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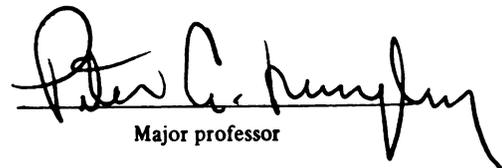
**The Multiple-Stemmed Growth Form of
Trees in a Subtropical Dry Forest**

presented by

Brian K. Dunphy

has been accepted towards fulfillment
of the requirements for

M.S. degree in **Botany &
Plant Pathology**


Major professor

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THE MULTIPLE-STEMMED GROWTH FORM OF TREES IN A SUBTROPICAL DRY
FOREST

By

Brian K. Dunphy

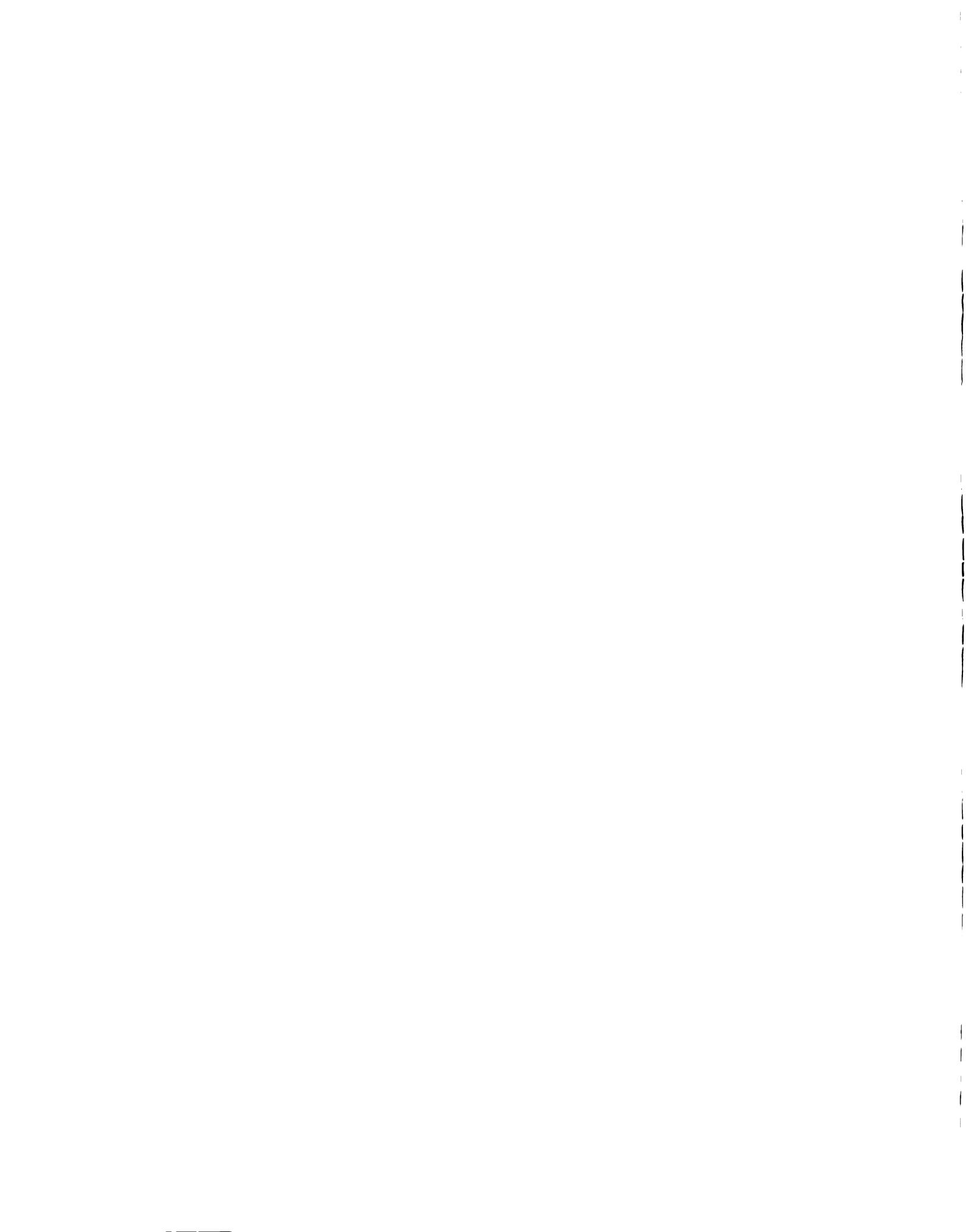
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ABSTRACT

THE MULTIPLE-STEMMED GROWTH FORM OF TREES IN A SUBTROPICAL DRY FOREST

By

Brian K. Dunphy

Caribbean dry forests are characterized by large numbers of small-diameter, multiple-stemmed trees. The current study addressed the question of whether the growth form of these trees is natural or simply a relict of the extensive disturbance to which these forests have been subjected. Eleven dominant woody species in Guánica Forest, Puerto Rico were examined and evidence was found that suggested that the multi-stemmed growth form occurs naturally for at least nine of these species. Among the strongest evidence was the persistence of original main stems (19.9% of multi-stemmed trees), and the presence of small multi-stemmed trees (20.7% of saplings below 3-cm diameter at ground height) which were considered too young to have been present prior to forest protection when the last major cutting episodes occurred. All considered, it appears that the overall structure of the forest at the study site, including the abundance of small multi-stemmed trees, is natural for this region.

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INTRODUCTION

To restore and protect natural communities, reasonably intact examples are essential to serve as benchmarks for the evaluation of restoration or conservation efforts. Despite past disturbance, Guánica Forest in southwestern Puerto Rico is considered to be an excellent example of subtropical dry forest (Ewel and Whitmore 1973), and could potentially serve as a model of the community type as it occurs in the Caribbean. Nevertheless, there has been uncertainty concerning the extent to which disturbance has altered its structure. Its low stature with multi-stemmed trees has in the past been attributed to cutting (Murphy and Lugo 1986b). This notion is contradicted by a recent examination of multi-stemmed trees which revealed a notable lack of stumps (P. Murphy and A. Lugo, pers. com.), suggesting that many of the trees may not have been cut. Although the multi-stemmed growth form has been noted in various dry forests worldwide (Josse and Balslev 1994; Lacey and Johnston 1990; Murphy and Lugo 1986b; Nyerges 1989; Smith and Vankat 1992; Sussman and Rakotozafy 1994), no study to date has directly addressed the question of whether the growth form of these trees is natural. It was to answer this question that the present study was initiated.

Tropical and subtropical dry forests, as defined by Holdridge (1967), receive between 500-2,000 mm of rain on a yearly basis, possess a potential evapotranspiration to precipitation ratio of greater than one, and have a mean annual biotemperature greater than 17° C. Of all the world's tropical forests, 42% would be classified as tropical or subtropical dry forest according to these criteria (Murphy and Lugo 1990).

The climate in which dry forests occur tends to be favorable for human habitation. In addition, the soils tend to be more suitable for agriculture than

those of moist tropical environments. Soils are richer in nutrients and easier to clear since dry forest is not as large or structurally complex as forests of moister regions (Murphy and Lugo, 1990). For these reasons, few examples of pristine dry forest remain. In Central America, for instance, less than 1% of the original dry forest remains (Janzen 1988), most of it having been cleared for pasture and farm land. In Jamaica, dry forest is found below 1,370 m, among other vegetation types which "have been so seriously modified by human interference as to be only imperfectly recognizable" (Shreve 1914).

Worldwide, tropical and subtropical dry forests are being cleared at a rate of 2.2 million ha/yr (Peter 1993), an area nearly as large as New Jersey. Jha and Unni (1994) used remote sensing data to look for change in 169,000 ha of dry forest in the northern Indian province of Uttar Pradesh between 1982 and 1989. During this period, only 52,390 ha (31% of total) remained unchanged, while 77,740 ha (46% of total) were converted from closed forest (cover > 50%) to open forest (cover 30-50%), and 38,870 ha (23% of total) were converted from open forest to tree savanna. Unlike the tropical wet forest and rain forest, there are no large blocs of unbroken tropical and subtropical dry forest remaining (Janzen 1986). For these reasons, Josse and Balslev (1994) consider the history of human disturbance to be one of the key factors in determining structure and composition of tropical dry forests.

Structure of tropical and subtropical dry forest

Structurally, dry forests tend to be less complex than wetter tropical forests (Table 1). Canopies of dry forests have only 1-3 canopy strata, whereas wet forests have three strata or more; canopy heights of dry forests are about

Table 1. Community-level structural characteristics of tropical and subtropical dry forest relative to tropical and subtropical wet and rain forest (adapted from Murphy & Lugo 1986a).

Trait	Forest type	
	Dry ^a	Wet ^b
Number of tree species ^c	35-90	50-200
Complexity index ^d	5-45	180-405
Canopy height, m	10-40	20-84
Number of canopy strata	1-3	3 or more
Leaf area index, m ² /m ²	3-7	5-8
Ground vegetation cover	low-high	<10%
Basal area of trees, m ² /ha	17-40	20-75
Plant biomass, t/ha		
Stems and branches	28-266	209-1163
Leaves	2-7	7-10
Roots	10-45	11-135
Total	78-320	269-1186
Root biomass as % of total	8-50	<5-33

^a Annual rainfall 500-2000 mm; strongly seasonal; annual PET/P normally >1.

^b Annual rainfall >2000 mm; little or moderate seasonality; annual PET/P normally <1.

^c Based upon surveys of 1-3 ha; includes trees at least as small as 10-cm dbh.

^d Calculated as the product of number of species, basal area (m²/0.1 ha), maximum tree height (m), and number of stems/0.1 ha, times 10⁻³ in a 0.1 ha plot (Holdridge *et al.* 1971).

half those of the wet forests. Within dry forests, the number of strata is related to precipitation, with fewer strata in areas receiving less rain (Sussman and Rakotozafy 1994). Dry forests tend to have smaller individuals; community basal area is typically 30-75% that of wet forest and overall biomass is about 30% that of wet forest (Murphy and Lugo 1986a). Ground cover is higher in dry forest due to generally lower canopy cover (Murphy and Lugo 1986a).

Guánica Forest resides at the lower end of the precipitation spectrum for documented dry forests (Murphy and Lugo 1990). Therefore, it is not surprising that it tends to show lower values for key community structural traits. Total biomass of dry forest ranges from 98-320 t/ha, with Guánica Forest having the lowest of these values (Murphy and Lugo 1990). In basal area, values range from 17 to 52 m²/ha (Murphy and Lugo 1990). Guánica Forest is found near the lower end of this spectrum with 19.8 m²/ha for trees at least 2.5-cm dbh (Murphy and Lugo 1986b). The largest tree found at a study site in Guánica Forest by Murphy and Lugo (1986b) was a *Pisonia albida* with a dbh (diameter at breast height) of 23 cm. In contrast, 5% of trees exceeded 25-cm dbh in a dry forest in southwestern Madagascar (Sussman and Rakotozafy 1994), and 3% of stems exceeded 50-cm dbh near Varanasi, India (Singh and Singh 1991). In a dry forest in Ecuador, 8.6% of stems exceeded 10-cm dbh (Josse and Balslev 1994), while in Guánica Forest only 2.3% of stems exceeded this size (Murphy and Lugo 1986b).

Tree stems in Guánica Forest exhibit a small-biased structure. Among trees with a dbh of at least 2.5 cm, 80% were less than 5-cm dbh (Murphy and Lugo 1986b). Singh and Singh (1991) found a similar pattern in a dry forest in India where 64-72% of stems were below 10-cm dbh. In an Ecuadorian dry forest, 60% of trees were between 5- and 10-cm dbh (Josse and Balslev 1994).

The density of stems in Guánica Forest was particularly high for dry forests, with 14,007 stems/ha of at least 2.5-cm dbh (Murphy and Lugo 1986b). In comparison, a dry forest in Madagascar had only 1,112 to 1,656 stems/ha (Sussman and Rakotozafy 1994). In Ecuador, Josse and Balslev (1994) found 655 stems/ha above 5-cm dbh, while there were 2,487 stems/ha above 5-cm dbh in Guánica Forest (Murphy and Lugo 1986b).

Leaf area index (LAI) ranged from 2.1 to 4.3 in Guánica Forest, depending upon time of year (Murphy and Lugo 1986b). This was lower than values reported for other dry forests. Murphy and Lugo (1990) report values of 3-6.6 for forests in Thailand, and a LAI of 8 for a dry forest in India.

Below-ground biomass formed a significant portion of the biomass in Guánica Forest. Root biomass was 45 metric tons/ ha, with 90% of this within 40 cm of the soil surface and 57% within 10 cm of the surface (Murphy and Lugo 1986b). Roots that were less than 5 mm in diameter accounted for 40% of the total root biomass. Dry forests tend to have more extensive root systems than do tropical moist and rain forests. Brown and Lugo (1982) examined data from 33 moist and wet forests, and estimated that roots accounted for around 16% of the total biomass. In contrast, Murphy and Lugo (1986b) examining four dry forests, estimated that 33.5% of the total biomass occurred below ground. The explanation offered for this difference was that larger root systems allow for increased water and nutrient uptake, two features that are especially advantageous in a water-limited ecosystem. Additionally, an extensive root system may help anchor trees, thus helping them withstand strong winds during hurricanes.

Forest structure is influenced by precipitation. The importance of precipitation is recognized by Holdridge (1967), who uses it along with potential evapotranspiration and biotemperature to classify life zones.

Nevertheless, a good deal of variation can exist among different forests that receive similar amounts of precipitation. Despite very similar levels of precipitation, four tropical dry forests had very different canopy heights (Table 2). In fact, the forest receiving the most annual precipitation (860 mm) had the lowest canopy height (9 m). Similarly, Singh and Singh (1991) found total basal area in a dry forest near Varanasi, India to be between 9.0 and 14.8 m²/ha. In an earlier study by Bandhu (1970), a dry forest in the same area of India was reported to have a basal area of 30.6 m²/ha. Clearly, precipitation is only one of numerous factors affecting the structure of tropical dry forests. Proximity to surface water is one additional factor. In Madagascar, forest plots along a river course had canopy heights of 15-20 m, while plots well away from the river ranged from 2 to 15 m (Sussman and Rakotozafy 1994). Larger trees (>25 cm dbh) and a lower density of stems were also characteristic of plots near the river.

Local soil conditions can also have an influence on forest structure. This is well illustrated by the range of different forest types found within Guánica Forest (Lugo *et al.* 1978). On shallow, rocky soil, scrub vegetation predominated, with many shrubs, cacti and some grasses interspersed among a few large deciduous trees, with open areas and exposed limestone. In areas with deeper soils, such as deep valleys, the forest was much taller with evergreen foliage. Precipitation, which would not vary significantly between these sites, can not explain this variation. Variation in soil depth, slope angle and orientation, and soil moisture availability, are the main determining factors (Lugo *et al.* 1978).

Information is not readily available regarding numbers of multi-stemmed trees in tropical forests. In Colombia, Josse and Balslev (1994) found that among trees ≥ 5 cm dbh, 15% of trees were multi-stemmed, with an

Table 2. Canopy heights and annual rainfall for four tropical and subtropical dry forests.

<u>Location</u>	<u>Canopy height</u>	<u>Rainfall</u>	<u>Source</u>
Ecuador	12 m	650 mm	Josse and Balslev (1994)
Madagascar	15 m	750 mm	Sussman & Rakotozafy (1994)
India	18 m	800 mm	Bandhu (1970)
Puerto Rico	9 m	860 mm	Murphy and Lugo (1990)

average of 2.4 stems/ tree. The multi-stemmed condition was not the norm for any particular species, however, and all were mostly single-stemmed. They also reported that in another 1-ha dry forest plot in Ecuador there were roughly twice as many stems as trees. On North Andros Island in the Bahamas, Smith and Vankat (1992) found that in a dry forest with floristic similarities to Guánica Forest, 31 of 65 overstory species had at least one individual that was multi-stemmed or low-branched (≥ 3 stems at breast height).

Origin of the multi-stemmed form

A woody plant can have a multi-stemmed growth form either obligately (i.e., it is a shrub), or it can develop such a structure through stress-induced sprouting of vegetative buds (Kozlowski *et al.* 1991; Rundel 1991). Buds are either preformed or form adventitiously, the latter usually as a result of injury (Kozlowski *et al.* 1991; Kormanik and Brown 1967). Adventitious buds are fairly common on the roots of many tree species (Church and Godman 1966), and

Kormanik and Brown (1967) found adventitious buds on the boles of six temperate tree species that they examined, usually as the result of small, localized injuries. Since they form as a result of injury (i.e., are not preformed), adventitious buds can be distinguished from preformed buds by the lack of a vascular connection to the central vascular cylinder. Such a criterion does not confirm a bud as adventitious, however. Hoop pine (*Araucaria cunninghamii*), as well as other members of the Araucariaceae, possesses an unusual sprouting mechanism (Burrows 1990). In these trees, axillary meristems arise in apparently blank leaf axils. Like pre-formed buds (described below), this tissue is formed and buried beneath the periderm with the normal growth of the tree. Unlike preventitious buds, the tissue remains undifferentiated until disturbed. They also lack a vascular connection to the central vascular cylinder, which makes them appear similar to adventitious buds. Upon cutting, Burrows (1990) found that 50-60% of 200 20-year-old hoop pines coppiced. This makes them unusual in being one of the few conifers with the ability to coppice.

The usual mechanism of sprouting involves pre-formed ("preventitious") buds which have lain dormant below the tree's bark (Kozlowski *et al.* 1991; Burrows 1990). The buds are formed in the leaf axils with the normal development of the tree, but do not burst and eventually are buried by the expanding periderm. They grow only enough to keep ahead of the expanding vascular cambium, and a connection, or bud trace, is usually maintained with the central vascular cylinder (Kozlowski *et al.* 1991).

