The Structure and Composition of Seasonally Dry Tropical Forest Communities on St. Lucia

by

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Abstract

Dry forests of the Caribbean islands are regarded as highly disturbed ecosystems and have been characterized as having a high density of small diameter stems, a lower basal area at maturity and a lower species-richness than continental Neotropical dry forests. However, the emerging view regards these ecosystems as phenologically complex, where taxonomic and structural composition is variable over time and space, due to local hydraulic regimes induced by high topographic and climactic variability and varying forms and intensities of disturbance. The former view is derived from a few studies, the majority of which have been conducted in Puerto Rico and from one data review of small 0.1 ha plots representing 4 sites in the Antilles and 25 sits in the continental Neotropics. Overall, little is known about the less-disturbed dry forest formations of the Antilles. Given the emerging view and lack of research in less-disturbed Antillean dry forests, a case study of dry forest structure and composition on the island of St. Lucia is used to examine heterogeneity in dry forest floristic and structural composition on the topographically, floristically and climactically complex island of St. Lucia. Amongst twenty-two 15 x 15 m widely distributed plots, only 11/64 species/genera were found in ¿50% of plots and clustering was observed amongst uncommon species, supporting evidence of floristic heterogeneity. Significant differences between the total basal area of each plot (Kruskal-Wallis test, p ¡0.05) were observed; each plot differed significantly with at least 2 other plots, 6 differed significantly with 10 or more plots, providing evidence for structural heterogeneity.

Comparisons were also made with prior research to question generalizations about Antillean dry forests. Amongst large diameter stems, species richness and stem density was higher in this study, when compared to more-disturbed Antillean dry forests. The most speciose dry forest genus was *Zanthoxylum*, while four families were found to be equally speciose namely, Myrtaceae, Fabaceae, Rutaceae and Rubiaceae, highlighting inconsistencies with prior generalizations. Species-richness values reported amongst Neotropical dry forests were highly variable amongst similar regions, let alone the continental Neotropics, relative to the Antillean Archipelago. Stem density and basal area in St. Lucia was similar to ranges reported throughout the Neotropics, further supporting evidence for intra-island structural variability. The intra-region heterogeneity observed in Antillean and Neotropical continental dry forests indicates that results from localized plot-based studies of structure and composition, should not be extrapolated to broad geo-political regions.

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Dedication

This thesis is dedicated to every amateur botanist who finds adventure in discovery and sees the importance of biodiversity protection to cultural heritage preservation, particularly Melvin Smith and Roger Graveson. Without Melvin's ethnobotanical knowledge of St. Lucia's flora and Roger's profound knowledge of tropical flora and dedication to the field, St. Lucia's plant collection would not be what it is today. We know where it lives, when we know how it lives, but also, how it has been used. Linking traditional knowledge with traditional science only enhances what we know about the world. Thank you for all your teachings, I hope you can pass your knowledge on.

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Chapter 1

Introduction

Ecological research conducted in local contexts (narrow spatial scales), does not seek to explain places or process in isolation and often refers to pre-existing theories and prior generalizations to provide context to results. It may also serve to revise, extend or improve on existing theories or generalizations (*Trudgill and Richards*, 1997). While the nature of scientific research, leads to additional questions and increased complexity that can potentially impede environmental policy development and implementation (*Trudgill and Richards*, 1997) the absence of research which questions preceding theories or generalizations can lead to management decisions built off of weak generalizations.

In the tropics, research efforts of biologists and preservation initiatives of conservationists can be hampered by inadequate information (*Phillips and Raven*, 1996). A considerable amount of tropical forest research has been directed towards tropical moist and wet forests biomes, while similar activities in tropical dry forests lags behind despite pleas for more research (*Murphy and Lugo*, 1986a; *Janzen*, 1988; *Mooney et al.*, 1995; *Sánchez-Azofeifa et al.*, 2005a; *Pennington et al.*, 2006). Unfortunately, tropical dry forests are also recognized as a highly threatened ecosystem on regional scales (*Ceballos and Carcía*, 1995; *Mooney et al.*, 1995; *Gillespie et al.*, 2000; *Gillespie and Jaffré*, 2003; *Gonaález-Rivas et al.*, 2006; *Pennington et al.*, 2006) and are regarded as the most degraded and inadequately protected vegetation type amongst tropical biodiversity hot spots (*Janzen*, 1988; *Gillespie*, 2005).

While there is evidence to show that these forests are rapidly depleting, understanding their historical and present extent is complicated by what actually characterizes a tropical dry forest. This complication is observed amongst those conducting global assessments of the worlds forests, as they have been challenged with harmonizing classification systems used in different regions (*Miles et al.*, 2006). This may be partially due to the historical use of bio-climactic based classification schemes to delineate areas of dry forest. These classification schemes only aid in identifying regions where dry forest is likely to be found but don't provide a means to differentiate vegetation of differing structural (and floristic) forms and rather presumes it will exist there. Regardless if it is due to the historical use of bio-climactic classification systems, dry forests are generally accepted to encompass a wide variety of vegetation formations. Terms and definitions may vary extensively due to multiple classification systems used for typifying vegetation associations (*Lugo et al.*, 2006). To provide one example formations can include dry evergreen forest, dry evergreen woodland, dry evergreen thicket, evergreen bushland, cactus scrub and thornland (*Beard*, 1949).

Existing phytogeographic research on the structure and composition of tropical dry forests is scattered and limited to a few sites worldwide and the majority of research is from the Neotropical realm (*Sánchez-Azofeifa et al.*, 2005b). Data comparisons between these studies are hampered by a lack of consistent methodologies due to varying research priorities and objectives. Where efforts have been made to identify and compare the structure and composition of dry forests between regions using similar methodologies (*Murphy and Lugo*, 1986b; *Gentry*, 1995; *Gillespie et al.*, 2000; *Gillespie and Jaffré*, 2003), it has helped to better our understanding of dry forest characteristics, but generalizations and theories from this research should be tested to examine their wider applicability.

Due to the general lack of research and inconsistent methodologies employed between tropical dry forest studies, literature reviews which attempt to characterize tropical dry forests must try to resolve the effect of different methods on study results, while simultaneously extracting evidence of trends that may be characteristic of vegetation from certain regions (*Murphy and Lugo*, 1986a; *Lugo et al.*, 2006; *Pennington et al.*, 2006). Such literature must be interpreted with these limitations in mind. To date, the most geographically widespread study of dry forest structure and composition, which employed similar methodologies between sites was completed by *Gentry* (1995) is limited to data collected from the Neotropics. While this is the most extensive study and replicate methods are useful for comparing sites of different locations, the results were extrapolated to larger geo-political regions particularly the continental dry forests of South and Central America and the dry forests of the Caribbean islands (Antilles). Additionally, the research didn't address past or present disturbances that may have influenced the vegetation within each of the study sites.

Caribbean dry forests are regarded as heavily disturbed ecosystems and their structural form has been attributed to varying levels and types of disturbances. This has promoted considerable debate over the influence of cutting, grazing, hurricanes, and edaphic factors such as, nutrient limitation and drought on the on the structure and composition of Caribbean dry forests for over a decade (*Murphy and Lugo*, 1995; *Gonzalez and Zak*, 1996; *Ramjohn*, 2004; *Van Bloem*, 2004; *Van Bloem et al.*, 2005; *Imbert and Portecop*, 2008). While effort had been made to understand the cause and effects of disturbance on forest structure, disturbance regimes are regional and variable over time and space, considerably less research has focused on the cause and effects of low-disturbance. Our understanding of dry forest ecosystems that may be considered remnant old-growth formations or recovered forest is extremely limited, however some progress has recently been made.

Roth (1999) compared two dry forest types in the Dominican Republic, that she defines as “old-growth’ and “scrub” forest. The old-growth formation was found to be more developed than scrub forest in structure and species composition and is attributed to more severe types and intensities of disturbance. Similarly, *Kalacska et al.* (2004) found several differences between species richness and community structure between early and late stage successional dry forests in Costa Rica. The differences in species composition and dominance between the sites was attributed to historical land use. These studies reveal that less-disturbed formations of dry forest exist within the Neotropics and the former reveals some clear distinctions between two dry forest formations within the Caribbean. Therefore, biogeographical comparisons of structure and composition across large geopolitical regions should clarify definitions of dry forest and account for disturbance.

Of interest to this study is the issue of broad generalizations made for tropical dry forests in the Greater and Lesser Antilles. Caribbean islands as a whole, have received remarkably less research than Neotropical continental dry forests (*Lugo et al.*, 2006). Caribbean dry forests are regarded as having certain structural and floristic traits that make them different from Neotropical continental forests. Much of these generalizations are supported by the previously mentioned research by *Gentry* (1995), however data from only two Antillean islands were used and the sample sizes were not reflective of either island’s total dry forests, let alone the Antillean Archipelago. Additionally, a large proportion of Caribbean dry forest research has been conducted in Puerto Rico, particularly Guánica Forest, where much of the aforementioned research the effects of high disturbances on forest structure and composition has been derived. Generalizing data within regions of immense topographic variability and high biodiversity, as seen amongst Caribbean islands, does not embrace their true character.

A more localized case of generalization was made for dry forests on the island of St. Lucia, in the Lesser Antilles (*Gonzalez*, 1994; *Gonzalez and Zak*, 1996). To date, this is the only plot-based quantitative study of dry forest structure and composition conducted on St. Lucia. Similar to *Gentry* (1995), plots were placed within a small fraction of St. Lucia’s dry forest but results are extrapolated to the entire dry forest region. The majority of plots were placed in forests that the author defined as “secondary scrub forests”, which were recognized as less diverse and variable in structure, particularly amongst large diameter stems, to one third of the plots that were defined as “less-disturbed forest” (*Gonzalez*, 1994). Although the authors noted differences in the two vegetation formations, data on forest structure and composition from this study were amalgamated and minimal comparisons were made between these two forms. The data presented by *Gonzalez and Zak* (1996) is believed to represent predominately more-disturbed forests.

