

## The tendency for trees to be multiple-stemmed in tropical and subtropical dry forests: Studies of Guanica forest, Puerto Rico

B.K. DUNPHY,<sup>1,3,4</sup> P.G. MURPHY<sup>1</sup> & ARIEL E. LUGO<sup>2</sup>

<sup>1</sup>*Department of Botany and Plant Pathology, Michigan State University, East Lansing, MI 48824, U.S.A.;* <sup>2</sup>*International Institute of Tropical Forestry, USDA Forest Service, Rio Piedras, PR 00928-5000, Puerto Rico*

**Abstract:** Multiple-stemmed trees are a characteristic feature of Caribbean dry forests. In a semi-deciduous forest stand in Guánica Forest, Puerto Rico, 43.3% of all trees have multiple stems. These multiple-stemmed trees account for 58.0% of total basal area. Ten of eleven common species examined had examples of multiple-stemmed individuals, varying between 13.9% and 80.8% of all individuals for a given species. The presence of multiple-stemmed trees with intact (unharvested) main stems, and the occurrence of multiple-stemmed trees too small to have been subject to cutting prior to forest protection, suggest that the multiple-stemmed condition may arise in the absence of human influence. Natural mechanisms that can promote a multiple-stemmed growth form are discussed.

**Resumen:** Los árboles con múltiples tallos constituyen un rasgo característico de los bosques tropicales secos del Caribe. En un rodal de bosque semideciduo en el Bosque Guánica, Puerto Rico, 43.3% de todos los árboles tuvieron múltiples tallos. A estos árboles con múltiples tallos correspondió el 58.0% del área basal total. Diez de las once especies comunes examinadas tuvieron ejemplos de individuos con múltiples tallos, con proporciones que variaron entre 13.9% y 80.8% de todos los individuos para una cierta especie. La presencia de árboles con múltiples tallos con troncos principales intactos (no cosechados), y la presencia de árboles con tallos múltiples suficientemente pequeños como para haber estado sometidos a cortes previamente a la protección el bosque, sugiere que la condición de tener múltiples tallos puede surgir en ausencia de la influencia humana. Se discuten los mecanismos naturales que pueden promover un crecimiento con múltiples tallos.

**Resumo:** As árvores com troncos múltiplos são uma característica das florestas secas das Caraíbas. Numa parcela de floresta semi-caducifólia na floresta de Guánica, em Porto Rico, 43,3% de todas as árvores apresentavam troncos múltiplos. Estas árvores representavam 58,0% da área basal total. Dez de onze espécies comuns examinadas tinham troncos múltiplos, variando entre os 13,9% e 80,8% de todos os indivíduos para uma dada espécie. A presença de árvores com troncos múltiplos com troncos principais intactos não explorados e a ocorrência de árvores de troncos múltiplos, muito novas para terem sido sujeitas a corte antes da proteção da floresta, sugere que a condição de apresentarem troncos múltiplos deve surgir na ausência de influência humana. Os mecanismos naturais que podem promover uma forma de crescimento com troncos múltiplos são discutidos.

**Key words:** Caribbean, forest recovery, multiple-stemmed trees, Puerto Rico, tree growth form, tropical dry forest, West Indies.

---

<sup>3</sup> *Current Address:* Department of Botany, University of Georgia, Athens, GA 30602, U.S.A.

<sup>4</sup> Author to whom all correspondence should be addressed.

## Introduction

Extensive human disturbance over several centuries (Beard 1949; Kelley *et al.* 1988) makes it difficult to interpret certain structural features that appear to characterize many Caribbean dry forests, or to determine the extent to which these forests resemble the pre-Columbian condition. For example, the multiple-stemmed growth form and shrubby stature of dry forest trees is frequently cited as evidence of past cutting (Beard 1955; González & Zak 1996; Kelly *et al.* 1988; Murphy *et al.* 1995; Rico-Gray *et al.* 1988). This growth form is common in dry forests throughout the islands of the Caribbean [*e.g.*, Bahamas (Britton 1920); Barbuda and St. Vincent (Beard 1949); Dominican Republic (Hager & Zanoni 1993)]. Warming (1909) described the trees of the “dry tropical bushland” of the West Indies to be similar to those of Mediterranean Maqui, which mostly occur “in the guise of dwarf-trees and shrubs”. Britton (1920) made several references to hardwood “coppice” in the Bahamas, and Beard (1949) described the “ever-green bushland” formation of the lesser Antilles as being composed of many low-branching trees and shrubs.