The dormancy of buds is imposed mainly through the balance of hormones (Rinne and Saarelainen 1994; Schier *et al.* 1985). Most important is the balance between auxins, synthesized in the young leaves at the apical portions of the plant, and cytokinins, which are believed to be synthesized in

the root tips. Auxins have been found to suppress lateral bud outgrowth, and cytokinins have been found to promote it. Consequently, a high auxin: cytokinin ratio inhibits sprouting, and a low ratio promotes it (Rinne and Saarelainen 1994; Schier *et al.* 1985). Removal or damage to the upper parts of a plant promote sprouting by lowering the auxin: cytokinin ratio. Abscissic acid (ABA) may also be involved, either directly or indirectly, in promoting apical dominance (Cline 1991; Schier *et al.* 1985). Likewise, gibberellic acid (GA) may play a role in bud burst, but it appears that its role may be confined to stem elongation following bud burst (Cline 1991).

Restriction of water to the dormant buds has been proposed as an additional mechanism that maintains dormancy (Blake and Tschaplinski 1986). Normally, water in trees moves preferentially through the major, as opposed to minor, axes (Tomlinson 1983). When the stem is snapped off by wind or otherwise removed, there is an initial decrease of xylem pressure in the remaining stump (Blake and Tschaplinski 1986). This temporary moisture stress can often lead to death of the remaining tissue. Within a few days, however, water availability increases for dormant buds, mainly due to the increased root/shoot ratio and decreased stem competition for moisture. Blake and Tschaplinski (1986) believe this increase in water availability releases the buds from apical control, increases stomatal conductance and hence net photosynthesis. This, they contend, leads to the accelerated growth of stump sprouts often seen after a tree is cut.

Sprouting after damage leads to what Tomlinson (1983) terms a "reiterative complex" forming from dormant buds, which is essentially a replication of the basic architectural model of the tree. There are numerous vegetative responses to injury. Among the more common are root sprouting, stump sprouting (from the root collar), and epicormic sprouting (sprouting

from above-ground tissue) (Lacey and Johnston 1990). This ability of trees to sprout following cutting (i.e., to coppice) has been exploited worldwide as a means of providing timber and fuel-wood (e.g., Barnard *et al.* 1987; Matsuda 1989; Nyerges 1989; Rinne and Saarelainen 1994), and much literature deals with these human-managed systems. Less prevalent are studies examining the ecology of stress-induced multiple-stemmed trees in natural settings, although such a growth form is common among trees in ecosystems around the world (Lacey and Johnston 1990). A few representative ecosystems include the cool temperate forests of Japan (Matsuda 1989; Peters and Okhubo 1990), the "mallee" forests of Australia (Lacey and Johnston 1990), and the chaparral of California (Biswell 1974). The question arises as to what natural stresses influence dry forests, and are these stresses capable of inducing a multi-stemmed growth form.

Natural stresses and tree growth form in the dry forest life zone

Due to severe non-anthropogenic (and often anthropogenic) stresses, there tends to be a relatively low survival rate of seedlings in the dry forest habitat (Ewel 1980). This is one likely reason why the ability to resprout after the death of above-ground tissue has been selected for worldwide throughout the dry forest life zone (Janzen, 1975; Murphy and Lugo, 1986b; Nyerges 1989; Sampaio *et al.*, 1993; Smith and Vankat, 1992). Coppicing is often the dominant mode of reproduction following disturbance. For instance, in abandoned "Coppice Swiddens" in Sierre Leone, 91-95% of trees coppiced after cutting, and within 7-8 years these trees accounted for 73% of the total basal area (Nyerges 1989). This ability to reproduce vegetatively gives dry forest a relatively high

degree of resilience in the face of disturbance (Dunevitz 1985; Nyerges 1989). Other factors favoring stump sprouting in the dry forest life zone include relatively slow rates of stump decay, seed mortality from predation and fungal action, and the ability of sprouts, which form during the dry season, to take advantage of water as it becomes available (Janzen 1975). In contrast, seeds germinate only during the rainy season, and there is a lag period before the seedlings are large enough to take advantage of available water. On St. John in the U.S. Virgin Islands, the seeds of many species remain dormant during the winter dry season and emerge with spring rains. Because the spring rainy period is so brief, mortality is high (Ray and Brown 1994).

Smith and Vankat (1992), studying dry limestone forest on North Andros Island in the Bahamas, found that the number of low-branching or multi-stemmed trees was more than three times greater along the coast than 500 m inland. They suggested that exposure to stresses such as hurricanes, salt spray and wind may be responsible, a process they refer to as 'natural coppicing', presumably since the natural stresses are mimicking the effects of cutting. The presence of small saplings with low branches and/or multiple stems suggested that cutting was not a factor.

The shrub life form is considered by Rundel (1991) to be especially well adapted to dry environments. He defined shrubs as low, woody or semi-woody, multi-stemmed plants that retain living tissues aboveground throughout the year. They are considered to be highly derived life-forms resulting from multi-stress interactions (Figure 1). According to Stebbins (1965), the earliest angiosperms evolved in semi-arid upland habitats as woody shrubs. These habitats are the same ones dominated by shrubs today. Shrubs tend to dominate water stressed systems, in particular desert and Mediterranean-type ecosystems. In addition, other systems can have a high percentage of shrub

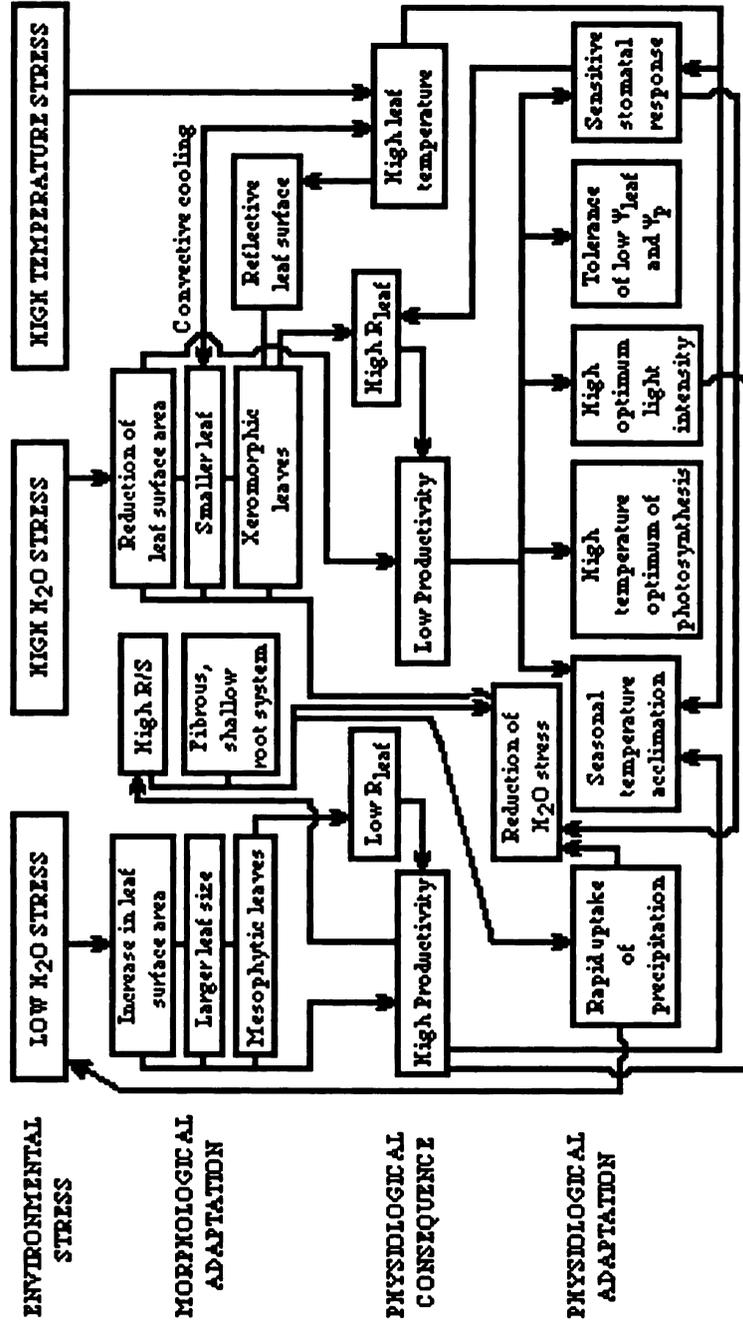


Figure 1. Multiple-stress interactions in the evolution of drought-deciduous desert shrubs (source: Rundel 1991).

species as well. For instance, in the tropical dry forest at Chamela, Mexico, 23.3% of the species present are shrubs (Bullock, 1985) and in Varanasi, India, shrubs accounted for 30 to 53% of the total basal area of the dry forest (Singh and Singh 1991). The ability of trees in Caribbean dry forests to facultatively assume a multi-stemmed (i.e., shrub-like) growth form could give them the ability to better adapt to local microsite conditions, especially very dry ones.

Possible causes of natural coppicing in the dry forest include drought, salt spray, wind stress, hurricanes, fire, grazing and browsing, and high light levels. A discussion of each of these follows.

Drought

According to Kramer and Kozlowski (1979), drought is "... a period without rainfall of sufficient duration to cause depletion of soil moisture and reduction in plant growth." Factors such as water storage capacity of the soil and the rate of evapotranspiration will determine whether plants are drought stressed. Drought stress occurs when leaf water potential drops to -2 or -3 bars (-0.2 or -0.3 MPa) or when cell turgor falls "well below" its maximum possible value, such that cell enlargement is decreased and essential physiological processes are disturbed (Kramer and Kozlowski, 1979).

Two of the main effects of drought stress on plants are a decrease in turgor pressure (Hsiao 1973), and a decrease in certain enzyme-mediated processes (Kramer and Kozlowski 1979). A decrease in turgor can in turn lead to a decrease in growth, mainly by reduced cell expansion (Hsiao 1973; Kramer and Kozlowski 1979). A consequent decrease in leaf area also can lead to a decrease in whole-plant photosynthesis (Kramer and Kozlowski 1979).

Additionally, low turgor can trigger stomatal closure, reducing CO₂ diffusion into the leaf, further reducing photosynthesis.

Enzyme-mediated processes negatively affected by drought stress include: respiration, the dark reactions of photosynthesis, formation of chlorophyll, and carbon and nitrogen metabolism (Kramer and Kozlowski 1979). Organelles such as mitochondria, ribosomes and cell membranes are disrupted by drought stress.

Drought stress can alter the balance of growth regulators, with levels of auxin and abscissic acid (ABA) increasing, and cytokinin decreasing. Since auxin and ABA promote apical dominance, while cytokinin promotes sprouting, death of the apical meristem, resulting in the curtailment of auxin production, is probably necessary for hormonal conditions which promote sprouting of dormant and/ or adventitious buds.

As water potential in the soil drops, tension on xylem water increases, and air is drawn into vessels and tracheids (Kolb and Davis 1994). With enough tension, the water column ruptures, or cavitates, which results in the formation of embolisms that block the flow of sap in the xylem (Kozlowski *et al.* 1991). Cavitation can seriously decrease xylem conductivity, reducing the supply of water to distal parts of the plant (Tyree and Sperry 1988).

Zimmerman (1983) suggested that a trade-off might exist between high specific conductivity and resistance to water stress-induced embolism. Long vessels with wide diameters are most efficient for water transport, but more prone to embolism. However, Tyree and Sperry (1989) do not believe that embolism formation is well correlated with the diameter of the conduits. Kolb and Davis (1994) claim that the severity of embolism is based largely on the size of the pores in the pit membranes of vessels and tracheids. Normally, 5-20% of xylem conduits are embolized (Tyree and Ewers 1991), which is

tolerable since most trees have more conducting tissue than is required (Kramer 1983), and can survive even after high levels of cavitation. Nevertheless, most woody species would be 100% embolized at a water potential of -9 MPa (Tyree and Ewers 1991).

Although important, susceptibility to embolism cannot be used as the sole index of drought stress tolerance (Kolb and Davis 1994), since drought tolerance is a highly coordinated, whole-plant process. This point is well illustrated by the study of Kolb and Davis (1994) comparing two species of coastal sage and chaparral. *Salvia mellifera* (coastal sage) is found in drier microsites than *Ceanothus megacarpus* (chaparral), despite the fact that *S. mellifera* is more susceptible to drought-induced embolism. Along with a high growth rate and drought-deciduous habit, what allows *S. mellifera* to persist is its ability to resprout from the base after stem die-back. *C. megacarpus* cannot resprout. In the dense chaparral stands, it also must reach greater heights than *S. mellifera* to compete for light. If its single stem dies back from drought stress, there is no mechanism for recovery.

Since most physiological processes require water, its availability is a major determinant of plant distribution and growth (Kozlowski *et al.* 1991). Vegetation can vary dramatically in composition and structure over a short distance given a substantial change in precipitation. In the Serrania Macuira, on the Guajira peninsula in northeastern Colombia, the boundary between the dry forest and the higher elevation (and wetter) cloud forest is rather abrupt, being at the approximate height of the average cloud base, below which fog rarely forms (Cavelier and Peñuela 1990). In Puerto Rico, species richness along the south side of the Cordillera Central increases with increasing levels of moisture (Lugo *et al.* 1978). In fact, if a normally dry ecosystem is supplied with additional water, a whole new suite of species can come to dominate, and

the biomass of the system can increase substantially (Lauenroth and Dodd, 1978).

If the drought kills the dominant stem, but dormant buds survive, resprouting may occur, leading to a multi-stemmed structure. In the case of *Quercus stellata* and *Q. marilandica*, the roots exhibit more resistance to dehydration than the shoots. If the shoots have been killed by drought, sprouting will often occur from the roots (Kramer and Kozlowski, 1979). Such root sprouting, as well as sprouting from stem tissue, is a valuable trait in an environment where periodic drought may be severe enough to kill the above-ground portions of a tree. In contrast, few trees in the rain forest produce sucker shoots from stumps or root sprouts (Janzen, 1975).

Schier *et al.* (1985) report that in spring before *Populus tremuloides* (quaking aspen) trees have opened their buds and initiated auxin production, temperatures are often high enough for suckering to occur for a short while before apical dominance is reasserted. The trees of Guánica Forest might experience a similar annual period of low auxin production. In a tropical dry forest near Veracruz, Mexico, Kavanagh and Kellman (1992) found a burst of root growth at the beginning of the rainy season. Since cytokinin production and transport seem to be related to root activity (Rinne and Saarelainen 1994), this active root growth might lower the auxin: cytokinin ratio enough to allow sprouting to occur.

Salt

By reducing the water potential gradient between the soil and the roots, excess soil salinity can cause coppicing by depriving the tree of water (i.e., by

inducing drought stress) (Kozlowski 1991). High intra-cellular concentrations of salt ions also can have toxic effects upon the plant (Kozlowski 1991).

Smith and Vankat (1992) listed salt spray as one of the possible explanations for why trees near the coast in the Bahamas possessed more stems than those inland. The inland trees they examined were closer to the coast (about 500 m) than those in the study plot at Guánica Forest (about 2 km), but it is still possible that salt could be having an effect. Moss (1940) found that after a hurricane, trees as far as 70 km inland were damaged by salt.

Wind

Winds of relatively low velocity, insufficient to cause stem breakage, may nevertheless play a role in sprouting. At low speeds, wind increases water loss through transpiration by reducing the boundary layer around leaves (Kozlowski 1991). This increased drought stress may contribute to death of the main stem, as discussed above in the section on drought, leading to resprouting and a multi-stemmed growth form. This drying effect is most pronounced at lower wind speeds. At higher speeds, stomata begin to close, and transpiration decreases. At a weather monitoring station in Ponce, Puerto Rico, approximately 30 km east of the study site, monthly wind speed between 1972 and 1990 averaged 9.1 to 13.1 m.p.h., with monthly maximum gusts averaging 28.4 to 34.2 m.p.h. (NOAA 1995).

Lawton (1982) found that wind stress affects the growth form of trees in a montane rain forest in northwestern Costa Rica. Trees exhibited an elfin (stunted) form characterized by an increase in trunk girth and twig thickness and a decrease in tree height with proximity to an exposed ridge crest. There

was no significant difference in leaf production between trees at a site protected from the wind and an exposed area where windspeeds were 1.5-1.8 times higher. This suggested to Lawton that morphometric changes have allowed the trees to adapt to the increased wind stress, thereby avoiding a loss in fitness. Shreve (1914) noted similar growth forms along ridges and peaks of the Blue Mountains of Jamaica.

Hurricanes

Hurricanes can have a significant effect on forest structure, causing trees to defoliate, snap, or uproot. Table 3 shows relative amounts of hurricane damage to trees in three tropical dry forests. Defoliation is the most common type of damage, followed by snapping and then uprooting. Tall trees are more likely to be defoliated, snapped or uprooted than shorter trees. When damaged, understory trees tend to snap whereas taller trees tend to uproot (Brokaw and Walker 1991; Lugo et al. 1983). On St. John in the U.S. Virgin islands, the tallest and shortest trees suffered more damage than medium sized trees, with the tallest being subjected to the greatest wind damage, and the shortest to falling debris (Reilly 1991).

Tree form is important in determining how trees respond to wind. Multi-stemmed trees tend to be more stable in wind than single-stemmed trees (Lacey and Johnston 1990). On the other hand, shallow root systems, caused by shallow clay horizons or impervious rock, increase the probability that a tree will be uprooted (Savill 1983). Trees in Guánica Forest are shallow rooted, with 90% of root biomass within 40 cm of the soil surface, and that could make them especially vulnerable to wind throw.