In order to improve our knowledge of the structure and composition of Antillean dry forests, this research presents a case study analysis of tropical dry forest structure and composition on on the island of St. Lucia. Effort is made to distinguish “less-disturbed” stands *a priori* so that results reflect forests of relatively low disturbance. While some comparisons are made to forests classified as more-disturbed, scrub, or early stage successional forests by other researchers, there are no universally accepted characteristics that distinguish disturbed ecosystems from less-disturbed ecosystems. Thus, definitions of vegetation types and levels of disturbance are dependent on a researchers classification and comparisons must be interpreted with this in mind.

Despite the lack of universally accepted definitions, albeit an arduous task, such nomenclature can be resolved amongst dry forest researchers. Improving our knowledge of community dynamics within and amongst dry forests, shrublands, cactus-scrub and numerous other formations, is critical given the conservation status of the dry forest biome as a whole. It is clear that research within tropical dry forests is wanted and motives are driven beyond traditional quests of scientific inquiry. *Hubbell* (2001) may have stated it best "the low investment in and slow pace of biodiversity research might be tolerable were it not for the overwhelmingly rapid destruction of the natural world".

1.1 Thesis Purpose

This study serves three main purposes: (1) to examine heterogeneity in structure and composition of woody tree species in a widespread sample of St. Lucia's "less-disturbed" dry forest; and (2) to compare these results to previous research within Antillean dry forests; and (3) to re-examine through comparative analysis, generalizations made by *Gentry* (1995) and other researches in regards to the floristic and structural differences observed between Antillean dry forests and continental Neotropical dry forests.

1.2 Thesis Framework

There are four remaining chapters to this thesis. Firstly, a review of literature largely derived from studies within the Neotropical realm is presented in Chapter 2. In this review, characteristics of tropical dry forests as a whole are presented, along with previous observations that have been extrapolated to St. Lucia's and Antillean dry forests overall. Given the three main purposes of this thesis require different analytical methods, it was deemed appropriate to place the comparative analysis in a separate chapter. Chapter 3 presents the methods, results/discussion and summary of research on woody tree composition and structure and composition within 0.495 ha of St. Lucia's dry forest. Chapter 4 presents a comparative analysis of results from Chapter 3 to results previously reported in tropical dry forest literature, particularly from studies conducted in St. Lucia, the Antilles and Neotropical dry forests as a whole. The conclusions from this entire thesis are brought together in Chapter 5 in a discussion of evidence of dry forest heterogeneity, issues with generalizations and is completed with a discussion of the implications of this study and recommendations for future research.

Chapter 2

Tropical Dry Forests

2.1 What is a Tropical Dry Forest?

The characteristics and extent of tropical and subtropical dry forests are contentious issues for debate (*Mooney et al.*, 1995). On one hand it is useful to characterize vegetation types found within larger bio-climactic regions as segments of continua, given that species move beyond structural forms and conservation strategies need to recognize this. On the other hand, without defining how a forest is different from other vegetation formations, biogeographical comparisons of the structure and composition of forests will be made amongst ecosystems of highly different structural forms. As a result, we have classification systems that define dry forests very differently, some are inclusive and encompass a variety of vegetation formations (within the tropical dry forest designation) and others separate dry forests from other vegetation types based on structural characteristics.

2.1.1 Classification Systems and Definitions

Dry forest research is often conducted in regions defined as sub-tropical and tropical dry forests according to the Holdridge Lifezone classification system, which separates the world's terrestrial biota into zones based on climactic parameters that are supposed to coincide with particular vegetation characteristics (*Holdridge*, 1947, 1967). By Holdridge's criteria, sub-tropical and tropical dry forests are found in frost-free areas where the mean annual biotemperature (average of the Celsius temperatures where vegetation growth takes takes place relative to the annual period) greater than 17 °C, there is a potential evapotranspiration to precipitation ratio of 1-2, and the mean annual rainfall is 500-2000 mm. Not surprisingly, dry forests have been been found in regions outside this definition, as observed in major reviews (*Mooney et al.*, 1995; *Pennington et al.*, 2006).

It appears that the only clear unifying climactic characteristic of these ecosystems is the strong seasonality of rainfall distribution, where a period of extended drought is harsh enough to induce water coping strategies in the regions vegetation (*Janzen*, 1988). As few as 2-3 months of drought may be sufficient to alter the composition and structure of moist, wet, or rainforest ecosystems (*Murphy and Lugo*, 1986a). Dry seasons have been found to range from 3-8 months in length depending on its geographic location and two periods of drought are characteristic of several regions (*Murphy and Lugo*, 1986a).

A more recent definition resulting from a plant diversity symposium, identifies seasonally dry tropical forest (SDTF) to occur where the rainfall is less than 1600 mm/yr, with at least a 5-6 month period of less than 100 mm of of rainfall. The vegetation is mostly deciduous during the dry season, increasing as rainfall declines, however in the driest forests there may be a marked increase in evergreen and succulent species (*Pennington et al.*, 2006). These forests were differentiated from savannas, where SDTF are defined as tree-dominated ecosystems with a continuous or almost continuous canopy layer and grasses are a minor element in the herb layer. Savannas may also include trees, but a xeromorphic, fire-tolerant grass layer is an important component. No clarification is provided on what characterizes a tree or what is meant by continuous or almost continuous canopy.

Interestingly, the same authors which recognize there is a difference between tropical dry forests and savannas, accept a wide interpretation of seasonally dry tropical forests (SDTF) so that it includes formations such as diverse tall forest (on moister sites) and cactus scrub (on the driest) (*Lugo et al.*, 2006; *Pennington et al.*, 2006). The reason, in part, may be due to the recognition that different formations found within dry forest bio-climactic regions are regarded segments of continua along various environmental gradients, rather than distinct easily defined communities (*Murphy and Lugo*, 1995).

Bio-climactic classification systems and broad structural definitions of seasonally dry tropical forests will include multiple vegetation types and forms (i.e. cactus scrub, shrublands, and forests), within various stages of regeneration (i.e. secondary, intermediate, old growth), subject to various types and intensities of anthropogenic and natural disturbances. While perceiving tropical dry forests as segments of continua is important for conservation efforts and ecological research concerned with all vegetation forms within the broad bio-climactic zone, we still need to distinguish tree-dominated ecosystems from shrub-dominated ecosystems for bio-regional comparisons of forest structure and composition.

It is extremely important for researchers whose work serves to characterize and compare dry forests from given regions to specify what is defined as a forest and how it is different from other vegetation forms. This requires a distinction of what is defined as a tree vs. a shrub or sapling, since the latter ecosystems will vary in structural form (and likely composition) from tree-dominated ecosystems. In addition, what researchers define as a stem or an individual, will influence the types of species that are measured and how important (see Importance Value) the species is to the ecosystem.

Classification schemes which denote forests based on minimum height parameters are reportedly inappropriate for the Antilles since the terminology for vegetation below minimum height parameters can have a derogatory connotation (i.e. shrubland, scrubland or woodlands) and it is feared this may result in less regulatory protection of shorter forests (*Lugo et al.*, 2006). While this is a reasonable assumption and could lead into debate of how we value different ecosystems, distinguishing taller, tree-dominated ecosystems from shrub or stunted tree formations, should not afford less regulatory protection to the latter ecosystems. If this is an issue, policy makers need to be further educated on the importance of short statured vegetation, be it shrubs or trees, to the local ecology.

Bounding, naming and describing important patterns in spatial imagery, requires observers to set the categories of analysis to convey real-world phenomena (i.e. deforestation, reforestation and desiccation) (*Robbins*, 2001). Given the lack of a universally accepted definitions that characterize tropical dry forests, spatial assessments and mapping activities aiming to define the existing extent of these forests are complicated. Resolving the numerous classification schemes has been a challenge for many vegetation mapping projects (*Areces-Mallea et al.*, 1999; *Miles et al.*, 2006) and global forest cover assessments have been criticized for providing unreliable estimates of forested areas and deforestation rates in the tropics (*Grainger*, 1996). This discussion simply serves to highlight a major issue encountered (by this research and others), when conducting regional comparisons of tropical dry forest structure and composition. Comparing classification schemes is not the focus of this research, and the larger issue of what is considered a tropical dry forest cannot be resolved with this study. Resultantly, the information presented in consecutive sections should be interpreted with this in mind.

2.1.2 Spatial Extent and Distribution

The challenges of harmonizing various classification schemes used by different regions were noted by *Miles et al.* (2006). Dry forests were identified to exist within three World Wildlife Fund-US ecoregions including ‘tropical and subtropical dry broadleaf forest’, ‘Mediterranean forest, woodland and scrub’, and ‘desert and xeric shrubland’, in addition to forests falling within the arid zones of the ‘tropical and subtropical grassland, savanna, and shrub biome’ of *Middleton and Thomas* (1997). *Miles et al.* (2006) was challenged with using broad definitions and excepting different vegetation formations under the dry forest designation or excluding ecosystems which varied in form. Evidently, dry forest was defined broadly due to issues with gradation of different forms and biomes were amalgamated to identify areas where tropical dry forests might occur. Thus, regions of forest are only a fraction of the estimates by *Miles et al.* (2006).

The spatial estimate of global dry forest distribution by *Miles et al.* (2006) indicates that 1,048 million km^2 of tropical dry forest and savanna remain. The two most extensive contiguous areas of dry forest were found to be located in north-eastern Brazil and south-eastern Bolivia, Paraguay and northern Argentina. Other extensive concentrations were found in Mexico's Yucatan peninsula, through northern Venezuela and Columbia, and throughout central Indochina including Thailand, Vietnam, Laos and Cambodia. Extensive but diffuse concentrations were located on the Pacific coast of Mexico, through India and Sri Lanka, on the island chain east of Java and in Northern Australia. Dry forests were also identified to be scattered throughout the African continent, mainly between two regions 1) western Ethiopia, southern Sudan and the Central African Republic, and 2) the Zambia, Zimbabwe and Mozambique, although scattered populations are also remain in western Madagascar and West Africa (mainly Mali) (*Miles et al.*, 2006). According to (*Pennington et al.*, 2006), the Neotropics alone, including South and Central America, the Mexican lowlands, the Antilles, and southern Florida, contain approximately 67% (700, 000 km^2) of the worlds remaining dry forests. Based on *Miles et al.* (2006) analysis of major threats to dry forests, including climate change, forest fragmentation, fire, conversion to agriculture and human population, only 3.3% of the remaining global area of tropical dry forests are not at a high risk from one of these threats.