Studies of dry forest structure rarely contain quantitative descriptions of the multiple-stemmed growth form. The following five studies are exceptions, however, and further support the regular occurrence of this growth form in dry forests. In Guánica Forest, Puerto Rico, 56.9% of stems  $\geq 2.5$  cm dbh (diameter at breast height) were part of multiple-stemmed clumps (Murphy & Lugo 1986); on North Andros Island in the Bahamas, between 3.6% and 7.3% of individuals greater than 1 m in height (246-492 individuals  $\text{ha}^{-1}$ ) had multiple stems or low branches (Smith & Vankat 1992); trees  $\geq 4.0$  cm dbh in five sites on St. John in the U.S. Virgin Islands averaged between 1.16 and 1.44 stems per tree (Ray & Brown 1995); in three dry forest plots at Chamela, Mexico, 17.8%, 20.5% and 25.3% of all non-vine woody plants  $\geq 2.5$  cm dbh had more than one stem (Lott *et al.* 1987); in a dry forest of western Ecuador, 15% of trees  $\geq 5$  cm dbh were multiple-stemmed, with an average of 2.4 stems/tree (Josse & Balslev 1994).

If the multiple-stemmed form were a response to cutting, these forests would presumably bear little resemblance to pre-Columbian forests in terms of the number and sizes of tree stems. If the form is natural, however, the stem structure of

these forests may be more similar to pre-Columbian forest structure than previously thought. In other dry ecosystems, such as chaparral (Biswell 1974), the multiple-stemmed form has been determined to occur naturally. There was a notable lack of stumps among multiple-stemmed trees of Guánica Forest, Puerto Rico (Murphy & Lugo, pers. obs.), suggesting that the occurrence of a multiple-stemmed growth form may be a natural occurrence in Caribbean dry forests.

The objectives of the present study were to describe the multiple-stemmed structure of trees in the dry forest of Guánica, Puerto Rico and to compile evidence to evaluate whether or not this form is due to cutting, natural causes, or both. Guánica Forest is considered an excellent example of Caribbean dry forest (Ewel & Whitmore 1973) and, if found to have a tree structure reflective of natural rather than anthropogenic factors, could serve as an example of relatively unaltered Caribbean dry forest. In this way, it could be used to assess and guide restoration efforts in more degraded forests.

## Methods

Guánica Forest, administered by the Commonwealth of Puerto Rico, comprises 4,000 ha along the Caribbean coast of southwestern Puerto Rico (approximately 18° north latitude) in the subtropical dry forest life zone (Holdridge 1967). The annual rainfall of 860 mm, recorded at Ensenada, 6 km west of the study site, is interrupted by a major dry season from December to April and a minor one from June to August. All work was performed within a 120 m x 120 m (1.44 ha) research site established by Murphy & Lugo (1986) in a section considered representative of the semi-deciduous forest type. This section of the forest is characterized by a high number of trees that are short in stature and small in diameter. The site has an average of 14,007 stems  $\geq 2.5$  cm dbh per hectare, only 19% of which have a dbh  $\geq 5$  cm. Fewer than 12 percent of all trees exceeded 5 m in height (Murphy & Lugo 1986). The forest presents a low, seasonally open canopy (leaf area index ranges from  $<1$  to  $>4$  depending on rainfall) where much light is able to penetrate to the forest floor.

