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# 15 Botanical and Ecological Basis for the Resilience of Antillean Dry Forests

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## ABSTRACT

Dry forest environments limit the number of species that can survive there. Antillean dry forests have low floristic diversity and stature, high density of small and medium-sized trees, and are among the least conserved of the tropical forests. Their canopies are smooth with no emergent trees and have high species dominance. Antillean dry forests occur mostly on limestone substrate, exposing them to more water stress and nutrient limitations than other dry forests. They also experience periodic hurricanes and anthropogenic disturbances. Many of the attributes that allow plants to survive in the stressful environment of the dry forest also provide resilience to disturbance. We attribute the high resilience of Antillean dry forests to the diversity of life forms, a high resistance to wind, a high proportion of root biomass, high soil carbon and nutrient accumulation belowground, the ability of most tree species to resprout and high nutrient-use efficiency. However, opening the canopy, eroding the soil and removing root biomass decreases forest resilience and allows alien species invasion.

## 15.1 INTRODUCTION

We may conclude that neotropical dry forests are intrinsically fascinating ecosystems, perhaps not so much for their diversity as for the coordinated way in which their relative low species diversity is organized.

Gentry, 1995: 189

Dry forests, seasonal and non-seasonal, are prominent features of the Caribbean landscape because they mostly occur on or near the coastal zone of the islands where they are visible to casual observers. Antillean dry forests occur on soils that can be shallow and rocky. They are not only exposed to low and variable rainfall, but also to winds that range from a breeze to hurricane-level intensity. Net primary productivity and biomass of these forests are low compared to tall moist and rain forests (Murphy and Lugo, 1995), but paradoxically Antillean dry forests are highly resilient to hurricanes, tree pruning, cutting and drought. A question of ecological interest, which builds on Gentry's quote (above), is how do the coordinated functions of Antillean dry forests species lead to high resilience?

Most of the ecosystems at tropical and subtropical latitudes are seasonally stressed by drought (Murphy and Lugo, 1986a). Research on population and ecosystem dynamics, and conservation efforts, however, rarely address the moisture gradient of forests from very wet to very dry. Indeed, the term tropical forest is usually understood as moist or rain forest. The extent of forests in the drier tropics and their characteristics are problematic subjects for those conducting global assessments using remote sensing techniques. In addition, dry forest degradation and conversion is far more advanced than that of wet forests, and yet they are less studied and less publicized (Lerdau et al., 1991; Sánchez-Azofeifa et al., 2005). Janzen (1988) noted that less than 2% of dry forest remains intact in Mesoamerica, and less than 0.1% is explicitly protected. This is unfortunate since tropical forests with prolonged annual drought occupy a greater area than forests in moist and wet regions, and have been of greater use to humans (Murphy and Lugo, 1986a).

What are tropical dry forests? We use the dry forest designation *sensu* Holdridge (1967) as described for the Neotropics by Murphy and Lugo (1995). In the simplest terms, dry tropical or subtropical forests occur in frost-free regions with a pronounced dry season and/or low annual rainfall. In the Holdridge life zone system, frost-free environments include both tropical and subtropical designations. However, because the Holdridge system does not account for seasonality, we expand the definition of dry forest to include forests receiving higher annual rainfall than the system specifies but behaving as dry forests because of an extended dry season. The dry season may be severe enough to select for drought-deciduous or even evergreen, drought-tolerant trees. Drought-deciduousness is, however, the principal adaptive mode found in this type of forest although at the dry extremes small evergreen trees may be important.

The vegetation of the Caribbean is classified into three phytogeographical units (Mexico and Central America, northern Venezuela/Colombia and the Antillean subregion), which in turn are subdivided into provinces according to vegetation affinities (Gentry, 1982; Samek, 1988). Borhidi (1996), however, lumped the two continental units into one. Our geographical focus is on the Antillean subregion, specifically on the dry forests. Lugo et al. (2000) reviewed the literature on the vegetation of the Antillean subregion while Bullock et al. (1995) reviewed the literature on seasonal dry tropical forests, including those of the Antillean subregion. Van der Maarel (1993) included reviews on coastal dry vegetation of the world, including two chapters dedicated to the Caribbean (Borhidi, 1993; Stoffers, 1993).

In this chapter we examine the floristic composition and botanical basis for the resilience of Antillean dry forests, and we explore their distribution and conservation status. We caution that the scarcity of research in the Antilles causes our presentation to be heavily influenced by Gentry (1995) and our research in the Guánica dry forest in southern Puerto Rico. We start with a description of the environmental setting of Antillean dry forests.

## 15.2 THE ENVIRONMENT OF ANTILLEAN DRY FORESTS

Antillean dry forests function in the context of three environmental conditions that together appear unique in the Neotropics. The first is common to all dry forests, namely, the low and seasonal availability of moisture. Drought stress has been characterized by climatic variables, mostly precipitation and temperature, as the balance between precipitation and evaporation and these are used in mapping the distribution of dry forests and correlating physiological and phenological patterns with climate (Murphy and Lugo, 1986a; Mateucci, 1987). The fundamental variable of soil moisture has been sparsely documented, and this hinders inter-site comparisons. The subject is complicated since soil physical characteristics as well as topography have great importance in dry forests as determinants of variation in water availability. Soils on limestone substrates are frequently very well drained, having a tendency to dry out quickly after rains, and they are therefore often drier than other soil types under the same rainfall regime.

Medina (1995) showed that the number of dry months, estimated through the Bailey Index (BI), was more indicative of water stress to plants than rainfall. The BI is calculated using basic evaporation laws with the formula:

$$BI = 0.18p/1.045t,$$

where  $p$  is the mean monthly precipitation in cm and  $t$  is the mean monthly temperature in °C.

The BI for which potential evapotranspiration equals rainfall during a given period is 6.37. This number allows separation of humid and dry climatic realms (Bailey, 1979). Dry forests not only experience more dry months than do moist or wet forests, but also more within-year variability of the Bailey Index (Medina, 1995). Soil moisture can also vary significantly during the wet season because of the sporadic occurrence of rains. The moisture limitations of Antillean forests are exacerbated by edaphic conditions. Gentry (1995) believed that many of the peculiarities of Antillean dry forests were due to edaphic factors, particularly the prevalence of limestone. Rocky limestone soils have low water holding capacity and nutritional limitations imposed by their calcareous composition. Growing on calcareous soils not only increases the potential water stress due to their comparatively low water retention capacity, but also restricts the availability of phosphorus (P).

The combination of low moisture availability, high number of dry months and dry days, variation in the availability of moisture and of occurrence of dry days in annual and decadal cycles makes the Antillean dry forest a highly stressful environment for plants. Wind exposure in coastal dry forests increases moisture requirements, putting further demand on water availability. The situation is often exacerbated by exposure to salt spray close to the sea (Stoffers, 1993). Salt spray causes death of exposed new leaves produced during the dry season, and this can be easily observed in wind exposed coastal forests. Flooding with seawater during tropical storms and hurricanes produces a more pronounced effect, causing the death of whole plants when the water percolates down to the root zone. Wright (1992) suggested that drought, and possibly nutrient stress, control floristic composition and relative density by limiting the number of species that can cope physiologically with such an environment. He also stated that seasonal water deficits contribute to mortality and limit diversity in epiphytes, terrestrial herbs and understory shrubs. These moisture limitations result in slow tree diameter growth rates (Weaver, 1979; Murphy and Lugo, 1986a).