2.2 Characteristics of Dry Forests

2.2.1 Dry Forests vs. Wet Forests

Tropical dry forests are reported to be less diverse than wet or moist forests (*Gentry*, 1995; *Pennington et al.*, 2006) and floristic affinities amongst dry forests of different islands, have been found to be more closely related than amongst wet forests of the the same island (*Trejo-Torres and Ackerman*, 2002). Dry forests have been found to average half the number of plant species found in wet forests (*Murphy and Lugo*, 1986a), however this comparison was based on 1-3 ha surveys only including trees >10 cm d.b.h., thus is a broad generalization. Nonetheless, the relationship between species richness and rainfall has shown significant patterns of increased richness in wetter areas of the Neotropics (*Gentry*, 1988). Similar patterns have also been observed on a local scale; in Puerto Rico, the number of plant species was found to increase along a moisture gradient from dry to wet (*Murphy and Lugo*, 1986a). Finally, dry forest families are reportedly less species-rich than wet forests (*Murphy and Lugo*, 1986b).

In comparison to wet forests, the basal area of dry forests has been found to be 30-75% lower on average (*Murphy and Lugo*, 1986a). Average biomass is also lower, approximately 30% that of wet forests (*Murphy and Lugo*, 1986a). This is attributed to the smaller stature of dry forest trees, as well as the low net primary productivity in dry forests, since growing only takes place during the wet season (*Mooney et al.*, 1995). Slower growth and shorter stature are characteristic of many dry forest tree species. Annual diameter growth tends to be half that of wet forests and average canopy heights have been found to be 50% shorter than that of wet forests (*Murphy and Lugo*, 1986a). In fact, the annual growth increment is so small and the wood so dense that it is usually not possible to identify growth increments of an annual or seasonal nature in dry forests (*Murphy and Lugo*, 1986a).

Many dry forests are characterized as having only one or two canopy strata, while three or more strata are commonly found it wet forests (*Murphy and Lugo*, 1986a). Dry forest species also tend to have a higher root shoot ratio, which averages twice that of wet forest species (*Holbrook et al.*, 1995); root biomass in dry forests ranges from 8-50% compared to 5-33% in wet forests (*Murphy and Lugo*, 1986a). Dry forest species have also been observed to deploy a greater proportion of their root biomass deeper into the soil profile (where moisture availability is higher) (*Holbrook et al.*, 1995).

2.2.2 Characteristics Amongst Tropical Dry Forests

In addition to the difficulties with classification, a large proportion of published literature on tropical dry forest structure and composition is from the Neotropical realm. Published studies within this realm, are generally from localized plot-based research largely conducted within continental Neotropical dry forests. Methodologies employed in this research are variable depending on the purpose of the study, which can often be influenced by logistics including time, financial support, and accessability.

2.2.3 Phenological Complexity

There is a great degree of variation in the structural components, physiological responses and the timing of phenological events (i.e. leaf growth and shed, flowering, seed dispersal, stem and root growth) which take place in dry forest ecosystems and their relationships are notoriously complex (*Holbrook et al.*, 1995). The morphological and anatomical structural components of dry forest trees are integral to the timing and rates of water uptake, transport and transpiration. Physical characteristics such as rooting depth, stem water storage, hydraulic architecture and sensitivity to water stress are diverse among plants and add to the complexity of phenological behaviors found in dry forest stands (*Mooney et al.*, 1995).

The rooting depth of individual plants may influence the occurrence and duration of phenological events in dry forests (*Holbrook et al.*, 1995). Stem and leaf physiology and architecture, also are important for regulating hydration within dry forest trees, this is reviewed extensively by *Holbrook et al.* (1995). Leaves of evergreen species have been found to be thicker, have a higher specific gravity and a lower nitrogen content than deciduous species and are described as schlerophyllous, leathery, and stiff (*Holbrook et al.*, 1995).

2.2.4 Hydraulic Influences

The temporal and spatial patterns in water availability largely influence the characteristics of tropical forests; local and regional hydraulic regimes influence the floristic diversity and composition, plant growth forms as well as phenology (*Bullock*, 1995). Differential spatial gradients in moisture often induced by topography and soils, as well as local rainfall intensity, cloudiness, latitude and elevation (*Mooney et al.*, 1995) can cause a wide variation in tree phenology within biomes exposed to the same seasonal climatic drought regime (*Borchert*, 1994). Low soil moisture availability can trigger leaf shed, thus regions which retain water efficiently may not contain as many deciduous trees (*Burnham*, 1997). Spontaneous rainfall can also trigger flowering events during the dry season, but may behave in a very site-specific manner. This was observed in Guancaste, Costa Rica where a rainfall induced mass flowering of *Tabebuia ochracea* in areas where surface and subsurface flow would collect (i.e. hill bottom), as opposed to the hill top, which did not flower (*Borchert*, 1994). This asynchronous timing in leaf shed and flowering amongst the same species within a given region highlights the phenological complexity of dry forests that is not shared with their wet forest counterparts and the importance of micro-climactic variables (*Burnham*, 1997). Overall, the phenological complexity of dry forests is not well understood. There is a large variation among species, as well as individuals of the same species and there is no single environmental factor responsible for phenological events (i.e. stem growth, leaf loss, leaf initiation, flowering and fruiting) (*Murphy and Lugo*, 1986a).

Seasonal availability of water and its distribution plays an important role in dry forest ecosystems. Many species of trees, vines and herbs within tropical dry forests are deciduous during the dry period creating a creating a heterogenic mosaic of habitat formations (*Janzen*, 1988). Seasonal rainfall can affect growth rates of plants, flowering and fruiting phenologies (*Pennington et al.*, 2006), and the geographic distribution of plants and animals (*Murphy and Lugo*, 1986a; *Borchert*, 1994). Flowering periods have been observed to be shorter and more synchronous among species as the duration of drought period increases and the majority of deciduous trees drop their leaves during the dry season and regrow their canopies with the onset of rain (*Mooney et al.*, 1995). Although drought-deciduousness is the most commonly reported phenological response (*Borchert*, 1994; *Pennington et al.*, 2006), drought tolerant evergreens are also common (*Mooney et al.*, 1995; *Lugo et al.*, 2006). The representation of deciduous trees is variable and ranges from 40 - 100% within any given dry forest stand (*Medina*, 1995), since deciduousness is dependent upon localized moisture and soil conditions (*Murphy and Lugo*, 1986a). The amount of annual rainfall and the duration of the rainy season may also be responsible for the variation observed in total biomass and canopy height, between different broad scale climactic regions (*Mooney et al.*, 1995).

2.2.5 Patterns of Dominance and Distribution

It is suggested that species dominance is never predictable within dry forest regions and is mostly determined by stochastic processes. This theory arose from consistent observations of species clumping and only few wide ranging species among dry forests of similar regions (*Hubbell*, 1979). Similar patters of clumping and small numbers of wide-ranging species have been seen throughout Neotropical dry forests. In Brazil, no species was encountered at all the study sites and there appeared to be a limited geographic distribution for some (i.e. restricted to the North or South) (*Sampaio*, 1995). In Central America (Costa Rica and Nicaragua), as well as Puerto Rico one species was observed to occur at all sites (*Murphy and Lugo*, 1986b; *Gillespie et al.*, 2000). *Balvanera et al.* (2002) observed >50% of the species that were censused in a Mexican tropical dry forest, were present in 3 plots or less and only 8/119 species were present in all dry forest transects and species clumping was common. *Hubbell* (1979) noticed that the highly clumped patterns were most commonly observed amongst rare species, while common species were more randomly distributed. Clumped patterns have been found to be significantly related to solar insolation, which might explain the importance of water availability in the changes in species composition and richness (*Balvanera et al.*, 2002).

2.2.6 Floristics

It is widely understood that comparing diversity between regions is a logistical and scientific challenge (*Pennington et al.*, 2006) and although dry forests may be less diverse than their wet forest counterparts, dry forests are species-rich ecosystems (i.e. 10,000 species of vascular plants have been identified in the Brazilian Cerrado Biome (*Myers et al.*, 2000). In regards to global assessments of richness amongst dry forest sites, there is yet to be a study which applies a consistent definition and methodology to allow for adequate quantitative comparison. The most geographically extensive quantitative comparison employing similar methods at each site was conducted by *Gentry* (1995), but was limited to 28 locations within the Neotropics. Locally, substantial progress has been made in the number of studies which employ uniform methodologies, particularly in the Brazilian cerrados, as outlined by (*Pennington et al.*, 2006). Additional studies of this type have been conducted in Central America (*Gillespie et al.*, 2000), Bolivia (*Killeen et al.*, 1988), Florida (*Gillespie*, 2006), Eastern South America (*Oliveira-Filho et al.*, 2006), however the methodologies employed in each of these studies are differing.