Table 3. A comparison of damage to trees from hurricanes in three different subtropical dry forests (adapted from Brokaw and Walker 1991).

Location	% of all individuals			Dead	Lowest dbh measured (cm)	Reference
	branch damage	Snapped trunks	Uprooted trunks			
Sri Lanka	43	-	39	14 (3.5) ^a	10	Dittus 1985
Virgin Islands	22	---3--- ^b		-	5	Reilly 1991
Mexico	72	12	4	11.4 (1.4)	10	Whigham <i>et al.</i> 1991

^a years after hurricane that mortality was estimated (in parenthesis).

^b Snapped and uprooted trunks combined.

Sprouting is a common response to hurricane damage (Whigham *et al.* 1991; Lugo *et al.* 1983) and recovery of leaf area is rapid. Vandermeer *et al.* (1995) found that 46-69% of the new trunks in plots from the Caribbean coast of Nicaragua following a hurricane were from resprouting. The abundant litter generated by windfall leads to rapid forest regrowth and increase in leaf area. Nutrients normally retranslocated before leaf-fall (especially P) may be unusually high in concentration in the litter (Whigham *et al.* 1991). Indeed, the diameter growth of trees on the Yucatan peninsula was greater in the first year after Hurricane Gilbert than in the five years prior to the hurricane. The authors attributed this regrowth to the increase in nutrients. Not discussed, however, is the possibility that the increased growth could be due to a thinning effect, in that the surviving trees are exposed to greater light levels.

Ten severe hurricanes struck Puerto Rico between 1700 and 1960 (Weaver 1986), although the eye of none of them passed over the subtropical dry forest life zone of Puerto Rico. Hurricane-force winds (greater than 65 knots (74.8 m.p.h.) on the Beaufort wind scale) have been infrequent. Between 1970-1992, at a weather monitoring station in Ponce, Puerto Rico (30 km east of the study site), hurricane-force winds were recorded only during January, 1980, the greatest being 81.7 m.p.h. (NOAA 1995). Storm force-winds (56-65 knots (64.4-74.8 m.p.h.)) were also measured during three monthly measuring periods between 1970-1992. Therefore, strong winds generated by tropical storms and hurricanes have likely played a periodic role in structuring Guánica Forest.

Fire

Some ecosystems are adapted to frequent fire; the loss of leaves generally releases dormant buds residing under the bark or stimulates the production of adventitious buds, leading to sprouting (Kozlowski 1991). For example, most of the important species of climax chaparral, which is prone to frequent fires, produce vigorous stump sprouts (Kozlowski 1991). Fire is not a normal occurrence in the dry forest. When it does occur, it is usually of human origin (Murphy and Lugo 1986a), and can be particularly destructive, especially when following other disturbances. After Hurricane Gilbert struck the Yucatan peninsula in 1988, fires occurred in dry forest areas, especially those with shallow and highly organic soils (Whigham *et al.* 1991). In the 17 months after the hurricane, 11.2% of the trees on unburned sites died (compared with 2.6% of trees dying during the five years prior to the hurricane). On sites that burned, 85.4% of stems died, and recovery of the forest was slowed (Whigham *et al.* 1991). A similar fate befell large regions of *Raphia* palm swamp forests in Nicaragua where sections of the forest that burned after a hurricane in October, 1988 still remain treeless (Vandermeer *et al.* 1995). In the Caatinga vegetation of Brazil, fire impeded the ability of cut vegetation to recover by stump sprouting. In the absence of fire, 94% of cut stems coppiced. When fires followed cutting, the number of stems coppicing dropped to 10-43%, depending upon the severity of the fire (Sampaio *et al.* 1993).

There has been no record of significant burning in the sections of Guánica Forest examined in the present study since the forest was first protected in the 1930's (Murphy and Lugo 1986a).

Grazing and browsing

Grazing or browsing of the terminal portions of a plant would have an effect similar to that of cutting, in that it can involve the removal of auxin-producing apical stem tissue. Although grazing by domestic animals poses a threat to other dry forests (Sussman and Rakotozafy 1994), including nearby Caribbean dry forests (e.g., feral donkeys on St. John (Brown, *et al.* 1992)), grazing has not been a problem in the studied area of Guánica Forest since its protection in the 1930's (Murphy and Lugo 1986a). Defoliation by insects and disease can also result in a multi-stemmed growth form mainly through epicormic shoot production (Burrows 1990). Drought often lowers resistance to attack by insects and pathogens, which in turn can lead to more severe attacks (Kramer and Kozlowski 1979).

Light

Both irradiance and spectral quality have a significant effect on apical dominance (Cline 1991). As irradiance of the upper crown increases, apical dominance decreases (Cline 1991) and high light levels have been found to promote the development of epicormic shoots (Burrows 1990). Likewise, apical dominance is weakened by red light, and strengthened by far-red light (Cline 1991). Schier *et al.* (1985) found that light is necessary to promote good sucker growth in quaking aspen. They report that in a clearcut in full sunlight, there were 98,840 suckers per ha. Where light was 50% or less of full intensity, the number of suckers fell below 7,400 per ha. Open-canopy

conditions with extensive light penetration in Guánica Forest should also be favorable for growth of root suckers as well as stump sprouts. This may especially be the case before bud burst at the beginning of the two annual rainy seasons beginning in April and September. It is at this time of higher than average light levels (Figure 2), that fine root growth, and hence cytokinin production, is probably at a maximum, and auxin production is probably at a minimum.

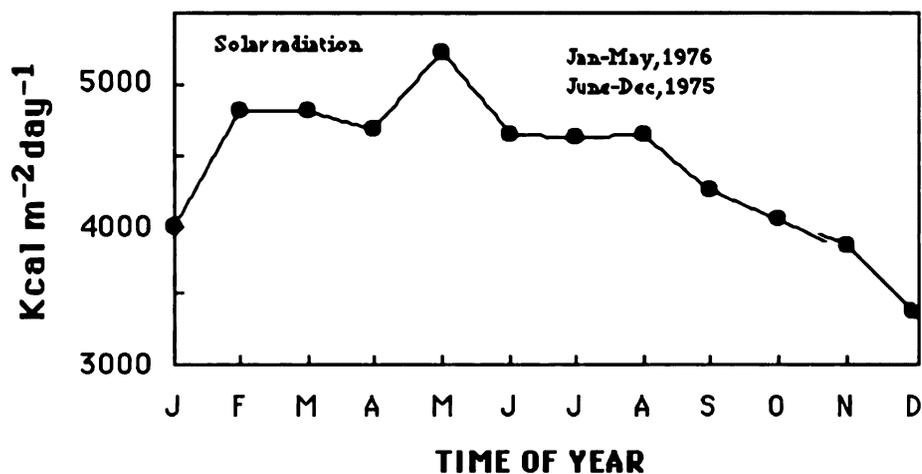


Figure 2. Annual course of incident solar radiation to Guánica Forest (adapted from Lugo *et al.* 1978).

High soil temperatures, resulting from high irradiance of the soil, can promote sprouting (Lacey and Johnston 1990; Schier *et al.* 1985). High temperatures may lower the auxin: cytokinin ratio by increasing cytokinin production, and by speeding degradation of auxin (Schier *et al.* 1985).

Summary: natural stresses and growth form

The development of multi-stemmed clumps as the result of environmental stress involves a change in plant hormone levels, most importantly the auxin: cytokinin ratio. Although "natural coppicing" implies death of the main stem leading to a release from apical dominance, other non-lethal alternatives exist which would promote a multi-stemmed growth form. In aspen, Schier *et al.* (1985) mention that if apical control is weak, or the concentration of growth promoting substances is high, sprouting can occur with very little disturbance. The same could be true for species in Guánica Forest.

History of human disturbance in Guánica Forest

According to Wadsworth (1950), the forests of Puerto Rico were little cut by the pre-Columbian Taíno Indians; disturbance consisted mainly of the farming practice of "conuco" or "shifting cultivation". A small plot of land was cleared and farmed for 2-3 years until most of the organic matter and available nutrients were exhausted, and then abandoned. Although the coast, along which Guánica Forest is located, was the site of Indian settlements, the population was probably too low (estimated to have been 30,000-60,000 when the Spaniards arrived) to have significantly impacted the vegetation (Wadsworth 1950).

Population densities of European settlers in Puerto Rico likewise remained low during the first few centuries, with about 45,000 people in 1765, and most of the forests remained intact. Soon after, the population began to

rise. At the beginning of the 19th century the population had risen to 155,000, and by 1899 it had reached 953,000. It was during the 19th century that destruction of the forests accelerated, especially along the coasts. In 1815, the Spanish government opened Puerto Rico to world commerce, and the value of total trade grew from \$57,500 in 1803 to \$5,600,000 in 1830. Timber products, coming from towns near Guánica Forest such as Ponce and San Germán, were among the items exported. Most of the forest destruction that occurred during the 1800's came not from timber harvesting, however, but from clearing for agriculture and pasture-land. In 1828, there were 634,000 acres of pastures. By 1899, this had nearly doubled to 1,200,000 acres, or nearly 55% of the island. Destruction of the forests was so extensive that it prompted the Governor General in 1879 to write a letter to the Spanish Foreign Minister in which he described the Puerto Rican forests to be in a very poor condition, particularly those in the southern part of the island. In 1898 forested lands near Guánica Forest (as well as other forested areas around the island) were still held as Crown lands, and theoretically protected from extensive clearing. However, settlers near government forests were permitted to collect timber for their own needs (Wadsworth 1950).

As part of the settlement of the Spanish-American War, Puerto Rico passed into U.S. hands in 1898 (Peraire-Vidal 1983). At the beginning of the 20th century, disturbance in what is now Guánica Forest consisted mainly of clearing for farming, trails, paths and homesteads, cutting for charcoal, and a baseball field (Figure 3). Selected trees were removed for timber and fenceposts, and grazing occurred throughout many areas of the forest (Murphy *et al.* 1995). In 1917, Guánica Forest became a Commonwealth Forest, and since the mid-1930's has been protected from farming or grazing. The area of the forest where the present study was undertaken appears little

Figure 3. Land use in a section (El Maniel) of Guánica Forest, 1935. Approximate location of the 'main site' and the '1969 site' (see Methods) are indicated towards the bottom of the map by 'M' and 'E', respectively. The inset shows the section of Guánica Forest represented (Map adapted from Sandra Molina, U.S.D.A. Forest Service, International Institute of Tropical Forestry, Rio Piedras, Puerto Rico.)

disturbed in 1936 aerial photographs. Since that time, there has been only occasional grazing by goats and cutting of post-sized timber, and these activities have been mostly confined to the outer margins of the forest (Lugo, *et al.* 1978).

Objectives and statement of hypothesis

The main hypothesis for this study was the following:

The multi-stemmed growth form prevalent among trees of Guánica Forest is in large part due to intrinsic growth patterns and/or environmental factors rather than to cutting or other disturbance (e.g., grazing) which removed the main stem.

In conjunction with this hypothesis, the following objectives were developed:

- (1) To develop a methodology for determining whether the multi-stemmed growth form of a tree is due to cutting versus other factors.
- (2) To determine the percentage of trees which are naturally multi-stemmed versus those that are multi-stemmed due to cutting.
- (3) To determine if any differences exist in the number of stems between individuals of different size classes.
- (4) To uncover any interspecific differences in multi-stemmed growth form.
- (5) To find evidence suggesting the environmental factors most responsible for the multi-stemmed growth form.

This study examined the growth form of select tree species growing in a drought-stressed ecosystem, the dry forest at Guánica, Puerto Rico. Cutting by humans and natural mechanisms leave unique signatures in a tree's growth form. Such signatures provide evidence to either support or refute the main hypothesis. Obtaining such evidence, as well as documenting the multi-stemmed growth form of key species, was the focus of this study.

Description of the study site

Guánica Forest is located at 18° north latitude in the subtropical dry forest life zone (sensu Holdridge 1967) which extends for about 120 km along the southwest coast of Puerto Rico (Figure 4). Little and Wadsworth (1964) recognize two climax forest types in this life zone, the dry coastal forest, and the dry limestone forest (Figure 5). It is within the latter forest type, the dry limestone forest, that stretches about 40 km from Ponce west to Ensenada, that Guánica Forest is located.

Rainfall records from Ensenada (a few km west of the study site) show a mean annual rainfall of 774 mm, falling mainly during two rainy seasons (Figure 6). These wet periods are interrupted by two dry seasons: a major dry season from December to April and a minor one from June to August. In the period from June, 1975-May, 1976, Lugo *et al.* (1978) measured soil moisture deficits for seven months of the year (Figure 7), although the passage of hurricane Eloise in September of 1975 led to higher than average precipitation levels for their study period. The climate station at Santa Isabel, also in the subtropical dry forest life zone, reported soil moisture deficits for ten months of the year (Ewel and Whitmore 1973). There tend to be pronounced year-to-year fluctuations in the amount of precipitation received. Between 1931 and 1981, values ranged from a low of 363 mm in 1967 to a high of 1,469 mm in 1979. The predominately northeasterly trade winds that bring rain to most of Puerto Rico are intercepted and drained of their moisture by the Cordillera Central, leaving the south coast dry. Moisture that does arrive in Guánica Forest tends to be from the southeast (M. Canals, pers. comm.). The ratio of temperature to precipitation was 2.9 (Lugo *et al.* 1978).

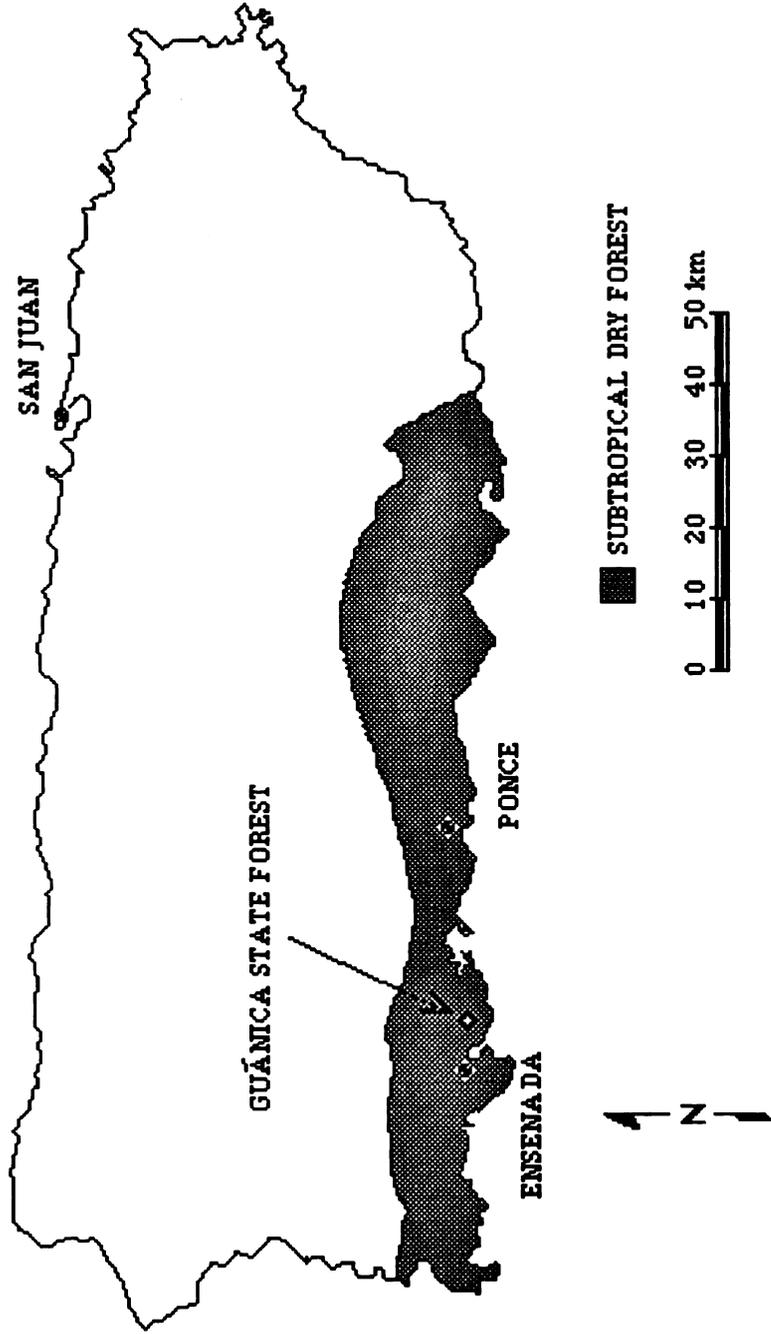


Figure 4. The subtropical, dry-forest life zone in Puerto Rico (adapted from Ewel & Whitmore 1973).