Disturbance has been minimal since the 1930s, when Guánica Forest was given protected status as a commonwealth forest. Subsequently, no cut-

ting has taken place or wildfire been observed in or near the area of the research site. Ten major hurricanes struck Puerto Rico between 1700 and 1960; none of them passed directly over the subtropical dry forest life zone of Puerto Rico (Salvia 1972), although the eyes of Hurricanes Hortense and Georges passed over Guánica Forest in 1995 and 1998, respectively, subsequent to this study.

To describe the multiple-stemmed growth form and to evaluate if it occurs naturally, the structure of individual trees was examined in detail along a 2-m wide and 100-m long transect that followed the slope of the hill where the study site is located. The transect was broken into 20 5-m segments, with measurements made in alternating segments. All individuals of all woody species were measured for height, diameter at ground height (dgh), diameter at breast height (dbh), and the number of stems originating <1 m above ground. For the purposes of the present study, a stem was differentiated from a branch in that the former is considered to have assumed vertical growth at its most distal end. In addition, the presence of a main stem or a stump was recorded, which would indicate either the absence or occurrence of cutting, respectively.

At the level of overall forest structure, the transect data documented the frequency and relative basal area of multiple-stemmed trees versus single-stemmed trees. The transformation from single-stemmed seedling to multiple-stemmed adult occurs over a period of several decades. To determine the way in which the transformation occurs we examined individuals from a wide range of DBH size classes. Changes in the numbers of stems from smaller to larger individuals was assumed to be similar to the changes that occur in a single individual as it grows from smaller into larger size classes. To gain greater insight into this process, attention was focused on the nine woody species with the highest importance values in the study site (Murphy & Lugo 1986). These were, in decreasing order of importance value, *Gymnanthes lucida* Sw., *Exostema caribaeum* (Jacq.) Roem. & Schult., *Pisonia albida* (Heimerl) Britton ex Standl., *Pictetia aculeate* (Vahl) Urban, *Thouinia striata* var. *portoricensis* (Radlk.) Votava & Alain, *Coccoloba krugii* Lindau, *Bursera simaruba* (L.) Sarg., *Erithalis fruticosa* L. and *Guettarda krugii* Urban. Two common understory species, *Croton humilis* L. and *Eugenia foetida* Pers., were also included for comparison, bringing the total

number of study species to eleven. All individuals of these eleven species from the transect were placed into one of the following dgh size classes: 0-0.99 cm, 1-1.99 cm, 2-2.99 cm, 3-3.99 cm, 4-4.99 cm, 5-10 cm and >10 cm. Comparisons were made among size classes to determine any size-related changes in growth form. No individuals greater than 10 cm dgh were found for *C. humilis* or *E. foetida*. Size classes were based on dgh rather than dbh because many individuals, especially in the smaller size classes, were under 1.4 m in height.

For several of the eleven species, fewer than five individuals were available in certain size classes in the original transect sampled. For this reason, a second transect was established in June, 1994 to bolster sample sizes up to five individuals where necessary. Since the individuals needed were likely to be at a low density (if they were not, at least five should have been found in the original transect), this second transect was made to be large in area. The transect was 10 m wide, 440 m long and positioned around the inside perimeter of the study site. Since the study site is embedded within the forest, and only a small footpath circumnavigates it, edge effects were unlikely. The second transect was thoroughly searched, beginning at the southwestern corner and moving in a counterclockwise direction. Only those individuals needed to bring a size class of a given species up to five individuals were measured. Since this second transect was not completely sampled, the data that were collected from it cannot be used to make quantitative statements regarding overall forest structure.

Differences between size classes in the number of stems was tested using the Kruskal-Wallis test (Sokal & Rohlf 1995). For those species where the null hypothesis of no differences between size classes was rejected, pair-wise Mann-Whitney U tests determined which size classes were significantly different from the others (Sokal & Rohlf 1995). For both tests, the Dunn-Sidak method was used to prevent multiple comparisons from raising the experimentwise error rate above 0.05 (Sokal & Rohlf 1995). This adjustment to the error rate resulted in a finding of non-significance for *G. lucida* and *G. krugii*, both of which had significant results before the adjustment. In several cases, small sample sizes, and the consequent reduction in power, are presumably responsible for non-

significant results. All statistical comparisons were made with PC-SAS (Joyner 1985).

