopy height is generally 5-7 m, and density of live stems (>2.5 cm dbh) averages 12,000 per hectare (Murphy & Lugo 1986b). About 42% of trees are multiple-stemmed and they include 56% of all stems (Murphy & Lugo 1986b). Annual rainfall averages 860 mm, 45% of which comes between September and November, corresponding to the height of hurricane season (Murphy & Lugo 1986a). Mean annual temperature is 25.1°C and the PET/precipitation ratio averages 1.4 (Murphy & Lugo 1986a). Previous investigations in the forest have determined that the multi-stemmed growth habit of the trees cannot be solely explained by cutting, although this is a likely explanation for a few species (Dunphy *et al.* 2000).

Hurricane Georges crossed over the island of Puerto Rico on September 21-22, 1998. The southern portion of the hurricane's eye passed over Guánica Forest. This category 3 hurricane (Saffir-Simpson Index) had sustained winds of 176-184 km h^{-1} with gusts up to 240 km h^{-1} (Bennett & Mojica 1998). Rainfall measured in the forest was 151 mm during the two days of Georges' passage. Average September rainfall in Guánica forest is 155 mm (Murphy & Lugo 1986b). Hurricane-force winds from Georges impacted Guánica forest for about four hours.

In the last 300 years, hurricanes have passed over the areas containing our research sites at an average return rate of 25 years (Miner-Solá 1996; Salivia 1972). The last hurricane that passed over Guánica Forest and had a strength similar to Hurricane Georges was San Felipe in 1928 (Salivia 1972).

We studied sprouting response in five plots in Guánica Forest ranging from 0.01 to 1.44 ha in size and located in various topographic settings that represent a gradient of wind conditions determined by slope, aspect, and elevation. Low elevation, topographically level plots had the least wind exposure while plots at higher elevation (e.g. 175-200 m) with steeper, south-facing slopes had the greatest exposure. All plots were comprised of semi-deciduous forest (Ewel & Whitmore 1973) and had trees permanently marked and censused for previous studies. Our plots included over 40 species of trees, but have relatively high species evenness (Murphy & Lugo 1986b), as is common in many mature subtropical forests. All plots were on the same type of soil, an alkaline clay mollisol over a limestone base. Within these plots, we had 1407 permanently tagged stems of at least 2.5 cm dbh (measured at 1.4 m).

We determined the type and severity of damage to the 1407 tagged stems in our plots within one week of Hurricane Georges. Snapped trunks, uprooting, loss of large branches, and permanent bending of trees beyond 45° from vertical were considered major structural damage. On stems without major damage, defoliation was estimated visually on a percentage basis. Some trees appeared to escape both major stem damage and defoliation and were considered to have no visible damage. The type and rates of damage and species effects resulting from Hurricane Georges will be reported elsewhere.

Following Hurricane Georges, we measured sprout development on the tagged stems within our plots six times over two years. We considered any woody twig growing from a mature stem below breast height at an angle < 45° from the trunk to be a sprout (Dunphy 1996). To quantify pre-hurricane rates of sprouting, we inventoried all old sprouts on 451 tagged stems along 6 transects totaling 680 m in our largest plot. Subsequently, we were able to distinguish new sprouts by their distinctive bark colors as compared to old sprouts. On all of the 1407 tagged stems, we counted all new sprouts growing at breast height (1.4 m) or lower. Technically, some of these sprouts would be considered branches rather than additional stems; therefore, we noted whether new sprouts arose from trunks or roots and where on the trunk new sprouts emerged from tagged stems. In mature trees, it can be difficult to distinguish between branches and stems when they attain diameters ≥ 2.5 cm, grow at angles < 45° from vertical and emerge from trunks below 40 cm, so we attempted to take this into account with our measurements. The length of the longest sprout on each tagged stem was measured to the nearest cm and its point of origin noted (i.e., ground, or height on trunk).

Results

Pre-hurricane sprouts were present on 16 of 451 stems (3.5%). No new sprouts emerged on the 1407 tagged stems in Guánica Forest within eight days of the hurricane. However, new sprouts were present by mid-November, 1998 (8 weeks post-hurricane), on both damaged and undamaged stems, and by January, 1999 (15 weeks post-hurricane), 481 total stems had new sprouts. In June, 2000 (90 weeks post-hurricane), 493 stems had post-hurricane sprouts (34.2%). The plots with the greatest exposure to hurricane winds had the greatest proportion of sprouting stems (Fig. 1). In each plot, the proportion of sprouting stems was 2–3 times the proportion of stems incurring major structural damage.

The proportion of stems sprouting after Hurricane Georges was 8–14 times higher than before the hurricane. The sprout rate (number of sprouts per stem) was 3–13 times higher than pre-hurricane rates (Table 1). While we expected stems with major structural damage to sprout, we were surprised at the increase in sprouting on defoliated stems and stems without any visible damage. The proportion of stems sprouting and sprout rates did not differ with severity of defoliation (Fig. 2).

New sprouts emerged from both roots and trunks of trees, sometimes in both locations for a single stem (Table 2). Over 73% of sprouting stems had sprouts emerging below 40 cm on a stem.

Tree species in Guánica Forest had different sprouting response patterns after the hurricane.