Centers of diversity and endemism amongst Neotropical tropical dry forests are identified to be located in western Mexico and southeast Bolivia (*Gentry*, 1995; *Mooney et al.*, 1995). *Gentry* (1995) found only three families which occurred solely in dry forests namely Zygophyllaceae, Canellaceae and Julianaceae. *Gentry* (1995) characterizes dry forests as a depauperate set of moist/wet forest flora, whereby they are reported to restrict the occurrence of many Neotropical families, rather than giving rise to distinctive flora. Dry forests families of the Caribbean are reportedly less speciose (species-rich) than continental dry forests (*Gentry*, 1995). It has been hypothesized that areas of high richness are not the wettest and there appears to be a pattern of high diversity near both the tropics of Cancer and Capricorn, departing from trends seen in tropical rainforests where diversity increases closer to the equator (*Gentry*, 1995). However, recent research questions the validity of this latter observation (*Pennington et al.*, 2006), since disturbance wasn't taken into account in site selection (*Gillespie et al.*, 2000; *Gordon et al.*, 2004) and areas of similar richness (found by *Gentry* (1995)) have been identified further south of Mexico (*Pennington et al.*, 2006).

As outlined by *Pennington et al.* (2006), previous reviews by *Gentry* (1995) and *Pennington et al.* (2000) may have overemphasized floristic similarities between different Neotropical dry forests. The emerging view is a greater heterogeneity amongst Neotropical dry forests, taxonomic composition is variable and floristic similarity is low (*Pennington et al.*, 2006). Somewhat contradictory to the previous point, *Pennington et al.* (2006) states that some common factors should be emphasized. According to *Pennington et al.* (2006), Leguminoseae s.s. (Fabaceae s.l.) is the most speciose family at all areas in the Neotropics, with the exception of the Caribbean, where Myrtaceae predominate. Cactaceae are very common and are one of the most speciose families. In addition, woody families Capparidaceae, Zygophyllaceae, are more abundant in Neotropical SDTF (see SDTF definition in Section 2.1) than elsewhere, particularly in Central America. Erythorxylaceae are common and are characteristic of the Brazillian cerrados, and the genera *Bursera*, is very common in Mexican seasonally tropical dry forests.

Of particular interest to this study is the statement by *Pennington et al.* (2006) that Leguminoseae is not the most speciose family in the Caribbean and Myrtaceae predominates. This statement is based from a review of literature by *Lugo et al.* (2006) and is essentially a reiteration of the generalization made by *Gentry* (1995), a study which was regarded by *Pennington et al.* (2006) to overemphasize floristic similarities. Additional observations made by *Gentry* (1995) regarding differences between Antillean and continental Neotropical dry forests are of interest to this study and are presented in the following section.

2.3 Tropical dry forests of the Caribbean

Global forest cover assessments indicate that 6.5% of the worlds tropical forest exist within the borders of 26 countries in Central America, Mexico and the Caribbean (115 million ha) (*FAO*, 1993). Along the coastal zones of many Caribbean islands exists tropical forests that have adapted to harsh climactic conditions of seasonal water availability, rocky and shallow soils, constant wind exposure and salt spray (*Lugo et al.*, 2006), as well as periodic and high-intensity disturbances from hurricanes (*Imbert and Portecop*, 2008). These dry forests are prominent features of the Caribbean landscape (*Lugo et al.*, 2006), as coastal hillsides are regularly viewed from beaches and passing sea vessels.

It is estimated that the Caribbean retains only 11% of its primary vegetation. Despite the decimation, the region holds approximately 2.3% of Earth's vascular plants and 2.9% of vertebrates (*Myers et al.*, 2000). The West Indies form part of the Caribbean Floristic Region, which is estimated to contain approximately 12, 000 vascular plant species, in 200 families, 50% of which have been identified to be locally endemic (*Myers et al.*, 2000). As a result, the Caribbean Floristic Region is considered one of the World's leading biodiversity hotspots (*Myers et al.*, 2000). However, our current knowledge of existing plant species within the Antilles is incomplete (*Lugo et al.*, 2006). Floristic inventories and species richness data is wanting *Gillespie* (2005) and to date, there has been no comprehensive comparative assessment of dry forest distribution between Caribbean islands that amalgamates remote sensing work with field data.

2.3.1 Environmental Complexity

The Caribbean has a notably heterogeneous environment including several thousand islands, encompassing 14 Holdridge life zones, a complex geology, variable soil composition and is affected by variable human induced and natural disturbances (*Lugo et al.*, 2000). Several islands contain mountainous interiors and steep slopes that descend towards the coast with a large degree of overall topographic variability (*Stoffers*, 1993). In addition, despite their close proximity, the islands of the Antilles are subject to large variations in localized climate over very small distances (*Stoffers*, 1993).

2.3.2 Forest Loss

Globally, coastal deforestation is steadily increasing (*Shi and Singh*, 2003). The dry forest zone is reported to be a preferred zone for human settlement and forest conversion (*Murphy and Lugo*, 1986a; *Helmer*, 2004) in Mesoamerica, South America, and the Caribbean (*Sánchez-Azofeifa et al.*, 2005b). Tropical forests in the Caribbean have been widely utilized and heavily exploited since European settlement at the end of the 15th century (*Murphy and Lugo*, 1995). *Lugo et al.* (1981) divides periods human activity on the Caribbean islands into four main eras: the era of early settlement of low intensity farming (1493-1630); the era of extensive monocultures (1630-1880's); the era of economic collapse and emancipation (1880's-1940's); and the era of increasing energy use (1940's-1980's).

Agricultural activities over the past few centuries have dramatically altered the plant formations in the Caribbean such that remnant or climax communities may only be found in some of the isolated and inaccessible portions of the islands (*Carlozzi and Carlozzi*, 1968). Those forests that have managed to escape agricultural conversion due to their unsuitability for farming (i.e. ultramorphic soils on Puerto Rico (*Helmer*, 2004)) may be of risk of removal and conversion, as land is sold to resort and vacation home developers, in response to proliferating Caribbean tourism markets. As many small island states are releasing dependence on export agriculture, several states have become more heavily reliant on tourism (*Momsen*, 2006; *IUCN*, 2007a).

2.3.3 Disturbance

Antillean dry forests are regarded as highly disturbed environments, thus a large amount of research is concentrated on the cause and effects of disturbance (*McDonald and McLaren*, 2003a,b; *McLaren et al.*, 2005; *Van Bloem et al.*, 2005, 2006; *Imbert and Portecop*, 2008); the effects of disturbance are often used to explain and characterize dry forest structure and composition. However, (to my knowledge) there is little emphasis on the opposite trend, the cause and effects of low disturbance. This may be do to our reluctance to define low-disturbance ecosystems, since in the tropics, we have very little understanding of what defines an intact system (*Crome*, 1997). While all forests are affected by disturbance, the intensity of disturbance and resiliency of the forest is extremely variable over time and space (*Parminter*, 1998). Therefore, structural attributes which may be caused by disturbance will be variable from one location to the next, since variability is dependent on the area affected, the return interval and the magnitude of disturbances (*Parminter*, 1998). The influence of these variables over the long term for a defined region are used to define a place's disturbance regime (*Parminter*, 1998).

Types of Disturbance

Parminter (1998) divides natural disturbances into abiotic and biotic categories, each varying in intensity. Those that may influence Antillean dry forests include wildfire, wind, landslides, volcanoes, and flooding; the effects induced of recent volcanic activity and flooding are unlikely for plot locations in this study. Biotic disturbances within Caribbean dry forests may include grazing by goats, sheep and cattle (*Murphy and Lugo*, 1995; *Lugo et al.*, 2006), the effects and extent of insect, pathogen and other animal disturbances is unknown. While high disturbance would be the complete removal of forested stands through land clearing, low disturbance activities are also common. Antillean dry forests are often used as sources of fuel (charcoal), construction materials, fence posts, fishing poles, craft supplies and traditional medicines (personal observation) (*Mooney et al.*, 1995; *McDonald and McLaren*, 2003a; *Lugo et al.*, 2006).

Effects of Disturbance

Antillean dry forests have been characterized as having a higher stem density, a larger proportion of multiple stemmed trees, less basal area at maturity, and a shorter height than dry forests in the continental Neotropics (*Murphy and Lugo*, 1986a; *Gentry*, 1995; *Van Bloem*, 2004; *Van Bloem et al.*, 2005; *Lugo et al.*, 2006).

The causes of these characteristics has been attributed to cutting, hurricanes, and edaphic factors such as nutrient limitation and drought (*Murphy and Lugo*, 1995; *Van Bloem*, 2004; *Van Bloem et al.*, 2005; *Imbert and Portecop*, 2008). These studies have triggered debate on whether the multi-stemmed growth form is a result of disturbance (both natural and anthropogenic) or whether it is a phenological trait of species regardless of disturbance. Overall, evidence has shown that the multi-stemmed growth form occurs both naturally in some tree species not affected by disturbance (*Dunphy*, 1996), stem breakage is common after hurricanes (*Van Bloem et al.*, 2005; *Imbert and Portecop*, 2008) and sprouting is a response of both cutting by humans and by hurricanes (*McDonald and McLaren*, 2003a; *Van Bloem et al.*, 2006). This reveals that the multi-stemmed form is both a natural phenological trait of some species but can also be induced or increased by disturbances; therefore we cannot assume that the multi-stemmed form is due to prior human disturbances.

Although the structure and composition forests of Antillean forests are influenced by disturbances, the effect is variable in time and space; not all forests are effected in the same manner and some forests have managed to escape or recover from high-level disturbances. These "less-disturbed" forests have not been a focus of research within the Antilles and little is known about their structure and composition.

2.3.4 Previous Research

Although a large proportion of global dry forest research is conducted within the Neotropics, the islands of the Caribbean have received considerably less research in comparison with continental forests (*Lugo et al.*, 2006). A large proportion of Antillean dry forest research has been generated from studies on the island of Puerto Rico (*Ramjohn*, 2004) (see *Lugo et al.* (2006) bibliography for literature). As a result, reviews which characterize Antillean dry forests (*Murphy and Lugo*, 1986a; *Gentry*, 1995; *Murphy and Lugo*, 1995; *Lugo et al.*, 2006), utilize data largely derived from research conducted within Puerto Rico, particularly within the the 4000 ha Guánica Forest, touted as one of the best remaining contiguous tracts of dry forest in the Caribbean (*Murphy and Lugo*, 1995). However, as outlined by *Ramjohn* (2004) and *Murphy and Lugo* (1995) the Guánica Forest has experienced a wide range of disturbances including cutting, plantation forestry and agricultural crop production. Puerto Rican dry forests are regarded as having a long history of wind disturbance via hurricanes and tropical storms, a phenomena that has been identified as responsible for the multi-stemmed nature of these forests (*Van Bloem et al.*, 2005).