The second environmental condition that helps delimit the unique environment of the Caribbean is the persistent exposure to hurricane conditions. The passage of hurricanes over the region is a large-scale, periodic and high-intensity disturbance to forests. A forest will experience anywhere from 10 to 70 hurricanes per century depending on its location in the Caribbean (Neuman et al., 1978). Hurricanes involve exposure to two environmental factors: water and wind. While the passage of hurricanes mitigates short-term water shortages for dry forests, their winds cause tree-fall and other structural changes and stimulate succession. Because of its geographical location, the Caribbean

is also continuously exposed to trade winds and these moderate air temperatures, redistribute aerosols, dust, nutrients and organisms throughout the region, and influence the structure of forest canopies. Epiphytic plants benefit from the moisture and nutrient inputs of trade winds to Caribbean forests (Lugo and Scatena, 1992).

The third environmental factor that helps shape present-day Antillean dry forests is human activity. Humans have been active in the Caribbean for over four millennia (Rouse, 1992) and they have modified and converted dry forests through cutting, grazing and burning, resulting in species extinction and introduction of alien species. Because of human activity, it is unlikely that there is any primary Antillean dry forest left. Most stands have been modified in some way.

### 15.3 FLORISTICS

Gentry (1995) compared the floristics of 28 neotropical dry forests (using data from 0.1 ha per site) and found that Antillean dry forests were different from continental dry forests in terms of structural and floristic composition. Antillean dry forests have more sclerophyllous leaves and higher small and medium tree densities (2.5–20 cm diameter at breast height (dbh)) than their continental counterparts. While dry tropical forests have lower species richness than moist or wet tropical forests, those from the Antilles have even lower species richness than their continental counterparts. Gentry (1995) also reported less than a third as many species of lianas (22/0.1 ha), but a similar number of tree species (46/0.1 ha with dbh  $\geq$  2.5 cm), in Antillean dry forests compared to continental sites. Although Gentry did find a low epiphytic species occurrence in dry forests, he nevertheless considered their absence, or near absence, as one of the most distinctive structural features of this vegetation type. However, Murphy and Lugo (1986b) observed a higher biomass of epiphytes in the Guánica Forest in Puerto Rico than in the moist forests of the Venezuelan Amazon, and they and Medina (1995) attributed this difference to the effect of sea breezes with high atmospheric humidity and the incidence of dew.

Antillean dry forests have almost as many plant families (26) as their Equatorial mainland counterparts (27.9). Myrtaceae is the pre-eminent West Indian dry forest family, averaging four species per sample examined by Gentry (1995). Cactaceae, Capparaceae, Zygophyllaceae and Euphorbiaceae are common families closely associated with dry forests in general. Families like Cucurbitaceae, Asclepiadaceae and Passifloraceae as well as papilionoid legumes are disproportionately well represented in dry forests compared to moist and wet forests. The first three of these families are predominantly herbaceous climbers as are many papilionoids found in this habitat, and their abundance reflects the success of this growth-type in dry forests. Also common are shrubby members of families that are predominantly arboreal or scandent in other habitats.

Among the genera over-represented in the Antilles, Gentry listed *Coccoloba*, *Eugenia*, *Erythroxylum* and to a lesser extent *Drypetes* and *Casearia*. Gentry (1995) found that the level of generic endemism in Antillean dry forests was low compared to that of northern Venezuela and Colombia. Regarding the level of endemism in the dry forests of Cuba, Borhidi (1993) found a greater number of endemics in dry forests on serpentine (ultramafic) soils on eastern Cuba, higher endemism in littoral thickets on limestone than in littoral forests on sandy beaches, a tendency for endemic species to increase towards the mature phases of vegetation succession, and that the endemic species are mostly local endemics.

Gentry (1995) observed that flowering and seed dispersal in dry forests contrasted with those of moist and wet forests. Two-thirds to three-quarters of dry forest woody taxa had conspicuous flowers pollinated by specialized pollinators such as large bees, hummingbirds or hawkmoths. Seed dispersal for woody plants in dry forests is by wind, occurring in about 80% of lianas and 5–33% of trees. In fact, of families with species showing both wind and animal dispersal, those dispersed by wind are predominant in dry forests. These characteristics apply to most tropical dry forests, but have not been studied in Antillean dry forests (though see Gillespie, Chapter 16).

Knowledge about the number of plant species in the Antilles is incomplete. This is also true for the dry forests. An estimate for the number of native plant species in the Antillean Archipelago is 12,000 (Myers et al., 2000). Part of the problem of fully documenting the richness of Antillean dry forest plants is that most ecological studies record only plants above a certain size (dbh) and this causes many shrubs, herbs, vines and epiphyte species to be missed since they do not reach the minimum size required. However, the preponderance of herbs, lianas and shrub species in dry forests in comparison to those in moist and wet forests is well known (Gentry and Dodson, 1987).

Irrespective of the size of the Antillean flora, half of the species are considered as endemic to the region, many of them endemic to a single island or to a small region inside one island. Several examples from dry forests in Puerto Rico demonstrate that in spite of the modification, fragmentation and conversion of dry forest stands, new species and records of species continue to be documented by botanical investigations.

- In the dry forests of the south-west of Puerto Rico (Sierra Bermeja, Cabo Rojo, Guánica) six new species of shrubs or small trees were described up to 1990 (Little and Wadsworth, 1964; Little et al., 1974). Also, Acevedo Rodríguez (1999) named the rare vine *Marsdenia woodburyana* Acev.-Rodr., and Kuijt et al. (2005) catalogued the parasitic epiphyte *Dendrophthora bermejiae* Kuijt, Carlo & Aukema.
- In Mona Island, the herbaceous species *Chamaesyce orbifolia* Alain, the orchid *Psychilis monensis* Saulea and the shrub *Lobelia vivaldii* Lammers & Proctor were published by Liogier (1980), Saulea (1988) and Lammers and Proctor (1994), respectively.
- In the dry forests of north-eastern Puerto Rican Bank, which includes the Virgin Islands, the new orchid *Psychilis macconnelliae* Saulea was published by Saulea (1988), and the shrubs *Eugenia earhartii* Acev.-Rodr., *Machaonia woodburyana* Acev.-Rodr. and *Malpighia woodburyana* Vivaldi (the latter is present in south-west Puerto Rico) were published by Acevedo Rodríguez (1993).

The early phytogeographical literature of the Antilles (mostly of the smaller islands) was reviewed by Stoffers (1993) who provided species lists for three communities on sandy beach substrates, two on sand spits and four on rock pavement. A more comprehensive analysis is that of Borhidi (1993) for Cuba. Borhidi segments the 5746 km coastline of Cuba into six main areas according to geography. The age of the substrates are about 30 million years, and most are on limestone substrate except for the eastern portion between Moa and Baracoa that also contains ultramafic soils. Borhidi identifies six main vegetation zonation types for which he presents vegetation profiles and species lists. The main zonation types are sandy beaches, low limestone benches, high limestone benches, coastal semi-desert terrace areas without wind effects, semi-desert areas with strong wind effects and the serpentine coast where in one 20 m × 20 m plot he found 80 species of which 73 were endemic. In all, Borhidi provides information for 16 littoral communities in Cuba: six on beaches, seven on rocky semi-arid shores and three on rocky arid shores. The works of Borhidi (1993, 1996) and Bisse (1988) contain species lists and phytogeographical data for Cuban vegetation.

A comparative overview of the flora of Antillean dry forests has been made in two studies based on parsimony analyses of species assemblages. These analyses search for the most parsimonious arrangement of shared species among geographical locations with the purpose of revealing biogeographical affinities in a hierarchical pattern (Rosen and Smith, 1988; Rosen, 1992).

