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Ecological and Physiological Aspects of Caribbean Shrublands

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and Olga Ramos González



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Cover Photograph: Montane Caribbean vegetation dominated by elfin shrublands (smooth canopy and wind-sculptured vegetation with scattered slope palm forests) on rain forest climate and volcanic substrate on the Luquillo Mountains in Puerto Rico. Photograph © Ariel E. Lugo.

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Ecological and Physiological Aspects of Caribbean Shrublands

Ariel E. Lugo^{1,*}, Ernesto Medina^{1,2}, Elvira Cuevas^{3,4}, and Olga Ramos González¹

Abstract - Shrubland vegetation has not received as much scientific attention in the Caribbean as forest vegetation has. However, shrublands constitute ~25% of the woody vegetation classification units in the Caribbean, and in 10 islands that we analyzed, the average cover of shrublands was 16% of the land area and 27% of the vegetation area. Caribbean vegetation is subject to strong environmental gradients, and many tree species change habit from arboreal to shrubby along those gradients. Shrublands usually occur at the extremes of edaphic and climatic gradients, which explains why many studies of forests in the Caribbean are actually studies of shrublands or include shrublands. Shrubland vegetation is of scientific interest because it possesses adaptations for dealing with extreme conditions of drought, oligotrophy, salinity, inundation, fire, temperature, and wind. These conditions have floristic, ecological, and ecophysiological consequences. Caribbean shrublands, particularly those on ultramafic or serpentine soils, have a high level of endemism and high species diversity. Shrublands exhibit a high level of leaf sclerophylly, high root-to-shoot ratios, and high resilience. We generalize the development of shrublands with a stress model that emphasizes environmental gradients and duration (chronic or acute) of limiting conditions. Human activity is creating shrubland habitat, a trend that is bound to intensify in the Anthropocene Epoch. These changes in environmental conditions are leading to novel shrublands where introduced species mix with native ones forming new species assemblages.

“... the term shrub conjures up an image of a woody plant of limited stature; usually with mature specimens of one third to twice human height and often with multiple stems.” E. Durant McArthur (2004:i)

Introduction

In this review, we summarize the geographic distribution and classification of Caribbean shrublands and their ecological attributes. We also present a heuristic model to illustrate the range of conditions that lead to a shrubby physiognomy, identify the ecological and ecophysiological characteristics of shrublands and shrub species, and review recent research on 3 dwarfed shrublands in Puerto Rico: a dwarfed *Rhizophora mangle* L. (Red Mangrove) community growing on old peats (Medina et al. 2010), a coastal dry shrubland growing on a limestone rocky

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substrate (Medina et al. 2012), and an elfin dwarf shrubland with an annual rainfall of about 5000 mm (Medina et al. 1981). All geographic locations mentioned in this manuscript are shown in Figure 1.

Our review of the literature showed that shrubs and shrublands are important components of the vegetation of the Caribbean, but in the process of highlighting their importance, we encountered difficulties with terminology and consistency in its use. While the distinction of what is a shrub vs. what is a tree is clear by measures of size and the origin and number of shoots (Box 1; Lawrence 1955), the distinction becomes less clear when trees are small, stunted, or dwarfed, or when terms such as bush, scrub, thicket, and woodland are introduced to describe vegetation (Box 2). Shrubs, *sensu stricto*, are part or dominant components of these vegetation types. To be true to the intentions of authors, we use the terms used in the publications that we reviewed. However, we also sought information in the publications that assured the presence or dominance of shrubs. We recognize that many times the absolute height of vegetation is used to define a shrubland, particularly in the absence of taxonomic information or quantitative vegetation analysis. The causes of the confusion with the distinction between shrub and non-shrub vegetation are many. We discuss some of them but in the last section highlight research questions that when addressed will contribute to improving understanding of shrubland vegetation and its functioning.

Shrubs, defined and characterized in Box 1, are common features of most Caribbean forests, either in mature forests or as part of their succession stages. In fact, the iconic images of Caribbean vegetation used to attract tourism to the region are shrublands (Figs. 2, 3). The number of shrub species in Puerto Rico and the US Virgin Islands is similar to the number of native tree species reported by Little et al. (1974). Francis (2004) found that Puerto Rico has about 540 shrub species and the US Virgin Islands has 527 in only 349 km², and he described 311 temperate

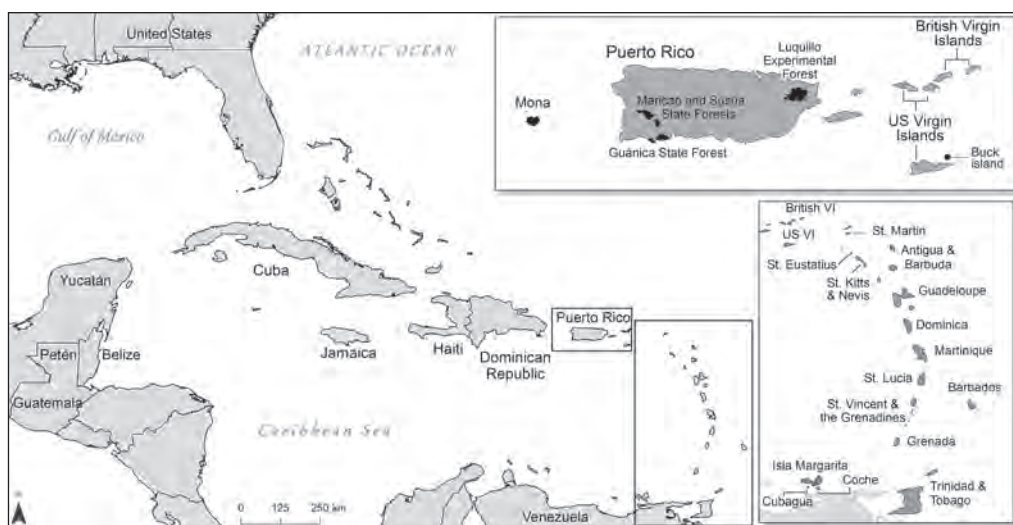


Figure 1. Map of the Caribbean showing the locations of islands and research areas mentioned in the text.

Box 1. Definition and characterization of “shrubs”.

Shrubs are distinguished from trees by their height (usually >0.5 m and <5 m), their production of multiple stems from the base, their lack of a single bole, and their aspect, which is not tree-like (Lawrence 1955). Lawrence (1955:175) pointed out that shrub is “a descriptive term not subject to precise circumscription”, which explains the subtle difference between the formal definition of shrub and the quote of Durant McArthur before the Introduction to this review. Ewel and Bigelow (1996:105) contrasted the tree and shrub habits in terms of the ecological functioning of shrubs as follows: “Evidence suggests that shrubs and trees are best treated as distinct life-forms and not just part of a continuum that is arbitrarily divided on the basis of size. Compared with trees, shrubs may have proportionally fewer thick, structural roots; a greater fraction of their roots concentrated near the surface; persistent, reproductively active shoots close to the ground; greater ability to reproduce vegetatively (by layering or rooting of crushed or broken branches); and the capacity to return to reproductive mode more quickly following crown damage. Excavation of shrubs and treelets on Barro Colorado Island, Panama, for example, revealed that shrubs have a larger ratio of root-surface area to leaf-surface area than saplings of co-occurring trees (Becker and Castillo 1990). Because shrubs invest in flowers and fruits (which can be major nutrient sinks), whereas tree saplings of equal height do not, Becker and Castillo hypothesized that shrubs allocate proportionately more carbon to shallow roots. The fact that shrubs have limited need for the thick, belowground anchors required to keep massive trees upright might also contribute to their concentration of roots near the surface”.

Götmark et al. (2016) explored the adaptive advantages of the shrub habit over the small-tree habit with the same aboveground woody volume. These advantages include a larger basal area, larger photosynthetic tissue in bark and stem, larger vascular cambium area, larger epidermis or bark area, and larger area for sprouting. All these attributes of shrubs contribute to faster growth rate, faster seed production, greater likelihood of survival and growth after a stem dies, and improved survival after disturbances relative to small trees with equal aboveground wood volume.

Box 2. General definitions of common vegetation terminology that includes the presence, and sometimes the dominance, of shrubs. These definitions are consistent with those in Hanson (1962), Art (1993), and McGraw-Hill (2003). Different authors define these terms differently to fit particular vegetation classification schemes.

Bush – shrubs, area covered by shrubs or forest.

Scrub – densely growing, low, often stunted or dwarfed bushes or trees; a track of land covered with a generally thick growth of dwarf or stunted trees and shrubs and a poor soil.

Shrubland – vegetation where shrub forms predominates.

Thicket – vegetation dominated by a dense growth of small trees and shrubs; sometimes used as synonymous with scrub.

Woodland – any land used for the growth of trees and shrubs such as permanent woodland cover and plantings along roadsides and stream banks; vegetation consisting of numerous trees, generally more spread apart than those of a forest, not close enough to form a continuous canopy.



Figure 2. Coastal Caribbean vegetation dominated by dry limestone shrublands on Cayo La Farola in the Dominican Republic. Photograph ©Jerry Bauer.