### Results and discussion

Of 187 woody plants sampled in the original north-south, 100-m transect, 43.3% were multiple-stemmed. Multiple-stemmed trees averaged 4.1 stems (3.4 live and 0.7 dead). Total dgh-based basal area for all stems was 36.2 m<sup>2</sup>ha<sup>-1</sup>, with multiple-stemmed trees accounting for 58.0% (21.0 m<sup>2</sup>ha<sup>-1</sup>). An estimate of total basal area based on dbh rather than dgh yielded 15.5 m<sup>2</sup>ha<sup>-1</sup>. This value compares to 19.8 m<sup>2</sup>ha<sup>-1</sup> the value found by Murphy & Lugo (1986) at the same site for trees at least 2.5 cm dbh.

Ten of the eleven study species had some multiple-stemmed individuals. The percentage of individual trees of each species possessing two or more stems ranged from 13.9% (*E. caribaeum*) to 80.8% (*C. krugii*). With the exception of *B. simaruba* (which had no multiple-stemmed individuals), all eleven study species had examples of multiple-stemmed individuals that showed no evidence of ever having been cut (Table 1). The strongest evidence for the natural development of multiple stems was the presence of original (uncut) main stems on larger multiple-stemmed individuals and

the occurrence of small multiple-stemmed saplings with no evidence of physical damage.

Persistent main stems were found in multiple-stemmed trees of all species studied except *P. aculeata*. In all, 19.9% of multiple-stemmed trees possessed an original main stem, ranging from 5% of individuals of *C. krugii* to 80% of individuals in *E. caribaeum* (Table 1).

Small multiple-stemmed individuals, clearly having arisen in the absence of cutting or grazing, were found in all multiple-stemmed species studied except *P. albida*. Of all individuals 2.99 cm dgh, nearly one-quarter (23.0%) were multiple-stemmed. In this size class, there was an order of magnitude difference in the percentage of individuals with multiple stems between *Exostema caribaeum*, which had the lowest percentage (6.3%) and *Coccoloba krugii*, which had the highest (61.5%). Similarly, a high number of multiple stems was reported for an unidentified species of *Coccoloba* from the Bahamas (Smith & Vankat 1992). Although the diameter growth rate in Guánica Forest is only on the order of 0.03 cm year<sup>-1</sup> (P. Murphy & A. Lugo, unpublished data), most of these individuals would have been far too small 60 years ago to have been cut for timber or fence posts. This is especially likely for those individuals (found in *G. lucida*, *C. krugii*, *E. fruticosa*, *C. humilis* and *E. foetida*) <1 cm dgh

**Table 1.** Tree growth-form properties inconsistent with cutting for the 11 study species: (a) the percentage of multiple-stemmed trees (all size classes, ranging from 0-2.99 cm dgh (diameter at ground height) to >9 cm dgh, included) with an original main stem still intact; (b) the percentage of saplings in four dgh size classes which possessed multiple stems. Values which are not statistically different share the same superscript. Sample sizes are in parenthesis.