Trejo-Torres and Ackerman (2001) studied the Antillean archipelago based on its orchid flora. Islands dominated by dry forests (those flat, low-lying, calcareous islands such as the Bahamas archipelago and the Cayman islands), form regional island groups with cohesive floristic assemblages. Islands physically similar to these archipelagos but found in other areas such as Mona (between Puerto Rico and Hispaniola), Anegada (north-east Virgin Islands) and Isla de la Juventud (south-west of Cuba) affiliate to the Bahamas and Cayman islands instead of to their respective

geographical neighbours. The conventional wisdom is that larger islands and regional archipelagoes are biogeographical units while small islands and small archipelagoes are subordinate to the other major neighbouring units (Borhidi, 1996; Samek, 1988). However, parsimony analyses for orchids indicate that floristic groups are concordant with physical factors of the islands (i.e. ecological settings) rather than with geological or geographical membership. This pattern is also understandable given the high vagility of dust seeds of orchids, and is hence expected for other vagile, passively dispersed organisms.

The study of limestone forests shows that dry forests can have closer floristic affinities with dry forests of other islands rather than with moist or wet forests on limestone substrate of their own island (Trejo-Torres and Ackerman, 2002), even when all of them share physiognomic and structural features (Dansereau, 1966; China, 1980). This simple observation also undermines the traditional idea that islands are equivalent to biogeographical floristic units. Instead, it seems that specific biota in complex islands have close affinities to equivalent biota in other islands. Meanwhile, in the study of orchids, regional groups of islands form cohesive floristic units, but other distant non-neighbouring islands can also have close affinities to them, rather than to their neighbouring islands (Trejo-Torres and Ackerman, 2001).

The importance of environmental factors as determinants of floristic composition of Antillean dry forests connects the floristic component of these forests to their response to environmental disturbances and hence to resilience, the temporal response to disturbance. This is particularly true for those resilience attributes that are species specific such as the ability to resprout or the nutrient-use efficiency. Resilience in Antillean dry forests is our next topic.

## 15.4 RESILIENCE OF ANTILLEAN DRY FORESTS

Ewel (1971, 1977) studied the resilience to cutting and herbicides of a dry forest stand in Guánica Forest. He conducted short-term experiments (1 to 3 years) in dry, moist and wet forests in the Caribbean and Central America and found that while dry forests had a slower rate of recovery than wet forests, their resilience was higher because it had less structure to restore after the disturbance. As an example, in terms of the total amount of a variety of structural parameters, the recovery at Guánica forest was on average 39% that of the wet forest at Osa Peninsula in Costa Rica. However, recovery of Guánica forest was 24 times more complete than Osa when assessed in terms of the expected structural values at maturity at each site (Ewel, 1971).

Thirteen years after Ewel's experiments, Dunevitz (1985) assessed the Guánica site and found that the forest recovered more quickly when it was cut than when herbicides were applied. She also evaluated six parameters of forest structure in cut sites and found the following rates of recovery (shown in parentheses) expressed as a percentage of the same parameter measured in an adjacent control stand: number of mature forest species present (59%), basal area (7–40% depending on tree diameter, with a smaller percentage for larger trees), mean height (40%), aboveground biomass (43%), leaf area index (64%) and epiphyte density (11%). Notably, the cut site had 60% more tree species than the control sites due to the invasion of pioneer species. Regeneration was by 81% stem sprouts, 3% root sprouts and 16% seed germination.

Molina Colón (1998) assessed the resilience of the same dry forest vegetation at Guánica by measuring regrowth and forest recovery after abandonment of agriculture, dwellings and charcoal production. Her study examined the effects of long-term recovery 45 years after the abandonment of land uses that had lasted over a century. Molina Colón confirmed Ewel's observation that canopy parameters such as leaf area index and leaf biomass recovered faster than other forest attributes such as stem biomass or basal area. She also showed that forest resilience was higher after disturbances that removed only aboveground biomass relative to disturbances that removed both above- and belowground biomass. *Leucaena leucocephala* (Lam.) de Wit, a naturalized alien species, dominated sites previously used for agriculture, houses and a baseball park.

Van Bloem et al. (2003) found that the dry forest was resistant to a category three hurricane. After the hurricane, more trees showed no effect than those affected in some way by the hurricane. The forest experienced low tree mortality (2% of stems) and low structural changes such as defoliation, stem breakage and loss of basal area. Wunderle et al. (1992) reported similar results for dry limestone forests in Jamaica after the passage of hurricane Gilbert, and attributed to hurricanes some of the observed characteristics of Caribbean avifauna, including its distribution. Van Bloem et al. (2003) suggested that hurricane winds damage larger trees and cause basal sprouting, thus contributing to the maintenance of the low and dense structure of these forests.

Dry forests in Puerto Rico were also found to be resilient to forest fragmentation. Fragments as small as <1 ha retained species richness and composition of trees (including representation of mature forest species), reptiles and termites (Molina Colón, 1998; Genet, 1999; Genet et al., 2001; Ramjohn, 2004). Ramjohn (2004) found 12 rare or endangered species (out of 53 in the south-west of Puerto Rico) in at least one of 40 fragments he examined. However, wood decomposition in the small fragments was slower than in controls (Genet et al., 2001), suggesting that fragmentation might influence some ecosystem functions while not affecting species composition.

Dickinson et al. (2001) proposed a combination of factors associated with seasonal drought and low annual rainfall in dry limestone forests of the Yucatán peninsula. They suggested that low annual rainfall, seasonal drought, low storm frequency, low epiphyte loads, large diameter-to-height ratios and strong anchorage of trees led to low rates of canopy disturbance between disturbance events in dry forests. We modified their model (Figure 15.1) to make it more applicable to Antillean dry forests. In the Antilles, the biomass of epiphytes can be significant in some locations due to the favourable environment produced by the trade winds and night water condensation in the canopy. Also, storms are more frequent than in the Yucatán, and fire is not a natural factor in the Antillean dry forests. Nevertheless, the general notion of a wind-resistant

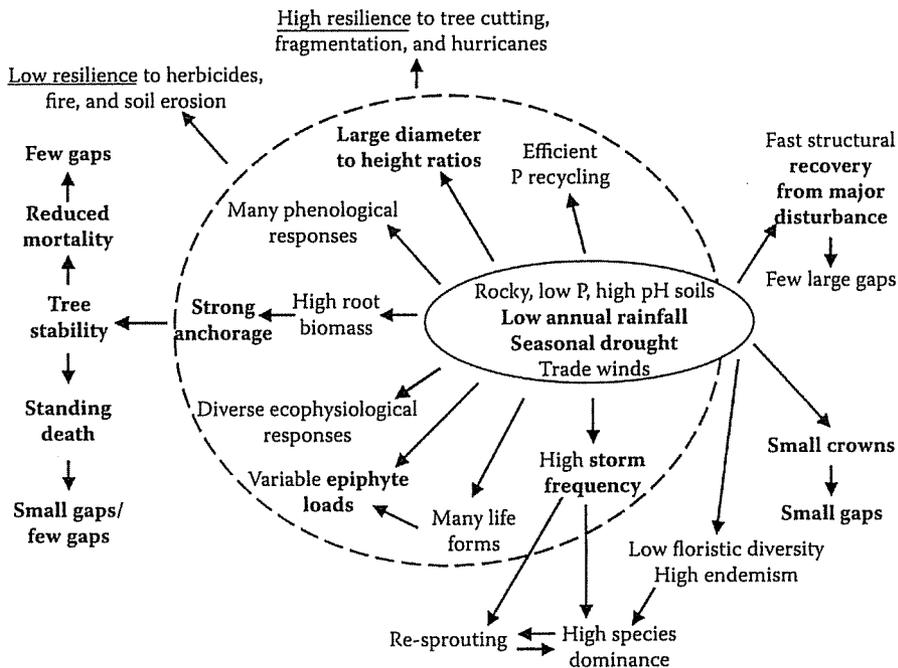


FIGURE 15.1 The combination of factors believed to contribute to high resilience of Antillean dry forests (modified from Dickinson et al., 2001). Bold entries represent information in Dickinson et al. and normal print text has been added.

canopy that has few and small gaps is also typical of Antillean dry forests. Tree stability through proper anchorage and standing tree mortality are also elements in common between Yucatán and Antillean dry forests. These common characteristics of dry forests lead us to a discussion of the botanical basis of their resilience.