Figure 3. Montane Caribbean vegetation dominated by elfin shrublands (smooth canopy and wind-sculptured vegetation with scattered slope palm forests) on rain forest climate and volcanic substrate on the Luquillo Mountains in Puerto Rico. Photograph © Ariel E. Lugo.

and tropical shrub species with information on range, ecology, reproduction, growth, management, and benefits. Despite the overlap between the tree and shrub species in both lists, or perhaps because of that reason, it is remarkable that so little scientific attention has been given to shrublands. “Forest” is the dominant vegetation formation of the Caribbean, and forests are the center of scientific attention even if, as we discuss below, almost 25% of the woody vegetation classification units of the Caribbean are shrub-dominated. However, these shrublands cover a smaller area than non-shrublands, and when studied, they are usually portrayed as woodlands, thickets, scrub, or low-stature forests, rather than as shrublands. The most influential and detailed vegetation analysis of Caribbean vegetation, i.e., that of Beard (1949), has no explicit category for shrublands, even though the description of the vegetation and vegetation profiles include shrubs.

The level of endemism of Caribbean seed plants, including shrubs, is 71% (Acevedo Rodríguez and Strong 2012), a factor that contributes to the classification of the Caribbean as a biodiversity hotspot by Myers et al. (2000). Plant endemism is particularly high in serpentine or ultramafic soils where shrublands predominate. Borhidi (1991) reports plant endemism levels of 81% for species and 91.7% for genera on old serpentine areas of Cuba. In contrast, shrublands in the Venezuelan Llanos, located only tens of kilometers from Caribbean islands, have only 1% plant endemism (Huber et al. 2006).

Borhidi (1991) observed a higher frequency of sclerophyllous vegetation in Cuba compared to globally. He also observed (Borhidi 1991:figure 54) that in contrast to tropical and Caribbean tree and shrub species, small leaf sizes prevailed in the Cuban endemic species. For example, 68% of microphyllous, 75% of leptophyllous, and 78% of nanophyllous tree and shrub species were endemic species. Borhidi (1991) concluded that this supported the role of drought as a driver of evolutionary processes in Cuban plants.

Shrubland vegetation is of scientific interest because it possesses adaptations for dealing with extreme conditions of drought, oligotrophy, salinity, inundation, fire, temperature, and wind (discussed below). These conditions are likely to be more prevalent in the Anthropocene Epoch because human activity induces extreme conditions on heavily used landscapes. In some cases, shrub-dominated vegetation is stunted and fails to attain greater stature because of the harsh conditions at the end of an environmental gradient in salinity, wind, or nutrient availability; while in other cases, shrub vegetation is dwarfed, *sensu stricto*, for reasons that are poorly understood, although a certain degree of genetic control is suspected in some cases (Grubb 1977, Specht 1979, Borhidi 1991). We will address this issue later.

Geographic Distribution of Caribbean Shrublands

Past studies have mapped the vegetation of Cuba (Borhidi and Muñiz 1980), including coastal vegetation (Borhidi 1993), where the location of shrub-dominated vegetation throughout the island is given. Similar vegetation or land-cover maps are available for several other islands including Buck Island (Moser et al. 2010); Isla de Margarita, Coche, and Cubagua (Sanz et al. 2011); St Kitts, Nevis, St. Eustatius,

Grenada, and Barbuda (Helmer et al. 2008); Trinidad and Tobago (Helmer et al. 2012); Puerto Rico (Gould et al. 2008, Helmer et al. 2002); and Mona Island (Martinuzzi et al. 2008). There is no consistency in the classification of vegetation or land covers among this diversity of maps, which makes comparisons difficult.

We used recent remote sensing studies of selected Caribbean islands to gain some insight into the area and geographic distribution of shrublands (Table 1). The results in Table 1 are not a definitive statement of the area of shrublands in Caribbean islands because the table is based on remote sensing information from a limited number of sources that used similar criteria to classify land cover. Shrublands are a high proportion of the land and vegetation in low islands like Barbados, which is also highly urbanized. Mona (Martinuzzi et al. 2008) and Buck Island (Moser et al. 2010) are also examples of low islands with a high representation of dry limestone shrublands. Shrublands include vegetation on mountaintops known as elfin woodlands and found in high islands like Grenada, St. Kitts and Nevis, Dominica, St. Vincent and the Grenadines, St. Lucia, and Puerto Rico. Elfin vegetation increases shrubland representation in the island floras. Shrublands in these islands tend to cover a small proportion of the land area. The larger area of flatlands in islands like Hispaniola and Cuba, coupled with the lower rainfall in the western Caribbean, accounts for the more extensive representation of shrublands there, including the large areas of serpentine shrublands of Cuba (Borhidi 1991). For islands represented in Table 1, the average cover of shrublands is 17% of the land area and 27% of the vegetation area.

Table 1. Area (ha), and percent of land and vegetation cover that is shrubland in selected Caribbean islands. All numbers are rounded to the nearest ha and percentage. Numbers in the table were derived by combining those reported land covers that were most likely to be shrublands. Because of differences in land-cover types and mapping criteria, these numbers are general indicators and approximations of the real areas of shrublands in the region. Sources: (1) Helmer et al. 2008, (2) Schill et al 2007, (3) Tolentino and Peña 1998, (4) Gould et al. 2008, (5) Helmer et al. 2002, and (6) Kennaway et al. 2008.

Island(s)	Land area	Vegetation area	Shrubland			Source
			area	% of land area	% of veg. area	
Barbados	43,431	7444	4258	57	10	1
Dominica	75,474	49,556	5546	11	7	2
Dominican Republic	4,818,172	2,868,706	861,395	30	18	2
Dominican Republic	4,222,491	2,156,535	681,017	32	16	3
Grenada	351,907	16,541	2500	15	1	1
Mona Island	5571	5496	4308	78	77	4
Puerto Rico	889,342	780,976	113,667	15	13	4
Puerto Rico	889,438	413,380	19,976	5	2	5
St. Kitts & Nevis	28,049	14,292	1776	12	6	1
St. Lucia	62,637	45,196	1854	4	3	2
St. Vincent & Grenadines	42,462	24,333	4170	17	10	2
US and British Virgin Islands	53,233	34,146	30,264	89	57	6
Total and weighted percent*	6,349,423	3,846,688	1,029,738	27	16	

*Used Gould et al. (2008) for Puerto Rico and Schill et al. (2007) for the Dominican Republic.

Classification of Caribbean Shrublands

The vegetation of the Caribbean has been classified using a variety of criteria, which has resulted in numerous classification schemes with different levels of detail. Lugo et al. (2000) did an overview of Caribbean vegetation with emphasis on the diversity of environmental conditions that lead to a high diversity of plant associations. That review contains a listing of life-zone conditions in the region, the importance of climate and geology to vegetation structure and functioning, and the overarching environmental factors that control vegetation including vegetation response to hurricanes.

The best-known and most comprehensive treatment of Caribbean vegetation is that of Beard (1944, 1949, 1955), who used floristic, physiognomy, habitat, and successional status to describe vegetation. Beard separated primary climax communities from secondary and sub-climax communities and under these he identified 4 climatic and 2 edaphic climax formations. Community types were identified for each of the formations, totaling 13 community types. Beard also identified 19 secondary and sub-climax communities for the Caribbean. Shrub-dominated vegetation was not highlighted as any of the community types in any of the above categories, but was included within the woodlands, thickets, sand dune, and rock pavement vegetation. Hager and Zanoni (1993) used the same approach as Beard in their classification of the vegetation of the Dominican Republic and did not include shrublands as a vegetation type. Asprey and Robbins (1953) applied the Beard classification to the vegetation of Jamaica and added vegetation types not recognized by Beard such as dry limestone scrub forest, thorn scrub, montane sclerophyll, and several secondary communities, some resulting from the effects of human activity (discussed below under novel shrublands).

Borhidi (1991) classified the Cuban vegetation by physiognomic units including shrublands and thickets associated with particular climates, soil types, and geologies (karst serpentine, volcanic), and located throughout the island from coastal to montane locations. Shrublands and thickets were subdivided into 3 groups: (1) evergreen broad-leaved thickets that included montane serpentine and elfin thickets; (2) semi-deciduous broad-leaved thickets including littoral limestone thickets, submontane serpentine, and lowland with fluctuating water table; and (3) extremely xeromorphic (thorny) thickets including on serpentine and in the sub-desert belt. Shrubs were prominent members of thickets as discussed next.

Borhidi (1991) also classified the vegetation of Cuba into physiognomic characteristics including the following 2 where shrubs are predominant: (1) Microphanerophyta consisting of shrubs and small trees 2 to 5 m tall, comprised of 194 species equivalent to 3.2% of the total flora of Cuba; these plants assemble into evergreen shrublands, scrub formations, and semi-desert; and (2) Nanophanerophytes consisting of shrubs between 0.5 and 2.0 m tall, comprised of 1249 species or 18.3% of the flora of Cuba; 76% of this flora is endemic, and these shrubs assemble into woodlands, shrublands, scrub formations, semi-desert, karstic woods, and montane thickets. Some shrublands also contain Microphanerophytes, which are small trees (5 to 10 m tall) represented by 798 species (12.2% of the flora of

Cuba). Borhidi's (1991) monumental synthesis, based in part on previous studies e.g., Borhidi et al. 1979, contains floristic, phytogeographical, phytosociological, taxonomic, ecological, and physiological details about the vegetation of Cuba. He later included a detailed description of coastal vegetation where many shrublands occur (Borhidi 1993).