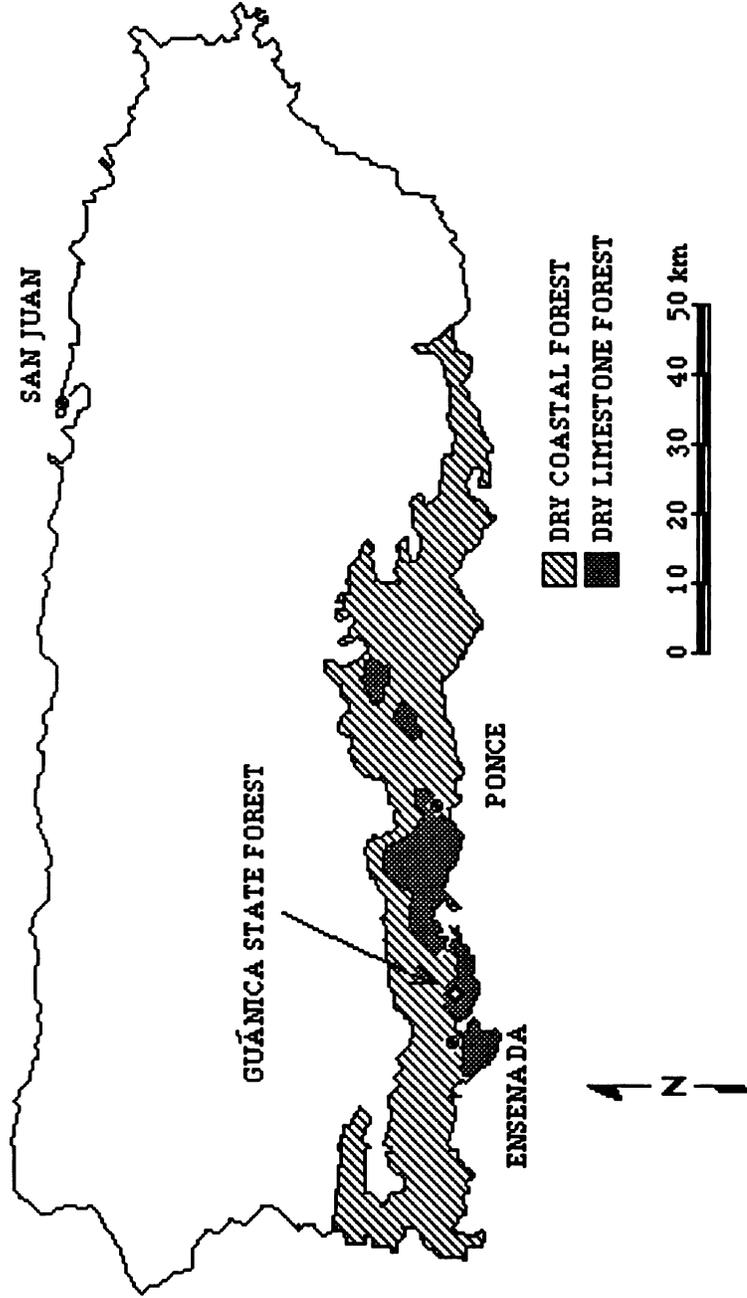


Figure 5. Dry climax forest types of Puerto Rico (adapted from Little & Wadsworth 1964).

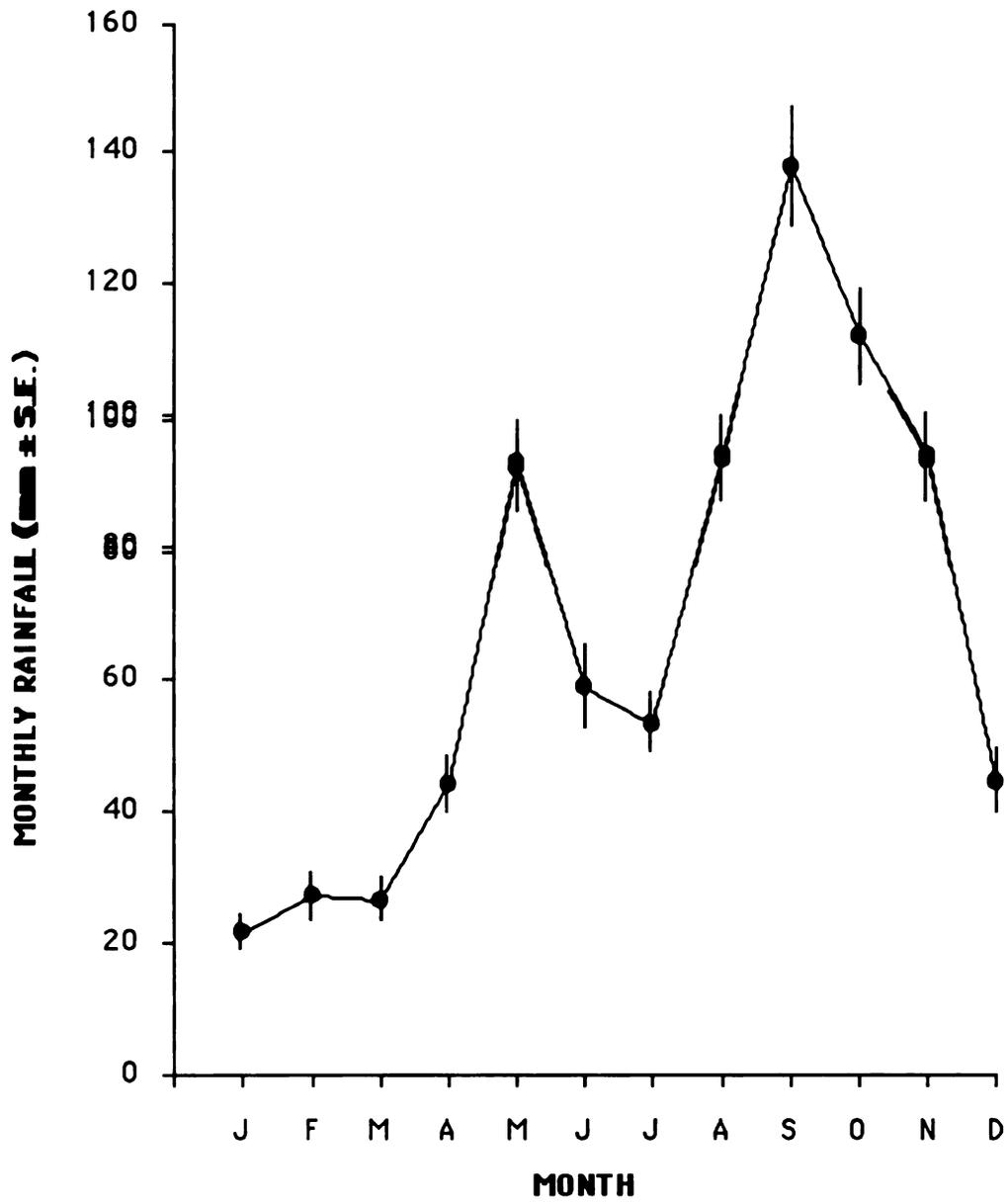


Figure 6. Monthly rainfall at Ensenada, Puerto Rico (1931-1953, 1956-1981).

Sources: United States Weather Bureau (1954); National Oceanic and Atmospheric Administration (1994).

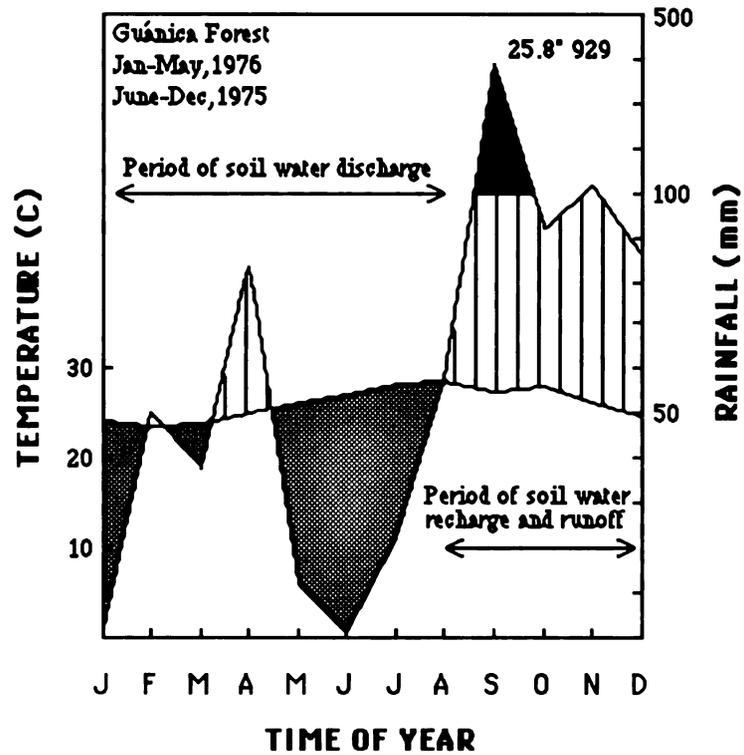


Figure 7. Climate diagram for the Guánica Forest for January-May, 1976 and June-December, 1975. Moist periods are shown with vertical lines, excess water with solid black, and periods of moisture deficit with dots. Source: Lugo, *et al.* (1978).

In July 1981, Murphy and Lugo (1986b) established a permanent 120 m x 120 m study site in a location considered representative of the deciduous forest type of Guánica Forest. This forest type accounts for 58% of the forest in Guánica Forest. The study site is located approximately 2 km inland on a south-facing slope of 13-14° at an elevation of 175 m. Structurally, the site is dominated by a large number of stems: 14,007 stems of at least 2.5 cm dbh per ha. Most of these stems were small, with only 2.3% exceeding a dbh of 10 cm, and short, with fewer than 12% exceeding 5 m in height, and none reaching 9 m. Twenty-one of 34 woody species found by Murphy and Lugo (1986b) in sample plots were reported by Little and Wadsworth (1964) to be capable of growing as shrubs (Table 4). This coincides with Murphy and Lugo's finding that 56.9% of the stems examined were members of multi-stemmed clumps. These multi-stemmed clumps were the focal point of the present study.

The 120 m x 120 m (1.44 ha) study site described by Murphy and Lugo (1986b) was the main location of the field work reported here, and hereafter will be referred to as the "main site" (Figure 3). In addition, two sets of plots which were experimentally cut in 1969 and 1981 to study regeneration following disturbance were also examined. The first, located within the main site, is comprised of five 10 m x 10 m plots from which all aboveground vegetation was removed in 1981 (Murphy and Lugo 1986b). These plots will be referred to as the "1981 plots". The second, a 1-ha site about 1 km west of the main site (Figure 3), was experimentally clearcut in 1969 (Ewel 1971), and hereafter will be referred to as the "1969 site".

Field work was performed during three trips to Guánica Forest on the following dates: July 13 through August 6, 1993, June 27 through August 5, 1994, and February 3 through February 22, 1995.

Table 4. Life form of 34 woody species (Little and Wadsworth 1964) found in 15 10-m x 10-m sample plots in the 1.44 ha study site (Murphy and Lugo 1986b), listed in order of decreasing importance value (IV).

<u>IV</u>	<u>Species</u>	<u>Life Form</u>
1	<i>Gymnanthes lucida</i>	small tree, shrub
2	<i>Exostema caribaeum</i>	small tree, shrub
3	<i>Pisonia albida</i>	tree
4	<i>Pictetia aculeata</i>	small tree
5	<i>Thouinia portoricensis</i> ^a	small tree, shrub
6	<i>Coccoloba, k & m</i> ^b	small tree, shrub
7	<i>Cephalocereus royenii</i>	cactus
8	<i>Bursera simaruba</i>	tree
9	<i>Erithalis fruticosa</i>	shrub
10	<i>Guettarda krugii</i>	small tree, shrub
11	<i>Tabebuia heterophylla</i>	tree
12	<i>Hypelate trifoliata</i>	small tree, shrub
13	<i>Coccoloba diversifolia</i>	tree
14	<i>Cassine xylocarpa</i>	small tree, shrub
15	<i>Krugiodendron ferreum</i>	small tree, shrub
16	<i>Jacquinia berterii</i>	small tree, shrub
17	<i>Bourreria succulenta</i>	small tree, shrub
18	<i>Crossopetalum rhacoma</i>	small tree, shrub
19	<i>Antirhea acutata</i>	small tree, shrub
20	<i>Amyris elemifera</i>	small tree, shrub
21	<i>Erythroxylum rotundifolium</i>	small tree, shrub
22	<i>Guettarda elliptica</i>	small tree, shrub
23	<i>Eugenia foetida</i>	small tree, shrub
24	<i>Forestiera segregata</i>	small tree
25	<i>Eugenia xerophytica</i>	small tree, shrub
26	<i>Leptocereus quadricostatus</i>	cactus
27	<i>Reynosia guama</i>	small tree
28	<i>Linociera holdrigii</i>	small tree
29	<i>Plumeria alba</i>	tree
30	<i>Comocladia dodonaea</i>	small tree, shrub
31	<i>Thrinax morrisii</i>	palm
32	<i>Zanthoxylum flavum</i>	tree
33	<i>Rochefortia acanthopora</i>	small tree, shrub

^a Now classified as *Thouinia striata* var. *portoricensis* (Liogier 1982).

^b *Coccoloba krugii* and *microstachya*.

METHODS

Description and causes of the multi-stemmed growth form

Buried in the present form of the tree species are clues to their origin. These include obvious features such as stumps due to cutting, and original main stems indicating lack of cutting. A gradual increase in the number of stems with increasing tree size could indicate that a gradual accumulation of stems is the natural development pattern for a species. This is particularly true for trees that began growth subsequent to the forest being protected from cutting and grazing. Alternatively, multiple stems that occur only in older trees (predating forest protection) or above a certain threshold size, could indicate that those trees were cut in the past or that environmental stresses intensify once a certain point is reached (e.g., exposure of the crown above the canopy). To investigate these growth forms, work was conducted within two transects during the summers of 1993 and 1994 (Figure 8). In 1993, a 2-m wide, 100-m long broken transect which traversed the main site in an upslope direction (from south to north) was established. The transect was broken into 20 5-meter segments, with observations made in alternating segments. In 1994, observations were made within a 10-m wide transect along the entire inside perimeter of the main site, thus avoiding the plots cut in 1981. The placement of the transects was intended to allow for a collection of individuals representative of the whole 1.44 ha study site.

All woody species encountered in the 1993 broken-transect were measured. In the 1994 perimeter transect, work was focused on eleven key species. The 1993 transect was intended to allow quantitative measurements of whole-forest structure to be made, while the 1994 transect allowed a more

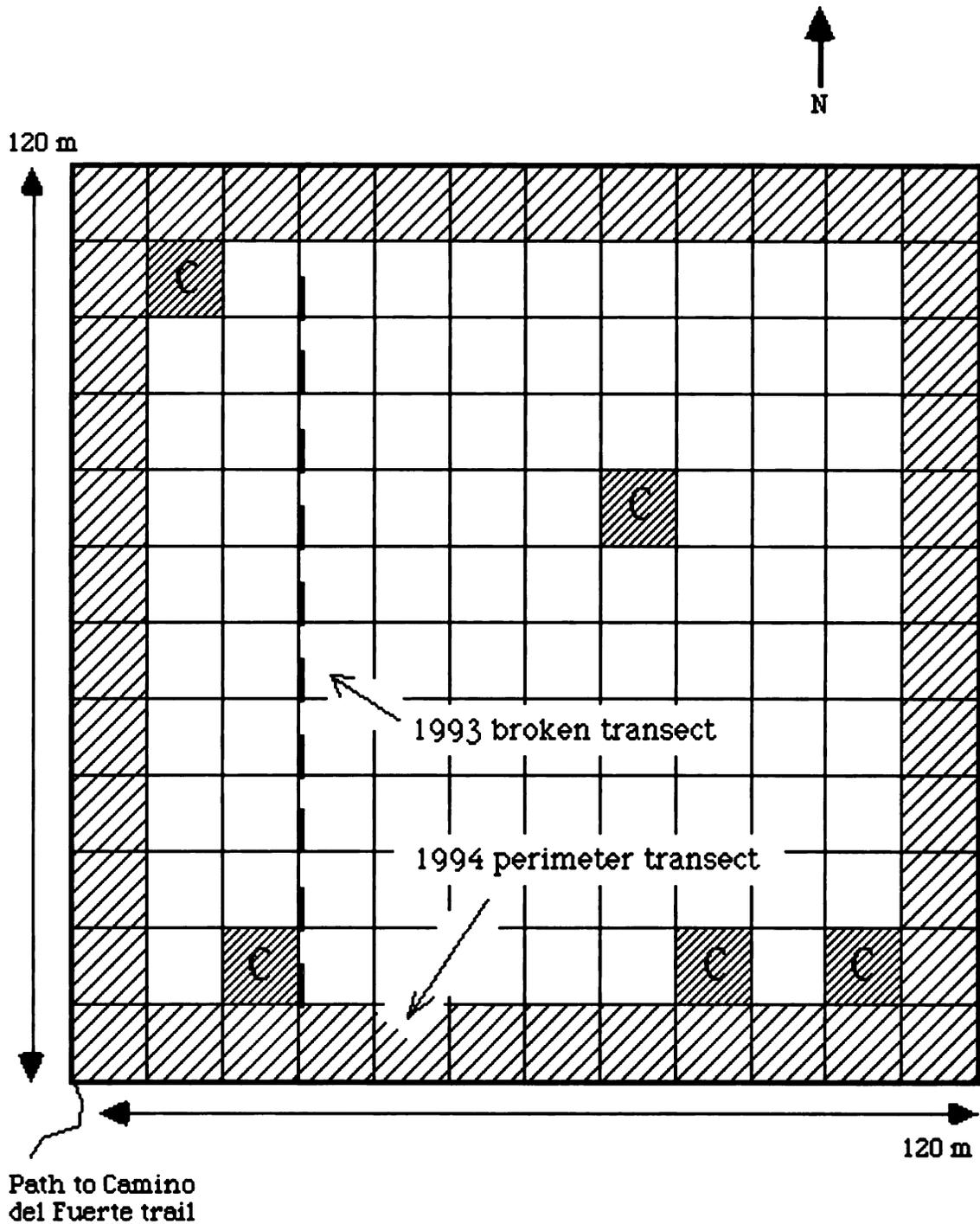


Figure 8. Diagram of 1.44-ha site ("main site") showing location of broken transect from 1993 and the 10-m wide transect within the perimeter of the main site where sampling was conducted in the summer of 1994. The 10 m x 10 m plots that were clearcut in 1981, indicated by the 'C's, also were sampled in the summer of 1994.

detailed assessment of the multi-stemmed growth form in the species chosen for study. For the latter, the nine top-ranked tree species in terms of importance values determined by Murphy and Lugo (1986b) for the main site were selected for study (Table 5). These trees, together with two common understory shrub species (*Eugenia foetida* and *Croton humilis*) which were included for comparison (see below), accounted for 62.8% (188.39 of a possible 300) of the total importance values for all plant species equal to or greater than 2.5-cm dbh (diameter at breast height) at the main site

In the 1994 transect, a minimum of five individuals from each of the following seven diameter size classes was measured for each species studied: 0-1 cm, 1-2 cm, 2-3 cm, 3-4 cm, 4-5 cm, 5-10 cm, >10 cm. These size classes are based on diameter at ground height (dgh). Instead of the more traditional dbh, dgh was chosen to allow for comparisons to be made between larger and smaller stems (especially those shorter than "breast height"). It was believed that significant changes in tree growth form were occurring in smaller trees. To more precisely document the sizes at which these changes occurred, 1-cm size classes were used for trees below 5-cm dgh. Larger trees were grouped into larger dgh categories of 5-10 cm and >10 cm.