## 15.5 BOTANICAL BASIS OF RESILIENCE

### 15.5.1 COMMUNITY ATTRIBUTES

Antillean dry forests are characterized by their lower height and higher tree density than mainland dry forests (Murphy and Lugo, 1986a, 1995; Gentry, 1995). The biomass distribution is also different (Table 5.1). Antillean dry forests have lower aboveground biomass but higher belowground biomass than continental dry forests. The total accumulation of nitrogen is higher in the Antillean forest, particularly in the belowground compartments but not aboveground. The weighted nitrogen concentration for the stand as a whole (including soil depth to 80 cm) is higher in the Antillean forest than continental forests (35 mg/g vs. 27 mg/g). This means that a gram of organic matter in Antillean dry forests contains on average 1.3 times more nitrogen than a gram of organic matter in continental dry forests.

A large number of tree species in Antillean dry forests sprout after cutting, and this accelerates the re-establishment of tree species after experimental (Ewel, 1971, 1977; Dunevitz, 1985; Murphy and Lugo 1986a) or subsistence cutting of stands (Molina Colón, 1998; McDonald and McLaren, 2003). Dunphy et al. (2000) reported that most tree species in the Guánica forest coppiced naturally as well as after cutting. They found 43% of all trees in the forest had multiple stems accounting for 58% of the total basal area. McDonald and McLaren (2003) found that only three out of 51 species tested in a Jamaican dry forest did not coppice. After a hurricane struck Guánica Forest, undamaged trees sprouted without any apparent reason (Van Bloem et al., 2003).

**TABLE 15.1**  
Above- and Belowground Carbon and Nitrogen Pools in  
a Mainland<sup>a</sup> and Antillean<sup>b</sup> Dry Forest

Parameter and Unit	Mainland Forest	Antillean Forest
Carbon (Mg/ha)		
Aboveground	58.3	37.8
Belowground		
Roots to 60 cm	6.7	22.5 <sup>a</sup>
Soil to 60 cm	76.2	86.5 <sup>a</sup>
Total	141.1	146.8
Nitrogen (kg/ha)		
Aboveground	940	631
Belowground		
Roots to 60 cm	106	546 <sup>a</sup>
Soil to 60 cm	6,659	9,100 <sup>a</sup>
Total	7,704	10,277

<sup>a</sup>To 85 cm depth

<sup>b</sup>Mg = Mega grams (metric tons)

Source: <sup>a</sup>Jaramillo et al., 2003

<sup>b</sup>Lugo and Murphy, 1986; Murphy and Lugo, 1986a

Lugo (1991) showed that all dry forest stands in Puerto Rico and Mona Island have high species dominance. In a mature forest at Guánica Forest for example, Molina Colón (1998) reported that from a total of 36 species, five accounted for 66% of total basal area, and six accounted for 66% of total tree density (Figure 15.2). Part of this dominance is due to the low floristic diversity of Antillean dry forests, but Lugo also attributed high dominance as a response to hurricane and anthropogenic disturbances and drought. Given the harsh environmental conditions of Antillean dry forests, those few species that thrive under the stress are able to dominate sites. Miller and Kauffman (1998) studied the effect of anthropogenic disturbances on species importance and dominance in Mexican dry forests. When exposed to slashing, burning, cultivation and grazing, the experimental sites had a reduction of species number and an increase in the dominance of the surviving species. The experiments also showed the importance of high root turnover to forest resilience (Castellanos et al., 2001).

The community attributes discussed above all contribute to forest resilience, each attribute contributing to resilience to one or more type of disturbance. For example, the low stature of the forest offers a reduced physical barrier to wind, which in turn gives strong resistance to high winds. The low fraction of biomass aboveground means that the necessity to rebuild after wind disturbance is comparatively small. This recovery is accelerated by the resprouting ability of most dry forest species. Moreover, the high amount of root biomass supports the recovery of the above-ground portion by supplying water, nutrients and organic matter reserves. The high proportion of root biomass is also adaptive in capturing scarce soil water resources. Similarly, high soil organic matter stores available nutrients for vegetation, and the high proportion of below-ground nutrients allows for multiple turnovers of aerial vegetation (Lugo and Murphy, 1986). These factors provide resilience to pruning and fuel-wood harvesting.

## 15.5.2 ECOPHYSIOLOGY

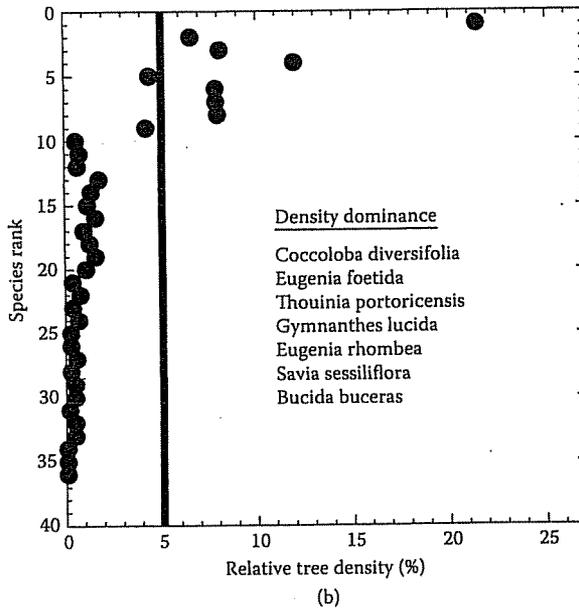
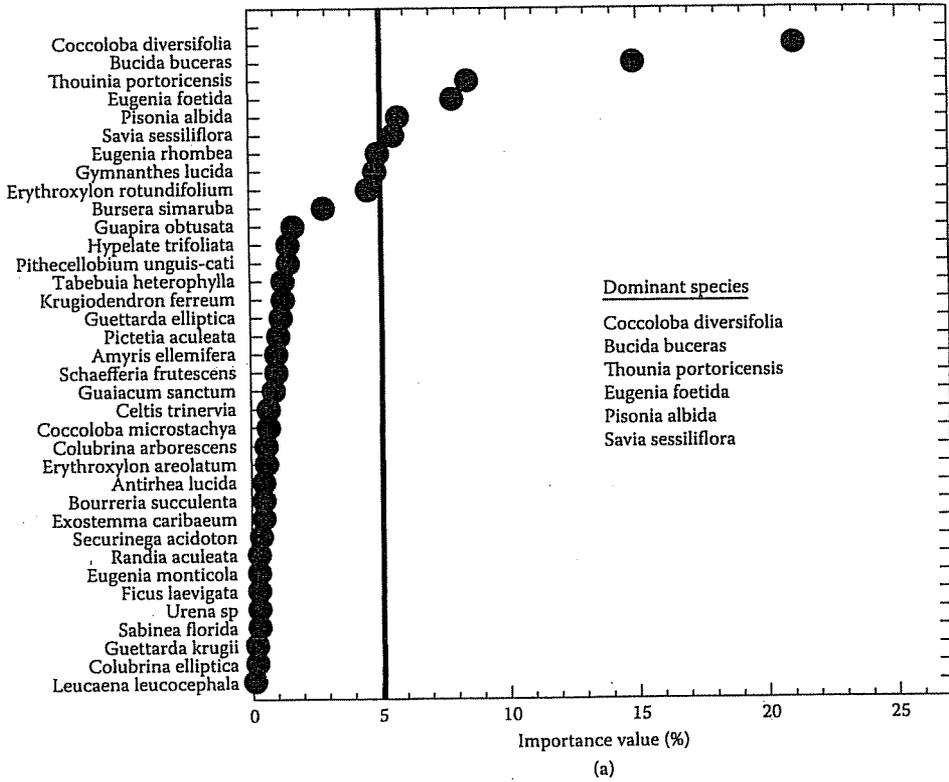
### 15.5.2.1 Life Forms