Consistent with the observations of Borhidi in Cuba, Stoffers (1993) described the coastal vegetation of the West Indies, including both the Greater and Lesser Antilles. The location of shrub-dominated vegetation along the vegetation profiles extending hundreds of meters from the coast and under wet montane conditions is clearly seen in Borhidi et al. (1979), Borhidi (1991, 1993), and Stoffers (1993). Shrub species grow in the non-saline zones of the dunes and usually in the sheltered inland locations. In a synthesis of sand dune vegetation of the Yucatan Peninsula, Espejel (1987) found that sand dune vegetation facing the Caribbean was floristically richer than that of other coastal dunes of the Peninsula facing the Gulf of Mexico. She attributed this difference to the influence of hurricanes and near-by rain forests.

Shrub-dominated vegetation was explicitly included in a Caribbean-wide hierarchical vegetation classification system assembled by Areces Mallea et al. (1999). These authors define shrubs as woody plants between 0.5 m and 5 m tall with several erect, spreading, or prostrate stems; and a bushy appearance. They indicated that in instances where the life form cannot be determined, woody plants greater than 0.5 m in height but less than 5 m in height will be considered shrubs in their study. Dwarf shrubs are multi-stemmed woody plants with a height of <0.5 m due either to genetic or environmental constraints.

In the Areces Mallea et al. (1999) classification, shrublands is a class of vegetation defined by areas dominated by shrubs, generally >0.5 m tall with individuals or clumps not touching to interlocking. Shrub cover in shrublands is generally $>25\%$ while tree cover is generally $<25\%$. In rare cases, shrub cover exceeds the tree, dwarf shrub, herb, and non-vascular plant cover and is less than 25% cover. Areces Mallea et al. (1999) define scrub vegetation as dominated by shrubs, including thickets. Thus, scrub vegetation is also a shrubland and vice versa. Dwarf Shrubland is a class of vegetation dominated by life forms of shrubs and/or trees <0.5 m tall. They generally have $>25\%$ cover of dwarf shrubs and $<25\%$ of trees and shrubs. Herbs and non-vascular plants may be present at any cover value in dwarf shrublands.

We highlight the last 3 categories used by Areces Mallea et al. (1999), which are relevant to an overview of the native shrublands of the Caribbean. Later we address novel shrublands, which Areces Mallea et al. (1999) categorized as Exotic and Altered Vegetation but classified with the same vegetation categories used for native shrublands. The concept of Formation is based on ecological groupings with broadly defined environmental and additional physiognomic factors in common. Alliance is a physiognomically uniform group of Associations sharing one or more diagnostic species usually found in the uppermost stratum of the vegetation. The species criteria include dominant, differential, indicator, or character

species. The term Association refers to a physiognomically uniform group of vegetation stands that share 1 or more diagnostic overstory and understory species. As with Alliances, the species criteria include dominant, differential, indicator, or character species.

The vegetation classification effort of Areces Mallea et al. (1999) led to the identification of 104 Formations (95% of the theoretical total), 187 Alliances (50% of the theoretical total), and 199 Associations (30% of the theoretical total) for the vegetation of the Caribbean. Shrub-dominated vegetation was included at the Order level (Table 2) and comprised 1 shrub-dominated Order, 2 Classes (shrublands or scrub, and dwarf shrublands or dwarf scrub), and 24 Formations. These Formations

Table 2. Classification of the shrublands of the Caribbean according to the comprehensive classification of Areces Mallea et al. (1999).

Order: Shrub dominated

Class III: Shrublands (scrub)

Subclass III.A: Evergreen Shrubland (scrub)

Group III.A.1: Tropical and subtropical broadleaved evergreen shrubland

Subgroup III.A.1.N: Natural/semi natural

8 Formations are listed including terrestrial (lowland, montane, and karst), freshwater wetland, and tidal wetlands.

Group III.A.4.N Microphyllous evergreen shrubland

Subgroup III.A.4.N Natural/semi natural

3 Formations are listed including lowland and montane.

Group III.A.5. Extremely xeromorphic evergreen shrubland

Subgroup III.A.5.N Natural/semi-natural

6 Formations listed including lowland and montane.

Subclass III.B. Deciduous shrubland (scrub)

Group III.B.1. Drought-deciduous shrubland

Subgroup III.B.1.N Natural/semi-natural

1 Formation listed in the lowlands.

Subclass III.C. Mixed evergreen-deciduous shrubland (scrub)

Group III.C.1. Mixed evergreen-deciduous-drought-deciduous shrubland

Subgroup III.C.1.N Natural/semi-natural

3 Formations listed in the lowlands and sub montane elevations, terrestrial and wetland.

Class: IV. Dwarf-shrubland (dwarf scrub)

Subclass: IV.A. Evergreen dwarf-shrubland (dwarf-scrub)

Group: IV.A.2. Extremely xeromorphic evergreen dwarf-shrubland

Subgroup: IV.A.2.N. Natural/semi-natural

1 tidal wetland Formation listed

Subclass: IV.C. Mixed evergreen-deciduous dwarf shrubland (dwarf scrub)

Group: IV.C.1. Mixed evergreen - drought-deciduous dwarf-shrubland

Subgroup: IV.C.1.N. Natural/semi-natural

2 Formations listed.

are associated with dry to extremely dry environments as well as environments periodically flooded by tidal or non-tidal waters. Some shrublands are exposed to dry, flooded, and poor soil-nutrient conditions. Their geographic location varied from coastal tidal wetlands to lowland and montane terrestrial. Those in montane environments have more fertile soils, although saturated, and are exposed to lower temperatures than those in the lowland environments. High wind velocities can occur in both coastal and montane shrublands.

Ecological Aspects of Caribbean Shrublands

The botanical and ecological work in the Caribbean, captured by the classification of Areces Mallea et al. (1999), identifies 3 contrasting environmental settings that lead to shrub dominance in the region: saline, climatically dry, and climatically wet conditions. All Caribbean shrublands under these settings face periodic hurricanes and steady winds, and shrublands under each particular setting face additional environmental challenges. For example,

- Saline shrublands can occur under salinity gradients that lead to hypersaline conditions or face oligotrophy, usually phosphorus and nitrogen limitations. Substrate varies from deep peats to rocky, and inundation levels vary from diurnal to chronic.
- Climatically dry shrublands occur along gradients of decreasing water, soil, and/or nutrient availability. When the substrate is limestone, plant stoichiometry is affected by calcium concentrations in soils and when the substrate is serpentine, plant stoichiometry is affected by high magnesium-to-calcium ratios and heavy metal concentrations.
- Climatically wet shrublands occur under chronic soil saturation, and some occur in areas with rocky substrate where elements like phosphorus can be limiting to plant growth. Plant stoichiometry is affected by heavy metal and magnesium concentrations on serpentine soils.

High diversity of shrubland communities in a small area

Moser et al. (2010) applied the vegetation classification scheme of Areces Mallea et al. (1999) to 70.4-ha Buck Island, St. Croix, US Virgin Islands. There, they found about half of the vegetation dominated by shrubs and distributed in 8 shrubland classes, plus 7 coastal sub-formations where shrubs were also prominent. This work resulted in 4 new Alliances and 11 new Associations added to the Caribbean-wide classification of Areces Mallea et al. (1999). The high number of species assemblages in a small land area is typical of Caribbean vegetation. This richness is why woody species–area curves are initially very steep and saturate at 0.2 ha for both dry and wet forests (Lugo et al. 2002) and why Molina Colón et al. (2011) found a high floristic dissimilarity among shrub species assemblages located close to each other. Fisher Meerow and Judd (1989) also found low similarity in the species composition of communities adjacent to each other on the southwest coast of Dominican Republic. Similarly, Ramjohn et al. (2012) found that despite past deforestation and fragmentation, the diversity of shrub assemblages within

fragments and their dissimilarity among fragments resulted in the conservation of species at the landscape level.

The botanists and ecologists that described and classified the vegetation of the Caribbean have shown that sharp environmental gradients result in many species assemblages responding to the particular conditions of the geography where they stand. However, we have not been effective in identifying the conditions that prevail along those gradients; thus we are unable to partition the relative contribution of different environmental gradients that converge simultaneously on a given geographic location. Advances in the right direction are the recent works of Bruijnzeel et al. (2010) on tropical montane cloud forests (including the Caribbean) and González et al. (2013) on the ecological gradients of the Luquillo Mountains in Puerto Rico. These works expand the scope of analysis of forest types along landscape-level gradients and uncover new complexities about the response of organisms, including microbes, to their environment.

It appears that shrub species can respond individually to a particular set of conditions to which they are adapted. Heartsill Scalley (2012) illustrated this along the elevational gradient of the Luquillo Mountains in Puerto Rico. Individual species responding individually to converging gradients along a landscape form different species assemblages across the landscape, leading to high plant diversity. Shrublands appear where the cost to survival cannot be met with a tree habit but can be dealt with in the shrub habit. Our heuristic model at the end of the manuscript uses the level of disturbance or of limiting conditions as an index of stress for explaining shrub-dominated vegetation and the changes of species that occur along environmental gradients.

Shrublands on dry and moist climates (500 to <2000 mm annual rainfall)

Del Risco Rodríguez (1999) contains observations of the ecological attributes of Cuba's shrublands. The following narratives, using their vegetation terminology, typify the physiognomy of non-flooded shrublands in the dry to moist climates of the Caribbean.