Species	(a) Percent with original main stem still intact	(b) Percent with multiple stems in dgh size classes			
		0-2.99 cm	3-5.99 cm	6-8.99 cm	>9 cm
<i>Gymnanthes lucida</i>	32 (19)	33.3 <sup>a</sup> (18)	42.9 <sup>a</sup> (14)	66.7 <sup>a</sup> (3)	100 <sup>a</sup> (5)
<i>Exostema caribaeum</i>	80 (5)	6.3 <sup>a</sup> (16)	16.7 <sup>a</sup> (12)	0 <sup>a</sup> (1)	28.6 <sup>a</sup> (7)
<i>Pisonia albida</i>	14 (7)	0 <sup>a</sup> (1)	16.7 <sup>a</sup> (6)	33.3 <sup>a</sup> (3)	83.3 <sup>a</sup> (6)
<i>Pictetia aculeata</i>	0 (11)	0 <sup>a</sup> (6)	16.7 <sup>a</sup> (12)	100 <sup>b</sup> (3)	100 <sup>b</sup> (6)
<i>Thouinia striata</i> var. <i>portoricensis</i>	17 (18)	37.5 <sup>a</sup> (8)	85.7 <sup>a</sup> (7)	80.0 <sup>a</sup> (5)	100 <sup>a</sup> (5)
<i>Coccoloba krugii</i>	5 (21)	61.5 <sup>a</sup> (13)	100 <sup>ab</sup> (4)	100 <sup>b</sup> (4)	100 <sup>b</sup> (5)
<i>Bursera simaruba</i> *	-	0 (16)	0 (10)	0 (3)	0 (7)
<i>Erithalis fruticosa</i>	21 (24)	33.3 <sup>a</sup> (15)	90.0 <sup>b</sup> (10)	100 <sup>bc</sup> (4)	100 <sup>c</sup> (6)
<i>Guettarda krugii</i>	14 (14)	20.0 <sup>a</sup> (15)	53.8 <sup>a</sup> (13)	100 <sup>a</sup> (2)	100 <sup>a</sup> (2)
<i>Croton humilis</i>	25 (12)	14.0 <sup>a</sup> (50)	100 <sup>b</sup> (5)	-	-
<i>Eugenia foetida</i>	30 (10)	20.0 <sup>a</sup> (35)	50.0 <sup>a</sup> (4)	100 <sup>a</sup> (1)	-

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

that were multiple-stemmed.

The evidence suggests that the multiple-stemmed growth form, as it exists in Guánica Forest, is not due to cutting. Furthermore, many of the trees in the forest have recovered from any disturbance they might have suffered 60 or more years ago, prior to legal protection, at least with respect to tree growth form. Nevertheless, past land use can have an effect on multiple stem production. In scattered sites throughout Guánica Forest, Molina-Colón (1998) found that the frequency of multiple stems at ground height in old charcoal pits was 46.1%, compared to 38.3%, 31.0% and 22.7% in forest sites where the land was used, respectively, for a baseball park, farmland and houses. Seen in the light of the present study, this suggests that human disturbance can affect tree growth-form not only directly via sprouting from cut stumps, but also by altering the microenvironment (i.e., through increased light levels, greater soil drying) in such a way as to promote conditions that favor sprouting.

Occasional drought, above and beyond that which occurs on a seasonal basis, can be a particularly important factor in structuring dry forests. For instance, of the 39 out of a total of 1,468 trees in dry forest plots on the Yucatán peninsula that died during five years of monitoring, 80.8% died during two years of a particularly severe drought (Whigham *et al.* 1991). Seasonal drought stress in Guánica Forest may be even more severe than the low levels of precipitation would suggest. This is due to the rocky, porous limestone soil that has a low moisture-retention capacity. The effect of this stress is well illustrated by the number of taller *G. lucida* with dieback at the upper portions of their terminal leaders (Dunphy 1996). No individuals shorter than 2 m had dieback, but above 3 m, 11 of 17 (64.7%) had dieback, and three of the four trees that were at or above the height of the canopy had dieback of their terminal leaders, with the dead portion averaging 0.87 m in length. In all cases, the lower portions of the stem remained alive. Severe and prolonged drought that kills the terminal leader, but does not cause extensive disturbance to the root system, can promote the development of multiple stems from sprouting of dormant buds (Kolb & Davis 1994; Kramer & Kozlowski 1979).