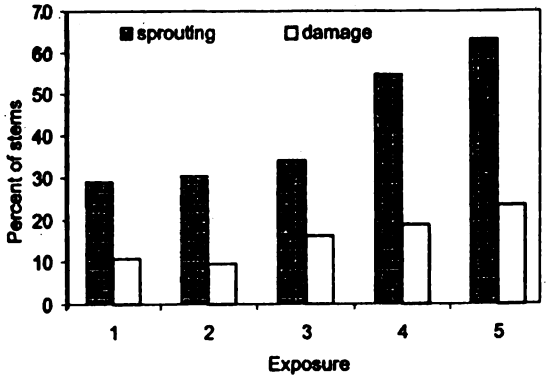

Fig. 1. Percent of stems in Guánica Forest incurring structural damage and with new sprouts relative to wind exposure. Sprouting data are from four months after Hurricane Georges. Structural damage includes snapping, permanent bending, uprooting, or loss of large branches. Exposure is determined by elevation and slope based on wind speeds and directions reported after Hurricane Georges (Bennett 1998), all plots face south. Exposure 1 is most protected at low elevation and a level slope. Exposures 4 & 5 are at the highest elevations, 5 has the steepest slope. Both damage and sprouting are greater at higher exposures (χ^2 tests: $p = 0.016$, $p < 0.00001$ respectively).

Table 1. Sprouting in Guánica Forest, Puerto Rico. Pre-hurricane sprouts were counted on 451 stems. Post-hurricane sprouts were counted on 1407 stems pooled from five plots. Only sprouts developing below breast height (1.4 m) were counted. A sprout was defined as any woody twig with an orientation greater than 45° relative to the ground. Post hurricane sprouts compared against pre-hurricane sprouts using z or t tests as appropriate.

	Total number of stems	% of stems with sprouts	Sprouts per sprouting stem (se)
Pre-Hurricane Sprouts	451	3.5	1.7 (0.3)
Post-Hurricane Sprouts			
Major structural damage	205	48.3***	21.3 (3.3)**
Defoliated stems†	1153	31.8***	10.1 (1.0)**
No visible stem damage	49	28.6***	5.8 (1.6)*

† Stems with defoliation but without major structural damage.

***p < 0.0002; **p < 0.0005; *p < 0.01

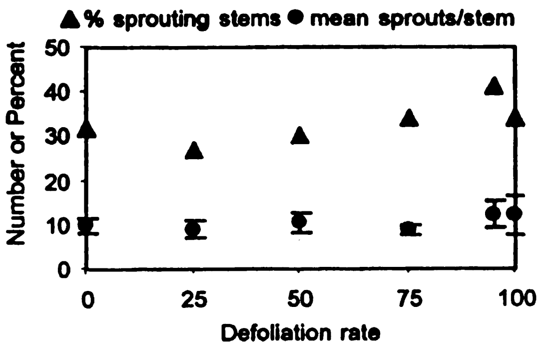

Fig. 2. Trends in proportion of sprouting stems or sprouting rate with defoliation severity in Guánica Forest following Hurricane Georges. Bars are ± 1 SE Pre-hurricane sprouting shown in Table 1. Severity of defoliation is not related to sprouting response. χ^2 tests: $p = 0.60$ for percent of stems sprouting; $p = 0.92$ for sprouts per stem.

Table 2. Percentage of post-hurricane sprouts arising from trunks or roots. Sample size is number of stems sprouting.

All stems (n = 481)	Percent
Only from roots	21.7
Only from trunk	61.1
From both trunk and roots	17.2
At or below 40 cm on trunk	73.4
Defoliated or no damage stems (n = 382)	
Only from roots	24.3
Only from trunk	58.6
From both trunk and roots	17.0
At or below 40 cm on trunk	75.1

For species with at least 10 stems in our plots, 4–100% of stems sprouted (Table 3). For our six most common species, each with at least 100 stems, 15–71% sprouted. Sprout rate ranged from 5–34 sprouts per stem for our 6 most common species. Some produced many short sprouts (e.g. *Exostema caribaeum*) while others produced few long sprouts (e.g. *Coccoloba diversifolia*). For species with at least 20 stems in our plots, the median length of the longest sprouts for each species showed was positively correlated with the number of stems per tree ($p = 0.012$, Fig. 3) and the percentage of multistemmed trees of a species ($p = 0.018$).

By January 1999 there were 5898 new sprouts on the 1407 stems in our plots. By June 2000 sprout mortality was 13.6%, leaving 5095 new sprouts. Mortality for sprouts growing from trunks was about 25%, but this was offset by a 20% increase in root sprouts. Mortality of sprouts was 15.8% on stems with major structural damage and 12.4% on defoliated or undamaged stems. By June 2000, 65% of all post-hurricane sprouts were on defoliated or undamaged stems. The longest sprout on each stem averaged 44 cm in January 1999 and doubled to 89 cm in June 2000.

Discussion

Trees responded to Hurricane Georges by producing a large flush of new sprouts, many at or near the base of trees. After two years, survival of sprouts has been surprisingly high. While we expect thinning of the sprout cohort to continue for some time, the proportion of stems producing post-hurricane sprouts suggests that hurricanes can have a long-term impact on forest structure by initiating the production of new stems. We cannot definitively relate the current structure of mature forest to previous hurricanes because we cannot completely quantify past human disturbance in

Table 3. Species effects in proportion of stems sprouting, sprout rates and sprout length for species with at least 10 individuals sampled. All sprouts are post-hurricane. Some individual trees were multi-stemmed, but only one stem per tree was sampled for sprouts.