The following measurements were made in both the 1993 and 1994 transects. For each individual, species, diameter at ground height of the whole tree, and overall tree height were determined (Figure 9). Within each tree, each stem was measured for dbh, total length, height of attachment to the main stem (secondary stems only), and diameter of the secondary stem at this point. For the purposes of the present study, a stem is differentiated from a branch in that the former has assumed vertical growth at its most distal end. Additionally, only stems with an origin (the point of emergence from the ground or from another stem) below 1 m in height were examined. This was to

Table 5. Tree species with the nine highest importance values (relative frequency + relative density + relative dominance) for plant species having a dbh equal to or greater than 2.5 cm in 15 10 x 10 m plots located in the 1.44-ha main site (adapted from Murphy and Lugo 1986b). The last two species are common understory shrub species in Guánica Forest.

Rank	Species	I.V.	Rel. freq.	Rel. den.	Rel. dom.
1	<i>Gymnanthes lucida</i>	43.51	8.15	21.52	13.84
2	<i>Exostema caribaeum</i>	25.16	8.76	7.28	9.12
3	<i>Pisonia albida</i>	22.46	5.87	4.38	12.21
4	<i>Pictetia aculeata</i>	21.47	5.26	10.19	6.02
5	<i>Thouinia portoricensis</i> ^a	21.00	5.26	10.68	5.06
6	<i>Coccoloba, k & m</i> ^b	19.78	5.87	7.61	6.30
8 ^c	<i>Bursera simaruba</i>	11.70	5.26	1.15	5.29
9	<i>Erithalis fruticosa</i>	9.97	3.50	3.83	2.64
10	<i>Guettarda krugii</i>	9.75	2.37	2.03	1.12
23	<i>Eugenia foetida</i>	3.59	2.37	0.66	0.56
n.r. ^d	<i>Croton humilis</i>	---	---	---	---
	Total	188.39			

^a Now classified as *Thouinia striata* var. *portoricensis* (Liogier 1982).

^b *Coccoloba krugii* and *microstachya*.

^c Rank 7 is held by the cactus, *Cephalocereus royenii*.

^d Not ranked. Most *Croton humilis* shrubs are shorter than 1.4 m in height (hence have no dbh) and at their thickest, are usually less than 2.5 cm in diameter. Hence they did not receive an I.V. rank despite their widespread occurrence.

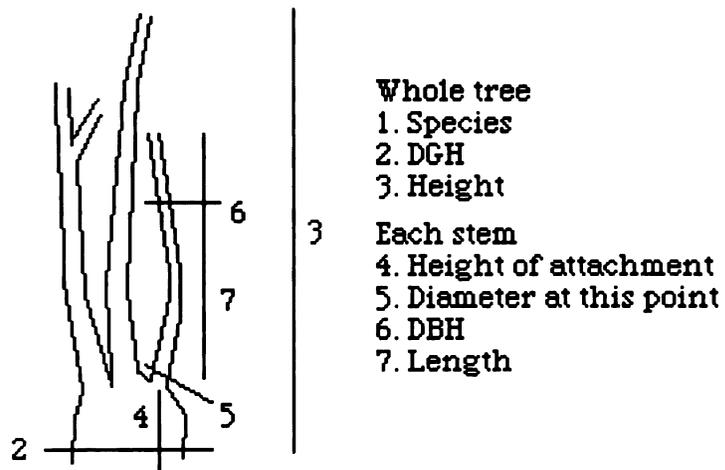


Figure 9. Data collected for each tree or shrub examined at the main site.

exclude those branches higher in the tree that may have assumed vertical growth (and therefore technically should be termed "stems"), yet do not change the overall physiognomy of the tree.

The following drawings were made:

- a) a vertical profile of the whole tree, showing its overall growth form;
- b) for multi-stemmed trees, a detailed drawing of the base of the tree, showing where the different stems were attached;
- c) an outline of the crown, as viewed from above, including orientation and position relative to the base of the tree; and
- d) a top view of the base of the tree showing where individual stems were positioned. Direction of magnetic north was also indicated in the drawings.

In a tropical dry forest of Sierra Leone, Nyerges (1989) found evidence in the growth form of multi-stemmed clumps that suggested that they arose

from cutting: "The coppices arise from old, burned stumps and often form rings or semicircles of stems that are connected at ground level and enclose pockets of soil". Likewise, Sakai (1990) in examining red maples (*Acer rubrum*) in northern lower Michigan noted that "ramets occurred in a characteristic circular pattern" and used that as a basis to determine if a ramet were a stump sprout. Similar visual inspection of multi-stemmed clumps at the main site at Guánica Forest allowed an evaluation of whether their origin was natural or the result of cutting. All multi-stemmed individuals received a rank of from 1 to 6 based on the criteria in Table 6.

Table 6. Ranking system for multi-stemmed individuals.

Rank	Explanation
1	Obvious cut stump present.
2	Degraded stump or stump-like structure, too degraded to determine if it had been cut.
3	Growth form consistent with cutting, in that the stems are gathered around an open central area where a stump may have been.
4	Growth form inconclusive.
5	Growth form inconsistent with cutting, in that the stems are closely packed together, suggesting that a stump was never present.
6	Not cut. All stems emerge from the intact, original main stem (which may be either dead or alive).

Self-thinning following cutting

Preliminary evidence from the first field season showed that the multi-stemmed trees in the 1981 cut plots had a higher average number of stems than those in the areas of the main site not cut in 1981. This suggests that either the trees in the surrounding main site were never cut, or that they were cut and subsequently thinned down to their present number of stems. To investigate this issue, multi-stemmed trees in the 1969 cut site were included for comparison. If self-thinning does occur among the eleven study species, trees that were cut in 1969 should have fewer stems, on average, than those cut in 1981. Therefore, five individuals from each of the eleven study species were examined in randomly placed transects in both the 1969 cut site and 1981 cut plots. The following data were collected: species, overall dgh, overall height, number of stems, and the dgh for the largest and smallest stems in multi-stemmed trees.

Growth form of two common understory species

Two common woody understory species (*C. humilis* and *E. foetida*) were included for comparison in the 1994 transect. These species offered a good opportunity to study the development of the multi-stemmed form in two species that are not exposed to the heightened water stress presumed to exist in the canopy. The same data that were collected for the nine tree species mentioned above were collected for these species as well.

Environmental influences on the development of multiple stems

Field conditions that could have an influence on the number of stems were measured at 5-m intervals along each of the transects. These conditions are summarized in Table 7.

Table 7. Field conditions^a measured along the study transects at the main study site in Guánica Forest.

Field Condition	How measured
slope orientation	compass
slope angle	clinometer
exposed rock	1-m x 1-m grid
bare soil	1-m x 1-m grid
canopy height	meter stick

^a Soil depth is potentially a very important factor affecting tree growth form. Nevertheless, to detect a correlation between soil depth and stem number, the former would have had to been measured in the vicinity of each tree examined. Time limitations, as well as the desire to limit disturbance to the study area, precluded such measurements.

RESULTS AND DISCUSSION

Determination of whether multi-stemmed form is natural

With the exception of *Bursera simaruba*, all eleven study species, including eight of the forest's leading tree species, had examples of multi-stemmed individuals that had not been cut (Table 8). The strongest evidence for the natural development of multiple stems was the presence of original main stems and small multi-stemmed saplings (Figures 10-13).

Persistent original main stems were found in multi-stemmed trees of all species studied except *Pictetia aculeata*, which regularly displayed a growth form consistent with past removal of the main stem. In all, 19.9% of multi-stemmed trees possessed an original main stem, ranging from 5% of individuals for *Coccoloba krugii* to 80% of individuals in *Exostema caribaeum*. It could be argued that following cutting in the past, new stems may have arisen that mimicked an original main stem. Contradicting this possibility was the absence of any stems resembling an original main stem among the multi-stemmed trees that had been cut in 1969.

Small multi-stemmed individuals, clearly having arisen in the absence of cutting or grazing, were found in all species studied except *Pisonia albida* and *B. simaruba*¹. Of all individuals below 3-cm dgh, 23.0% were multi-stemmed. *E. caribaeum* had the fewest small-sized multi-stemmed saplings, with multiple stems possessed by 6% and 8% of trees below 3-cm dgh and 5-cm dgh, respectively. *C. krugii* had the most, with multiple stems possessed by 62% and 69% of trees below 3-cm dgh and 5-cm dgh, respectively. Although the

¹ The smallest *P. albida* with multiple stems was 5.9-cm dgh and had 3 stems. All of the *B. simaruba* trees found at the main site were single-stemmed.

Table 8. Tree growth-form properties inconsistent with cutting for the eleven study species: (a) the percentage of multi-stemmed trees (all size classes included) with an original main stem; (b) the percentage of saplings in 0-3 cm or 0-5 cm dgh size classes which possessed multiple stems.

Species	(a)		(b)		
	% with original	n	% with mult. stems		n
	main stem		in dgh size classes:		
			0-3 cm	0-5 cm	
<i>Gymnanthes lucida</i>	32	19	33	37	18, 30
<i>Exostema caribaeum</i>	80	5	6	8	16, 26
<i>Pisonia albida</i>	14	7	0	0	1, 5
<i>Pictetia aculeata</i>	0	11	0	12	6, 17
<i>Thouinia striata</i> var. <i>portoricensis</i>	17	18	38	57	8, 14
<i>Coccoloba krugii</i>	5	21	62	69	13, 16
<i>Bursera simaruba</i> ^a	-	-	-	-	-
<i>Erithalis fruticosa</i>	21	24	33	56	15, 25
<i>Guettarda krugii</i>	14	14	20	35	15, 26
<i>Croton humilis</i>	25	12	14	20	50, 54
<i>Eugenia foetida</i>	30	10	20	22	35, 37

^a All *B. simaruba* trees in the present study were single-stemmed.



Figure 10. Naturally multi-stemmed *Erithalis fruticosa* in main study site.



Figure 11. Naturally multi-stemmed *Cocoloba krugii* in main study site. Note: all three sprouts at the base of the original main stem are alive.



Figure 12. Naturally multi-stemmed *Exostema caribaeum* in the main site showing an intact original main stem.



Figure 13. Multi-stemmed *Gymnanthes lucida* tree (dgh <5 cm) in the main site, which is too young to have been present during last cutting episodes of the 1930's.

diameter growth rate in the forest is only on the order of 0.13 cm/year (Murphy and Lugo 1990), most of these individuals would have been far too small 60 years ago to have been cut for timber or fenceposts. A few individuals (*Gymnanthes lucida* and *Erithalis fruticosa*) were multi-stemmed even below 1-cm dgh.

In some of the larger trees with no clear main stem, it is more difficult to determine whether cutting occurred or not. In the trees cut in 1969, many of the stumps were severely degraded by 1995, in 30% of the cases leaving no more than a ring of stems around a central area. Therefore, it is hard to imagine a cut stump at the main site surviving the 60 years since the last major cutting episodes. The most that remain are a few, degraded, stump-like structures (13.5% of multi-stemmed clumps) or a ring-like arrangement of stems (5.0% of multi-stemmed clumps). However, it can not be assumed that these latter tree forms are due to past cutting, since natural stem breakage (e.g., from high winds) would produce a similar structure. In addition, many of the larger trees have a growth form inconsistent with cutting, or their form seems to be a larger form of that found in smaller conspecifics (Figures 14, 15). Only in *P. aculeata* (see below) was there a growth form in the larger size classes that was different from that of the smaller size classes.

In dealing with species which are multi-stemmed at the base, there is a possibility that these clumps could represent multiple genetically-distinct individuals joined together (Frank Telewski, pers. comm.). *C. krugii*, for instance, has small, bird dispersed fruits (Ewel and Whitmore 1973). It is conceivable that a bird could ingest a number of these fruits and then deposit a group of seeds in very close proximity to each other, or that seeds could be stored together, or cached, for later use (Vander Wall 1990). After germination and a period of growth, these separate plants could appear as a



Figure 14. *Cocoloba krugii* shrub in the main site.



Figure 15. *Cocoloba krugii* shrub in the main site. Note that this shrub is simply a larger version of that in Figure 14.

single, multi-stemmed shrub. This possibility could confuse our interpretation of how single individuals develop. However, it does not pose a problem for the question of whether or not these clumps are natural or due to human disturbance, in that a multi-individual clump which mimics a single individual could still be considered a natural growth form.

Self-thinning following cutting

The trees in the plots cut in 1981 had more than twice the average number of stems as those in the main site (Table 9). Individual species showed even greater differences. *E. fruticosa* had 3.2 times as many stems in the cut plots, *E. foetida* had 3.1 times more, *P. albida* had 3.9 times as many, and *G. lucida* had 4.4 times as many stems in the 1981 cut plots as in the main site. *Guettarda krugii* actually had slightly fewer stems in the 1981 cut plots, with an average of 3.3 stems versus 4.2 stems at the main site. *B. simaruba*, which had no multi-stemmed trees in the main site, had one 5-stemmed individual in the 1981 cut plots.

Only eight of the eleven study species were found at the 1969 cut site. Overall, the average number of stems at the 1969 1-ha cut site shows little difference from that of the 1981 cut plots. A decrease in the number of stems was noted for *G. lucida* and *P. albida* (Table 9). For five species, the average number of stems was about the same or even slightly higher in the 1969 site compared to the 1981 plots. Significant thinning within multi-stemmed trees at the 1969 site seems to have occurred only in *G. lucida* and *P. albida*. This could indicate that they were cut in the past and thinned down to their present form. In the case of *G. lucida*, the high number of intact original main stems

Table 9. Average number of stems and percentage of different stump types found in the cut plots (1969 site and the five 1981 plots) and the main site (protected). (a) Average number of stems of multi-stemmed trees. In parentheses are the standard errors of the mean. (b) The percentage of multi-stemmed trees which had an obvious stump, a degraded stump, or a ring-like arrangement of stems.

Species	1981 cut plots			1969 cut site			Main (uncut) site		
	(a) Average number of stems								
	average (n)			average (n)			average (n)		
All	10.4	(1.2)	48	9.0	(1.0)	50	4.7	(0.4)	141
<i>Gymnanthes lucida</i>	16.0	(1.9)	5	9.6	(1.7)	7	3.6	(0.5)	19
<i>Exostema caribaeum</i>	5.0	(2.0)	2	5.1	(0.9)	8	3.0	(0.5)	5
<i>Pisonia albida</i>	14.0	(1.0)	2	6.2	(3.4)	6	3.6	(1.3)	7
<i>Pictetia aculeata</i>	8.4	(3.1)	5	12.1	(2.3)	8	3.5	(0.7)	11
<i>Thouinia striata</i> var. <i>portoricensis</i>	8.0	(3.7)	5	13.0	(2.9)	9	5.4	(1.5)	18
<i>Coccoloba krugii</i>	16.0	(4.7)	3	17.4	(2.8)	5	8.1	(1.9)	21
<i>Bursera simaruba</i>	5	(-)	1	4.3	(0.9)	6			0
<i>Erithalis fruticosa</i>	15.2	(4.7)	8			0	4.8	(0.5)	24
<i>Guettarda krugii</i>	3.3	(0.9)	3	8	(-)	1	4.2	(0.8)	14
<i>Croton humilis</i>	7.0	(1.2)	9			0	3.3	(0.4)	12
<i>Eugenia foetida</i>	8.3	(2.9)	5			0	2.7	(0.3)	10
	(b) Percentage with stumps								
obvious stumps	90-100 ^a			30.0			0		
degraded stumps	-			8.0			13.5		
ring arrangement	-			30.0			5.0		

^a Although not counted at the 1981 cut plots, almost all multi-stemmed clumps had a stump (B. Dunphy, pers. obs.).

and the presence of multiple stems in many of the smaller saplings would indicate that a natural multi-stemmed growth form is the norm for this species. *B. simaruba*, single stemmed at the main site, had an average of 4.3 stems per tree at the 1969 site.

None of the multi-stemmed trees at the 1969 site had an intact original main stem, nor were there any trees with a growth form inconsistent with cutting. In contrast, 29.8% of trees at the main site had a growth form inconsistent with cutting. What appeared to be a degraded stump was possessed by 8% of the trees at the 1969 site, and 30.0% had a ring-like arrangement of stems suggestive of a missing main stem. Where the main site and 1969 cut site are very similar is in the number of multi-stemmed trees with an ambiguous growth form (i.e., no clear evidence as to origin): 31.9% of trees at the main site, and 32.0% of trees at the 1969 site.