High soil temperatures (Schier *et al.* 1985), slow stem growth, and rapid root growth (Kavanagh & Kellman 1992), all of which characterize

Guánica Forest for at least part of the year, are factors that promote the development of multiple stems, but that do not necessitate death of the main stem. All do so by reducing auxin, and/or increasing cytokinin (Burrows 1990; Cline 1991; Schier *et al.* 1985). Auxins tend to suppress dormant buds whereas cytokinins promote sprouting. The low, open canopy of the forest allows much light to penetrate to the forest floor. This light and the accompanying increase in soil temperature will promote sprouting. Evidence for the importance of microenvironmental influences on forest structure in Guánica Forest was noted by Lugo *et al.* (1978), who detailed a dramatic shift in forest structure from scrub vegetation on shallow, rocky soil to much taller evergreen vegetation in areas with deeper soils, such as deep ravines.

Large-scale disturbances can also play an important role in structuring dry forest. This can be illustrated by comparing Caribbean dry forests with dry forests along the western coast of Central and South America. Relatively few hurricanes have struck the dry forests of western Central and South America (Hartshorn 1988), whereas the frequent occurrence of hurricanes has been suggested to limit tree stature in the Caribbean region (Kelly *et al.* 1988), creating open conditions that favor sprouting. This is in addition to the sprouting promoted by damage to trees from the hurricane itself. The dry forests of the Yucatán peninsula, for instance, were hit by 31 tropical depressions between 1871 and 1975 (Jáuregui *et al.* 1980). Within one month of the passage of Hurricane Gilbert in September, 1988, Whigham *et al.* (1991) found that most tree species at their study site in a Yucatán dry forest had resprouted, lending further credence to the ability of hurricanes to alter forest structure. Even in the case of Guánica Forest, where there is no record of a direct hurricane strike prior to this study, the indirect effects of a hurricane (e.g., strong, gale-force winds) have been proposed to play a significant role in structuring the forest (Murphy *et al.* 1995). In dry forests on low islands (e.g., the Bahamas), wind-transported salt has been implicated as an additional environmental factor partially responsible for the multiple-stemmed growth form (Smith & Vankat 1992). By reducing the water-potential gradient between the soil and the roots, excess soil salinity can deprive a tree of water, a process that mimics drought stress (Kozlowski *et al.* 1991).

The dry forests that are relatively free from hurricanes and salt stress tend to be taller and have more clearly identifiable canopy layers than most island dry forests (Gentry 1995). In fact, the structural differences between dry forests on islands and dry forests in western Central and South America have been suggested to be as great as the differences between wet and dry tropical forests (Gentry 1995). It is difficult to draw conclusions, however, on whether these forests differ in the frequency of multi-stemmed trees due to the dearth of literature on this topic. In addition to being a passive response to environmental stress and disturbances, sprouting may also be an active strategy for coping with a dry environment (Rundel 1991). Drought stress increases substantially with an increase in tree height (Ryan & Yoder 1997). A multiple-stemmed growth form may allow a tree to expand its canopy area with a minimum of vertical growth. This expansion in canopy area may also allow a tree to outcompete or exclude others in the competition for light. This possibility could be investigated by examining the growth form of the species from this study across a moisture gradient. In particular, *G. lucida*, *E. caribaeum*, *P. albida*, *E. fruticosa*, *E. foetida* and other species occur in moist limestone forests near the north coast of Puerto Rico (Little & Wadsworth 1964). Examples of multiple-stemmed trees can be found in these moist forests (B. Dunphy pers. obs.), as well as in other moist limestone forests in the Greater Antilles (e.g., Jamaica (Shreve 1914)), although quantitative descriptions of the multiple-stemmed growth form are not available. The extent to which the growth form of trees in the moist forest differs from that of dry forest conspecifics could suggest the extent to which the multiple-stemmed growth form is under genetic versus environmental control.

In summary, multiple-stemmed trees of various species represent a substantial portion of the Guánica Forest plant community. Intact main stems on multiple-stemmed trees and multiple-stemmed trees too small to have been cut during the last major cutting episodes of the 1930s suggest that the form occurs naturally in Guánica Forest. Consequently, the abundance of multiple-stemmed trees should not be used as evidence of past human disturbance. The factors most likely to be responsible for the low, shrubby forest structure include environmental stresses such as drought and salt stress as well as periodic hurricane dis-

turbances. Positive selection for a multi-stemmed form may also play a role.