Species	Number of stems	% sprouting	Sprouts per sprouting stem	Median longest sprout length (cm)	% Multi-stemmed trees	Mean number of stems per tree
Gymnanthes lucida	306	19.9	7.3	24	29.0	1.5
Amyris elemifera	140	10.7	17.3	8	29.2	1.5
Eugenia foetida	113	70.8	12.8	30	24.4	1.4
Exostema caribaeum	107	34.6	33.9	8	8.3	1.2
Coccoloba diversifolia	104	67.3	7.7	92	52.1	3.1
Pictetia aculeata	104	15.4	5.5	16	50.0	2.4
Bursesera simaruba	98	4.1	5.5	24	4.4	1.0
Guettarda krugii	57	22.8	3.0	17	66.7	3.4
Coccoloba microstachya	37	54.1	4.4	81	76.5	6.1
Bourreria succulenta	33	36.4	4.9	76	35.3	1.5
Thouinia portoricensis	33	90.9	18.9	34	68.6	4.2
Krugiodendron ferreum	31	71.0	20.3	17	16.1	1.2
Pisonia albida	29	10.3	14.3	71	34.5	1.6
Tabebouia heterophylla	28	39.3	9.0	61	92.9	6.5
Bucida bucerus	23	30.4	8.9	37	38.1	2.3
Erithroxylon rotundifolium	23	52.2	11.8	51	35.3	2.3
Leucaena leucocephala	14	100.0	19.1	29	23.1	1.4
Crossopetalum rhacoma	12	75.0	8.2	13	53.8	2.5
Eugenia xerophytica	10	100.0	9.1	11	80.0	6.4

the forest, however, the forest after Hurricane Georges is clearly primed to have more stems than before the hurricane. As the sprout cohort thins, we may see patterns begin to develop between the number of stems per tree and the percent of stems sprouting or sprout rate. By 90 weeks post-hurricane, the length of the longest sprout on each tree was positively associated with the mean number of stems per tree and the percent of stems sprouting within a species.

As expected, stems incurring major structural damage had the highest sprouting rates, but sprouting was also common on defoliated and apparently undamaged stems. Sprouting on defoliated stems was notable because allocation of resources to production of new leaves would be less costly than to leaves and woody tissues needed for sprouts. Root biomass is nearly equal to shoot biomass in Guánica Forest (Murphy & Lugo 1986b), so it appears that roots were able to provide enough resources for the production of new leaves and sprouts simultaneously which we ob-

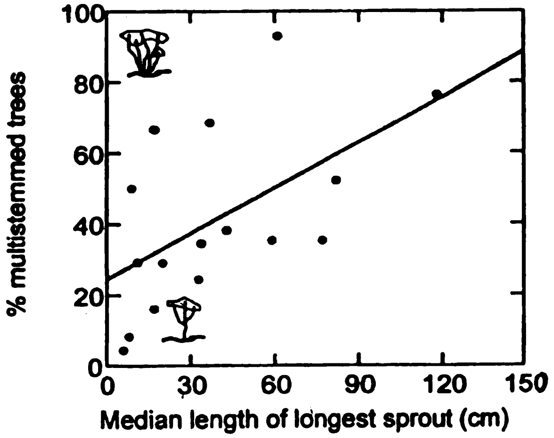

Fig. 3. The median length of the longest sprouts on stems in 16 species of dry forest trees is related to the number of stems of each tree. (p = 0.012) Median sprout length is similarly related to the percent of multi-stemmed trees (p = 0.018). The data are from species with at least 20 trees in our plots. Each point represents a tree species.

served on most stems after Hurricane Georges. The severity of defoliation did not affect sprouting rate, suggesting that defoliation itself was not the mechanism that elicited sprouting.

It is likely that sprout development following the hurricane was influenced by altered hormone balances in trees. High winds and vertical displacement are known to increase ethylene production (Brown & Leopold 1973; Leopold *et al.* 1972; Nelson & Hillis 1978; Telewski & Jaffe 1986). Ethylene production would be highest at the point of greatest bending – below breast height near the root collar (Vogel 1994; Wood 1995). Ethylene has been shown to block auxin transport (e.g. Wood 1985). Because auxin suppresses lateral bud development, blockage of auxin can release these buds (Cline 1991; Kramer & Kozlowski 1979). While we have no direct evidence of altered hormone concentrations following Hurricane Goerges, this model would explain the prevalence of basal sprouting, even on undamaged stems. A mechanism to explain basal sprouting must be applicable across species because basal sprouting occurred on undamaged stems of all species in our plots. Altered hormone balances would be a generalized response to wind stress among all species. Variation in the degree of sprouting response could be the result of unique characteristics of each species in hormone regulation as well as wood density, crown geometry, etc.

Conditions necessary to maintain sprouting as a disturbance recovery mechanism have recently been reviewed by Bellingham & Sparrow (2000). They suggest a tradeoff in recovery strategies between sprouting and seeding. This seems to be the case in Guánica Forest as seedling establishment is generally very low (Molina Colón 1998), while resprouting ability is widespread. Resprouting on mature trees would be supported by well-developed root systems and increasing leaf area to maximize photosynthesis after a disturbance. Resprouting would be a strategy for trees to maximize spatial coverage in order to access more resources (sunlight, water or nutrients) and would, therefore, be a case of reiteration (sensu Halle *et al.* 1978). Bellingham & Sparrow (2000) further suggest that the proportion of biomass lost from a tree following a disturbance will determine whether a tree will resprout and where resprouting will occur on the tree. They suggest that basal sprouting should only become prevalent when a large proportion of above-ground biomass is lost. In this context the amount of sprouting on defoliated stems and stems without any type of visible damage was surprising. Our results suggest that basal sprouting occurs even with the small biomass loss associated with partial defoliation, in contrast to the Bellingham & Sparrow model. Our results likely differ from their predictions because resources following the hurricane (water and nutrients in fresh litter) were high, and thus the reliance on storage organs to support sprouting would be low. Also, our mechanism for eliciting sprout development does not rely on biomass loss, but instead on internal hormone balance altered by exogenous factors.