At an individual tree level, the multi-stemmed growth form of many of the study trees can be concluded to be natural. Nevertheless, problems can arise when extrapolating from observations of individual tree structure to community-level structure. If, prior to protection of the forest, cutting had lowered the overall canopy height, this could have led to an altered microclimate (e.g., greater light penetration to forest floor, leading to higher soil temperatures and greater moisture stress) which could have promoted artificially high levels of sprouting. This does not seem to be the case in Guánica Forest, however, since aerial photographs from 1936 show that the main study site was well forested, and therefore any cutting in the years just prior to forest protection did not substantially alter forest structure.

Description of the multi-stemmed form

In the 1993 broken transect, 43.3% of 187 individuals encountered were multi-stemmed. Multi-stemmed trees averaged 4.1 stems, with 3.4 live stems and 0.7 dead stems. Total basal area for stems of at least 2.5-cm dbh² in the 1993 transect was 15.5 m²/ha, with multi-stemmed trees accounting for 58.4% of this amount (9.05 m²/ha). Also working in the main site, Murphy and Lugo (1986b) found a total basal area for trees at least 2.5-cm dbh of 19.8 m²/ha.

All species examined had some single-stemmed individuals (Figure 16). The percentage of individual trees possessing two or more stems ranged from 13.9% (*E. caribaeum*) to 80.8% (*C. krugii*). Three patterns of growth were evident in the trees examined (Table 10). The first, exemplified by *G. lucida*, *T. striata* var. *portoricensis*, *C. krugii*, *E. fruticosa*, *G. krugii*, *Croton humilis*, and *Eugenia foetida*, is characterized by multiple stems in all size classes, generally with the larger size classes possessing more stems than the smaller size classes. The second pattern, demonstrated by *E. caribaeum*, *P. albida*, and *P. aculeata*, is one in which single stems predominate in smaller size classes, with multiple stems appearing only in the larger size classes. The third pattern, which only *B. simaruba* (not shown) displayed, is characterized by single-stemmed individuals in all size classes³.

One key difference between the two patterns is in the strength of the relationship of dgh with number of stems (Figure 17). With the exception of *G. lucida*, the trees with the first pattern have higher r² values (0.59 to 0.91), than those with the second pattern (0.19 to 0.57). *Thouinia striata* var.

² Area was calculated using dbh instead of dgh to allow for comparison of results with those of Murphy and Lugo (1986).

³ Multi-stemmed *B. simaruba* trees were found at the cut sites, as well as alongside the road leading to the study site.

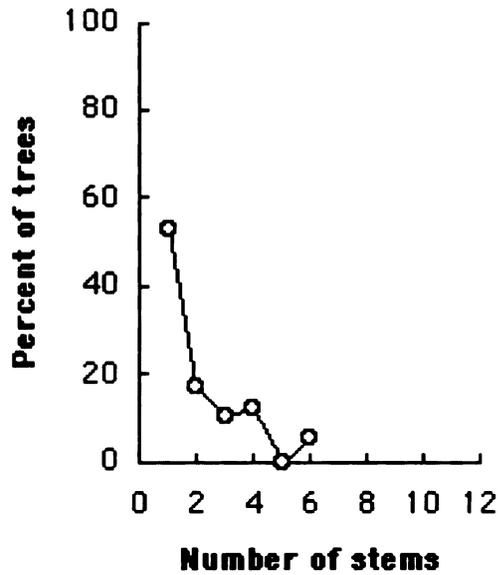
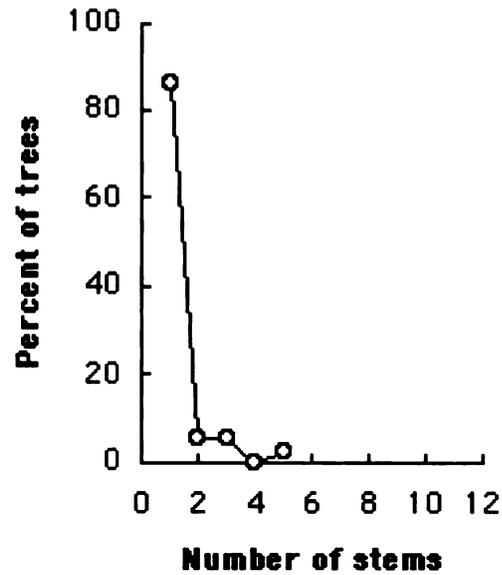
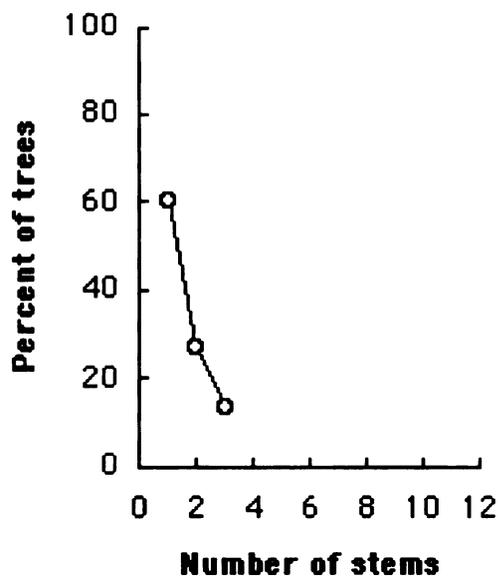
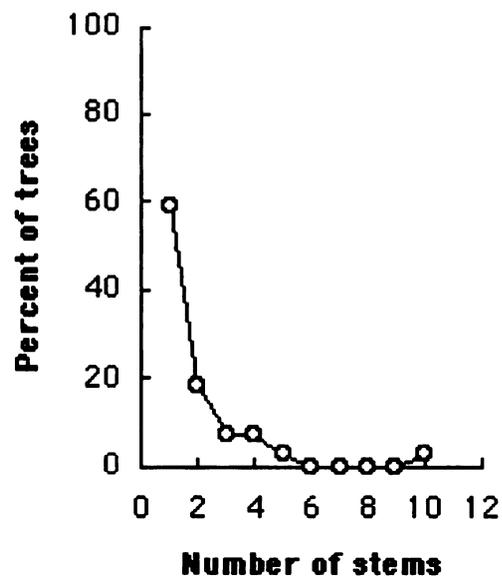
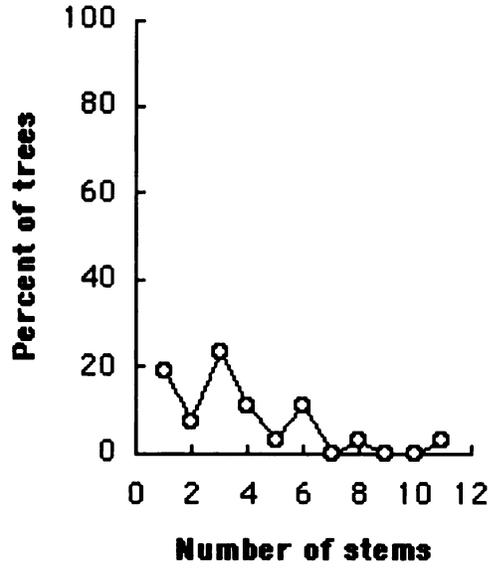
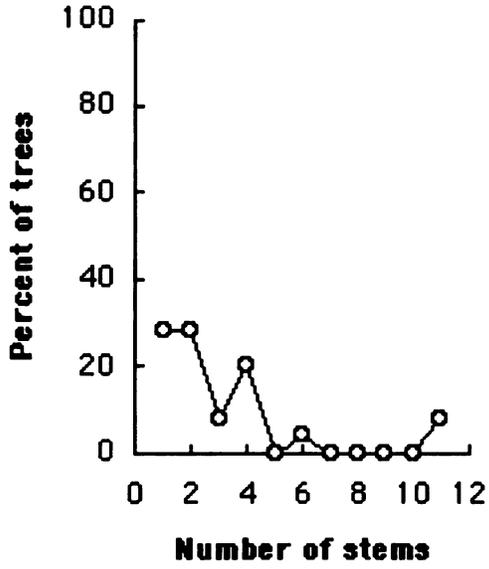
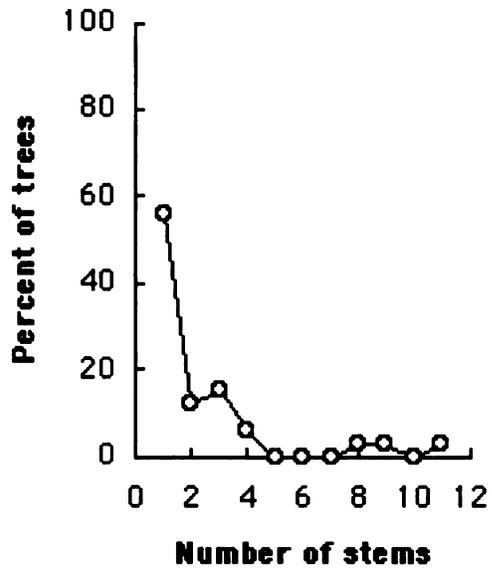
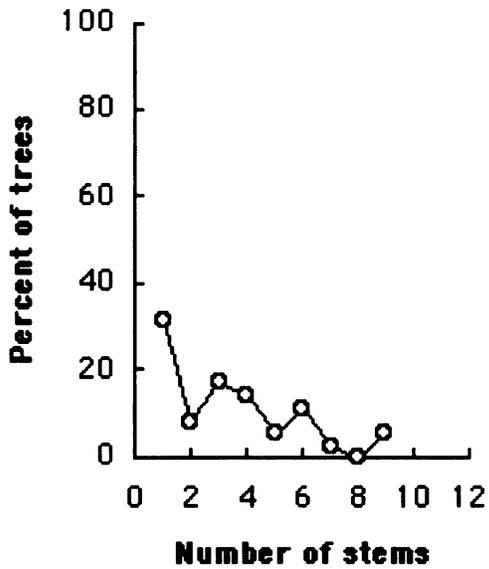
(1) *Gymnanthes lucida* (n=36)(2) *Exostema caribaeum* (n=35)(3) *Pisonia albida* (n=14)(4) *Pictetia aculeata* (n=27)

Figure 16. Percent of trees with a given number of stems for ten of the eleven study species. *Bursera simaruba* is not represented since only single stems were found.

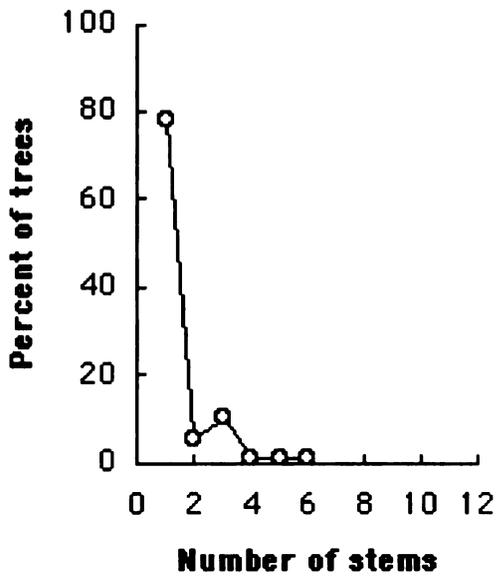


(5) *T. striata* var. *portoricensis* (n=22) (6) *Coccoloba krugii* (n=21)

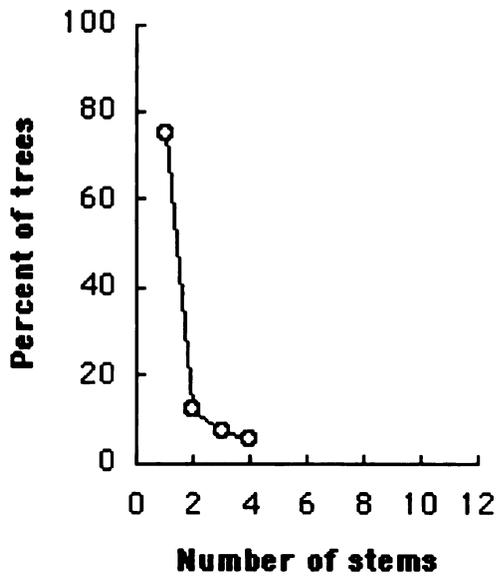


(8) *Erithalis fruticosa* (n=35) (9) *Guettarda krugii* (n=32)

Figure 16 (cont'd).



(10) *Croton humilis* (n=55)



(11) *Eugenia foetida* (n=40)

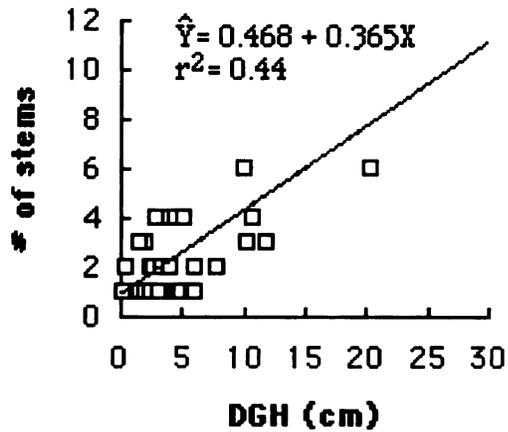
Figure 16 (cont'd).

Table 10. Average number of stems in seven different dgh size classes.

Standard errors of the mean are in parentheses.

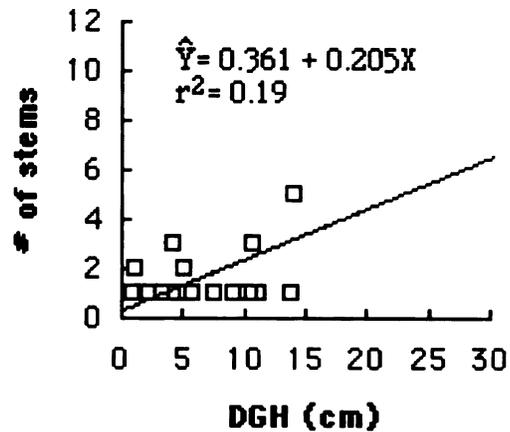
Species	DGH Size Classes (cm)							
	0-1	1-2	2-3	3-4	4-5	5-10	>10 ^a	
<i>Gymnanthes lucida</i>	Average:	1.2 (.2)	1.4 (.4)	1.6 (.3)	1.8 (.6)	2 (.5)	2 (.5)	4.4 (.7)
	Max/ Min:	2/ 1	3/ 1	3/ 1	4/ 1	4/ 1	4/ 1	6/ 3
	n:	5	5	7	5	7	10	5
<i>Exostema caribaeum</i>	Average:	1(0)	1.2 (.2)	1 (0)	1 (0)	1.4 (.4)	1.2 (.2)	2.2 (.8)
	Max/ Min:	1/ 1	2/ 1	1/ 1	1/ 1	3/ 1	2/ 1	5/ 1
	n:	5	6	5	5	5	5	5
<i>Pisonia albida</i>	Average:	--	--	1	1 (0)	1(-)	1.6 (.4)	3.5 (1.5)
	Max/ Min:	--	--	1/ 1	1/ 1	1/ 1	3/ 1	11/ 1
	n:	0	0	1	3	1	5	6
<i>Pictetia aculeata</i>	Average:	--	1 (0)	1 (0)	1 (0)	1.3 (.2)	2.6 (.5)	4.6 (1.5)
	Max/ Min:	--	1/ 1	1/ 1	1/ 1	2/ 1	4/ 1	10/ 2
	n:	0	2	4	5	6	5	5
<i>Thouinia striata</i> var. <i>portoricensis</i>	Average:	1 (-)	1.3 (.3)	1.7 (.3)	1.5 (.5)	2.8 (.5)	3.7 (.7)	11.6(4.3)
	Max/ Min:	1/ 1	2/ 1	2/ 1	2/ 1	4/ 2	6/ 1	26/ 2
	n:	1	4	3	2	4	6	5
<i>Coccoloba krugii</i>	Average:	1.8 (.5)	2.3 (.6)	3 (0)	4 (-)	4.5 (1.5)	6.2(1.3)	20.6(4.3)
	Max/ Min:	3/ 1	4/ 1	3/ 3	4/ 4	6/ 3	11/ 3	34/ 8
	n:	5	6	2	1	2	5	5
<i>Erithalis fruticosa</i>	Average:	1.8 (.6)	1 (0)	2 (.5)	2.8 (.5)	4.6 (.8)	5.2(1.1)	7.8 (1.2)
	Max/ Min:	4/ 1	1/ 1	3/ 1	4/ 1	6/ 2	9/ 3	12/ 5
	n:	5	5	5	5	5	5	5
<i>Guettarda krugii</i>	Average:	1 (0)	1.6 (.6)	1.4 (.2)	2.3 (.5)	1.6 (.4)	3.8(1.5)	10 (1)
	Max/ Min:	1/ 1	4/ 1	2/ 1	4/ 1	3/ 1	8/ 1	11/ 9
	n:	5	5	5	6	5	4	2
<i>Croton humilis</i>	Average:	1.1 (.1)	1.2 (.1)	1.8 (.4)	3.5 (.9)	-	5 (-)	-
	Max/ Min:	2/1	4/1	3/1	6/2	-	5/5	-
	n:	10	34	6	4	0	1	0
<i>Eugenia foetida</i>	Average:	1.1 (.1)	1.3 (.2)	2.4 (.6)	1.5 (.5)	-	2 (.6)	-
	Max/ Min:	2/1	4/1	4/1	2/1	-	3/1	-
	n:	10	20	5	2	0	3	0

^a The large jump in the number of stems seen in some species for the > 10 cm dgh size class is due to very large individuals with large numbers of stems.