### Acknowledgements

The study was performed in collaboration with the Commonwealth of Puerto Rico Department of Natural Resources and the Environment and the University of Puerto Rico and was funded under USDA Forest Service Agreement 19-91-090, administered jointly through the USDA Forest Service and Michigan State University. We thank M. Canals for providing logistical support. We also thank L. Leege, S. Molina, C. Peterson, I. Ramjohn and S. Van Bloem for their valuable comments and reviews of the manuscript.

### References

- Beard, J.S. 1949. *The Natural Vegetation of the Windward and Leeward Islands*. Oxford Forestry Memoirs 21. Clarendon Press, Oxford.
- Beard, J.S. 1955. The classification of tropical American vegetation-types. *Ecology* **36**: 89-100.
- Biswell, H.H. 1974. Effects of fire on chaparral. pp. 321-364. *In*: T.T. Kozlowski & C.E. Ahigren (eds.) *Fire and Ecosystems*. Academic Press, New York.
- Britton, N.L. 1920. *The Bahama Flora*. Published by the authors. New York.
- Burrows, G.E. 1990. The role of axillary meristems in coppice and epicormic bud initiation in *Araucaria cunninghamii*. *Botanical Gazette* **151**: 293-301.
- Cline, M.G. 1991. Apical dominance. *The Botanical Review* **57**: 318-358.
- Dunphy, B.K. 1996. *The Multiple-Stemmed Growth Form of Trees in a Subtropical Dry Forest*. M.S. Thesis, Michigan State University, East Lansing.
- Ewel, J.J. & J.L. Whitmore. 1973. *The Ecological Life Zones of Puerto Rico and the U.S. Virgin Islands*. U.S.D.A. Forest Service, Institute of Tropical Forestry, Rio Piedras, Puerto Rico, ITF-18.
- Gentry, A.H. 1995. Diversity and floristic composition of neotropical dry forests. *In*: S.H. Bullock, H.A. Mooney & E. Medina (eds.) *Seasonally Dry Tropical Forests*. Cambridge University Press, New York.
- González, O.J. & D.R. Zak. 1996. Tropical dry forests of St. Lucia, West Indies: Vegetation and soil properties. *Biotropica* **28**: 618-626.
- Hager, J. & T.A. Zanoni. 1993. The natural vegetation of the Dominican Republic: a new classification. *Moscosoa* **7**: 39-81.
- Hartshorn, G.S. 1988. Tropical and subtropical vegetation of Meso-America. pp. 365-390. *In*: M.G. Barbour & W.D. Billings (eds.) *North American Terrestrial*