Conclusions

Hurricane Georges clearly stimulated the development of sprouts above pre-hurricane levels. The production of post-hurricane sprouts was higher in stems with major structural damage than defoliated stems, but not limited to damaged stems nor related to defoliation severity. Sprouts produced on defoliated stems or stems without visible effects of the hurricane accounted for over half of all new sprouts. The amount of production of basal sprouts varied by species, but the phenomenon was not species-specific. After two dry seasons, sprout mortality was low. Our results suggest that hurricane disturbance leaves subtropical dry forest with the potential to greatly increase stem density and the proportion of multiple-stemmed trees, characteristics common to dry forests in the hurricane-prone Caribbean region.

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CHAPTER 7

OVERALL CONCLUSIONS

Forest growth and structure are influenced by a variety of factors, each of which operates on varying spatial and temporal scales and with different intensities. Two factors that shape the structure and function of dry forests in the West Indies are hurricanes and nutrients. Hurricanes impact large swaths of forest, but the timing and intensity of hurricane effects depend on storm strength and trajectory. Nutrients appear to affect some functional traits in the forest, such as limitation of growth, and may be important during the rainy seasons when water is abundant. As a result of this dissertation research, I conclude that hurricane disturbance has a greater influence than variation in nutrients on forest structure. Hurricane Georges arrested forest development, damaging large stems and causing basal area losses that equaled decades of growth. Furthermore, the hurricane resulted in a widespread sprouting response that could increase stem density and the proportion of multi-stemmed trees as sprouts mature into stems. Even though strong associations between tree growth and soil nutrient content were absent, trees still exhibited symptoms of nutrient stress, such as high phosphorus use efficiency and the satisfaction of 65% of annual P budget by retranslocation.

Within the broad interpretation reached above, a number of specific conclusions regarding nutrient effects, hurricane effects, and long-term growth have been generated by this research. These include:

NUTRIENT EFFECTS

1. Pool sizes of most nutrients in Guánica Forest were large compared to other dry forests. Guánica Forest had the highest amount of total N (0.5-1.8%), available Ca (5-12 mg/g), organic matter (17-49%), and pH (7.7-8.0) reported for dry forest areas. Only forests in the Yucatan had more total P (2.2 mg/g) than Guánica (0.5-1.0 mg/g). Despite large amounts of total P, only 1.3 to 2.9% was available. High organic matter in the soil suggested that a large proportion of soil nutrients could be immobilized in microbial pools to facilitate decomposition. (Chapter 2)
2. While studies in other forest life zones have indicated that soil nutrient patches tend to be the same size or smaller than crown diameters of mature trees, this was not the case in Guánica Forest. Based on spatial analyses, patch sizes of nutrients were inferred to be 17-25 m, much larger than the 3-5 m crown diameters of mature trees in Guánica Forest. Patches tended to be about the same size for different nutrients as well as from site to site in the forest and appeared to be the result of microtopography. (Chapter 3)
3. Among soil properties, spatial patterns of N and organic matter were the most similar, reflecting strong correlations in their pool sizes. Total P was also strongly correlated to N and OM pools at three of the four research sites. Spatial autocorrelation was able to explain at least 70% of variability in soil properties for a majority of nutrients. (Chapter 3)
4. Neither Ca nor pH was consistently related to pool sizes of TP or P_{av}, despite the potential for occlusion of P by Ca at the high pH found in the forest soils. The control of P pools was therefore not simply a matter of soil chemistry, but probably

also strongly affected by biotic influences, such as cycling through plant and microbial communities. (Chapter 3)

5. Microtopography interacted with nutrient pools. Small depressions or rocky areas with crevices accumulated litter and had higher nutrient contents, even when these areas were in exposed locations or had smaller trees growing in them. On the other hand, mean elevation of sites was not related to nutrient pool sizes. (Chapter 3)
6. All common tree species appeared to be able to grow across the entire portion of each nutrient gradient measured in Guánica Forest. The presence of some mature individuals of each common species, even at the lowest end of a nutrient gradient, suggested that all species were able to survive the most extreme nutrient conditions in the forest. However, some species grew more frequently along portions of nutrient gradients, suggesting either greater tolerance to low nutrient conditions or competitive exclusion from high nutrient locations. (Chapter 4)
7. Nutrient limitation of growth affected only smaller stems and sprouts. Growth or survival of sprouts and smaller trees responded to nutrient pool sizes, most frequently to P, but often in relation to OM or N. There was no strong evidence for nutrient limitation on the growth of mature trees based on nutrient pool size. Smaller trees would be able to access a smaller volume of soil and thus be restricted in nutrient uptake. Trees resprouting after hurricane disturbance would have lost a significant portion of internal nutrient pools to defoliation. Therefore, growth of small and sprouting trees would have been more likely to respond to nutrient pool size. (Chapter 4)
8. Nutrient limitation of tree growth appeared to result from the combined effects of N and P. Co-limitation by both N and P was indicated by root in-growth experiments.