- Dry thorny shrub vegetation is characterized by microphyllous, sclerophyllous, thorny bushes and trees, which are adaptations that diminish the barren effect of the dry variation of the tropical climate, with 2 dry seasons that comprise up to 7 or 8 months of each year and a total of 750–800 mm annual rainfall. Evergreen shrubland (scrub) is an example community under this type of vegetation. There are no characteristic deciduous species in these shrublands. They have an arboreous stratum below 2–4 m height with emerging small trees and palms 5–6-m tall. Cylindrical and leaf-bearing cacti are abundant but not dominant. They grow on rock of limestone terraces and lapiaz coasts.
- Semidesertic shrublands are open bush or thickets 4–5 m tall that are formed by small trees and mostly thorny bushes, with large representation of cactaceae, that are mainly dominant in the bush stratum. They are conditioned by the barren, hot, semidesertic climate, with 9 to 10 dry months per year, a mean annual temperature of 27–28 °C, and annual rainfall of 500 mm on rocky or sandy soils.

- Cuabales are low subperennial communities (i.e., most species are evergreen, some deciduous), xerophytic, sclerophyllous, microphyllous, and thorny. They grow on skeletal soils with low capacity to retain moisture., and in areas that experience 3 to 6 months of dry season and 1000–1800 mm annual rainfall. They have a dense stratum 3–6 m tall, small trees and bushes, with emerging small trees and palm trees 5–8 m tall with an 80–100% cover. These cuabales contain epiphytes and lianas with 50–70% deciduous elements and many endemic species.
- Sea-grape shrublands are evergreen-dominated by *Coccoloba uvifera* (L.) L. (Sea Grape). Sea Grape can grow as a shrub or small tree (Little and Wadsworth 1964). Some deciduous species form a thin belt that grows on the dunes of sandy or rocky coastlines. Plants are generally 4–5 m tall, but can be 10 m in height, with a poor composition of species. The bush and herbaceous strata are also species poor, and there are some palm trees and lianas.

The Cuban vegetation contains an extensive shrubland area on serpentine soils that cover ~5000 km² (Brooks 1987). Cuba is second to New Caledonia in the global diversity of endemic plant taxa with 854 taxa (Anacker 2011). Leaf size in limestone and serpentine shrublands decreases linearly (becoming more xeromorphic) with decreasing rainfall, but serpentine vegetation had smaller leaves than limestone vegetation at all levels of rainfall (Borhidi 1991). In montane shrublands, leaf size decreased linearly with elevation, decreasing temperature, and increasing rainfall, and the effect was greater in serpentine vegetation than on granodiorite substrates (Borhidi 1991). Similarly, a thorn-index (based on frequency of taxa with thorns) increased nonlinearly with decreasing rainfall, but serpentine vegetation had a higher index at all rainfalls than limestone vegetation (Borhidi 1991).

Jamaica has large areas of vegetation growing on limestone substrates and limestone-derived soils (Asprey and Robbins 1953). Asprey and Robbins describe this vegetation in detail, including its species composition and presence of shrubs and small trees in those communities growing under moisture stress and exhibiting shrubby and/or scrubby and thorny habits. This vegetation predominates in dry coastal limestone hills, dry southern alluvial coastal plains, and dry southern slopes.

Xerophytic shrublands dominated (68% cover) and contained the highest floristic richness of the landscape of the Venezuelan Araya Peninsula at Sucre (Cumana Campos 1999). The vegetation did not exceed 5 m in height and contained a diverse number of life-forms including columnar cacti, trees, shrubs, herbs, prostrate climbers (annual and perennial; herbaceous or woody), thorny shrubs, and epiphytes-hemi parasites. Cumana Campos (1999) listed some of the adaptations of the xerophytic shrublands to dry and abrasive trade winds and low precipitation including: deep tap roots or an intricate network of surface roots that quickly intercepts low rainfall, leaves with few stomata (sometimes cryptic) and a thick cuticle that reduces water loss, and some leaves that store water or are modified into spines. Non-succulent plants can be deciduous or reduce leaf exposure by superimposing leaflets at mid-day.

In the Puerto Rico archipelago, shrublands predominate in the limestone subtropical dry forest life zone that represent the common geology and climate combination of most of the smaller islands as well as in the southern coastal zone of the main island. For example, there are more shrub species than tree species in the vegetation of Mona Island (Table 3). Brandeis et al. (2012) found the vegetation of Mona to have a

Table 3. Plant habits by Family in Mona Island, Puerto Rico (Medina et al. 2017a). [Table continued on following page].

Family	Species	Habit
Anacardiaceae	<i>Comocladia dodonaea</i> (L.) Urb.	Shrub-tree
	<i>Metopium toxiferum</i> (L.) Krug & Urb.	Tree
Apocynaceae	<i>Plumeria obtusa</i> L.	Shrub
Arecaceae	<i>Thrinax morrisii</i> H. Wendl	Shrub
Bignoniaceae	<i>Tabebuia heterophylla</i> (DC.) Britton	Shrub-tree
Boraginaceae	<i>Bourreria succulenta</i> Jacq.	Tree
	<i>Varronia bullata</i> L.	Shrub
Burseraceae	<i>Bursera simaruba</i> (L.) Sarg.	Tree
Capparaceae	<i>Quadrella cynophallophora</i> (L.) Hutch.	Shrub-tree
Canellaceae	<i>Canella winterana</i> (L.) Gaertn.	Shrub-tree
Celastraceae	<i>Crossopetalum rhacoma</i> Cranz	Shrub
Erythroxylaceae	<i>Erythroxylum areolatum</i> L. (Swamp-redwood)	Shrub-tree
Euphorbiaceae	<i>Croton betulinus</i> Vahl (Beechleaf Croton)	Shrub
	<i>Croton discolor</i> Willd.	Shrub
	<i>Croton glabellus</i> L.	Shrub
	<i>Euphorbia petiolaris</i> Sims	Tree
	<i>Gymnanthes lucida</i> Sw.	Shrub-tree
Fabaceae	<i>Chamaecrista nictitans</i> (L.) Moench	Shrub
Malpighiaceae	<i>Byrsonima lucida</i> (Mill.) DC.	Shrub-tree
	<i>Malpighia setosa</i> Spreng.	Shrub
Malvaceae	<i>Melochia tomentosa</i> L.	Shrub
	<i>Corchorus hirsutus</i> L.	Shrub
	<i>Helicteres jamaicensis</i> Jacq.	Shrub-tree
Meliaceae	<i>Swietenia mahagoni</i> (L.) Jacq.	Tree
Moraceae	<i>Ficus citrifolia</i> Mill.	Shrub-tree
Myrtaceae	<i>Calyptanthus pallens</i> Griseb.	Shrub
	<i>Eugenia foetida</i> Pers.	Shrub
	<i>Eugenia monticola</i> (Sw.) DC.	Shrub
	<i>Myrcianthes fragrans</i> (Sw.) McVaugh	Shrub-tree
Nyctaginaceae	<i>Pisonia albida</i> (Heimerl) Britton ex. Standl.	Shrub-tree
Phyllanthaceae	<i>Phyllanthus epiphyllanthus</i> L.	Shrub

mean canopy height of 4.6 m, with the tallest trees averaging 6.6 m. This vegetation had a mean basal area of only 8.7 m²/ha, a mean aboveground biomass of 28.8 Mg/ha, and a mean stem density of 3408 stems/ha. Shrubs were present on all vegetation strata but dominated at <1.8 m height. An inventory of 3.502 ha yielded 104 plant species, of which 26 were shrub species on 0.871 ha and 43 were tree species on 1.742 ha. Forb and herbaceous plant species were also recorded.

In the main island, Weaver and Chinae (2003) inventoried 3.4 ha of secondary vegetation in southwest Puerto Rico and found 103 dicotyledonous tree species and an additional 58 tree species outside their plots. The greatest number of stems belonged to *Pilosocereus royenii* (L.) Byles & G.D. Rowley (Sebucán), a cactus, while *Leucaena leucocephala* (Lam.) de Wit (Zarcilla) was the most common shrub. Ten species accounted for 60% of the stems. Shrubs covered 50% of the 110-ha property. Twenty introduced species accounted for about 20% of the stems, and an ordination of the vegetation showed that land-use history was the most important factor explaining the distribution of species. Slope and distance to drainages were the next most-important factors in determining species distributions.

An analysis of floristic composition patterns for limestone vegetation from 3 Caribbean Islands (Hispaniola, Mona, and Puerto Rico) included vegetation from very dry to wet climates and ridge-top, slopes, and plateaus topographic location (Trejo Torres and Ackerman 2002). The various analysis techniques that they used, including parsimony analysis of species assemblages, yielded similar ordination results. Species assemblages were separated by climate (humid and dry) and then by topographic location. Dry species assemblages had more affinity among themselves regardless of island location than when compared to moist locations within island, meaning that climate is better at defining floristic affinities than geographic location.

Table 3, continued.

Family	Species	Habit
Polygonaceae	<i>Coccoloba diversifolia</i> Jacq.	Tree
	<i>Coccoloba microstachya</i> Willd.	Shrub
	<i>Coccoloba uvifera</i> (L.) L.	Shrub–tree
Rhamnaceae	<i>Krugiodendron ferreum</i> (Vahl) Urb.	Shrub–tree
	<i>Reynosia uncinata</i> Urb. (Sloe)	Shrub
	<i>Ziziphus taylori</i> (Britton) M.C. Johnst.	Shrub–tree
Rubiaceae	<i>Stenostomum acutatum</i> DC.	Shrub
	<i>Erithalis fruticosa</i> L. (Black Torch)	Shrub
	<i>Exostema caribaeum</i> (Jacq.) Roem. & Schult	Shrub
	<i>Guettarda elliptica</i> Sw.	Shrub
	<i>Randia aculeata</i> L.	Shrub
Rutaceae	<i>Amyris elemifera</i> L.	Shrub–tree
Sapindaceae	<i>Hypelate trifoliata</i> Sw.	Shrub–tree
Sapotaceae	<i>Sideroxylon obovatum</i> Lam.	Shrub–tree
	<i>Sideroxylon salicifolium</i> (L.) Lam.	Shrub–tree
Verbenaceae	<i>Lantana involucrata</i>	Shrub

The extreme dry communities in Mona and hilltops in Puerto Rico that stood out in the ordinations (Trejo Torres and Ackerman 2002:figure 7) were shrubs—which they termed open, low forest to scrub—and semi-deciduous vegetation.