- Vegetation*. Cambridge University Press, Cambridge.
- Holdridge, L.R. 1967. *Life Zone Ecology*. Tropical Science Center, San José, Costa Rica.
- Jáuregui, E., J. Vidal & F. Cruz. 1980. Los ciclones y tormentas tropicales en Quintana Roo durante el período 1871-1975. pp. 47-63. *In: Memorias de Problemática y Perspectiva de Quintana Roo*. Instituto de Geografía, UNAM, y CIQRO, Cancún, Mexico.
- Josse, C. & H. Balslev. 1994. The composition and structure of a dry, semi-deciduous forest in Western Ecuador. *Nordic Journal of Botany* **14**: 425-434.
- Joyner, S.P. 1985. *SAS/STAT Guide for Personal Computers*. Version 6 Edition. SAS Institute Inc. Cary, North Carolina.
- Kavanagh, T. & M. Kellman. 1992. Seasonal pattern of fine root proliferation in a tropical dry forest. *Biotropica* **24**: 157-165.
- Kelly, D.L., E.V.J. Tanner, V. Kapos, T.A. Dickinson, G.A. Goodfriend & P. Fairbairn. 1988. Jamaican limestone forests: floristics, structure and environment of three examples along a rainfall gradient. *Journal of Tropical Ecology* **40**: 121-156.
- Kolb, K.J. & S.D. Davis. 1994. Drought tolerance and xylem embolism in co-occurring species of coastal sage and chaparral. *Ecology* **75**: 648-659.
- Kozlowski, T.T., P.J. Kramer & S.C. Pallardy. 1991. *The Physiological Ecology of Woody Plants*. Academic Press Inc., New York.
- Kramer, P.J. & T.T. Kozlowski. 1979. *Physiology of Woody Plants*. Academic Press, New York.
- Little, E.L. & F.H. Wadsworth. 1964. *Common Trees of Puerto Rico and the Virgin Island*. USDA Forest Service, Agr. Handbook 249.
- Lott E.J., S.H. Bullock & J.A. Solis-Magallanes. 1987. Floristic diversity and structure of upland and arroyo forests of coastal Jalisco. *Biotropica* **19**: 228-235.
- Lugo, A.E., J.A. González-Liboy, B.B. Cintrón & K. Dugger. 1978. Structure, productivity and transpiration of a subtropical dry forest in Puerto Rico. *Biotropica* **10**: 278-291.
- Molina-Colón, S. 1998. *Long-term Recovery of a Caribbean Dry Forest after Abandonment of Different Land Uses in Guánica, Puerto Rico*. Ph.D. Dissertation. University of Puerto Rico, Rio Piedras, PR.
- Murphy, P.G. & A.E. Lugo. 1986. Structure and biomass of a subtropical dry forest in Puerto Rico. *Biotropica* **18**: 89-96.
- Murphy, P.G., A.E. Lugo, A.J. Murphy & D.C. Nepstad. 1995. The dry forests of Puerto Rico's south coast. pp. 178-209. *In: A.E. Lugo & C. Lowe (eds.) Tropical Forests: Management and Ecology*. Springer-Verlag, New York.
- Ray, G.L. & B. Brown. 1995. The structure of five successional stands in a subtropical dry forest, St. John, U.S. Virgin Islands. *Caribbean Journal of Science* **31**: 212-222.
- Rico-Gray, V., J.G. Garcia-Franco, A. Puch & P. Sima. 1988. Comparison and structure of a tropical dry forest in Yucatan, Mexico. *International Journal of Ecology and Environmental Science* **14**: 21-29.
- Rundel, P.W. 1991. Shrub life-forms. pp. 345-370. *In: H.A. Mooney, W.E. Winner & E.J. Pell (eds.) Response of Plants to Multiple Stress*. Academic Press, New York.
- Ryan, M.G. & B.J. Yoder. 1997. Hydraulic limits to tree height and tree growth: What keeps trees from growing beyond a certain height? *Bioscience* **47**: 235-242.
- Salvia, L.A. 1972. *Historia de los temporales de Puerto Rico y la Antillas (1492 a 1970)*. Editorial Enid, Inc. San Juan, P.R.
- Schier, G.A., J.R. Jones & R.P. Winokur. 1985. Vegetative regeneration. pp. 29-33. *In: N.V. DeByle & R.P. Winokur (eds.) Aspen-Ecology and Management in the Western U.S.* U.S. Dept. of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Shreve, F. 1914. *A Montane Rain-Forest; a Contribution to the Physiological Plant Geography of Jamaica*. Carnegie Institution of Washington, no. 199. Washington, D.C.
- Smith, I.K. & J.L. Vankat. 1992. Dry evergreen forest (coppice) communities of North Andros Island, Bahamas. *Bulletin of the Torrey Botanical Club*. **119**: 181-191.
- Sokal, R.R. & F.J. Rohlf. 1995. *Biometry*. W.H. Freeman and Company, New York.
- Warming, E. 1909. *Oecology of Plants: An Introduction to the Study of Plant Communities*. Oxford University Press, London.
- Whigham, D.F., I. Olmstead, E.C. Cano & M.E. Harmon. 1991. The impact of Hurricane Gilbert on trees, litterfall, and woody debris in a dry tropical forest in the Northeastern Yucatan peninsula. *Biotropica* **23**: 434-441.