Species-specific growth responses, either to pools of P or N, or N:P ratios, also suggested that the forest responded to both nutrients. (Chapter 4)

HURRICANE EFFECTS

1. Hurricane winds resulted in greater damage to larger stems than smaller stems. However, wind damage overall was relatively low (12.4% of stems) even though Georges was a strong hurricane and its eye crossed over Guánica Forest. (Chapter 5)
2. Topography, aspect, and forest type influenced the amount and type of damage a forest stand incurred from high winds. Forests in exposed areas had greater damage than those in valleys or on leeward slopes. Mahogany plantations and stands dominated by the exotic species *Leucaena leucocephala* incurred less damage than native forests. (Chapter 5)
3. The majority of damage was caused by the strongest winds, which gusted up to 240 km/hr and came from the southeast. A critical wind speed between 176 (Category 3 hurricane level) and 240 km/hr was necessary to cause the majority of damage, based on tree fall directions. Hurricane Hortense crossed over Guánica Forest in 1996, but its winds of 130 km/hr did very little damage. (Chapter 5)
4. Forest fragmentation had little effect on hurricane damage rates in a collection of forest fragments in SW PR. Rates of damage and the effects of aspect and topography in fragments were similar to Guánica Forest. (Chapter 5)
5. Compared to annual litterfall, hurricane litterfall was enriched in nutrients. Nutrient return to the forest floor by leaf litterfall during the hurricane was equal to or greater than annual nutrient return for N and P although leaf litterfall biomass was only 55% that of annual rates. Wood litter was 11 times greater than annual rates as were its contributions of N and P. (Chapter 5)

6. Stem mortality due to Hurricane Georges was only 2%, lower than damage rates and mortality rates reported from other dry forests. Although 2% mortality was tenfold greater than background rates in Guánica Forest, hurricanes do not occur frequently enough to kill as many stems as are lost to other factors (senescence, thinning, drought, etc.) over time. (Chapter 5)
7. Basal sprouting that occurred after Hurricane Georges minimized mortality and may have a long-term influence on forest structure. Basal sprouting occurred on 34% of stems, nearly three times the rate of stem damage. After two years, sprouts continued to survive, suggesting that the incidence of multi-stemmed trees will increase as a result of Hurricane Georges, maintaining wind-resistant physiognomy. (Chapter 6)
8. Basal sprouting following the hurricane appeared to be the result of gravitational displacement by high winds rather than structural damage to or defoliation of stems. Sprouting was 10 times higher than pre-hurricane rates on undamaged and defoliated stems, but the severity of defoliation was not related to sprout rates. It is suggested that high winds may trigger an ethylene response at or near the base of a stem, where flexure would be greatest, altering hormone balances sufficiently to reduce inhibition of basal sprouts. (Chapter 6)

LONG-TERM GROWTH PATTERNS

1. Native forest stands in Guánica Forest appear to be mature, based on species turnover, mortality and in-growth rates, and stable size distributions, densities, and basal areas of stems. Stable soil properties over the 18-year period between sampling events also indicated forest maturity. (Chapter 2)

2. The tree species assemblage changed little in the Main site over an 18-year period and the changes that did occur are typical of a mature forest. Putative pioneer species in the forest became less important over time. Individuals of three new tree species entered the smallest diameter class measured (2.5 cm), but only one of these species had not been noted in the understory previously. (Chapter 2)
3. Without the effects of Hurricane Georges, the forest would appear to be aggrading, with increasing stem density and in-growth exceeding mortality. Stem losses resulting from the hurricane nearly equaled growth over the 18-year period. Considering that hurricanes are a permanent part of the environment, the forest has reached a dynamic equilibrium and can therefore be considered mature. (Chapter 2)

FUTURE RESEARCH

The findings of this research highlight additional avenues of inquiry which would further our understanding of tropical dry forest structure and function. Potential topics include:

1) Continued follow-up of long term research sites in Guánica Forest. Long term permanent plot studies with multiple sampling periods are rare in tropical dry forest (see Chapter 2). Future measurements will provide more complete insight into background mortality rates, in-growth patterns, species turnover, invasion of exotic species, and the relationship between tree growth and annual precipitation.

2) Microbial mediation of nutrient flux. My research only focused on nutrient pools, an important first step in understanding nutrient dynamics. The role of microbes, particularly mycorrhizae, in cycling nutrients needs to be addressed in more detail. Studies should focus on timing of major fluxes, amount of nutrients in flux, the effects of high

amounts of organic matter in soil, and forms of nutrients (e.g., Ca-bound P or organic P) accessed and released by various microbial populations.

3) Water effects. Mainly due to logistical considerations, water limitation has never been explicitly studied in Guánica Forest. Manipulative studies which control the quantity and timing of water availability would be useful to understand how much tree growth is determined by water supply and how much nutrient limitation is determined by transport (or lack thereof) or nutrients through soil by water.

4) Hormonal control of the sprouting response. The sprout response following Hurricane Georges was likely to have been generated by the hurricane altering hormone balances in stems, as discussed in Chapter Six. This mechanism is the subject of a grant to Skip Van Bloem recently funded by the US Department of Agriculture.

5) Genetic determination of sprouting after high winds. Once the hormone mechanism for sprouting is identified, we should determine if this is a trait common to all trees, or only species and populations growing in wind-stressed areas. The flora of Guánica Forest contains species found in Florida, Central America, and South America. Dry forests in these areas exist along a hurricane gradient, and it should therefore be possible to determine whether the sprouting is an adaptation or simply a physiological response.