One of the most studied limestone dry forests in Puerto Rico is the Guánica Forest Biosphere Reserve with vegetation gradients associated with elevation and soil depth that vary from evergreen and semi-deciduous woodlands to shrublands near the littoral (Lugo et al. 1978) and dwarfed vegetation over rocky substrates (Medina et al. 2012). The dwarf vegetation had stunted trees such as *Pisonia albida* (Heimerl) Britton ex Standl. (Corcho Blanco), *Jacquinia arborea* Vahl (Barbasco; identified as *J. armillaris* in the paper), *Conocarpus erectus* L. (Mangle Botón), *Ficus laevigata* Vahl (Jagüey Blanco), and *Tabebuia heterophylla* (DC.) Britton (Roble Blanco), as well as genetically determined shrubs such as *Erithalis fruticosa* L. (Jayajabico), *Reynosa uncinata* Urb. (Cascarrolla), *Croton rigidus* (Muell. Arg.) Britton (Adormidera), *Antirhea acutata* (DC.) Urban (Quina), *Coccoloba microstachya* Wild (Uverillo), and *Strumpfia maritima* Jacq. Enum (Lirio).

Martinuzzi et al. (2013) applied light detection and ranging (LiDAR) technology and Landsat images to the study of vegetation cover in the Guánica Forest Biosphere Reserve and could separate vegetation types and successional stages in developing a vegetation map at 30-m resolution. The technique allowed the differentiation of scrub, dwarf, and *Prosopis juliflora* (Sw.) DC. (Mesquite; identified as *P. pallida* in the paper) shrublands and robust statistical descriptions of the stature of vegetation over the landscape.

Shrublands on moist to wet climate and serpentine soils

Shrublands on serpentine soil also occur in Puerto Rico's moist and wet life zones in the Susua (Álvarez 1983) and Maricao (Medina et al. 1994, Rivera et al. 1983, Tschirley et al. 1970) Commonwealth Forests. The climate at Susua is moist and at Maricao is moist and wet. The leaves at both locations are sclerophyllous and reflect phosphorus limitation (Medina et al. 1994). The vegetation structure is complex with low basal area and high density of woody plants that includes trees of up to 15 m tall and shrub layers as well as shrub-dominated canopies <5 m tall (Álvarez 1983, Rivera et al. 1983, Tschirley et al. 1970). Álvarez (1983) found a diverse number of life forms in these forests, including bromeliads growing on the ground. These serpentine shrublands are notable for the high species density, including high Shannon diversity indices. Tschirley et al. (1970) found that the species area curve did not saturate at 0.92 ha with 105 woody species with a diameter at breast height ≥ 2.5 cm. This richness was 1.2 times higher than in volcanic soils with similar rainfall and elevation. The shrublands had high levels of loose litter, root biomass, and soil organic-matter accumulation in the top 20 cm of the soil profile (Álvarez 1983, Rivera et al. 1983).

Cedeño Maldonado (1997) surveyed 2.89 km² of serpentine forests in the Maricao river watershed between 460 and 900 m elevation in wet and lower montane wet-forest life zones. He found 178 tree and 88 shrub species, with 10 families of shrubs represented by more than 2 species. The most common shrub families were

Rubiaceae (15 species), Asteraceae (10 species), Polypodiaceae (10 species), and Piperaceae (7 species). At 700 m elevation, Caminero Rodríguez (1991) conducted a quantitative analysis of twelve 10 m x 10 m plots, and from his data we estimated the Holdridge vegetation complexity index (CI = product of stem density, number of species, basal area, and tree height expressed in 0.1 ha and divided by 1000). Mean vegetation height varied from 2.7 m to 7.1 m and was linearly correlated with the complexity index (CI = 52.3[tree height in m] - 118; $r^2 = 0.8$; $P < 0.01$). Those shrublands accumulated a high concentration of soil organic matter (varying from 5.0% to 24.5%) at 0–13 cm depth.

Shrublands on wet and rain environments (>2000 mm annual rainfall)

Shrublands in the Caribbean also occur on wet to rainforest environments at high elevations, and their physiognomy is similar to shrublands in dry environments. An example is the elfin woodland vegetation, which has attracted scientific attention for over a century (Schimper 1903) because it is a vegetation type that occurs globally in all tropical continents. In the Caribbean, the literature is also abundant with a rich diversity of accounts of species composition and woody plant stature, and multiple interpretations of the causes of stunting and dwarfing (Howard 1968). Howard (1970:B-325) observed that “each descriptive phrase has an element of truth, but the variety of terms indicates the lack of understanding and the inability to ascribe a dominant causal factor”.

Howard (1968) reviewed the literature of Caribbean elfin woodlands and described the peculiarities of dwarf shrubby vegetation in the Luquillo Mountains of Puerto Rico. These shrublands include both stunted and dwarfed shrubs with a mixed composition of small trees and shrubs, depending on aspect and exposure to wind. The epiphytic flora is impressive in terms of both the diversity and number of bryophytes and vascular plants and both woody and herbaceous twiners. Three of 12 species of woody plants present accounted for 81% of the crown cover, with the first 2 species accounting for 70%: *Tabebuia rigida* Urb (Roble de Sierra), *Ocotea spathulata* Mez, Jahrb (Nemosé), and *Calypttranthes krugii* Kiaersk (Limoncillo). Elfin woodlands also occur in other islands such as in Jamaica, under lower rainfall conditions, but still retain the shrubland physiognomy and abundance of shrubs observed in the wetter conditions of Puerto Rico (Asprey and Robbins 1953).

Shrublands on saline estuarine environments

Stunted and shrub form (sensu Tomlinson 2016) *R. mangle* grow throughout the dry coastal areas of Caribbean islands as described by Beard (1944), Borhidi (1991), and nearly all vegetation descriptions in the region, e.g., Asprey and Robbins 1953) and Stoffers (1993). *Avicennia germinans* (L.) L. (Black Mangrove; Feller et al. 2015) and *Laguncularia racemosa* (L.) C.F. Gaertn (White Mangrove; Moser et al. 2010) also exhibit stunting in response to increased salinity or nutrient limitation. The stature of these mangrove shrublands responds to salinity (Cintrón et al. 1978) and nutritional gradients (Feller et al. 2015). Under the extreme oligotrophy characteristic of limestone coastal environments around the Yucatan Peninsula and the everglades, mangrove dwarfing occurs (Lugo and Snedaker 1974,

Reef et al. 2010). These mangroves grow in oligotrophic waters and limestone substrates devoid of sediment and nutrient inputs from terrestrial sources. Below, we discuss ecophysiological responses to oligotrophic peats of dwarfed mangroves on a moist climate and the effects of hurricanes on these mangroves.

Novel shrublands

Humans can induce environmental conditions that lead to changes in vegetation physiognomy towards shrubby habits. These anthropogenic disturbances have increased in importance in the Anthropocene Epoch. For example, increasing frequency of anthropogenic fires favor the formation of shrublands. Similarly, deforestation followed by extensive or intensive agricultural activity changes soil conditions through erosion and lead to oligotrophy, soil compaction, and shrubby vegetation (Molina Colón et al. 2011). In the Bahamas, anthropogenic disturbances to vegetation have also favored the establishment of shrublands (Wunderle et al. 2007). In these islands, shrub succession is desired for supporting the habitat of the endangered *Setophaga kirtlandii* (Baird) (Kirtland Warbler), and scientists have devised management techniques to favor 2 shrub species (*Erithalis fruticosa* L. [Black Torch] and *Lantana involucrata* L. [Wild Sage]) on whose fruits the warblers feed (Fleming et al. 2013, Larkin et al. 2012). The shrub-inducing management techniques involve manipulating levels of disturbance using *Capra aegagrus hircus* (L.) (Domestic Goat) and machines with the purpose of favoring open habitats that benefit the target shrub species. Students of Caribbean vegetation classified many of these shrublands as disclimax vegetation (e.g., Asprey and Robbins 1953, Roth 1999). Asprey and Robbins (1953) list many of the species that have naturalized in Jamaica and now form “ruinate” secondary communities recognized as vegetation that develops in marginal and abandoned lands. Today, because of the introduction of species that colonize these degraded lands, we recognize that the species composition of resulting shrublands is different from native shrublands. They are thus classified as novel because the species assemblages are new to these landscapes (Lugo and Helmer 2004, Molina Colón et al. 2011).

Areces Mallea et al. (1999) listed a shrubland alliance in the Caribbean involving introduced species and altered vegetation: *Piper aduncum* L. (Bamboo Piper), *Lantana camara* L. (Cariaquillo), and *Psidium guajava* L. (Guayaba). Of these 3 plants, *P. guajava* is the only non-native species in the Caribbean. Other examples of Caribbean novel shrublands dominated by introduced woody shrub species include those of *Leucaena leucocephala* (Lam.) de Wit (White Leadtree; dry soil condition) and *Mimosa pigra* L. (Black Mimosa; moist and wet soil conditions). In Puerto Rico, these introduced shrub species can colonize highly degraded lands and in the short-term establish monocultures that slowly thin and diversify with other native and introduced woody species (Francis 2004). Through the succession process, both soil structure and fertility and conditions for the growth of native species improve. However, in all observed examples, the novel species composition remains because introduced species regenerate as well as native ones, particularly after disturbances.