However, dry forests are found throughout the rest of the Antilles, with stands remaining on the Greater Antilles (Cuba, Hispaniola, Jamaica), the Virgin Islands, St. Croix, the volcanic and limestone arc's of the Lesser Antilles, as well as the flat limestone islands of the Bahamas archipelago, the Cayman islands, Mona and Anegada (*Lugo et al.*, 2006). Due to the larger size of these islands, the most extensive areas exist in the larger Greater Antilles on the island of Cuba, Haiti and the

Dominican Republic (*Miles et al.*, 2006). Outside of Puerto Rico, published inventories and localized studies of forest structure and composition have been completed for other Antillean islands including Martinique (*Kimber*, 1988), Cuba (*Borhidi*, 1996), the Dominican Republic (*Hager and Zanoni*, 1993; *Roth*, 1999), Jamaica (*Asprey and Robbins*, 1953; *Kelly et al.*, 1988; *McLaren et al.*, 2005), Mona Island (*Lugo*, 1991) and St. Lucia (*Gonzalez*, 1994; *Gonzalez and Zak*, 1996). Overall, methodologies from these studies are highly variable and few reliable inferences can be made from comparing results reported in literature from these studies.

Broad Comparative Studies

One of the earliest widespread study of Caribbean vegetation (*Beard*, 1949), classifies forest types observed throughout the Antilles based on physical field data of various vegetation communities. While it is the most extensive review, replicate quantitative methods were not employed and mapping efforts were completed prior to the availability of spatial data. The first (and only) replicate quantitative study that compares Antillean dry forests to continental dry forests is the previously mentioned study by *Gentry* (1995). Data from four 0.1 ha plots in Jamaica and Puerto Rico (two in each) were compared with twenty-four 0.1 ha continental plots in South and Central America. From this data, *Gentry* (1995) observed some floristic and structural differences between Antillean dry and Neotropical continental dry forests.

Antillean dry forests were noted for having a lower species richness (particularly in regards to lianas), a high proportion of sclerophyllous leaves and a low species representation amongst most families, although the number of families represented were similar (26). Legiminosae, the most speciose arborescent family in continental forests, was under represented in the Antilles and instead the Myrtaceae or myrtle family, was identified to the pre-eminent West Indian dry forest woody species family (*Gentry*, 1995). The genera *Coccoloba*, *Eugenia*, *Erythroxylum* and to a lesser extent *Drypetes* and *Casearia* were identified to be over-represented in the Antilles. In regards to structure, Antillean dry forests were found by *Gentry* (1995) to have a higher density of small and medium trees. The large number of small diameter multiple stemmed trees was identified as a peculiarity of Antillean dry forests. *Gentry* (1995) also reported a lower basal area, a lower average height and less than a third as many liana's as continental forests.

This study has largely contributed to reviews attempting to characterize the structure and composition of Neotropical and Antillean dry forests (*Pennington et al.*, 2006; *Lugo et al.*, 2006) and is likely due to the lack of comparative research which questions the aforementioned generalizations. Given that (*Gentry*, 1995) only included plots from Jamaica and Puerto Rico the study is interpreted as a broad generalization and further research is needed to question the applicability of such generalizations.

Dry forests of the Antilles have also been identified to have a high species dominance, particularly in dry forest stands on Puerto Rico and Mona island, as observed by *Lugo* (1991). The high species dominance was attributed drought, hurricanes and anthropogenic disturbances and low floristic diversity of Antillean dry forests (*Lugo et al.*, 2006). However, the statement that Antillean dry forests have a low floristic diversity is debateable for several reasons. Firstly, no comparative inventory of Antillean dry forest diversity has been published to support the claim that these forests have a low floristic diversity. Secondly, this is one small example and more research is needed to draw such broad generalizations. Lastly, continental dry forests have been found to exhibit interesting spatial patterns, where regional restrictions and clustering has been observed amongst rare species and the most abundant species are also widespread (*Hubbell*, 1979). If these spatial patterns are not unique to continental dry forests, species diversity should be variable and diversity measurements (i.e. species richness/area) will largely be affected by plot, transect or inventory methods.

Given the environmental complexity of Antillean dry forests, broad generalizations extrapolated to regions where data is collected may misrepresent the characteristics of regions that are lacking data. In response, this thesis presents a comparative analysis of data collected from 22 plots dispersed amongst St. Lucia's dry forest to determine if generalizations made about Antillean dry forests are applicable to St. Lucia. In addition, a comparison of species richness data reported in Neotropical dry forest literature is presented, in attempt to identify whether these forests should be regarded as having a lower species richness. It is hypothesized that some Antillean dry forests may exhibit the similar species distribution trends observed in other Neotropical continental forests of a few widespread species, clustering and restricted distributions. As discussed, Caribbean islands exhibit a high degree of complexity and are known to support a large variety of forest types within relatively small areas (*Lugo et al.*, 1981). It is assumed that clustering of rare species is most likely to occur on islands with a high degree of topographic complexity, thus the study area of St. Lucia is appropriate.

2.4 St. Lucia

The island of St. Lucia is located midway through the inner windward island arc of the Lesser Antilles, situated at 14 °N and 61 °N. St. Lucia is a small island with a land area of 616.4 sq. km, 42 km long and 22 km wide (*Isaac and Bourque*, 2001) and is topographically complex due to it's volcanic history. The Antillean island chain began to form as submarine volcanoes during the late Oligocene, emerging as active volcanic peaks between the Miocene and ending the late Pliocene (*Carlozzi and Carlozzi*, 1968). As a result, the islands are physiographically complex, varying sharply in dissection and maturity according to their age and may be characterized by having lofty interior peaks with steep slopes that descend to the sea (*Stoffers*, 1993). This topographic complexity influences St. Lucia's hydrologic regimes, where precipitation and mean annual temperature decreases along elevation gradients from the interior to the coast, with the driest regions located in the extreme North and South of the island (*Isaac and Bourque*, 2001). This complexity is responsible for numerous micro-climactic conditions on St. Lucia, which has resulted in a large variety of forest types within a small area. This variation is common to most of the islands along the main volcanic arc from Saba to Greneda (*Lugo et al.*, 1981; *Stoffers*, 1993).

St. Lucia's climate has been characterized as tropical maritime, where average day-time temperatures range from 26-32°C with an average relative humidity around 75% (*Cox*, 1997). Mean annual biotemperatures for all locations measured by *Isaac and Bourque* (2001) were greater than 17 °C, precipitation ranged from 1152-2000 mm/year along most of the coast and potential evapotransporation ratio's were between 1-2 in only the extreme north and south of the island. Resultantly, the life zone characterization by *Isaac and Bourque* (2001) revealed subtropical dry/moist forest to only be located on the extreme north and south of the island, comprising 6% of the land area; most of the coastal forests fell under the subtropical moist and subtropical moist/wet life zones. However, Isaac and Bourque's rainfall station data was limited to 49 stations, a large proportion of which were located in wet areas. Secondly, as previously mentioned, life zone characterization does not take into account seasonal rainfall distributions; a period of prolonged drought occurs on St. Lucia from December to April (*Cox*, 1997). Thus, seasonally dry vegetation has been identified outside the dry/moist life zone as delineated by *Isaac and Bourque* (2001).

2.4.1 Dry Forest's of St. Lucia

In the 1940's, J.S. Beard (*Beard*, 1949) conducted floristic inventories of vegetation on several Caribbean islands and later classified vegetation communities of the Caribbean based on their structural characteristics and primary environmental determinants (*Beard*, 1955). During Beard's visit to St. Lucia, he notes that most of the shallow soiled coastal hillsides are covered with a "degraded secondary community", which he termed "dry scrub woodlands". To provide more detail to the survey, Beard preferentially selected a location near Praslin, halfway down the island's east coast and laid a 1 acre quadrat in what he defines as the "least damaged example" of dry evergreen forest that could be found on his expedition through St. Lucia and possibly the entire Windward and Leeward Islands (*Beard*, 1949).

The site near Praslin had a moderate slope with a north aspect and was located approximately half a mile from the sea at 200 ft. elevation. The largest trees identified included two representatives of the Myrtaceae family, as well as *Coccolobis pubescens*, *Pimenta racemosa* and *Tabebuia pallida*; the latter was noted as the only tree which "reaches a great size". The majority of the growth was identified as shrubby and the woodlands were reported to resemble the eastern coastal woodlands of Dominica, rather than the secondary dry woodlands of St. Vincinent, Antigua, and Barbados. According to *Beard* (1949), this forest was dominated by evergreen species and only *Bursera simaruba* could properly be called deciduous. The forest also appeared to have several trees that were bent over, leaning, or crooked. According to *Beard* (1949), the majority of dry woodlands on St. Lucia did not include trees as large as those identified in Praslin (6-7 ft girths), and instead consist of a low dense thicket of saplings and the most severely degraded areas were covered with a thicket of *Croton* spp. Other species noted closer to the sea included *Bourreria succulenta*, *Calliandra tergemina* and *C. purpurea*, *Plumeria alba*, *Erythroxulum squamatum*, *Termstroemia peduncularis*, *Randia mitis*, *Diospyros ebenaster* and *Amyris elemifera* (*Beard*, 1949). Although few areas were actually inventoried and spatial data wasn't available at the time, Beard developed a map of vegetation communities on St. Lucia, which reveals that "dry scrub-woodlands" dominate the coastal hillsides.