Medina (1995) compiled the variety of life forms in dry forests (Table 15.2) and observed that diversity of life forms in dry forests appeared higher than in other types of tropical forests. He attributed this diversity to habitat (including surface) heterogeneity coupled with strong rainfall seasonality. This combination of factors leads to broad gradients of water availability so that each life form finds a sector of the gradient to which its particular physiological responses are competitively adaptive (Lugo et al., 1978; Medina, 1995). The diversity of life forms is accompanied by diversity in structure and physiology, for example, plant habit, leaf size, drought tolerance and growth seasonality (Medina, 1995). Sap concentration increases with aridity (Medina, 1995).

### 15.5.2.2 Phenology

Phenology of tropical deciduous forests is characterized by phenomena determined by pulses, such as the sudden increase in water availability at the beginning of the rainy season, moisture availability after sporadic rainfall events, and those triggered by slow reductions in resources availability, such as the decrease in water availability at the end of the rainy season (Table 15.3). These phenomena can be initiated, particularly near the outer fringes of the tropical regions, by photoperiod and temperature changes at the beginning and end of the rainy season.

Activation of the soil microbiota leads to rapid cascades of decomposition of below- and above-ground litter produced during the previous growing season, and active fluxes of gases derived from soil respiration ( $\text{CO}_2$ , NO,  $\text{N}_2\text{O}$ ) (Matson and Vitousek, 1995). In these processes significant amounts of nutrients are released which can be leached or taken up by newly formed fine roots. Much research is still required to understand the synchronization of events related to water supply, particularly processes of decomposition and release of nutrients and trace gas fluxes.



**FIGURE 15.2** Importance values based on (A) relative density + relative basal area, (B) relative density and (C) relative basal area of the most common tree species in a mature dry forest in Guánica, Puerto Rico (from Molina Colón, 1998). Data are for trees with dbh  $\geq$  5 cm. The total number of species was 36 in a sampled area of 400 m<sup>2</sup>. Absolute basal area was 19.1 m<sup>2</sup>/ha and absolute tree density was 5085/ha. The most important species representing >5% of the relative values are shown in each graph in decreasing order.

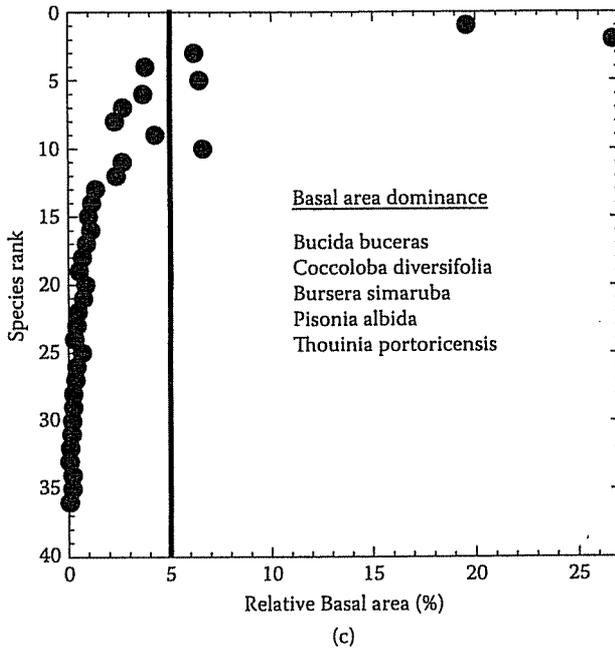


FIGURE 15.2 (Continued).

**TABLE 15.2**  
**Dominant Life Forms and Functional Attributes of Higher Plants from Tropical Dry Forests**

Life Form and Morphological Features	Functional Attributes
<b>Trees and Shrubs</b>	
Mesophyllous	Deciduous
Sclerophyllous	Evergreen
Succulent	C <sub>3</sub> and CAM photosynthesis
<b>Herbaceous</b>	
Grasses	Annual, C <sub>3</sub> and C <sub>4</sub> photosynthesis
Dicotyledonous	Perennial
Succulents	C <sub>3</sub> and CAM photosynthesis
<b>Vines</b>	
Herbaceous	
Woody	
Mesophyllous	Deciduous
Sclerophyllous	Evergreen
Succulent	C <sub>3</sub> and CAM photosynthesis
<b>Epiphytes</b>	
Mesophyllous	Deciduous
Sclerophyllous	Evergreen
Succulent	C <sub>3</sub> and CAM photosynthesis
Parasites	Xylem-tapping mistletoes

Source: Medina, 1995

**TABLE 15.3**  
**Characteristic Ecosystem Processes Regulated by Seasonality of Water Availability**

Phases	Primary Producers	Decomposers	Consumers
<i>Rainy Season</i>			
Beginning	Leaf flushing and fine root production	Rapid decomposition of above- and below-ground organic matter	Activity of detritivores, herbivores, and seed and fruit eaters
	Carbohydrate transport	Net loss of CO <sub>2</sub> and N oxides	
	Water transport		
Middle	Full canopy development	Accumulation of microbial biomass	Maximum herbivore activity
	Carbohydrate accumulation		
	Litter production		
End	Growth slows down	Slow reduction of microbial activity	Reproduction and beginning of resting phase
	Leaf and fine root shedding		Faunal migrations
<i>Dry Season</i>			
	Carbohydrate expenditures for flowering and maintenance respiration of roots and stems	Soil biological activity reduced or nil	Pollinators Nectar consumption Reproduction

*Note:* Ecosystem adaptive features are related to the duration and variability of the growing period (beginning to end of the rainy season, lasting 4–10 months)

Leaf flushing takes place at the beginning of the rainy season as a consequence of full hydration of meristems, while leaf shedding takes place at the end of the rainy season as a consequence of leaf dehydration and senescence (Frankie et al., 1974; Reich and Borchert, 1984). Similar processes take place by the production and sloughing of fine roots. Activity of insect herbivores (leaf and seed eaters) increases dramatically at the beginning of the rainy season, while activity of pollinators is high during the dry season, when numerous deciduous tree canopies are covered with dense flower crops (Janzen, 1981; Filip et al., 1995; Borchert et al., 2004). Essential determinants for the long-term dynamics of these forests are the duration and variability of the four phases of water availability (Table 15.3).

### 15.5.2.3 Nutrients

In the tropics, seasonal dry forests and savannas occur under the same climatic conditions. Separation of seasonal forests and savannas under undisturbed environmental conditions is possible on the basis of the fertility status of the soil. In the Neotropics, deciduous forests are found on soils of significantly higher fertility than savannas (Ratter et al., 1973; Furley et al., 1988; Oliveira-Filho and Ratter, 2002). Sarmiento (1992) developed a simple model based on the number of months with water deficit and on soil fertility, which allows the separation of evergreen forests, deciduous forests and seasonal savanna systems. The extension of deciduous forests has decreased because of deforestation for agriculture and pastures. Deforestation is associated in the tropics with an increase in the frequency of fires, leading to nutrient impoverishment and to the encroachment of fire-tolerant savanna communities. In Antillean forests, the soil nutritional conditions are not as favourable as on the continent due to the predominance of calcareous substrates. Low phosphorous availability probably accounts for the higher proportion of evergreen sclerophyllous trees in Antillean dry forests compared to dry forests in Central and South America (Lugo and Murphy, 1986).