APPENDICES

APPENDIX 1: FULL SITE DESCRIPTIONS

The Main site was located on the north side of Camino Couto (or Fuerte), approximately 50 m past the K5H2 marker. The SW corner of the site was 81 m north of the road. Elevation at the Main site ranged from 120-140 m (Figure 2). The site was dotted with dogtooth limestone outcrops which averaged 25% of surface area. Previous excavations have shown that the outcrops form a crust on the surface rather than being extensions of bedrock (Murphy and Lugo 1986b). The northeastern portion of the site was flat with shallow litter layers and few outcrops. The northwestern, center, and southern portions of the site were sloping and rocky with deep (>10 cm) litter layers. Where outcropping was prevalent, soil was only found at the surface in crevices between rocks and plants rooted in loosely consolidated humus layers. The western side of the site consisted of a shallow draw which drained the northeast corner and most of the western half of the site. Surface rocks were absent in the draw and the litter layer varied in thickness, presumably accumulating in the bottom both from transport from the sides and direct deposition from trees overhead. Along the eastern edge of the site, the ground sloped toward the east, so the topography of the entire site was like a knob or protrusion sticking out of a south-facing slope. The site had been used before 1930 for small-scale charcoal production, where pits of 3-5 m diameter were dug, filled with wood cut from nearby, lit on fire, and covered with soil. The pits have been refilled and the soil surface was leveled. One pit was located in the draw and at least three were located in the northeastern portion of the site. There was no evidence of charcoal pits in sloped areas. In 1999, there were at least 37 tree species with stem diameter ≥ 2.5 cm in the site (Table 1). *Gymnanthes lucida* was most important, followed by *Coccoloba microstachya, Pictetia aculeata,* and *Pisonia albida.* The most common exotic tree species in the dry forest region of Puerto Rico are *Leucaena leucocephala* and *Prosopis juliflora.* Neither of these species were present in the Main site.

The 1-ha Lluberas site was located off Camino Lluberas. The NW corner of the plot was about 30 m off the road, to the east, about 100 m south of the intersection of Lluberas and Granados Trail. Most measurements were taken within a 30 x 30 m block in center of the NW quadrant of the site, but twelve 5 x 5 m blocks were sampled in the remainder of the site to verify that patterns found in the 30 x 30 m block were representative of the whole. This same scheme was used at the Ventana site (described below). Elevation ranged from 141-151 m (Figure 2). The northwestern portion of the site formed a very shallow draw that flowed out of the site to the west (Figure 2). This area had few outcrops. The eastern two-thirds of the site had numerous outcrops and sloped generally southward. There were no signs of human use since 1930. Trees from 33 species (minimum diameter 2.5 cm) were censused at the site (520 trees in 900 m^2). The species assemblage was similar to the Main site (Table 2), with *Gymnanthes lucida* most important, followed by *Coccoloba diversifolia, Pictetia aculeata,* and *Eugenia foetida.* Two trees of *Leucaena leucocephala* were present.

The 1-ha Ventana site was located in a shallow draw which eventually becomes a gully about 100 m southeast of the site. The gully leads to Punto Ventana and crosses the forest boundary about 300 m southeast of the site. The eastern edge of the plot was about 50 m west from the old barb wire fence marking the eastern boundary of Guánica Forest. The 30 x 30 m plot was in the SE quadrant. Elevation ranged from 20-36 m and the draw rans N-S through the site, turning out the SE corner. The soil surface was rocky, resulting in rooting in the lower layers of litter. Of all the sites, Ventana was the most open, having about 65% of the stem density and 90% of the basal area found elsewhere. There were no signs of human use since 1930, but before 1920 there had been extensive ranching to the west of this plot and old two-tracks were faintly visible between the site and Camino Lluberas. In the 1600s there was a Spanish settlement about 1.5 km west (M. Canals, personal communication), so the site probably incurred human disturbance in the past, perhaps more so than the other sites. Like Lluberas and Main, *Gymnanthes lucida* was the most important tree species (Table 3). *Amyris elemifera, Coccoloba diversifolia,* and *Bursera simaruba* followed in importance. There were 32 tree species at the site (320 trees in 900 m^2), including three *Leucaena leucocephala* trees.

Table A-1. Importance values for stems ≥2.5 cm at the Main site in Guánica Forest in 1999. I.V. is the sum of relative frequency (RF), relative density (RD), and relative dominance (RBA; basal area).

Rank	Species	IV	% of Total IV	RF	RD	RBA
1	*Gymnanthes lucida*	48.45	16.15	8.38	25.38	14.68
2	*Coccoloba microstachya*	23.38	7.79	7.26	8.57	7.55
3	*Pictetia aculeata*	23.38	7.79	5.59	11.19	6.60
4	*Pisonia albida*	21.56	7.19	5.03	2.75	13.78
5	*Thouinia portoricensis*	17.76	5.92	5.03	8.95	3.78
6	*Exostema caribeaum*	15.88	5.29	7.26	3.77	4.84
7	*Bursera simaruba*	10.83	3.61	5.03	1.02	4.78
8	*Bourreria succulenta*	9.32	3.11	5.03	2.11	2.18
9	*Coccoloba diversifolia*	9.21	3.07	4.47	1.34	3.39
10	*Tabebuia heterophylla*	8.82	2.94	3.91	2.37	2.54
11	*Hypelate trifoliata*	8.29	2.76	2.23	1.79	4.26
12	*Guettarda elliptica*	7.53	2.51	2.23	3.58	1.72
13	*Pilosocereus royenii*	7.30	2.43	1.68	0.64	4.99
14	*Erithalis fruticosa*	7.26	2.42	2.79	2.75	1.72
15	*Cassine xylocarpa*	7.20	2.40	2.79	2.37	2.04
16	*Leptocereus quadricostatus*	7.12	2.37	1.12	2.17	3.83
17	*Krugiodendron ferreum*	7.10	2.37	3.91	0.83	2.35
18	*Jacquinia berterii*	6.76	2.25	3.35	1.28	2.13
19	*Antirhea acutata*	6.15	2.05	1.68	2.56	1.92
20	*Guettarda krugii*	5.53	1.84	2.23	2.17	1.12
21	*Amyris elemifera*	5.48	1.83	2.79	0.96	1.73
22	*Crossopetalum rhacoma*	5.31	1.77	2.23	1.85	1.22
23	*Erithroxylum rotundifolium*	4.62	1.54	2.23	0.90	1.49
24	*Coccoloba krugii*	3.88	1.29	1.12	1.85	0.91
25	*Forestiera segregata*	3.76	1.25	1.12	1.85	0.79
26	*Eugenia xerophytica*	3.70	1.23	1.68	0.96	1.07
27	*Linociera holdridgii*	2.43	0.81	0.56	1.02	0.85
28	*Comocladia dodonaea*	1.95	0.65	1.12	0.58	0.26
29	*Reynosia guama*	1.73	0.58	1.12	0.38	0.23
30	*Plumeria alba*	1.64	0.55	1.12	0.32	0.21
31	*Colubrina arborescens*	1.54	0.51	0.56	0.77	0.21
32	*Zanthoxylum flavum*	1.01	0.34	0.56	0.26	0.19
33	*Eugenia foetida*	0.93	0.31	0.56	0.26	0.12
34	*Eugenia rhombea*	0.89	0.30	0.56	0.26	0.07
35	*Thrinax morrisii*	0.83	0.28	0.56	0.06	0.21
36	*Rochefortia acanthophora*	0.75	0.25	0.56	0.06	0.13
37	*Reynosia uncinata*	0.71	0.24	0.56	0.06	0.09