St. Lucia's dry forests were investigated approximately 45 years later by O.J. Gonzalez and D.R. Zak (*Gonzalez*, 1994; *Gonzalez and Zak*, 1996). The research was conducted in three contiguous areas of dry forest on the island's east coast, the majority of which the authors characterize as "secondary scrub forest", with relatively short canopies <4 m tall and are dominated by small diameter stems (< 5 cm) (*Gonzalez*, 1994; *Gonzalez and Zak*, 1996). Although the majority of their plots (two thirds) were placed in this "secondary scrub forest", 1/3 were placed in a "relatively undisturbed" dry forest. Within the entire study area (6200 m^2), 50 species were identified (7 only to family level). The species included herbs, vines and cactus in addition to woody shrubs and trees. Less species were observed in the relatively undisturbed forest but this was attributed to the smaller sampling area.

Interestingly, a greater diversity was observed amongst large diameter stems in the the relatively undisturbed forest (*Gonzalez and Zak*, 1996) and was the only comparison discussed between the two vegetation formations. The data derived from both formations were amalgamated and were used to characterize the island's dry forests. Like *Beard* (1949), *Gonzalez and Zak* (1996) noted that the island's dry forest is dominated by a secondary scrub formation. While this forest type does exist on St. Lucia, the observation that it is the dominant dry forest type has yet to be verified by any sort of field or spatial inventory. Other less-disturbed formations of dry forest were identified by both authors and are found in scattered patches along the slopes of coastal hills often in areas of difficult accessibility (personal observation).

It appears that the use of a broad definition of dry forest was used by *Gonzalez and Zak* (1996), despite the recognition of two different structural forms. Given that the majority of plots were placed in what the authors defined as "secondary scrub forests" the results of this study are believed to be representative of more disturbed forest and the study area is further regarded as "predominately disturbed" dry forest. Given the lack of understanding of the structure and composition of less-disturbed dry forest on St. Lucia, the research presented in this thesis is exploratory in nature and serves to improve our understanding of the island's less-disturbed dry forests. Comparisons with results presented in *Gonzalez* (1994) and *Gonzalez and Zak* (1996) are made to identify differences in structure and composition between "less-disturbed" and "predominately disturbed" dry forest formations.

Chapter 3

Less-Disturbed Dry Forests of St. Lucia

3.1 Purpose

The structure and composition of St. Lucia's seasonally dry forests are examined using a sampling regime that is widely dispersed amongst remnant or recovered dry forests of St. Lucia and is classified as "less-disturbed", relative to other tree or shrub-dominated ecosystems found within vegetation classified as woodland/shrublands (*Areces-Mallea et al.*, 1999). Widely dispersing plots over the island, captures the floristic and structural heterogeneity expected on a tropical island with high topographic variation.

It is difficult to give context to the results of this study since it is the first of its kind and serves as baseline exploratory descriptive research. This research is the first replicate quantitative analysis of "less-disturbed" dry forests, where plots are dispersed widely amongst St. Lucia's dry forest rather than being concentrated in localized area of the island (i.e. *Gonzalez and Zak* (1996)). Therefore, results are mainly descriptive and serve to broaden our understanding of floristics and structural characteristics of this vegetation type. This information should aid further research efforts, which need to understand characteristics of "less-disturbed" dry forests prior to the placement of field plots. Geographic context is given to these results through a comparative analysis and discussion in Chapter 4.

3.2 Methods

3.2.1 Site Selection

Using GIS software (ArcGIS 9.2), a digital image of the most recent vegetation map of the island (*United States Geological Survey*, 2007) was georeferenced and rectified onto a 1: 25,000 digital topographic map of St. Lucia (*Government of St. Lucia*, 1981). *Areces-Mallea et al.* (1999) categorized insular Caribbean vegetation types (as used in the aforementioned map) using the International Classification of Ecological Communities (ICEC) system, which has been adopted by the United States Federal Geographic Data Committee (FGDC 1997) as standard for describing vegetation communities in the United states (*Areces-Mallea et al.*, 1999). Seasonal forests (both evergreen and deciduous) are recognized in the aforementioned classification scheme, however all dry forest vegetation on St. Lucia was classified as "woodland/shrublands". Shrublands are defined as vegetation dominated by shrubs >0.5 m tall, with individuals or clumps not touching, shrub cover is > 25%, while tree cover is <25 %; no definition of vegetation classified as woodlands is given (*Areces-Mallea et al.*, 1999). Based on previous literature (*Beard*, 1949; *Gonzalez and Zak*, 1996), site visits and consultation with local forestry experts, it was determined that less-disturbed stands of seasonally dry forest would be found within the vegetation classified as woodlands/shrublands by *Areces-Mallea et al.* (1999). Thus, despite issues with nomenclature, it was assumed regions of woodland/shrublands would likely have less-disturbed stands of dry forest.

A definition of "less-disturbed" dry forest was developed in order to separate study sites from shrub-dominated ecosystems[1] and ecosystems indicative of recent disturbance. It was determined that regions containing closed canopies with contiguous forest cover (≥75 % coverage in an area ≥5 ha), were likely to contain dry forest formations but could include shorter shrub-dominated stands. In order to separate forests from shorter shrub-dominated ecosystems, a minimum height parameter was selected. Seasonal and semi-deciduous forests of Martinique have been classified as having a a minimum canopy height of 4 m (*Kimber*, 1988) and scrub forests of St. Lucia were identified to have an average canopy height of 4 meters (*Gonzalez*, 1994). It was thus determined that a minimum average canopy height of 4 m would be used as a condition for study site selection prior to plot placement.

Colour composite digital aerial photographs from 2004, obtained from the St. Lucia Forestry Department, were rectified to the base topographic map to aid in identifying recent areas of continuous tree cover within the woodland/scrubland classification of the vegetation map. While historical aerial photos were available for some regions, coverage was incomplete for the island, thus a systematic historical analysis of land cover change could not be conducted. In order to compensate for the lack of imagery, reconnaissance site visits and consultation with forestry officials, local land owners and guides with knowledge of land use activities, assisted with identifying specific areas od dry forest with low disturbance. In addition, oblique aerial photos taken a month prior to the study from helicopter became available and were useful at identifying existing site conditions.

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[1] Vegetation formations which are mostly comprised of a dense array of saplings and shrubs (vegetation that does not arise from a raised >1 ft trunk) generally <4 cm d.b.h. that that form one canopy layer which does not exceed heights >4 m due to the absence of tall, larger diameter trees.

Through this preliminary investigation, several regions were determined to have forest subjected to relatively low disturbance. A total of four regions of continuous, less-disturbed dry forest fragments were identified and included the central-east and north-east coast, the slopes of the central west coastal hills and the southern peninsula, Moule à Chique. Two other regions of dry forest are known but were not included in the study due to accessibility difficulties. Petit Piton, a 770 m high steep sided conical mountain (*Cox*, 1999) and the protected Maria Major Island just South of Moule à Chique (*SLUMAFFE*, 2006). In total 22, 15 x 15 m plots were dispersed amongst these four regions with 5 in the North East, 5 in the Central East, 9 in the Central West and 3 on the Southern Tip (Figure 3.1).

The potential plot locations within each region were selected *ex situ* using the base topographic map and aerial photographs. These potential locations were systematically placed so that they were separated by a minimum distance of 250 m and were spaced in incremental distances from the coast in order to account for some variation in structure induced by coastal winds. Slope, aspect and elevation were also taken into consideration so that plots within clusters were scattered to represent variation in these parameters. The hilly topography of St. Lucia's coastal zone made this relatively easy (i.e. if a plot was located on a south facing hillside, the next would be located on a north facing hillside).

The coordinates of each potential plot location were recorded in a Garmen handheld GPS unit *ex situ*, which facilitated easy navigation. In order to minimize the selection of heavily used forests and the edge effects expected by forest fragmentation, all plots were also located > 50 m from any road, farm or other land cover and > 10 m from any trails. As *Ramjohn* (2004) notes, the effects of edge on desiccation within dry forests may be less severe than wetter forests (especially in the Antilles), since these trees have more open canopies and trees have adapted to drier conditions. However, more research is needed to determine if the effects of edge differ from wet forests. *Turton and Freiburger* (1997) found micro-climate edge effects to penetrate 30 m into a 20 ha remnant of Australia's rainforest. Given the severity of edge effects are expected to be less for dry forests the conservative estimate of 50 m is believed to be suitable for avoiding micro-climactic effects induced by roads.

If "less-disturbed" forest was absent at a pre-defined location, an alternative location was chosen nearby following the aforementioned rules. In addition, if evidence of cutting, grazing or stem damage was clearly evident upon arrival at a site, a new location would be selected. Plots were not placed in areas with slopes > 45 degrees, rocky outcrops, or riparian lowlands (due to differences in vegetation types expected from intermittent flooding). At each site, elevation was recorded using the GPS, slope was measured using a digital clinometer and aspect was measured with a compass. Tree canopy height was approximated upon arrival at a potential location using a digital clinometer. The reported canopy heights are reflective of the largest tree (in girth) in one of four quadrants within each plot. Given that these were not always the tallest trees within the plot it is an approximation of the canopy height. Environmental parameters of plots are presented in Table 3.1 are reflective of the actual site conditions rather than potential plot locations.