In the Dominican Republic, Roth (1999) found that century-level anthropogenic activities so modified dry forestlands that native mature dry forest communities were substituted by thorn scrub of low stature where 70% of the stems belong to just 1 native (*Acacia macracantha* Humb. & Bonpl. ex Willd [Tamarindo Silvestre]) and 2 introduced (*Haematoxylon campechianum* L. [Campeche] and *Prosopis juliflora* (Sw.) DC.) species. Over time, the stands diversify somewhat and develop similar structure to native stands, but the original species composition is not re-established as the 3 shrubby species maintain dominance. In Cuba, the introduced shrub *Calotropis procera* (Aiton) W.T. Aiton (Algodon de Seda) thrives in slopes with degraded soils due to intensive grazing. Wezel (2006) found that the shrub mitigates the erosion and soil degradation caused by grazing. Quantitative and large-scale sampling of vegetation in St. Johns, US Virgin Islands, revealed that scrub vegetation is associated with rocky soils with low concentrations of nutrients and some compaction, and that introduced species dominate sites with a history of human land use and degradation (Oswalt et al. 2006).

Follow-up measurements of vegetation studied 20–60 yr previous in the island of St. Eustatius where most of the lowland vegetation is of low stature (<6 m), found an increase in canopy height and floristic richness (Van Andel et al. 2016). Some of these changes were associated with the establishment of introduced species and protection from fire on deciduous woodlands and open shrublands that still had free-roaming cattle. This colonization was restricted to open shrubby vegetation and did not extend into closed or partially closed vegetation, much as found by Molina Colón and Lugo (2006) in Puerto Rico and Atkinson and Marín Spiotta (2015) in the US Virgin Islands. In all cases, land-use legacies after abandonment of agriculture provide the conditions for this development of novel vegetation types.

Ecophysiological Characteristics of Caribbean Shrubs and Shrublands

The stressful environments under which shrublands dominate, select for similar ecophysiological and physiognomic plant responses. For example, they can occur in extremely dry or extremely wet climates, and grow in saturated soil conditions, extremely dry soil conditions, or in the absence of soil as on rocky substrates. Saturated soils can be oligotrophic or eutrophic and inundated or not by fresh or salty waters. Also, shrublands can grow in areas exposed to high velocity winds and periodic fires. These contrasting environmental conditions, or “syndrome of challenges” (Anacker 2011), all lead to water and nutrient limitations, which in turn select for similar ecophysiological responses such as evergreen sclerophylly (Specht 1979). Because of the contrasting environmental challenges that lead to shrub dominance, the shrub species composition is different for different types of shrublands, while their ecophysiological responses remain similar. Leaf size differs—larger leaves in wet shrublands, smaller or deciduous leaves in dry shrublands, but the common factor is sclerophylly (high leaf mass to leaf area ratio).

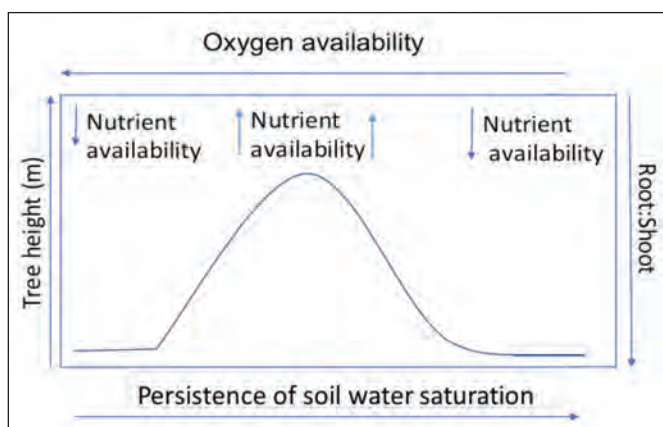
Plant traits that govern carbon and nutrient conservation dominate where edaphic conditions such as nutrients, water, oxygen, pH, and salinity limit growth (De Deyn et al. 2008). Community convergence of plant functional forms is basically

determined by the persistence of abiotic conditions, such as soil water saturation, degree of soil aeration, and salinity, that can affect plant functioning independently or as concurrent factors. These factors affect photosynthetic performance, soil biological activity, nutrient availability, and assimilate distribution such as is reflected in root-to-shoot ratios (Titlyanova et al. 1999). In Figure 4, we present how some of these abiotic factors affect tree height and root-to-shoot ratios. In the drier sites, there is low nutrient availability due to low levels of water availability, affecting assimilate production and distribution, not only related to photosynthesis but also to low levels of bacterial and fungal activity. In these systems, microbial structure, diversity, activity, and biomineralization processes (discussed below) occur during pulses of water availability and are also determined by the plant species specific substrate, such in the dry dwarf forest located in the semi-arid region of Puerto Rico (Rivera 2017, Rivera Rivera et al. 2018). In saturated sites, there is low nutrient availability, as oxygen is limiting to soil bacterial and fungal activity, therefore affecting photosynthetic performance of the plants. In this case, soil biological activity occurs in the oxic soil zone established between high and low tide, and/or during dry and wet seasons (Das et al. 2016). Increased anoxic conditions with soil depth also reduce soil microbial and enzymatic activity due to unfavorable conditions for microorganisms to carry out bio-mineralization processes (Das et al. 2016). Thus, soil biological activity has a strong effect on the productivity and biomass allocation of plants.

Sclerophylly

Schimper (1903) recognized the common features of xerophytic vegetation, one of which was sclerophylly, and the physiological implications of those adaptations to drought, regardless of the causes of drought, i.e., edaphic or climatic. Sclerophylly is a complex leaf response to environmental conditions measured by mechanical characteristics such as hardness, toughness, and stiffness, which are parameters that are difficult to characterize and quantify. Medina et al. (1990) showed that sclerophylly was not necessarily an adaptation to drought, but to low levels of nutrient availability. Compared to lower montane forests in Puerto Rico, leaves of elfin forest shrubs have smaller areas and are more sclerophyllous (larger mass/area

Figure 4. Schematic diagram of the factors and gradients that contribute to tree height and root-to-shoot ratios in plants. Shrubs occupy the space with low height and high root-to-shoot ratios in the diagram.



ratio) (Medina et al. 1981). Therefore, their concentrations of phosphorus and nitrogen by unit leaf area are also much larger. In these habitats, soil saturation leading to hypoxia increases energy expenditure for active nutrient uptake and transport. Read et al. (2006) confirmed these findings by comparing the sclerophylly of plants growing in areas of low levels of nutrient vs. those growing in areas of low levels of rainfall (drought) in New Caledonia. Leaves from the nutrient-limited maquis were more scleromorphic than the ones in dry forest and had similar concentrations of nitrogen and phosphorus per unit leaf area. Read et al. (2006) suggested that sclerophylly was a complex response of plants to stress involving both an adaptive mechanical response to stress and non-adaptive mechanical consequences that also provide protection to environmental conditions. They also suggested that leaf thickness allows for efficient packing of biomass and reduces branching costs in sunny but stressful environments.

Stoichiometry

Adult leaf elemental composition of shrublands from contrasting geological substrates and rainfall reveals the interaction of soil environment and plant physiological properties (Table 4). The first emerging pattern is the higher concentrations of organic matter-forming elements nitrogen and phosphorus in shrublands from drier areas. Those shrublands are strongly seasonal in their phenology and have smaller leaves. In addition, they grow on substrates where organic matter decomposes rapidly during humid periods (below). The data indicates that those plants are not phosphorus- or nitrogen-limited. The second pattern is represented by the higher concentrations of potassium in dry shrublands. Potassium is an essential element for enzyme activation, which also plays an important role in the cellular osmotic relations. In environments with abundant rainfall, potassium can be leached from both soils and leaves. Finally, calcium concentration is much higher in shrublands on calcareous substrates, certainly due to the higher availability of this ion in the soil solution.

In predominantly calcareous substrates, magnesium concentrations are similar to those of shrublands on serpentine substrates, but the Ca-to-Mg ratio is markedly higher in the former (Table 4). Shrublands on serpentine substrates are remarkably

Table 4. Stoichiometric parameters of adult leaves of shrubland species growing under different climates and geologies. Element concentrations (mmol/kg dry mass) are means of the number of indicated species. Data are from Medina et al. (1981, 1994, 2017b). All sites are located in Puerto Rico. # = number of species sampled.

Site	Shrubland	#	Elements						
			P	N	K	Ca	Mg	K/Ca	Ca/Mg
Pico del Este	Wet volcanic	7	20	707	130	167	65	0.8	2.5
Maricao	Wet serpentine	29	14	828	190	207	181	0.9	1.1
Susua	Moist serpentine	28	18	799	146	215	152	0.7	1.4
Mona Island	Dry limestone dolomite	47	31	1039	258	472	157	0.5	3.0
Guánica Upland	Dry limestone	13	25	1361	315	409	162	0.8	2.5
Guánica Dwarf	Dry limestone	26	21	991	212	340	138	0.6	2.5

capable of compensating for the unfavorable Ca-to-Mg ratios in the soil through preferential absorption of calcium. In Susua Commonwealth Forest, the Ca-to-Mg ratio increased from 0.08 in the soil to 2.1 in leaves, and in Maricao, from 0.16 in the soil to 1.6 in leaves (Medina et al. 1994). Shrublands on wet volcanic soils have a Ca-to-Mg ratio similar to those in dry limestone in spite of concentration differences. All shrublands maintain similar K-to-Ca ratios in spite of differences in the concentrations of calcium and potassium.