Table A-2. Importance values for plant species having dbh ≥2.5 cm in nine 10 x 10 m blocks in the Lluberas site in 1998. See Table A-1 for abbreviations.

Rank	Species	I.V.	% of total I.V.	RF	RD	RBA
1	*Gymnanthes lucida*	49.24	16.41	6.72	29.68	12.85
2	*Coccoloba diversifolia*	28.38	9.46	6.72	10.96	10.70
3	*Pictetia aculeata*	25.87	8.62	6.72	6.62	12.54
4	*Eugenia foetida*	24.46	8.15	5.97	13.61	4.88
5	*Bursera simaruba*	21.91	7.30	5.97	3.59	12.35
6	*Guettarda krugii*	17.42	5.81	6.72	6.81	3.90
7	*Amyris elemifera*	15.66	5.22	6.72	5.48	3.46
8	*Pisonia albida*	14.54	4.85	5.22	3.02	6.29
9	*Krugiodendron ferreum*	14.13	4.71	6.72	3.21	4.20
10	*Tabebouia heterophylla*	13.55	4.52	4.48	1.89	7.18
11	*Thouinia portoricensis*	9.68	3.23	5.22	3.21	1.24
12	*Bourreria succulenta*	8.85	2.95	4.48	2.27	2.10
13	*Coccoloba microstachya*	8.30	2.77	2.99	0.95	4.37
14	*Pithecellobium ungis-cati*	6.68	2.23	3.73	1.51	1.44
15	*Bumelia obovata*	5.21	1.74	2.24	0.76	2.21
16	*Leptocereus quadricostatus*	4.90	1.63	2.24	1.13	1.53
17	*Pilosocereus royeni*	4.88	1.63	1.49	0.38	3.01
18	*Bucida bucerus*	3.22	1.07	0.75	0.76	1.72
19	*Hypelate trifolia*	2.32	0.77	1.49	0.38	0.45
20	*Exostema caribaeum*	2.24	0.75	1.49	0.57	0.18
21	*Guaiacum sanctum*	2.20	0.73	1.49	0.38	0.33
22	*Capparis cynophyllophora*	2.02	0.67	1.49	0.38	0.15
23	*Leucaena leucocephala*	2.01	0.67	1.49	0.38	0.14
24	*Eugenia rhombea*	1.76	0.59	0.75	0.38	0.64
25	*Guaiacum officinale*	1.73	0.58	0.75	0.19	0.79
26	*Linocera holdridgii*	1.57	0.52	0.75	0.19	0.63
27	*Calyptranthes sp.*	1.39	0.46	0.75	0.19	0.46
28	*Cassine xylocarpa*	1.00	0.33	0.75	0.19	0.07
29	*Eugenia xerophytica*	1.00	0.33	0.75	0.19	0.06
30	*Erithroxylon areolatum*	0.99	0.33	0.75	0.19	0.06
31	*Comocladia dodonaea*	0.97	0.32	0.75	0.19	0.04
32	*Colubrina arborescens*	0.97	0.32	0.75	0.19	0.03
33	*Coccoloba krugii*	0.96	0.32	0.75	0.19	0.03

Table A-3. Importance values for plant species having dbh ≥2.5 cm in nine 10 x 10 m blocks in the Ventana site in 1998. See Table A-1 for abbreviations.