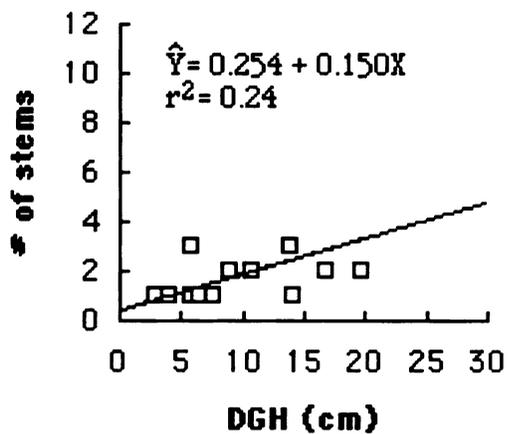
Gymnanthes lucida (n=39)

Rank: 1



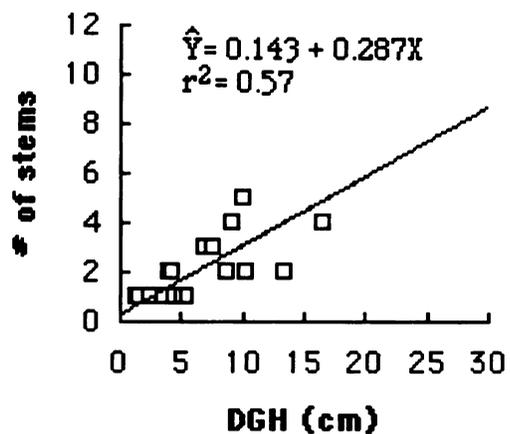
Exostema caribaeum (n=36)

Rank: 2



Pisonia albida (n=16)

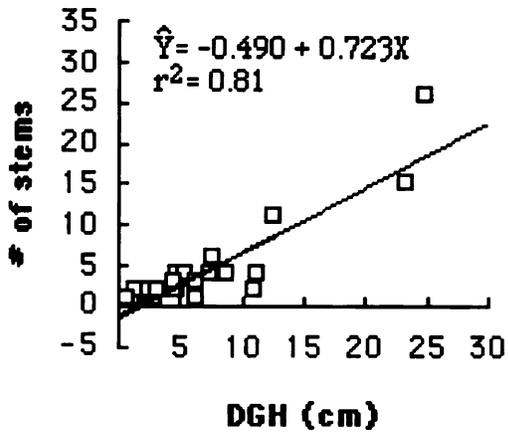
Rank: 3



Pictetia aculeata (n=27)

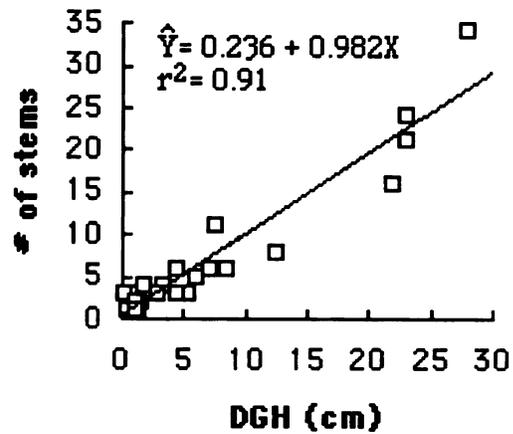
Rank: 4

Figure 17. Number of stems versus dgh (diameter at ground height for whole clump) for ten of the eleven study species at the main site. *Bursera simaruba* (rank: 7) is not presented here since only single stems were found. Rank is based on importance values for all woody species found at the main site (see Murphy and Lugo, 1986b). n.r.- not ranked.



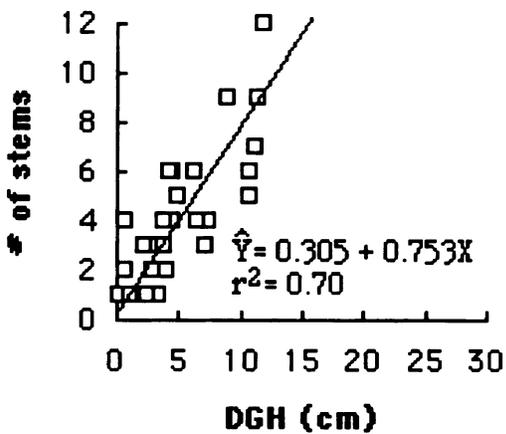
T. striata var. *portoricensis* (n=25)

Rank: 5



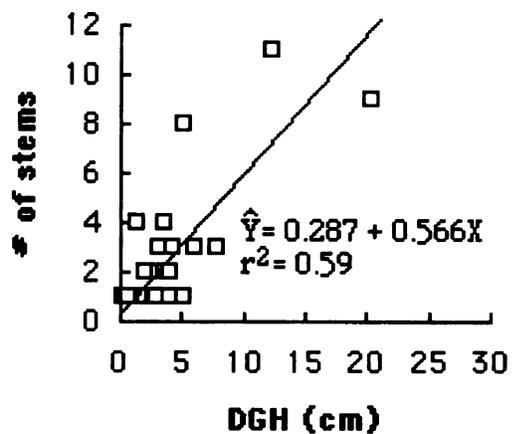
Coccoloba krugii (n=26)

Rank: 6



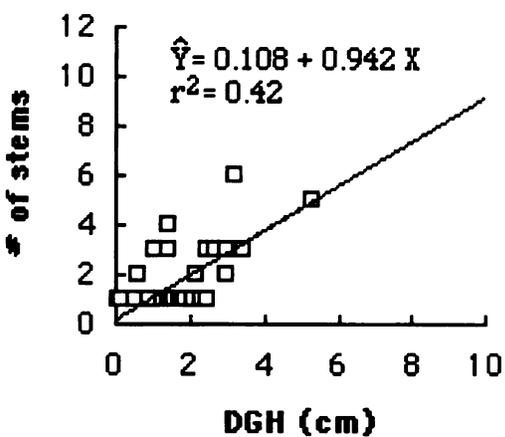
Erithalis fruticosa (n=35)

Rank: 8



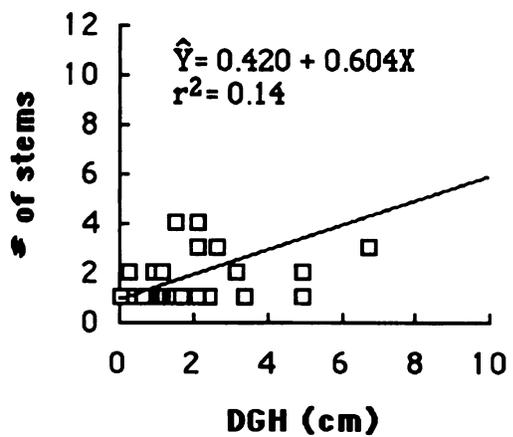
Guettarda krugii (n=32)

Rank: 9



Croton humilis (n=55)

Rank: n.r.



Eugenia foetida (n=40)

Rank: 23

Figure 17, continued.

portoricensis and *C. krugii* had particularly high values, with $r^2=0.81$ and $r^2=0.91$, respectively. The second pattern seems to be more prevalent. Three of the top four species, accounting for 27.4% of the total basal area, possess this pattern of stem acquisition. Although *G. lucida* had multiple stems in smaller size classes, it usually had only one or two dominant stems, and so has more in common with the second pattern than the first. With *G. lucida* included, the trees with the second pattern would account for 41.2% of the total basal area. This would suggest that although the multi-stemmed condition is common in Guánica Forest, the most important tree form, in terms of basal area, is characterized by a single stem in smaller size classes, with multiple stems appearing in larger trees.

Not surprisingly, trees with multiple stems in all size classes acquire additional stems at a lower tree height than those trees where only larger individuals have multiple stems (Figure 18). For the latter, multiple stems appear mainly in individuals which emerge above the canopy.

Multiple stems usually arose near the base of trees (Table 11). For nine of the eleven species examined, the average height of attachment ranged from 1.6 (*C. humilis* and *E. foetida*) to 9.0 cm (*P. albida*) above the ground. For *G. lucida* and *E. caribaeum*, additional stems were attached above the ground at average heights of 19.7 cm and 17.4 cm, respectively.

Growth form of individual study species

(1) *Gymnanthes lucida*

Small sprouts (seedlings and root sprouts) of this species were frequently encountered throughout the forest. Even in the smallest size

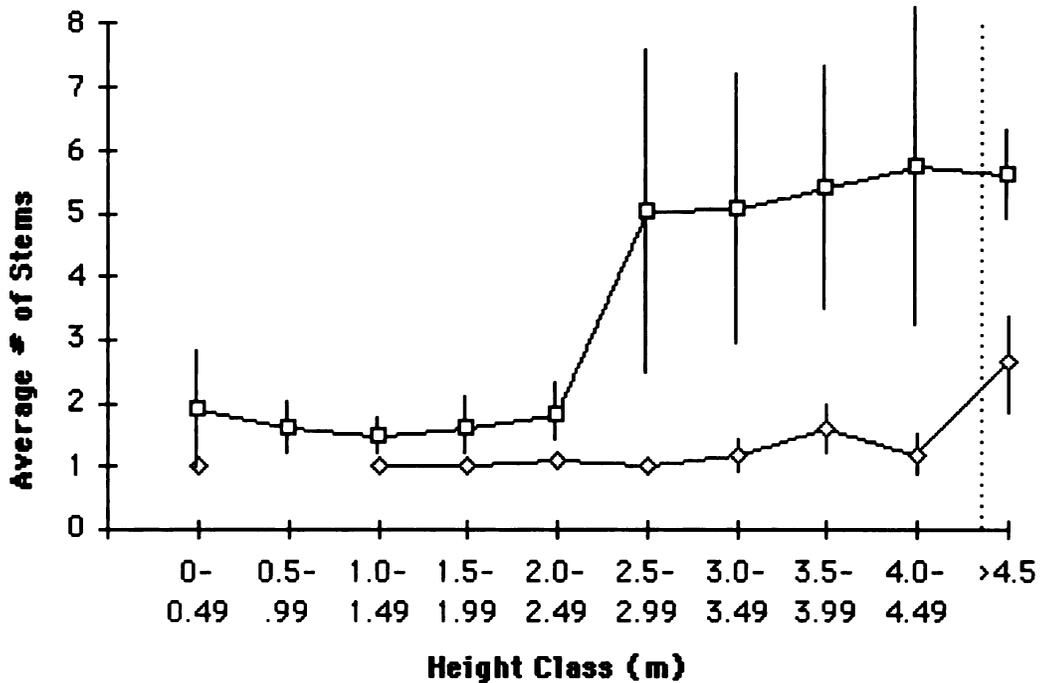


Figure 18. Average numbers of stems per tree in 0.5 m height classes. The overstory tree species were separated into two groups for this comparison. The first group (—□—) is comprised of species which are multi-stemmed in all dgh size classes (*G. lucida*, *T. striata* var. *portoricensis*, *C. krugii*, *E. fruticosa*, and *G. krugii*). The second group (—◇—) is comprised of species which are single stemmed in small dgh size classes, with multiple stems appearing mostly in larger size classes (*E. caribaeum*, *P. albida*, *P. aculeata*). The dotted line marks the average height of the canopy (4.4 m).

Table 11. The average height of attachment of multiple stems on trees found in the 1.44 ha study site. Note: single stems were excluded from the calculations used to construct this table. In parentheses are the standard errors of the mean.

Species	Average height of attachment (cm)	n
1) <i>Gymnanthes lucida</i>	19.7 (3.7)	19
2) <i>Exostema caribaeum</i>	17.4 (5.9)	5
3) <i>Pisonia albida</i>	9.0 (4.0)	6
4) <i>Pictetia aculeata</i>	7.4 (4.2)	11
5) <i>Thouinia striata</i> var. <i>portoricensis</i>	3.8 (1.0)	16
6) <i>Coccoloba krugii</i>	3.4 (1.3)	16
8) <i>Erithalis fruticosa</i>	7.2 (2.1)	24
9) <i>Guettarda krugii</i>	8.8 (3.9)	14
10) <i>Croton humilis</i>	1.6 (1.2)	12
11) <i>Eugenia foetida</i>	1.6 (0.9)	10

classes (0-1 cm dgh), one of the five individuals examined had two stems. Below 3-cm dgh, 33% of all *G. lucida* trees had more than one stem (Table 8). In the adult trees, the most common form was either a single-stemmed tree, or a double-stemmed tree with the split averaging 19.7 cm above the ground (Table 11). One of the two stems tended to be 2-3 times larger than the other. The split was narrow, not suggestive of cutting. The average number of stems ranged between 1.2 and 2.0 stems in size classes below 10-cm dgh, and only increased to 4.4 after 10-cm dgh.

The presumed water stress of exposure in the canopy can be seen in the number of taller *G. lucida* trees with dead tops (Figure 19). No individuals shorter than 2 m had a dead top, but above 3 m, 11 of 17 (64.7%) had a dead top, and three of the four trees that were at or above the height of the canopy were dead at the top. In all cases, however, the lower portions of the stem remained alive, and the dead portion averaged 0.87 m of the top portion of the tree. It did not appear that the death of the apical portion of the tree lead to sprouting in this species, however. In fact, the two *G. lucida* trees with the most stems had live tops. Curiously, few dead tops were found in other species. Of the 332 trees examined, only 30 had a dead top; 15 of these were *G. lucida* trees.

In the main site, a 2-m tall dead *G. lucida* tree (2.3-cm dgh) was found with eleven small live sprouts arranged around the base. A few of these were taller than 1 m in height. This was not a typical form for *G. lucida* at the main (i.e., protected) site, but was similar to that displayed by *G. lucida* trees at the 1969 and 1981 cut plots. Therefore it does demonstrate for this species that a multi-stemmed form can arise through basal sprouting following the natural death of the main stem.

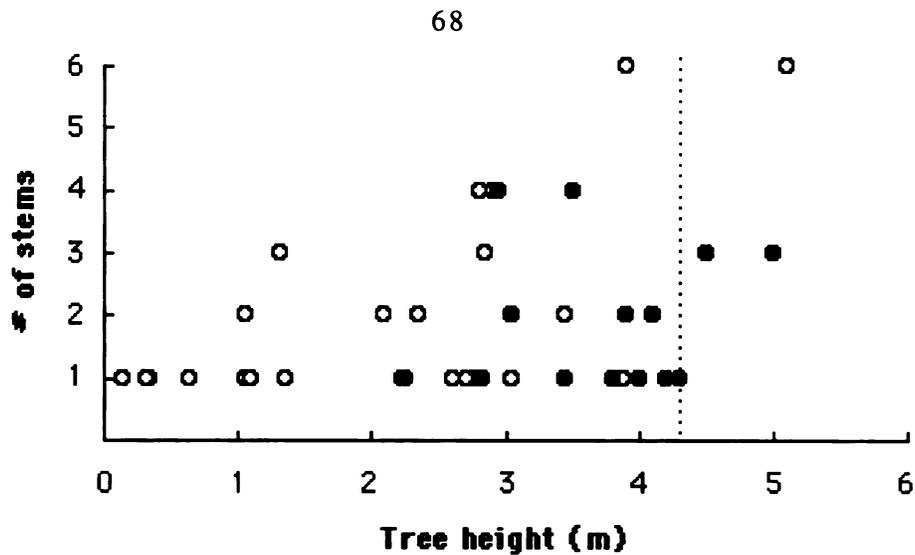


Figure 19. Tree height versus number of stems for *Gymnanthes lucida* trees with a dead (●) or live (○) top. Canopy height is indicated by the dotted line.

(2) *Exostema caribaeum*

E. caribaeum is mostly single-stemmed, with only 13.9% of trees possessing multiple stems. Only one of the multi-stemmed trees was below 4-cm dgh: a two-stemmed sapling with a dgh of 1.1 cm. Where multiple stems were present, there was an average of 3.0 stems (range: 2-5 stems). In 80.0% of multi-stemmed trees, an original main stem was present (Table 8). Evidence of a short-lived double-stemmed stage was frequently encountered. Many trees had a branch scar at their base that was nearly half as wide as the dgh of the main stem. The small, two-stemmed sapling mentioned above appears to be an example in which the second stem survived.

Evidence suggestive of possible cutting was found for one *E. caribaeum* that was not located in the study transects. This tree had an overall dgh of 20.4 cm with eight even-sized stems arranged around an open area. However, *E. caribaeum* appears to be successional, and considerable die-back has been

found among trees being monitored for growth (P. Murphy, pers. comm.) Therefore, the tree mentioned above is probably an example of natural die-back. For the multi-stemmed trees in the study transects, the presence of intact original main stems was the main evidence that this form is natural.

(3) *Pisonia albida*

The largest tree of any species that Murphy and Lugo (1986b) recorded was a *P. albida* with a dbh of 23 cm. Smaller trees are single-stemmed, and additional stems only appear in trees larger than 5-cm dgh (Table 10). In the present study, the smallest *P. albida* tree to acquire an additional stem had a dgh of 5.9 cm. Since *P. albida* trees are estimated to increase their diameter by only 3.3 cm over 60 years (P. Murphy and A. Lugo, unpublished data), even the smallest multi-stemmed trees could have been present prior to forest protection in the 1930's. Only 14% of multi-stemmed trees had an original main stem (Table 8), so evidence for this species that the multi-stemmed growth form is natural is mostly indirect. Namely, there were no examples of trees with a growth form consistent with cutting (i.e., a ring of stems surrounding an open area). Rather, there was a regular growth form that was very different from that seen among trees cut in 1969 or 1981 (Figures 20, 21).



Figure 20. Characteristic two-stemmed growth form of *Pisonia albida*.



Figure 21. Characteristic two-stemmed growth form of *Pisonia albida*, in a larger individual than the one in Figure 20.

It is typified by the largest stem growing at a slight angle. The second largest stem, with a basal area averaging one-fourth that of the first, grows out at a different angle. Subsequent stems grow out at intermediate angles from the first two stems. Larger trees are characterized by three to four large main trunks with few basal sprouts. Trees in the cut site, on the other hand, had stems that were relatively equal sized in diameter and were arranged around a degraded stump (Figure 22).