Root-to-shoot ratios

Larger root-to-shoot ratios make plants more tolerant to drought, more competitive in nutrient acquisition in nutrient-poor environments, more resilient to fires, and more tolerant to freezing aboveground temperatures. Among the factors that influence the root-to-shoot ratio are species characteristics, site moisture and nutrient availability, regeneration strategies, and competition for light. The root-to-shoot ratio varies with vegetation types. The ratio is negatively correlated with mean annual precipitation and positively linked with stand age (Waring and Powers 2017). Mokany et al. (2006) found that the root-to-shoot ratio of shrublands and grasslands along a precipitation gradient was an order of magnitude higher than for forests and woodlands. Shrublands and grasslands exhibited lower root-to-shoot ratios as air temperatures increased. For forests, the median root-to-shoot ratio tended to be higher in forests with low levels of shoot biomass. Shrublands had a high median root-to-shoot ratio (1.84), most likely related to a wide range of factors including their common occurrence in drier environments and their ability to resprout from rootstocks following disturbances. On sandy soils (Tropaquod soil) of the Amazonian forest of Venezuela, Medina and Cuevas (1989) found that the root-to-shoot ratio increased along a soil fertility gradient from 0.5–0.7 in tall Caatinga forest to 7.0 in sclerophyllous woodlands with a mixture of small trees and shrubs.

Under coastal conditions, increased pore-water salinity induces root branching due to auxin effects, which affects lateral root development and direction of root growth (Bernstein and Kafkaki 2002). This effect is accompanied by a reduction of aboveground biomass in relation to belowground biomass. Adame et al. (2013) used allometric equations for both below- and aboveground biomass estimations of dwarf *R. mangle* in the Mexican Caribbean Petén and found 3 times more root biomass than in tall *R. mangle* areas, with a root-to-shoot ratio of 2.79 ± 0.08 in the dwarf mangroves versus 0.96 ± 0.05 in the tall ones. Kauffman et al. (2014) found the same difference in the mangroves of the Montecristi Province in Northwest Dominican Republic although root-to-shoot ratios were lower, 1.41 ± 0.4 for dwarf mangroves versus 0.38 ± 0.03 for tall mangroves.

Bio mineralization

In drier sites, there is low availability of nutrients due to low levels of water availability, affecting assimilate production and distribution, not only related to photosynthesis but also to a low degree of bacterial and fungal activity. Pulses of water availability in dry systems favor microbial structure, diversity, and activity, and bio-mineralization processes related to enzymatic activity. The effects of these

pulses on microbial and enzyme dynamics are also influenced by plant species-specific substrate, such as in the dry dwarf shrubland located in the semi-arid region of Puerto Rico (Rivera 2017, Rivera Rivera et al. 2018). Barberena Arias and Cuevas (2018), studying the same location and tree species, found that in mono-specific shrub clumps, arthropod abundance in litter did not differ among plant species. However, arthropod species richness and trophic composition was different. Detritivore arthropod species composition co-varied with physicochemical characteristics of mature green leaves of plants, affirming that, even under extreme stressful conditions such as those experienced by the dwarf forest in a semi-arid region, plant idiosyncratic characteristics affect the structure of litter/humus arthropods up to the first consumer level as well as the microbial and enzymatic dynamics of the system.

Dwarfing

Differentiating between dwarfed vs. stunted shrublands is difficult at best, and while recognized as a reality, the distinction is not commonly made. Dwarfism is genetic, while stunting is growth inhibition. Isolating the causes of the reduction in size of vegetation requires ecophysiological and genetic research, both of which are generally not available. We thus caution that while we use the term “dwarf” to describe vegetation, as do others (e.g., Areces Mallea et al. 1999, Borhidi 1991), we are not aware that the genetic causes have been identified conclusively, and in fact the dwarfing could be a result of growth inhibition. This is the case of “dwarf” mangroves. We have observed that dwarfed *R. mangle* have larger leaf area (28 to 35 cm²) than stunted ones (Medina et al. 2010). Their leaf length (mean of 10.9 cm) is larger than expected from mangroves growing at the same soil salinity (8.5 cm; Lugo et al. 1981). If a larger leaf size is maintained when reduction is expected due to salinity or nutrient stress, and if that parameter was shown to be genetically determined, one might then conclude that these mangroves are dwarfed *sensu stricto*. But such information is not available; vegetation ecologists rely on the size and aspect of individuals for the determination of dwarfness. However, such a criterion for maintaining leaf size did not apply in dwarf dry shrublands on karstic rocky surface with a small amount of soil (Medina et al. 2012). Stunted growth of true trees is probably related more to drought, toxic soils (salinity in coastal areas, heavy metals or Ca/Mg imbalance in serpentine), low air temperature, and/or prevalent heavy winds.

Dwarfism seems to be related to “nutrient stress” generated either by intrinsic soil deficiency or by reduced uptake caused by metabolic inhibition due to hypoxic soils. It also may be genetically related, although this has not been shown. Nevling (1969) found that the size and number of chromosomes in elfin shrub species of Pico del Oeste in Puerto Rico were relatively small, and those species had low levels of polyploidy undercutting expectations that plants under extreme environments should have high levels of polyploidy and thus a greater possibility evolutionary change. Stunting factors are those that “convert” trees into “shrubs”. Shrubs can also be stunted when they do not attain their maximum structural development

under stress as is common with mangroves when exposed to high levels of soil salinity (Cintrón et al. 1978). The point is that under those stresses, shrubs are probably more competitive than trees, because of their higher root-to-shoot ratios. Competing hypotheses for explaining plant dwarfing on wet environments suggest that dwarfing is due to atmospheric conditions limiting nutrient uptake, i.e., low atmospheric saturation deficit leads to low transpiration rates that then limit nutrient uptake (Odum 1970) vs. dwarfing resulting from low levels of nutrient supply due to edaphic conditions (Grubb 1977).

Mangrove dwarfing occurs under 3 contrasting conditions. Under high salinity, *Avicennia* forms dwarfed communities of less <0.5 m tall. High salinity and soil saturation lead to water stress and ion imbalances, including phosphorus deficiency (Naidoo 2006). In addition, those environments may have nitrogen limitations both for tree plant development and soil microbial communities (Whigham et al. 2009). In the south coast of Puerto Rico, Lugo et al. (2007) reported reductions in net photosynthesis rates with increased soil salinity. Concentration of osmotically active solutes in plant cells increased with salinity, leading to higher plant respiration and lowering net energy available to develop aboveground structure.

In coastal Belize, dwarfing of *Rhizophora* occurs in response to phosphorus deficiency resulting from slow mineralization of soil organic matter (Feller 1995). Long-term fertilization experiments at Twin Cays elegantly showed that on calcareous substrates phosphorus was the limiting factor to vegetation growth (Feller et al. 1999). Subsequent research revealed the complex relationship between phosphorus availability and nitrogen utilization in coastal mangroves throughout the Caribbean and the Gulf of Mexico (Feller et al. 1999, 2002; Lovelock et al. 2006). More recently, Feller et al. (2015) found that those shrub mangroves that had accelerated their growth rates as a result of experimental nitrogen fertilization experienced greater loss of leaf area after the passage of a hurricane, and took 2 years more to recover their pre-hurricane leaf area than unfertilized controls. A third cause of mangrove dwarfing is a strong phosphorus deficit associated with restrictions in nitrogen supply (Medina et al. 2010). The deficiencies were revealed by negative $^{15}\text{N}/^{14}\text{N}$ isotopic values.

Non-mangrove shrublands are also dwarfed on dry calcareous coastal substrates as a result of the combination of reduced space for root development and drought stress revealed by comparatively smaller $^{13}\text{C}/^{12}\text{C}$ isotopic ratios (Medina et al. 2017b). On mountain tops, annual rainfall of ~5000 mm saturates soils leading to hypoxia, which reduces the capacity of nutrient uptake while increasing the cost of active nutrient uptake and transport (Elzenga and van Veen 2010, Grubb 1977). In these dwarf shrublands, leaves are comparatively large and sclerophyllous with large weight-to-area ratios. In contrast with the dry shrublands and dwarf mangroves, nutrient concentration in elfin shrubland leaves do not reflect limitation of phosphorus or nitrogen (Medina et al. 1981). There is an inherent trade-off in nitrogen allocation between high rates of leaf photosynthesis and leaf longevity. A leaf cannot maximize both photosynthetic nitrogen use efficiency (PNUE) and leaf life span simultaneously; low-PNUE leaves generally have longer life spans (Wright

et al. 2004). At the elfin shrublands, plants maximized longevity while functioning at slow rates of metabolism and investing in large amounts of leaf mass per area (Harris and Medina 2013).

Resilience

The ecological, physiological, and floristic responses of shrublands to the diverse environmental challenges of Caribbean islands that we have discussed above all contribute to the resilience and persistence of these ecosystems, even considering anthropogenic disturbances, which appear to favor them as novel shrublands. Lugo et al. (2002) and Lugo et al. (2006:figure 15.1) discuss the attributes of these ecosystems believed to contribute to the high resilience in Antillean seasonally dry shrublands to cutting, habitat fragmentation, and hurricanes. The attributes include habit, physiognomy, allometry, biomass distribution favoring belowground, diversity of life forms, high species dominance, high re-sprouting capacity, high efficiency of nutrient and water use, and others. The undisturbed conditions of these systems exhibit low resilience to herbicides, fire, and soil erosion. The response to these anthropogenic disturbances includes change in species composition towards introduced species as well as further changes in vegetation stature.