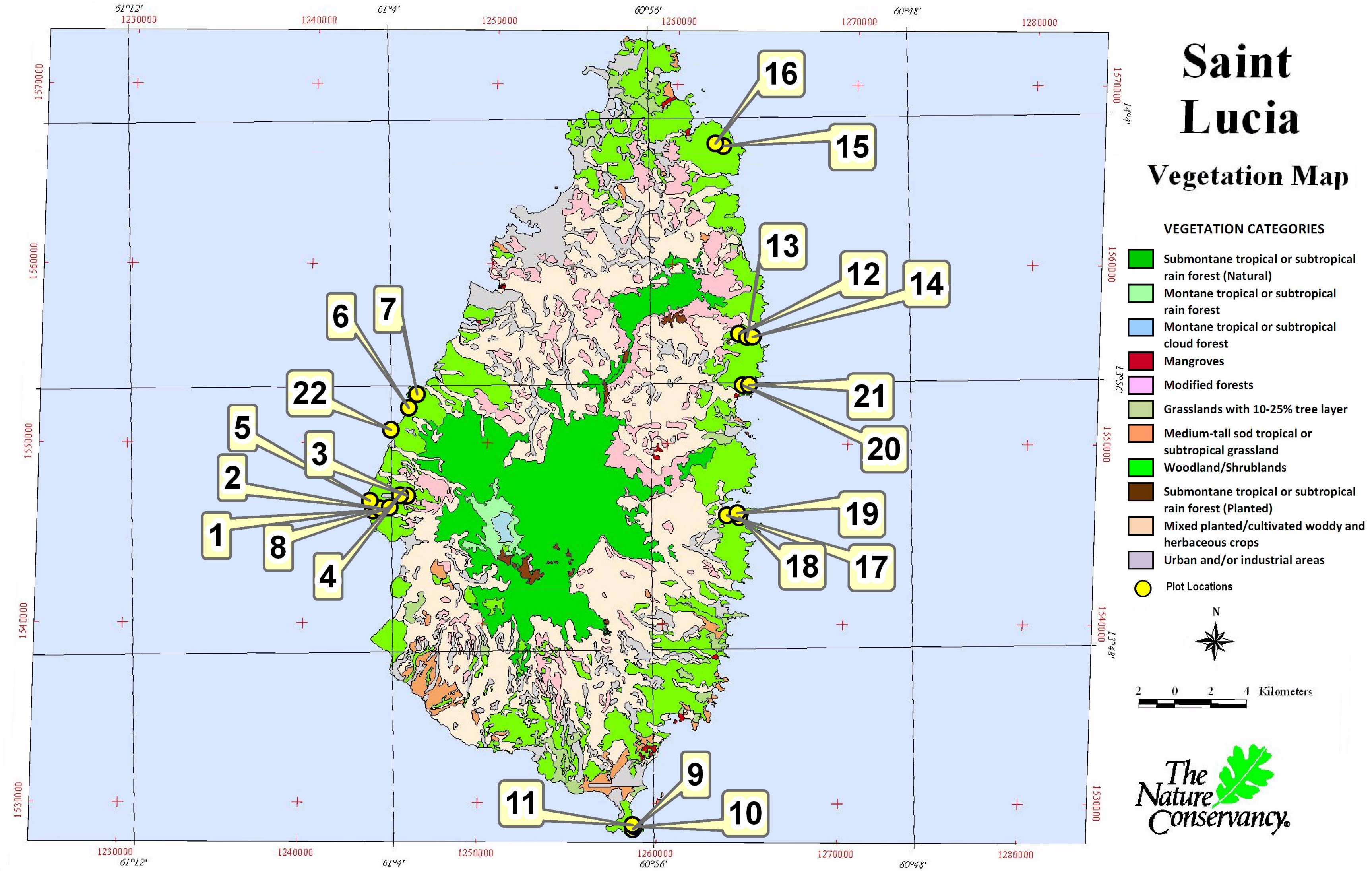

Figure 3.1: Dry Forest Plot Locations (modified from *United States Geological Survey* (2007)

Table 3.1: Elevation (m.a.s.l), slope, aspect and canopy height (m), measured at 22 plots within St. Lucia's dry forest

Plot	**Elev.**	**Slope**	**Aspect**	**Canopy Height**
1	58	26.7	198	7.6
2	185	31.1	24.6	7.4
3	280	34.4	357	6.5
4	276	27.5	80	5.4
5	42	27.5	230	7.9
6	50	11.5	326	7.4
7	95	31	212	5.7
8	253	29.1	250	4.9
9	188	20.9	267	6.6
10	226	32.4	5	6.3
11	131	32.6	22	5.1
12	180	6.5	230	6.5
13	113	27.9	170	6.7
14	64	18.8	76	7.5
15	165	27.8	24	6.3
16	177	34	128	8.3
17	49	29.6	352	5.0
18	41	12.1	168	6.9
19	26	25.8	22	11.2
20	37	14.3	312	6.7
21	111	18.4	280	8.0
22	30	23.8	314	11.9
$\bar{x}$	126	24.7	184	7.1
Range	(26-280)	(6.5-34.4)	(5-357)	(4.9-11.9)

While this method of site selection attempts to preferentially select sites with low disturbance, both anthropogenic and natural disturbances have likely influenced the structure and composition of these forests in one way or another. It would be incorrect to assume that any of these sites are undisturbed, intact or pristine ecosystems, however they are considered to be relatively less-disturbed than other vegetation formations found within St. Lucia's dry forests. The length of time that these stands have been "forest" could not be determined due to the lack of historical information, thus I do not attempt to define the types, degrees, and influences of disturbance within these "less-disturbed" plots. Essentially, 'less-disturbed" sites may represent remnant (old-growth) or recovering ecosystems (in varying stages of succession). Comparisons made with dry forests characterized as secondary scrub, disturbed and early stage successional dry forests (Chapter 4), support the classification of the study sites as less disturbed relative to other dry forests in the Neotropics. The results and discussion presented in this Chapter are largely descriptive, as it is the first of its type. It serves to give context to future research on the structure and composition on dry forests of St. Lucia and the Antilles, just as research which precedes this study has done (chapter 4), as is the nature of science (*Trudgill and Richards*, 1997).

3.2.2 Data Collection

Fieldwork was conducted between June and August 2007. During this time frame, Hurricane Dean passed over the island, therefore plots 20-22 were completed following the hurricane. Despite the storm, little evidence of disturbance was observed in the location where plots 20-22 were placed, besides a few snapped branches from the over-story. No significant evidence of disturbance was observed to stems >4 cm at 1.3 cm height. Within all plots (which were adjusted for slope) all standing woody stems (non climbing) $\geq$ 4cm d.b.h. and rooted within the plot, were measured, identified, mapped and classified as either alive standing (AS), dead standing (DS), alive leaning (AL), dead leaning (DL), broken (BS) or cut (CS). Leaning trees were identified as those which were found at angles $\geq 45^\circ$ to my upright stance.

Based on observations of stem diameters of shrub growth forms, 4 cm was selected as a minimum d.b.h. as it was deemed suitable to eliminate many shrub growth forms and most herbaceous species from the study, thereby limiting the majority of stems measured to trees. Eliminating stems <4 cm d.b.h. from this study also allowed for the completion of more plots. Stems on multi-stemmed trees were only measured if they bifurcated under the 1.3 m mark; measurement height followed the Canadian Environmental Monitoring and Assessment Network's forest monitoring protocol for trees on sloped ground (*Roberts-Pichette and Gillespie*, 1999). While this minimum d.b.h. omits juvenile trees, in addition to many shrubs, I do not neglect the importance of shrubs and juveniles within St. Lucia's dry forests and rather intended to focus this study on the structure and composition of larger trees amongst St. Lucia's dry forests. In addition, the inclusion of stems smaller than 4 cm d.b.h. would have had the following research disadvantages:

1. In order to identify and measure stems < 4 cm, subplots would have to have been used due to time constraints. Extrapolating subplot information to the per hectare level can largely over estimate overall plot stem density.
2. The inclusion of shrubs into community assessments adds unnecessary complexity and can render it more difficult to group plots into forest types (*Nolet et al.*, 1995).

All species >4 cm d.b.h. were identified *in situ* by local guides in the local dialect (Patoi). Given that I had developed prior knowledge of the Patoi names of St. Lucia's flora assisting Dr. Bradley Walters with taxonomic identification a year prior, I was already familiar with many of the tree species. However, samples were collected and photographs were taken for every new species identified and those which were questionable. Samples were pressed and a library was developed of all project plant species to allow for verification with subsequent plots. An electronic database complete with photographs and descriptions of species developed by local botanist and St. Lucia's herbarium curator Roger Graveson, aided in species identification. All voucher specimens and photographs were later verified at St. Lucia's national herbarium using local flora and *Howard* (1974).

3.2.3 Nomenclature

Given that this study includes a comparative analysis of dry forest floristics from other literature (Chapter 4), careful attention was paid to the classification systems used by studies for comparison, namely *Gentry* (1995), *Gonzalez* (1994) and *Gonzalez and Zak* (1996), which were completed prior to the development of the APG systems of plant taxonomy. The classification systems used by both studies differ from the APG system in the following instances:

1. Species identified in the subfamilies Caesalpinoideae, Mimosoideae, and Papilionoideae were included in Leguminoseae; all of which are currently classified as Fabaceae under the APG system.
2. According the the APG system, Sterculiaceae has been moved into the Malvaceae family, but was treated as a separate family by *Gentry* (1995); no speciments of Sterculiaceae or Malvaceae were identified by *Gonzalez* (1994).

Nomenclature for this study follows the APG system so that all Leguminoseae (s.s.) are considered as Fabaceae. The fact that the aforementioned studies recognized Leguminoseae, in a broad sense (includes the subfamilies) likened to the APG system, the analysis is not affected. However, since *Gentry* (1995) recognized Stericuliaceae separate from the already existing Malvaceae, *Guazuma ulmifolia* and *Symplocos martinicensis* are considered Stericuliaceae (s.s.) in order to provide an adequate comparison of species richness amongst dry forest families with results from *Gentry* (1995), presented in Section 4.4.3.