Only a small percentage of the nitrogen (N) (10%), phosphorous (P) (2%) and potassium (K) (3%) in the Guánica forest stand in Puerto Rico was stored above ground (Lugo and Murphy, 1986).

**TABLE 15.4**  
**Percentage of Nutrient Demand Required for Leaf Growth (Measured by Either Area or Weight) that Could be Satisfied by Retranslocation in Eight Selected Tree Species of Tropical Dry Forests in India**

Nutrient	Nutrient Demand Potentially Satisfied by Retranslocation (%)	
	Area	Weight
Nitrogen	50–100	46–80
Phosphorus	29–100	20–91
Potassium	29–100	20–57

Source: Lal et al., 2001

Trees retranslocated the N and P required for above-ground net primary production (30% and 65% respectively), while immobilizing P in dead roots. Lal et al. (2001) found that nutrient retranslocation by dry forest species in India could account for a significant portion of the nutrient demand for leaf and biomass expansion during the dry season (Table 15.4). These dry season leaves were capable of taking advantage of the changing moisture conditions at the onset of the rainy season. The result was that they maximized the length of time biomass accumulation could take place through net photosynthesis. Moreover, the ratio of organic matter to phosphorus in litterfall was 6057 to 1 in a mature stand in Guánica forest, one of the three highest P-use efficiencies reported in the literature (Lugo and Murphy, 1986). The storage and cycling of P in these dry forests contribute to resilience by facilitating organic matter production and use in spite of low P availability.

#### 15.5.2.4 Limestone Substrates

In Caribbean islands, a thick layer of limestone deposits of marine origin up to several hundred meters deep may cover volcanic substrates. On top of these deposits a variety of plant communities develop according to rainfall, from open thorn thickets to predominantly deciduous forests with a similar tree flora throughout the lowlands of the Caribbean (Asprey and Robbins, 1953; Kelly et al., 1988; Tanner, 1977). Soil development on top of hard limestone leads to formation of terra rossa above soft rendzinas. Limestone also presents strong hardening processes. The dissolution process of the limestone leads to the formation of deep holes (dolines). In time, these holes can be connected and form wide flat areas surrounded by steep walls of limestone covered with hardened calcareous crusts. In the Greater Antilles, this process is well developed particularly in the moister areas and has led to the Mogotes formation (Lötschert, 1958; Zanoni et al., 1990; Borhidi, 1996; Lugo et al., 2001).

Limestone is homogeneous in chemical composition, mainly containing calcium carbonate, with varying amounts of magnesium (dolomites) and clay (Marschner, 1995; Lugo et al., 2001). On limestone bedrock a variety of calcium-rich soils develop, particularly the rendzinas. Climatic differences determine variations in ion accumulations in the upper soil layers. In drier climates, rapid evaporation causes water-soluble salts to accumulate at the surface. In more humid regions, rainfall leaches out both nutrients and calcium carbonate leading to a 'secondary acidification'.

Water and nutrient relations differ markedly at the base, slope and tops of Mogotes, determining changes in density and species composition of the woody vegetation (Weaver, 1979; China, 1980; Serrano et al., 1983; Álvarez Ruiz et al., 1997). The limestone areas in Puerto Rico have been divided into northern, southern and dispersed limestone areas (Lugo et al., 2001). Since little is

known about the dispersed limestone areas, we will concentrate our attention on the northern and southern limestones. The northern limestone area includes the Karst belt, while the southern limestone area occupies some of the lower rainfall areas in Puerto Rico. On these limestone areas, three large geoclimatic units are differentiated according to their rainfall regime, supporting dry, moist and wet forest types. These forests grow under similar pedological conditions but intensity of carbonate dissolution varies in association with the amount of run-off and of percolating waters acidified by CO<sub>2</sub> from the air and root and microbial respiration. In these limestone forests, structural development and biomass production are tightly associated with rainfall regime (Lötschert, 1958; Lugo et al., 1978; China, 1980; Medina and Cuevas, 1990).

## 15.6 VEGETATION ON CALCIUM CARBONATE-RICH SUBSTRATES

The occurrence or exclusion of plant species in karst environments has been studied in detail in temperate latitudes, and this has led to the ecological classification of plants as *calcicoles*, species frequently growing on calcium carbonate-rich soils, and *calcifuges*, species that avoid, or are not found, on those soils (Kinzel, 1983). This differentiation, however, is not necessarily related to physiological properties or modification of the competitive ability of those plant species under natural conditions.

Calcium carbonate-rich soils generally have lower availability P and iron (Fe) because of the formation of insoluble salts, and may create physiological stress in the plants due to the accumulation of large amounts of calcium (Ca) ions. Often these soils generate nutrient stress through the following:

- Inhibition of K uptake by high concentrations of Ca ions in the soil solution.
- Low P availability because the high pH and high concentration of Ca leads to the formation of insoluble calcium-phosphate. However, activity of roots and rhizospheric microorganisms may increase P availability through the excretion of organic acids.
- Reduction of Fe availability, which in calcifuge species cultivated on calcareous soils causes a yellowish discoloration of leaves (lime-induced chlorosis).

Calcium concentrations in the cytoplasm have to be below the micromolar level for Ca to act as a secondary messenger in the regulation of membrane permeability and root growth (Marschner, 1995). The excess of Ca availability in karst soils can be precipitated around roots or cells (as calcium carbonate or calcium oxalate), or is maintained in soluble conditions within the vacuoles, frequently as chelates of malate and citrate (Kinzel, 1989).

Higher plants have been classified into two groups according to their soluble K and Ca concentrations. Those with a soluble K/Ca molar ratio below one are termed *calcitrophs*, whereas *calciophobes* are species containing little or no soluble Ca, either because it is precipitated inside the cell as calcium oxalate, or outside the plant tissues as calcium carbonate or calcium oxalate (Kinzel, 1983, 1989). Most of the species investigated are of temperate climates and mainly herbaceous. Calcitrophic species are frequent within the Leguminosae, and calciophobes have been described within the Polygonaceae. These families are well represented in Caribbean dry forest on calcareous soils but have not been investigated yet. Other important families that deserve to be analyzed because of their adaptation to karst soils in the Caribbean are the Palmae, Piperaceae, Moraceae and Rhamnaceae.

In calcium-rich environments, both physiological types (or physiotypes *sensu* Kinzel, 1983) can coexist if water availability is high. In semi-arid environments, calciophobic plants cannot use Ca as an osmoticum, therefore they osmoregulate by accumulating large amounts of photosynthetically expensive organic compounds, particularly sugars. This physiological constraint may explain the calcifuge character of those species (Kinzel, 1989; Marschner, 1995). Mycorrhizal fungi play a role in adaptation of perennial plant species to calcareous soils through the release of siderophores that enhance iron acquisition.

The ecophysiological aspects of Antillean dry forests that we have just reviewed reveal complex adaptations to the diverse environmental conditions typical of these forests. The environmental complexity is revealed in a list of conditions that change spatially and temporally. For example: (1) variable gradients of soil moisture, (2) variable nutrient availability, (3) chemical challenges associated with high soil pH and calcium concentration, (4) pulses of resource availability associated with temperature and rainfall seasonality, (5) limited space for tree anchorage and roots due to rocky soils, (6) periodic hurricanes and others.