Heuristic Model of Conditions Leading to Shrub Dominance

Figure 5 is a heuristic framework for conceptualizing the dominance of shrubs as a physiognomic and ecophysiological response of woody plants to different levels of environmental stress. Borhidi (1993) reached a similar conclusion regarding xeromorphism, which could be attributed to a variety of ecological conditions but

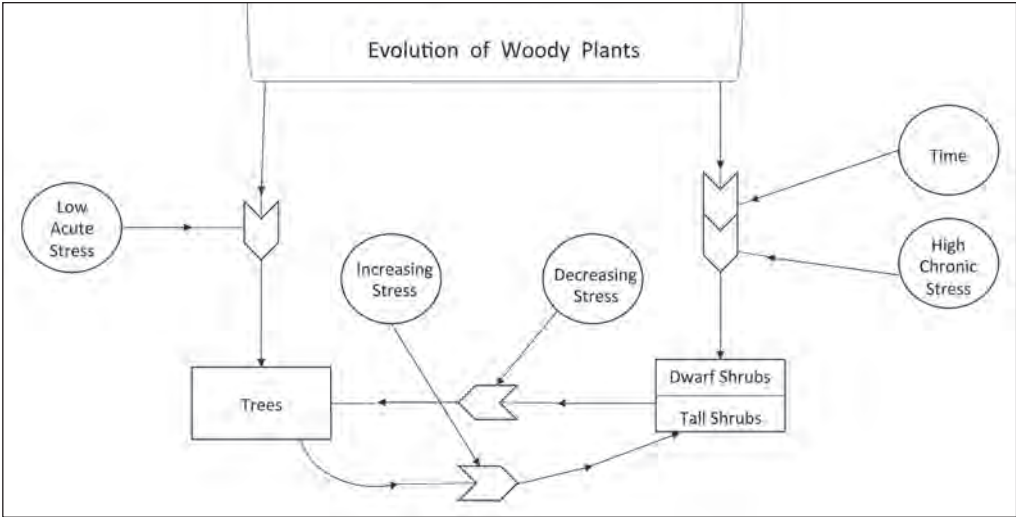


Figure 5. Heuristic model of the conditions that lead to tree and shrub habits. Circles are outside forces, boxes represent plant habits, lines show the direction of influence, and the arrows illustrate the interaction between outside forces and the direction of change of woody habits. The text explains and provides examples of the types of stressors and their intensity and duration.

in fact was a general response of plants to environmental stresses, i.e., a general adaptation syndrome. Following the discussion on heathlands in Specht (1979), we show 2 origins for shrubs. One is driven by plant evolution going back to the Mesozoic Era in response to aridity and infertile sandy and peaty waterlogged soils. The other origin for the shrub habit is through acclimation to numerous gradients of increased stress conditions faced by woody plants throughout the world. These extreme conditions on the one hand serve as selective forces for evolution of plant habit and ecophysiology, and on the other hand, they limit plant growth. We depict these gradients as leading to plant stunting as environmental conditions become more stressful to plants. Under low stress conditions, tree physiognomy is the predominant woody plant response.

By low stress condition we mean a ratio of potential evapotranspiration to precipitation (PET/P) near 1, a high level of soil nutrient availability, aerated soils, moderate air temperatures, low salinities of soils in tidal forests, moderate wind velocity, and low frequency of cool fires where fire is part of the environmental setting. The tree physiognomy changes to a shrub physiognomy along gradients of increasing stress due to the increased harshness of environmental factors. For example, when the water balance changes towards extreme high or low values of PET/P or when soils become oligotrophic, reducing nutrient availability to plants. Specht (1979:figure 6.9) illustrated how soil phosphorus limitation and water balance influence changes in aeration and combine to affect vegetation sclerophylly and physiognomy.

In tidal environments of arid climates, soil salinity increases to double sea water strength or more, thereby causing stunting of mangroves and the formation of mangrove shrublands (Cintrón et al. 1978). Chronic inundation by salty or freshwater or soil saturation lowers soil oxygen (Silver et al. 1999), which affects aeration and root functioning and triggers numerous adaptive plant responses that connect roots to leaves through several metabolic and hormonal mechanisms with influence on transpiration rates (Armstrong 1981:figure 12.5).

Warm, mild, and cool air temperatures either increase or decrease towards hot or frigid. In the Caribbean, temperature extremes do not include the frigid low temperatures associated with shrublands in other parts of the world such as the arctic (Bliss 1979) or the African mountain heathlands (Killick 1979). However, Whendee Silver (University of California at Berkeley, 15 January 2018 pers. comm.) found that in the montane wetland forests of the Luquillo Experimental Forest, ecosystem processes such as litterfall were affected by small reductions in air temperature. Annual mean temperature decreased 1.7 °C (from 21.2 °C to 19.5 °C) from 600 m to 1000 m elevation ($r^2 = 0.84$) while mean annual litterfall (based on 5 years of measurement) decreased from 10.5 g/m² to 1.6 g/m² ($r^2 = 0.91$). Both elevation patterns had the same shape with the lowest flux rates at the lowest air temperatures where elfin shrublands grew. However, lower rate of litterfall could also be related to leaf longevity, a character of sclerophyll leaves, not necessarily related to decreasing temperature.

Where fires occur, their higher frequency favor shrub dominance. The importance of the fire regime to heathland ecology, species composition, productivity,

succession, and plant life-history strategies was reviewed by Gill and Groves (1981). Chronic high wind speed, as in coastal and montane locations, sculpture tree canopies and induce shrub habits. The shrub vegetation of Caribbean dry forests is fairly resistant to strong hurricane winds (Van Bloem et al. 2005, 2006). However, hurricane winds induce sprouting in this vegetation (Van Bloem et al. 2003, 2007). Sprouting results after terminal buds are affected by wind decapitation or shaking, thus hormonally stimulating dormant buds in roots and stems. Trees and shrubs of the dry woodlands of Puerto Rico have thinner bark in comparison with trees and shrubs of other parts of the world (Wolfe et al. 2014), which makes them susceptible to fire mortality. However, the tree species in locations with greater fire presence due to human activity had thicker barks than those in the woodlands. Saplings of the introduced shrub *Leucaena* are more resistant to fire than native dry forest saplings because it outgrows them and competing grasses when colonizing deforested old fields (Wolfe and Van Bloem 2014). *Leucaena* is a nitrogen fixer, which is an advantage over native dry forest saplings also not adapted to fire.

Shrublands predominate at the high and chronic levels of environmental stress of those gradients discussed above including those conditions listed in Table 5. Some shrub species have the capacity to revert to a tree physiognomy when the stress level is reversed, as shown experimentally by Beadle (1966) and Fang et al. (2006), but others are genetically bound to the shrub physiognomy.

Chronic or high-frequency acute disturbances favor the establishment of shrubs. Depending on their intensity, low-frequency acute disturbances may or not cause the shrub habit. For example, in the Bahamas, understory growth after hurricanes

Table 5. Extreme conditions under which shrub vegetation functions. These conditions can be chronic or occur in pulses. Not all conditions occur simultaneously in all shrublands.

Environmental factor	Condition
Substrate	When present it can be saturated or flooded; eutrophic or oligotrophic; and hyper saline or freshwater. When absent it is an oligotrophic rocky substrate with our without standing oligotrophic saline or freshwaters.
Nutrient conditions	Low or high phosphorus and nitrogen concentrations; excessive Ca and low Ca/Mg, high concentrations of Fe ₂ O and Ni, Mn, and Cr oxides associated with serpentine soils.
Air temperature	Hot (>30 °C) or frigid (<-17.8 °C)*
Wind	High velocity (up to 13 m/s) either chronic as in coastal or montane summits locations, or episodic as during storms and hurricanes (~18 to >54 m/s).
Rainfall	≤500 mm per year or >4000 mm per year.
Dry season or dry days	Absent or present with variable duration.
Hydroperiod	Periodically or chronically flooded or saturated; or neither flooded or saturated.
Fire	Frequent

*This low temperature extreme is not present in the Caribbean.

(acute, intense disturbances but at low frequency) included many shrub species with ecological value to wildlife (Wunderle et al. 2007). In contrast, after the passage of hurricane Hugo, shrub cover and diversity in the Luquillo Mountains declined steadily because the canopy closed above the shrubs and non-arborescent vegetation dominated the understory (Royo et al. 2011). However, increased hurricane frequency reduces vegetation height, as does continuous wind sculpturing in the Caribbean, resulting in lower stature shrubby vegetation as occurs in the high-frequency typhoon region of Taiwan (Chi et al. 2015).

Research Questions

Research is needed to resolve several observed phenomena associated with the development of the shrub habit and shrublands in the Caribbean. For example:

- What is the relative importance of adaptation vs. acclimation in the response of shrub species to environmental extremes?
- What are the life-history and life-form tradeoffs that lead to the formation of the shrub habit?
- What are the stress thresholds for each of the factors listed in Table 5 that tilt plant response towards stunting or dwarfing?
- Do all stress factors in Table 5 lead to dwarfing or is dwarfing strictly associated with plant nutrition?

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