(4) *Pictetia aculeata*

Below 4-cm dgh, all stems found were single-stemmed (Table 10). In the next highest size class (4-5 cm dgh), there was an average of 1.3 stems/ tree. This average climbed to 4.6 stems/ tree in the largest size class (>10 cm dgh). The stems surrounded either a degraded stump (54.5% of multi-stemmed trees) or a central open area (18.8% of multi-stemmed trees). This is one species where cutting may be responsible for the multi-stemmed growth form. Little and Wadsworth (1964) support this notion in writing that *P. aculeata* was "formerly reported to 30 ft tall, but now rarely seen that size because most large individuals have been cut". Since the time of their comment, trees in the forest have presumably increased in height, for in the present study, several trees reached heights close to 7.5 m (24.6 ft.). One single-stemmed tree at the main site (but not included for study) was 8.1 m (26.6 ft) tall with a dgh of 12.3 cm, which is additional evidence that the multi-stemmed growth form is not the usual growth form for this species. However, this large individual grew along the edge of a narrow ravine where conditions for growth tend to be more favorable. Trees in harsher microsites may be more likely to harbor multiple stems.



Figure 22. *Pisonia albida* tree cut in 1969, showing growth form very different from that in Figures 20 and 21.

Among *P. aculeata* trees at least 2.5 cm in dbh, Murphy and Lugo (1986b) found an average of 346.7 trees/ha and 1427.3 stems/ ha in the main site of Guánica Forest. If these trees are normally single-stemmed, and assuming that there would have been 346.7 trees/ha had cutting not occurred, then cutting has resulted in an addition of 1,080.6⁴ *P. aculeata* stems/ha to the forest. This represents an extreme scenario, however, and the actual number of stems due to cutting is probably much lower.

(5) *Thouinia striata* var. *portoricensis*

Multi-stemmed trees were found throughout all size classes, with stems gradually accruing with an increase in size (Table 10). An original main stem was present in only eight of 25 (17%) trees examined (Table 8); six of these were below 3 cm in dgh. The main factor arguing for a natural origin to multi-stemmed trees in *T. striata* var. *portoricensis* was the high percentage of smaller multi-stemmed trees: 38% of trees in the 0-3 cm dgh size class, and 57% of trees in the 0-5 cm dgh size class.

(6) *Coccoloba krugii*

Throughout all size classes, *C. krugii* had multi-stemmed trees. In the smallest size class (<1 cm dgh), there was an average of 1.8 stems per individual, with a maximum of three stems (Table 10). These numbers increased at a regular rate as trees in larger size classes were examined. Only in 5% of individuals examined was there an original main stem (Table 8), and

⁴ Assume that there would be an average of 346.7 single-stemmed trees/ha. This would mean:

1,427.3 stems/ha	; actual number of stems
- 346.7 stems/ha	; theoretical number of stems
1,080.6 stems/ha	; theoretical number of actual stems due to cutting.

the clumps had a very disorganized, shrubby appearance with stems often following a sinuous path through the canopy to the light above. Large *C. krugii* trees had some of the greatest numbers of stems among trees in the main site. In the present study, twelve trees with greater than ten stems were found; five of these were *C. krugii*, with an average of 21.2 stems/ tree. Like *T. striata* var. *portoricensis*, the main factor which shows the multi-stemmed growth form to be natural for this species is the presence of small multi-stemmed saplings: 62% of individuals in the 0-3 cm dgh size class, and 69% in the 0-5 cm dgh size class (Table 8).

(7) *Bursera simaruba*

In the main study site, all *B. simaruba* trees sampled were single-stemmed. *B. simaruba* trees are among the fastest growing trees in Guánica Forest, with an average growth rate of 0.10 cm per year in dbh (P. Murphy and A. Lugo, unpublished data). Although only one tree occurred in the 1981 cut plots, it had five stems, which was similar to the average number of stems found among *B. simaruba* trees in the 1969 cut site (Table 9). In addition, multi-stemmed trees were found along the road leading to the study site. The species tends to be distributed rather sparsely throughout the forest (i.e., it has a low relative density, Table 5) in comparison to the other study species. It does not appear to engage in clonal spread.

(8) *Erithalis fruticosa*

In the 0-1 cm dgh size class, two of five *E. fruticosa* sprouts were multi-stemmed, one with two stems and the other with four. This presence of multi-stemmed sprouts argues for a natural origin of this growth form. In the 0-3 cm dgh size class, 33% of trees examined were multi-stemmed; in the 0-5 cm

dgh size class, this value was 56% (Table 8). *E. fruticosa* trees had fewer stems, on average, in the largest dgh size class (>10 cm) than the structurally similar *T. striata* var. *portoricensis* and *C. krugii* trees (Table 10). It is possible that the latter two species devote more energy to producing new stems from the base of trees, whereas *E. fruticosa* may put more effort into clonal spread through root sprouting. Clumps of *E. fruticosa* trees were common in the forest.

(9) *Guettarda krugii*

Original main stems were found in only 14% of multi-stemmed trees (Table 8). Evidence that the multi-stemmed form is natural came mainly from smaller trees: multiple stems were found in 20% of trees 0-3 cm dgh, and 35% of trees 0-5 cm dgh. Included among the multi-stemmed saplings was an individual with four stems that had a dgh of 1.3 cm. Below 5-cm dgh, there was an average of 2.8 stems per tree. In the 5-10 cm dgh size class, only four stems were found, with an average of 3.8 stems (Table 10). Despite extensive searching, only two *G. krugii* trees were found with a dgh above 10 cm. One was 12.4 dgh and had eleven stems, and the other was 20.4 cm dgh with nine stems. *G. krugii* seems to put much of its resources into vegetative spread, with runners between ramets often visible at the soil surface.

Understory woody species:

In terms of stem acquisition, both understory species showed a similarity to the type I trees, with a gradual increase in the number of stems with increasing dgh. Multiple stems were present even in the smallest size classes for both species.

(10) *Croton humilis*

There was an intact original main stem in 25% of multi-stemmed *C. humilis* shrubs. The average number of stems increased from 1.1 in the 0-1 cm dgh class to 3.5 in the 3-4 cm dgh class (Table 10). Beyond this, only one stem was found: an unusually large specimen that was 5.3 cm in dgh with five stems. These shrubs tended to stay small, with none rising above 2.9 m in height. Throughout the main site, *C. humilis* was found often in very dense clumps. Below-ground connections between individuals were often found.

(11) *Eugenia foetida*

Multi-stemmed individuals were found in all size classes, generally with an increase in the average number of stems with increasing dgh. In the 0-1 cm dgh size class, there was an average of 1.1 stems per tree. This average rose to 2.4 stems per tree in the 2-3 cm dgh size class, but dropped down to 1.5 stems per tree in the 3-4 cm dgh size class (Table 10). Like *C. humilis*, few large trees were found. Despite intensive searching, only three trees were found that were larger than 4-cm dgh. One particularly large single-stemmed tree was found with a dgh of 9.5 cm and a height of 5.7 m. It was growing at the top of a rocky slope in an area that did not seem especially favorable for growth. Also like *C. humilis*, below-ground connections between trees were often apparent. A natural explanation for the origin of multiple stems is shown by the fact that 30% of multi-stemmed trees had an original main stem (Table 8). Additionally, multiple stems were found in 20% of trees in the 0-3 cm dgh size class, and 22% of trees in the 0-5 cm dgh size class.

Environmental influences on the development of multiple stems

Since the data on multiple stems and environmental factors were not distributed as bivariate normal, they were ranked and Spearman correlations were calculated to determine the degree of relatedness between the factors mentioned in Table 7 and the number of stems in trees of the eleven study species. Only a few significant relationships were revealed (Table 12). Two correlations were significant at $P < 0.5$, and four were significant at $P < 0.02$. This is not different from what would be expected by chance, however, and thus it must be concluded that the environmental factors examined did not account for any significant variation in the number of stems.

Similarly, Josse and Balslev (1994) found no correlation between number of stems and slope steepness among Ecuadorian dry forest trees. Nevertheless, there are some variables that may be important. Shallow soils appear to harbor more multi-stemmed trees than deeper soils (S. Molina, pers. comm.). For instance, in a shallow ravine that traversed the main study site, trees had, on average, twice as many stems per tree as those growing on a neighboring slope. Deeper soil, along with greater soil moisture and increased shading from a more developed canopy, is likely to be the responsible factor.

Sprouting as a result of environmental stresses implies a feedback response. A tree grows as a single stem, stress reduces apical dominance, inhibited buds are released, and a multi-stemmed form results. An alternative mechanism might exist, namely multiple stems may be a "feedforward response" to drought. Schulze *et al.* (1987), define a feedforward response as "an environmental perturbation [that] causes a change in the controller (e.g., the stomata) that is independent of any change in the flux being controlled." In regards to dry forests, trees may develop multiple stems as a way to cope

Table 12. Spearman correlations for number of stems versus six different environmental factors for ten of the eleven study species in the 1.44-ha study plot. Only *B. simaruba* is excluded, since no multi-stemmed individuals were found. Critical values varied due to differences in sample sizes. Of the 60 correlations reported, 3.0 are expected to be significant by chance at $P < 0.05$ and 1.2 are expected to be significant by chance at $P < 0.02$.

Species	Exposed rock	Bare soil	Canopy height	Canopy coverage	orien- tation	slope angle
<i>Gymnanthes lucida</i>	-0.06	-0.14	-0.09	-0.03	0.11	-0.05
<i>Exostema caribaeum</i>	0.06	0.31	0.41**	-0.10	0.28	0.30
<i>Pisonia albida</i>	0.05	-0.34	0.31	0.09	0.64	0.64
<i>Pictetia aculeata</i>	-0.11	0.17	0.35	0.19	0.44*	0.46**
<i>T. striata</i> var. <i>portoricensis</i>	0.24	0.04	-0.19	-0.18	0.29	-0.13
<i>Coccoloba krugii</i>	0.51**	-0.17	0.40	0.39	-0.30	-0.25
<i>Erithalis fruticosa</i>	-0.26	-0.11	0.20	-0.04	0.17	0.00
<i>Guettarda krugii</i>	0.24	0.32	0.37*	0.02	-0.17	-0.19
<i>Croton humilis</i>	-0.06	0.04	0.06	-0.33**	0.13	0.03
<i>Eugenia foetida</i>	-0.20	-0.19	0.03	-0.09	-0.04	0.12

* $P < 0.05$, ** $P < 0.02$

^a Refers to the cardinal direction the slope faces.

with "anticipated" drought conditions. For some aspen clones, Schier *et al.* (1985) describe that apical control may be so weak that they sucker after the slightest disturbance. Since the shrub life form is selectively advantageous in dry environments (Rundel 1991), a simple genetic weakening of apical control, thereby allowing additional basal buds to sprout, may be enough to increase the fitness of individuals. Trees where multiple stems are common in smaller size classes (*T. striata* var. *portoricensis*, *C. krugii*, *E. fruticosa*, and *G. krugii*), may represent species where feed-forward responses are especially active.

The instability of the hormone auxin is likely to be important in trees where an original main stem persists and additional stems appear only after the tree reaches above the canopy. Schier *et al.* (1985) describe auxin as "a relatively unstable compound that must be transported a considerable distance from its source in developing buds and young leaves to the roots for it to have its effects". In taller trees, the auxin concentration at the base of the tree may not be great enough to suppress bud burst, and sprouting may result.

As discussed in the introduction, there are numerous non-lethal factors that promote sprouting. High levels of irradiation, high soil temperatures, slow growth rate of trees, and rapid root growth at beginning of wet season (before bud burst) all promote sprouting and can lead to the multi-stemmed form without requiring the death of the main stem. Drought stress increases auxin levels, and decreases those of cytokinins (Kramer and Kozlowski 1979). So unless it leads to death of the main stem, drought stress should actually promote apical dominance and suppress basal sprouting. Therefore, in the many cases where a live main stem persists, one of the above mentioned factors must be responsible for the multi-stemmed growth form.

CONCLUSIONS

In a subtropical dry forest, multi-stemmed trees were examined in a 120-m x 120-m (1.44 ha) study site protected from cutting for over 60 years. Along a 100-m broken transect, 43.3% of 187 trees were multi-stemmed. Data from this transect were combined with those from a 10-m wide transect located around the interior margin of the study site. Intact original main stems were found in 19.9% of multi-stemmed trees. Small, multi-stemmed trees (less than 5 cm dgh) were found in nine of eleven woody species studied, accounting for between 8 and 69% of trees below 5-cm dgh. Only *Pictetia aculeata* was lacking strong evidence as to whether its form is natural, and all of the *Bursera simaruba* trees were single-stemmed.

In *P. aculeata*, a degraded stump or a central open area surrounded by stems, both possible from either cutting or natural stem breakage, was found in 73.3% of trees examined. No multi-stemmed *P. aculeata* trees had an intact main stem. In the 60 years since forest protection, a *P. aculeata* stem would have increased its dbh by an average of 1.26 cm, with an upper 95% confidence limit of 5.98 cm (P. Murphy and A. Lugo, unpublished data). Therefore, it is possible that the trees below 5-cm dbh that were multi-stemmed (12% of trees were below 5-cm dbh) arose after protection of the forest, and were unlikely to have been cut. Considering the extent to which the wood of *P. aculeata* has been put to use in the past (e.g., for large poles; Little and Wadsworth 1964), it is possible that several of the larger trees were cut prior to forest protection.

The presence of a few, large (> 15 cm dgh) isolated trees in the main site which do have a pattern consistent with cutting (i.e., a ring of stems around a central open area) indicates that evidence of cutting does persist. The lack of

such evidence in other trees supports the notion that cutting is not a major cause of the multi-stemmed growth form. Only 18.4% (26 of 141) of multi-stemmed trees had a growth form which might be attributable to cutting, although natural stem breakage, rather than cutting, could be responsible. As in *P. aculeata*, 30.8% (9 of 26) of these trees were below 5-cm dgh, and therefore probably arose after protection of the forest. The rapid decomposition of stumps prevents a more definitive analysis of the larger trees.

Multi-stemmed trees in the main ("protected") site had very different growth forms from those in experimental plots that were cut in 1981. Multi-stemmed trees in plots cut in 1981 showed between 0.8 and 4.4 times as many stems as those in the main site. Although it is possible that trees in the main site were cut in the past and naturally thinned down to their present form, the similarity in numbers of stems between trees cut in 1981 and those cut experimentally in 1969 argues against this possibility. In comparing the 1969 site and the 1981 plots, only *Gymnanthes lucida* and *Pisonia albida* showed any signs of self-thinning.

Growth of multi-stemmed trees followed two patterns. The first pattern, displayed by five of the top nine species, as well as the two understory species studied, was characterized by multiple stems in all size classes, generally with a gradual increase in number from smaller to larger trees. The second pattern was characterized by mostly single-stemmed growth in smaller size classes, followed by acquisition of multiple stems beyond a certain threshold dgh, usually coinciding with the tree reaching canopy height. Three of the top four species in importance value displayed this latter pattern.

In summary, the regular occurrence of original main stems in multi-stemmed trees and the high frequency of multiple stems in smaller dgh size

classes demonstrate that the multi-stemmed growth form was natural for nine of the eleven species studied. The most common growth form among multi-stemmed trees was characterized by single-stemmed growth in smaller size classes, with additional stems appearing as trees reached the canopy. The scarcity of multi-stemmed trees with a growth form consistent with cutting, as well as the dissimilarity of multi-stemmed trees in the protected, main site versus those in the cut plots, is further evidence that few, if any, multi-stemmed trees in the 1.44 ha study site owe their form to cutting.

Issues for further study

The study of multi-stemmed trees in subtropical dry forest could be expanded in several ways. Similar studies could take place in other dry forest sites both in Puerto Rico and throughout other islands of the Caribbean. Within Guánica Forest, four different forest associations are found (Lugo *et al.* 1978). The present study focused only on the deciduous forest association. The relative abundance of multi-stemmed trees in all four forest types could be revealing. In particular, the scrub forest, where stresses are greater, should show a higher number of multi-stemmed trees than the evergreen forests, which lie in the relatively moist ravines traversing the forest. Similarly, the present study focused on eleven study species. It would be valuable to examine the growth form of the other species in Guánica Forest.

Several of the species in Guánica Forest, including *G. lucida*, *Exostema caribaeum*, *P. albida*, *Erithalis fruticosa* and *Eugenia foetida* are also found in moist limestone forests near the north coast. Examples of multi-stemmed trees are common in these forests (Figures 23-26), as well as other moist limestone



Figure 23. Example of a multi-stemmed tree from Guajataca Forest (moist limestone forest).



Figure 24. Example of a multi-stemmed tree from Guajataca Forest (moist limestone forest).



Figure 25. Example of a multi-stemmed tree from Guajataca Forest (moist limestone forest).



Figure 26. Example of a multi-stemmed tree from Guajataca Forest (moist limestone forest).

forests in the Greater Antilles (e.g., Jamaica (Shreve 1914)). The extent to which the growth form of trees in the moist forest differ from dry forest conspecifics could indicate the extent to which the multi-stemmed growth form is under genetic versus environmental control.

Studies examining the ecological role of hormones in adapting growth form to specific environments would be worthwhile. For instance, lower levels of auxin would be expected in dry forest trees compared to moist forest conspecifics. This would permit sprouting to occur more readily. Similarly, high levels of cytokinins, which promote sprouting, might be found in dry forests where there is a flush of root activity prior to the start of the wet season, such as those near Chamela, Mexico.

It would be valuable to search for correlations between abiotic factors not examined in this study (e.g., salinity, soil depth) and growth form. Finally, this study focused on vegetative reproduction through basal sprouting. Another important mode of vegetative reproduction is clonal spread through root sprouting. Determining the size and stem distribution of clones would greatly improve our understanding of dry forest community patterns.

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LITERATURE CITED

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