Ecophysiological responses that contribute to resilience within this environmental complexity include: (1) a diversity of plant life forms where different life forms function optimally on different sectors of the environmental gradients (Table 15.2), (2) metabolic specialization to deal with calcium-rich and high pH soils, (3) capacity to concentrate and use P at high levels of efficiency, (4) distribution of biomass and chemical resources in live vegetation and soils, (5) a variety of phenological clocks to deal with seasonality and climate variability, (6) stem and root sprouting and vegetative propagation capabilities, (7) a variety of gas exchange mechanisms in plants and others.

## 15.7 THE DISTRIBUTION, AREA AND CONSERVATION STATUS OF CARIBBEAN DRY FORESTS

Dry forests are widespread in the Antillean islands. A general distributional scheme for the Antilles includes:

- The Greater Antilles (Cuba, Hispaniola, Jamaica and Puerto Rico). In these islands, dry forests are of limited extension compared to other vegetation types, and are typically found on narrow strips of limestone on the northern and southern coastal areas. In Cuba, isolated areas of dry forests are also found along the centre of the island over ultramafic soils, many times associated with limestone. Puerto Rico also contains dry forests on ultramafic soils in the vicinity of dry forests over limestone. A peculiarity of Hispaniola (Dominican Republic and Haiti) is that dry forests are also present in interior valleys at the bases of the major mountain ranges.
- The islands of the Virgin Islands platform (British Virgin Islands, U.S. Virgin Islands, including St. Croix — which is outside the platform — and the Puerto Rican islands of Vieques and Culebra). These are volcanic, low mountainous islands with elevations up to 521 m. Dry forests and scrubs dominate except on islands with protected uplands, ravines and valleys, which sustain moist vegetation.
- In the Lesser Antilles two groups of islands are distinguished based on geomorphology: the volcanic arc and the limestone arc. The volcanic arc (from Saba to Grenada) is comprised of topographically abrupt islands up to 1467 m elevation, where dry forests are limited to reduced coastal areas, mainly on the leeward sides. The limestone arc of the Lesser Antilles (from Sombrero to Marie-Galante) as well as Barbados in the south, comprise islands up to 402 m elevation. They have similar conditions to the islands of the Virgin Islands platform in terms of dry forest coverage.
- Dry forests and shrubby vegetation dominate the flat and low-lying (up to 100 m elevation) limestone islands like the extensive Bahamas archipelago, the Cayman islands, Mona and Anegada (the last an atypical member of the otherwise volcanic Virgin Islands).

Brown and Lugo (1980) estimated that dry forests comprised 50%, 23%, 14% and 10% of the area of Bahamas, Dominican Republic, Puerto Rico and Trinidad, respectively. More recently, Helmer (2004) analyzed the areas of the various geoclimatic zones of Puerto Rico in relation to the level of development, forest cover and conservation as public lands (Table 15.5). Her analysis shows that 15% of Puerto Rico is in the dry forest life zone. A total of 24% of the island's development has occurred in this life zone, which means that the development burden is disproportionately high

**TABLE 15.5**  
**Areas of Ecological Zones of Puerto Rico, Zonal Proportion of Island-Wide Land Development, Proportion of Each Zone Under Protection, Upland Non-Cultivated Woody Vegetation within Zone, and Areas and Percentage of Each Zone that is Protected Upland Woody Vegetation**

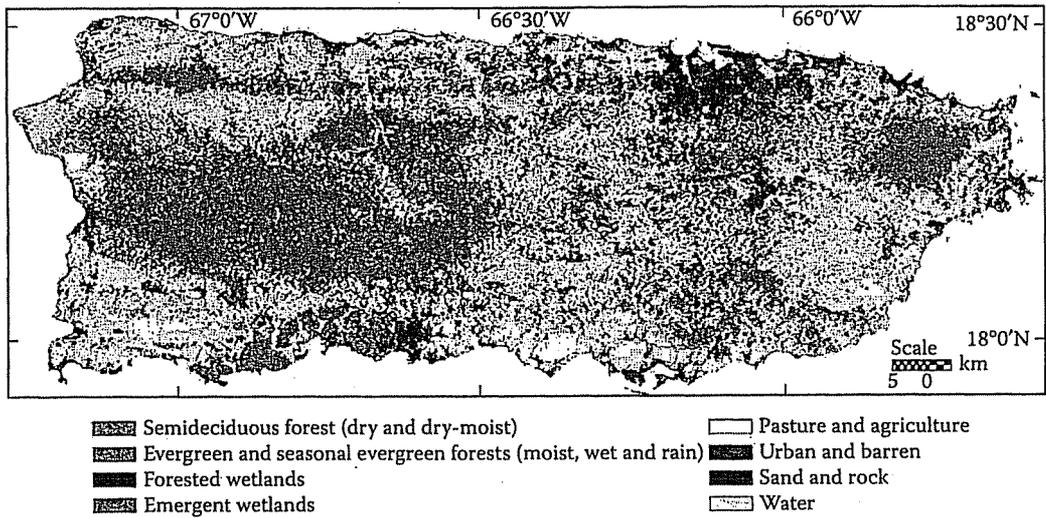
Ecological Zone	% of Island-wide Development	Area of Ecological Zone (ha)	% Protected	Upland Woody Area (ha)	Protected Upland Woody Vegetation	
					Area (ha)	% of zone
Dry-alluvial	10.5	45,179	5.5	5,368	211	0.5
Dry-volcanic/ sedimentary/ limestone	11.8	82,379	4.6	30,441	3319	4.0
Dry-moist serpentine (ultramaphic)	1.9	6,411	25.1	3,690	1517	23.7
Total for dry forest zone	24.2	133,969	6.0	39,748	5047	3.8
Rest of the island	75.8	735,187	5.1	325,412	28,979	3.9
Total for Puerto Rico	100	869,156	5.2	365,160	34,026	3.9

Source: Helmer, 2004

in relation to the geographic representation of the zone. The dry forest life zone of Puerto Rico is 30% forested, has 6% of the land under conservation protection and 3.8% of its forest cover is protected. Within the dry forest zone, the alluvial portion has the lowest forest cover (12%) and lowest area under protection. This situation contrasts with the serpentine or ultramaphic geoclimatic zone, which is 58% forested, and has the highest proportion of land cover under conservation protection. Dry forest over ultramaphic soil is quite rare ecologically and floristically and this region of Puerto Rico, which also includes moist and wet forest, is well protected for its biodiversity value. This, together with its unsuitability for agriculture, is why the proportion of island development that has occurred on this zone is the lowest among those reported in Table 15.5.

In general, Helmer's analysis for Puerto Rico reflects the situation elsewhere of Antillean dry forests. These forests suffer a disproportionate effect of human activity because human populations tend to be high in this life zone (Murphy and Lugo, 1986a). In addition, humans convert Antillean dry forests to alternative uses particularly where soils are nutrient rich, as is the case of forests on alluvial soils. Moreover, local people use these dry forests as a source of fuel-wood and grazing for goats and cattle, which results in altered forest structure and species composition (McDonald and McLaren, 2003).