			% of total			
Rank	Species	I.V.	I.V.	RF	RD	RBA
1	*Gymnanthes lucida*	35.84	11.95	7.09	22.50	6.25
2	*Amyris elemifera*	34.51	11.50	7.09	18.44	8.99
3	*Coccoloba diversifolia*	26.55	8.85	6.30	7.81	12.44
4	*Bursera simarouba*	24.20	8.07	7.09	5.00	12.11
5	*Tabebouia heterophylla*	19.35	6.45	5.51	5.63	8.21
6	*Bucida bucerus*	19.23	6.41	4.72	2.19	12.32
7	*Pilosocereus royeni*	17.08	5.69	3.15	2.19	11.74
8	*Pisonia albida*	16.45	5.48	5.51	2.50	8.44
9	*Pictetia aculeata*	15.52	5.17	7.09	6.25	2.18
10	*Coccoloba microstachya*	13.97	4.66	4.72	3.75	5.49
11	*Exostema caribaeum*	10.03	3.34	4.72	4.06	1.25
12	*Thouinia portoricensis*	7.13	2.38	3.94	2.50	0.70
13	*Guettarda krugii*	7.09	2.36	3.94	2.19	0.96
14	*Krugiodendron ferreum*	5.82	1.94	3.15	2.19	0.48
15	*Erythroxylon rotundifolium*	5.11	1.70	2.36	1.25	1.49
16	*Eugenia xerophytica*	4.42	1.47	2.36	1.25	0.81
17	*Bourreria succulenta*	4.08	1.36	2.36	0.94	0.78
18	*Guettarda elliptica*	3.85	1.28	2.36	0.94	0.55
19	Unknown species	3.45	1.15	0.79	0.31	2.35
20	*Comocladia dodonaea*	3.45	1.15	2.36	0.94	0.15
21	*Bourreria virgata*	3.43	1.14	2.36	0.94	0.13
22	*Eugenia foetida*	2.95	0.98	1.57	1.25	0.13
23	*Coccoloba krugii*	2.90	0.97	1.57	0.94	0.39
24	*Leucaena leucocephala*	2.66	0.89	1.57	0.94	0.15
25	*Jacquinia berterii*	2.36	0.79	0.79	0.94	0.63
26	*Pithecellobium ungis-cati*	1.61	0.54	0.79	0.31	0.51
27	*Ximenia americana*	1.25	0.42	0.79	0.31	0.15
28	*Securinega acidoton*	1.19	0.40	0.79	0.31	0.09
29	*Canella winterana*	1.14	0.38	0.79	0.31	0.04
30	*Crossopetalum rhacoma*	1.13	0.38	0.79	0.31	0.03
31	*Plumeria alba*	1.13	0.38	0.79	0.31	0.03
32	*Erithroxylon areolatum*	1.13	0.38	0.79	0.31	0.03

APPENDIX 2: PROPERTIES OF SOIL NUTRIENTS NOT DISCUSSED IN CHAPTER THREE.

Chapter Three focused on a selection of nutrients that were considered the most relevant for limiting tree growth in Guánica Forest. However, other nutrients were analyzed as well, as reported here.

Table A-4. Means of elevation (m above sea level) and soil properties of four sites in Guánica Forest. Means across sites were different unless indicated with the same letter. Samples were analyzed as described in Chapter Three. Subscripts *av* and *to* refer to available and total forms of elements. All concentrations are in mg/g unless specified.

	Main		**Lluberas**		**Ventana**		**Honda**	
	mean	SD	**mean**	SD	**mean**	SD	**mean**	SD
C (%)	**14.86a**	5.19	**26.35**	8.37	**17.46**	8.06	**13.54a**	1.46
K_{to} (mg/g)	**10.07a**	1.90	**6.87**	1.63	**8.60**	0.97	**10.03a**	0.47
K_{av} (mg/g)	**0.69a**	0.22	**0.70a**	0.19	**0.49**	0.17	**0.54a**	0.15
% K_{av}	**6.9**		**10.2**		**5.7**		**5.4**	
Ca_{av} (mg/g)	**8.27**	2.52	**12.08**	3.02	**10.16**	1.30	**5.19**	0.77
% Ca_{av}	**4.6**		**13.8**		**19.2**		**2.0**	
Mg_{to}	**3.5**	1.2	**4.6a**	1.0	**6.7**	1.6	**4.6a**	1.2
Mg_{av}	**0.51a**	0.29	**0.95b**	0.34	**0.95b**	0.35	**0.46a**	0.20
% Mg_{av}	**14.6**		**20.7**		**14.2**		**10.0**	
Al	**19.6**	10.1	**17.1**	9.6	**35.7**	13.1	**8.5**	1.9
Fe	**24.1**	12.6	**17.5**	10.3	**35.8**	14.5	**9.5**	2.3
Mn	**0.36**	0.21	**0.49**	0.21	**0.70**	0.21	**0.20**	0.03
S	**1.1**	0.7	**2.5**	0.8	**1.7**	0.7	**0.6**	0.1
Na_{av}	**0.12a**	0.10	**0.16**	0.05	**0.11a**	0.05	**0.04**	0.03

Table A-5. Parameters for variogram models of soil C, available Ca, available K, and total K. Spatial analyses were performed as described in Chapter Three.

Site	Max lag	Model	Effective Range (m)	r^2	PSV %
Carbon					
Honda	27	spherical	27.34	0.97	99
Lluberas	32	spherical	21.49	0.97	82
Ventana	32	spherical	20.82	0.94	100
Main	32	spherical	16.55	0.76	91
Main	150	spherical	125.70	0.87	81
Available Ca					
Honda	27	spherical	20.20	0.92	89
Lluberas	32	spherical	6.35	0.66	86
Ventana	32	spherical	19.10	0.86	74
Main	32	spherical	23.39	0.93	90
Main	150	spherical	58.50	0.78	85
Available K					
Honda	27	spherical	20.20	0.92	89
Lluberas	32	nugget only			
Ventana	32	spherical	19.10	0.86	74
Main	32	spherical	17.33	0.93	89
Main	150	spherical	56.90	0.78	88
Total K					
Honda	27	nugget only	0		
Lluberas	32	spherical	26.67	0.96	100
Ventana	32	linear	*	0.77	
Main	32	exponential	12.24	0.82	88
Main	150	exponential	10.20	0.36	88

* greater than maximum lag interval

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