In some Antillean dry forests, particularly those recovering from disturbance, trees can have low stature or coppiced growth form, and succulents are common. Consequently, there are certain classification systems that would categorize such dry forests incorrectly as shrub-, scrub-, or woodlands. These terms, often regarded as derogatory, can lead to less overall regulatory protection from human exploitation. Several global classification systems, for example, use a height threshold to determine whether a woody vegetation formation is a shrubland or forest, which is inappropriate for Antillean dry forests. The Land Cover Classification System (LCCS) (Di Gregorio and Jansen, 2000) uses a minimum forest height of 3 m, which would mistakenly classify a large proportion of recovering Antillean dry forest as shrubland. The UN Food and Agriculture Organization (FAO) forest classification system (FAO 1996, 1998) uses a 5 m height threshold to distinguish forest from shrubland. A recent global map of terrestrial ecosystems (Olson et al., 2001) refers to some Antillean dry forest



**FIGURE 15.3** (See colour insert following page 208) Distribution of woody vegetation formations typical of dry and dry-to-moist forest formations of Puerto Rico (Helmer et al., 2002). Dry forest formations include woodlands, shrublands and forests that are drought deciduous or semi-deciduous. Unlike most other maps of Puerto Rican forest formations, this map recognizes that dry forest types dominate karst substrate along the north-western coast of the island, which receives less rainfall than inland sites. Based on field observation, Helmer et al. (2002) delineated this area with maps of total annual precipitation and geology, assuming that over karst substrate, where annual rainfall is less than 1500 mm, drier forest formations dominate on limestone hills.

formations as cactus scrub. Even Beard (1955), for example, refers to young secondary dry forests with names like cactus bush, logwood thicket, logwood-acacia bush, *Leucaena* thicket and thorn savanna. This discussion underscores another reason why tropical dry forests fail to receive the attention they deserve. It appears that even their classification and identification are still inconsistent and this hinders the development of a coherent conservation argument for these forests.

A map of forest types for Puerto Rico (Colour Figure 15.3) shows that 44% of the potential forest cover of Puerto Rico is either dry or seasonally dry forest (Table 15.6). This new perception of the forests of this well-studied island is based on more rainfall data than previously available and field verification of vegetation physiognomy (Helmer et al., 2002). The results of the analysis underscore the point already discussed above, that drought-adapted vegetation is more common in the tropics than previously believed.

## 15.8 FUTURE FORESTS: ALIEN AND ENDEMIC SPECIES COEXISTING?

We have discussed how community structure and ecophysiology of dry forests are important to their resilience to natural and anthropogenic disturbances. We have also reviewed the floristic composition of these forests and its relation to resilience through taxon specialization, endemism and life form diversity. However, given the high level of global anthropogenic change predicted for the future, the last question we address is whether the Antillean dry forests will sustain or lose their resilience in the future through irreversible changes to their biota and to below-ground accumulation of nutrients, biomass and soil organic carbon.

It is clear that the Antillean dry forests are vulnerable to human exploitation and degradation. Typically, wood is extracted for charcoal production and domestic animals graze heavily within

**TABLE 15.6**  
**Areas of Forest Types in Puerto Rico as Generalized from Helmer et al. (2002) and Figure 15.3**

Forest Type	Area (ha)
Mixed evergreen drought-deciduous shrubland with succulents	1,052
Mixed deciduous evergreen forest on serpentine <sup>a</sup> substrate	3,535
Mixed deciduous evergreen forest on serpentine <sup>a</sup> substrate	90
Drought deciduous and semi-deciduous forest and woodland/shrubland on karst and other substrates	46,509
Seasonal evergreen and semi-deciduous forest on karst substrate	52,283
Seasonal evergreen and evergreen forest and forest/shrub	256,371
Active sun/shade coffee and evergreen forest/shrub	26,879
Area of dry and seasonally dry forests	386,719
Forested wetlands	7,157
Other forest types	475,280
Total area of Puerto Rico	869,156

<sup>a</sup>ultramaphic

forest stands. Fire is frequently introduced and this results in destruction of trees and invasion by alien grasses. Degraded dry forests are characterized by a combination of the following: compacted soils, loss of soil organic matter, erosion, grazed or trampled understorey vegetation, species composition altered towards the dominance of a few species that are usually thorny, fewer trees, ragged canopies and invasion of alien tree species. Such degraded stands are common in the Caribbean and it is very difficult to reverse these changes because once a fire regime is in place and the soil loses its fertility, succession is arrested at a grassy or thorny scrubland stage. However, management actions in Guánica forest demonstrate that the rehabilitation of degraded dry forests is possible (China, 1990; Wadsworth, 1990).

For rehabilitation to be successful in such areas it is necessary to remove grazing animals and fire. Tree planting and maintenance then follow these changes in disturbance regime until trees are re-established at the site. After that, natural succession can proceed to mature stages but not necessarily to the original species composition. In Puerto Rico, this formula has proven effective in the dry forest region of the island. A recent island-wide forest inventory documents the emerging new dry forests on the landscape (Lugo and Brandeis, 2005). The authors found that dry forests, although degraded, do not have an alien species that exerts dominance, as does *Spathodea campanulata* P.Beauv. elsewhere in Puerto Rico (Table 15.7). Apparently, the harsh natural conditions

**TABLE 15.7**  
**Percentage of Endemic and Alien Tree Species, Contribution of Aliens to the Importance Value (IV), and Number of Species (Alien and Native) by Size Class in Dry Forests in Puerto Rico (Data for 2002; Based on 21 Random Plots and 1.47 ha Sample)**

Total Number of Species (%)		IV (%)	Number of Species Sampled			
Endemic Species	Alien Species	Alien Species	Seedlings	Saplings	Trees	Total
5.7	13.6	7.8	65	56	30	88

Source: Lugo and Brandeis (2005)

of dry forests prevent the dominance of alien species, but not their presence, as aliens contributed to 13.6% of the dry forest tree species vs. 5.7% for endemic species, with the remaining species native non-endemics. Alien species combined accounted for 7.8% of the importance value of all species in dry forests (in contrast with 40–65% in other forest types in the island).

*Bursera simaruba* (L.) Sarg. and *Andira inermis* (W. Wright) DC, both native, were the most important dry forest species, and both species show signs of regeneration. *Leucaena leucocephala*, a naturalized alien, however, dominates the sapling and seedling classes. Of the 88 species found by Lugo and Brandeis (2005) in dry forest, 75 were native. They reported endemic species to Puerto Rico such as *Psidium insulanum* Alain, *Thouinia striata* Radlk., *Rondeletia inermis* (Spreng.) Krug & Urb. and *Tabebuia haemantha* (Bertol. ex Spreng.) DC, of which the last three species are regenerating (Table 15.7). *Prosopis pallida* (Humb. & Bonpl. ex Willd.) Kunth., *Pithecellobium dulce* (Roxb.) Benth., *Albizia lebeck* (L.) Benth., *Tamarindus indica* L., *Spathodea campanulata*, *Melicoccus bijugatus* Jacq., *Acacia farnesiana* (L.) Willd., *Persea americana* Mill., *Sterculia apetala* (Jacq.) H. Karst., and *Parkinsonia aculeata* L., in order of importance, were the alien species found in dry forest as upperstorey species. Most of these also showed sapling and seedling regeneration in undisturbed conditions.

From the above, it appears that alien species coexist with native and endemic species in dry forests. In fact these pioneer alien species appear to facilitate (*sensu* Callaway, 1995) the establishment of native species on degraded forestlands (Molina Colón, 1998). However, the alien species do not appear to dominate natural stands, although they do so in the colonization of sites where all vegetation has been removed. In this instance, the alien species form forest stands that slowly mature into communities with mixed species composition, including aliens and native species. It is possible that these new forests (*sensu* Lugo and Helmer, 2004) represent the forests that will prevail in human-dominated landscapes, assuming that humans learn to manage fire and grazing there. The level of resilience of these new forests will require additional research, particularly as they become the predominant vegetation of the Antillean dry forest.

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# Neotropical Savannas and Seasonally Dry Forests

Plant Diversity, Biogeography, and Conservation

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