3.3 Data Analysis

3.3.1 Importance Values

The sum of the relative dominance, relative density and relative frequency were used to generate an importance value index for woody tree species within the study area. The importance value index is used to provide an indication of the ecological importance of a species within a stand of forest (*Curtis and McIntosh*, 1950, 1951). The formula gives a maximum value of 300 for each species, thus the values were divided by 3 to display the relative proportion (on a 0-100 scale) of each species importance ranking within the index.

$$\begin{aligned}\text{Relative Density of Species A} &= \frac{\text{No. of stems of species A}}{\text{Total number of stems (all species)} \times 100}\\ \text{Relative Frequency of Species A} &= \frac{\text{Frequency of species A}}{\text{Sum of all species frequencies} \times 100}\\ \text{Relative Dominance of Species A} &= \frac{\text{Basal area of species A}}{\text{Total basal area (all species)} \times 100}\end{aligned}$$

$$\text{Species Importance Value} = \sum \div 3$$

Using a similar framework adapted from *Mori et al.* (1983), an importance value ranking for each family within the study area was also generated. This formula does not account for the frequency of the family (number of plots which it occurred in) and instead accounts for the number of species within each family represented within the entire study area.

$$\begin{aligned}\text{Relative Diversity of Family A} &= \frac{\text{No. of species in family}}{\text{Total no. of species} \times 100}\\ \text{Relative Density of Family A} &= \frac{\text{No. of stems in family}}{\text{Total no. of stems} \times 100}\\ \text{Relative Dominance of Family A} &= \frac{\text{Basal area of family}}{\text{Total Basal area} \times 100}\end{aligned}$$

$$\text{Family Importance Value} = \sum \div 3$$

3.3.2 Structural Heterogeneity

Total basal area within a given forest community is considered an appropriate indication of its structural composition, since it accounts for both the number and size of stems that are measured. Variation in the basal area distributions of different communities (when replicate measures are employed), can be analyzed by using statistical tests that report variation between populations. In order to examine the structural composition between plots, the total basal area (πr^2) of stems was compared using a (non-parametric) Kruskal-Wallis test. This test was used because the data did not represent a normal distribution due to a high proportion of stems (88%) <10 cm d.b.h within the study area (Figure 3.3A). A Kruskal-Wallis test transforms data from numerical values into ranks and tests for similarity, equality and significant differences between population medians in rank groups (*Zar*, 1984). It is expected that there would be significant differences in basal area between plots, given that dry forests of St. Lucia are regarded as highly complex heterogeneous ecosystems and dispersing plots widely across the island would account for some of this variation.

3.4 Results and Discussion

3.4.1 Condition of Stems

A total of 1972 stems were censused on 1484 individuals in 4950 m^2 (0.495 ha) of St. Lucia's dry forest. Of the 1972 stems censused, only 4.6 % were deceased and were classified as cut (CS) or broken (DB) above 1.3 m, dead standing (DS) or dead leaning (DL) (Table 3.2). Species which were identified as cut included *Amyris elemifera, Calliandra tergemina, Croton bixoides, Erithalis odifera, Foresteria rhamnifolia, Lonchocarpus heptaphyllus, Miconia cornifolia, Myrcia citrifolia*, and the genera *Tabebuia*. 9.8 % of stems classified as alive leaning; 52% of alive leaning stems were from the species *Croton bixoides*.

Table 3.2: Condition of all censused stems within study area.

Condition	No. of Stems	Percentage
Alive Standing (AS)	1700	86.2
Alive Leaning (AL)	177	9.8
Broken Stem (DB)	7	0.4
Cut Stem (CS)	14	0.7
Dead Standing (DS)	65	3.3
Dead Leaning (DL)	9	0.5
Total	1972	100

3.4.2 Taxonomic Composition

Of the 1,972 stems, censused on 1,484 individuals, 1,911 (97%) were identified to species, 47 (2.3%) were identified to genus and 14 (0.07%) were classified as unknown (Table 3.3). With the exception of *Coccothrinax barbadensis* (a palm), all species identified were woody. Overall, a total of 9 individuals were unidentified, while 61 species and 4 genera were identified and are represented within 32 families in an area of 4950 m^2. *T. pallida* and *T. heterophylla* were the only two species identified within the genera *Tabebuia* but were not recognized as separate species on every occasion, thus both species were grouped into the genera *Tabebuia* spp. As a result of the grouping, 59 species, 5 genera (64 species/genera) and 9 unidentified (unknowns) individuals were found in the study area.

Table 3.3: Woody tree species recorded in 22 plots in St. Lucia's dry forest.

Family	**Species**	**Patois/English***
Anacardiaceae	*Mangifera indica* L.	Mago, Mango*
Anacardiaceae	*Comocladia dodonaea* (L.) Urban	Bwa houk, Bwa di hou
Apocynaceae	*Plumeria alba* L.	Pashipeen, Frangipani*
Apocynaceae	*Tabernaemontana citrifolia* L.	Bwa let
Aquifoliaceae	*Ilex sideroxyloides* (Sw.) Griseb.	Ti siton
Bignoniaceae	*Tabebuia* spp.[2]	Powyé
Boraginaceae	*Bourreria succulenta* Jacq.	Pis a cheval, Pis a bouwik, Di bas blan
Boraginaceae	*Cordia nesophila* I.M. John.	maho nwé, black sage
Boraginaceae	*Cordia sulcata* DC.	Bwa sip, Sip blan, Maho gwan fey
Burseraceae	*Bursera simaruba* (L.) Sarg.	Gonmyé modi
Canellaceae	*Canella winterana*(L.) Gaertn.	Bwa kannel
Celastraceae	*Gyminda latifolia* (Sw.)	
Dichapetalaceae	*Tapura latifolia* Benth.	Bwa cot wouj
Ebenaceae	*Diospyros revoluta* Poir.	Babawa
Erythroxylaceae	*Erythroxylum havanense* Jacq.	Bwa vinet
Euphorbiaceae	*Argythamnia polygama* (Jacq.) Kuntze	
Euphorbiaceae	*Croton bixoides* Geiseler	Gwo bomn, ti bomn blan
Euphorbiaceae	*Croton* spp.	
Fabaceae	*Cassia fistula* L.	Kas
Fabaceae	*Calliandra tergemina* (L.) Benth.	Lyenn Myann
Fabaceae	*Haematoxylon campechianum* L.	Kanmpéch
Fabaceae	*Inga laurina* (Sw.) Willd.	Pwa dou
Fabaceae	*Lonchocarpus heptaphyllus* (Poir.) DC	Savonnét gwan fey
Fabaceae	*Lonchocarpus punctatus* Kunth	Savonnét ti fey
Flacourtiaceae	*Casearia decandra* Jacq.	Bwa koko kawét
Lauraceae	*Ocotea cernua* (Nees) Mez.	Lowyé gwo gwenn, Lowyé ti fey

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[2] The genera (and family) were represented by two closely related species, *T. pallida* and *T. heterophylla*

Table 3.3 – Continued

Family	**Species**	**Patois/English***
Lauraceae	*Ocotea membranaceae* (Sw.) R.	Lowyé sann, Lowyé gwan fey
Malpighiaceae	*Byrsonima spicata* (Cav.) DC.	Bwa tan
Melastomataceae	*Miconia cornifolia* (Desr.) Naudin	Bwa senn
Moraceae	*Ficus citrifolia* Mill.	Fijé
Moraceae	*Maclura tinctoria* (L.) D. Don ex Steudel.	Bwa dowanj
Myrtaceae	*Eugenia ligustrina* (Sw.) Willd.	Bwa hetti
Myrtaceae	*Eugenia monticola*(Sw.) DC.	Bwa (di bas) ti fey
Myrtaceae	*Eugenia* spp.	
Myrtaceae	*Eugenia tapacumensis* Berg.	
Myrtaceae	*Myrcia citrifolia* (Aublet) Urb. var.	Bwa gwiyé, Blackberry*
Myrtaceae	*Pimenta racemosa* (Miller) J. Moore	Bwa den
Nyctaginaceae	*Pisonia fragrans* Dum.-Cours.	Mapou
Nyctaginaceae	*Pisonia* spp.	
Nyctaginaceae	*Pisonia suborbiculata* Hemsley ex Duss.	Mapou ti fey
Ochnaceae	*Ouratea guildingii* (Planch.) Urb.	
Oleaceae	*Forestiera rhamnifolia* Griseb.	Bwa kaka wavet
Arecaceae	*Coccothrinax barbadensis* Becc.	Latanyé
Polygonaceae	*Coccoloba pubescens* L.	Bwa gwan fey
Polygonaceae	*Coccoloba swartzii* Meissner	Bwa lanmowi, Wezinyé
Rhamnaceae	*Krugiodendron ferreum* (M. Vahl.) Urb.	Bwa di fer
Rubiaceae	*Erithalis odifera* Jacq.	Bwa flambo
Rubiaceae	*Guettarda scabra* (L.) Vent.	Bwa madamn
Rubiaceae	*Morinda citrifolia* L.	Kosol chyenn, Nooni*
Rubiaceae	*Psychotria microdon* (DC.) Urb.	Bwa genton
Rubiaceae	*Randia aculeata* L.	Bwa lans
Rubiaceae	*Rondeletia parviflora* Poir.	Myen
Rutaceae	*Amyris elemifera* L.	Bwa flambo blan
Rutaceae	*Zanthoxylum microcarpum* Griseb.	Arko kwa
Rutaceae	*Zanthoxylum monophyllum* (Lam.) P	Lepinni
Rutaceae	*Zanthoxylum punctatum* Vahl.	Bwa kaptann, Lepinni
Rutaceae	*Zanthoxylum* spp.	Lepinni
Rutaceae	*Zanthoxylum spinifex* (Jacq.) DC.	Bwa bandé, Lepinni
Sterculiaceae (Malvaceae s.s.)	*Guazuma ulmifolia* Lam.	bwa lonm

Table 3.3 – Continued

Family	**Species**	**Patois/English***
Symplocaceae	*Symplocos martinicensis* Jacq.	bwa blé, zolivyé
Theaceae	*Ternstroemia peduncularis* DC.	Zabwiko pwanti, Zabwiko blan, Pan dowey
Thymelaeaceae	*Daphnopsis americana* (Miller) J.	Maho piment
Verbenaceae	*Aegiphila martinicensis* Jacq.	Bwa kabwit
Verbenaceae	*Cornutia pyramidata* L.	Bwa kasav
	Unknown 1	
	Unknown 2	
	Unknown 3	
	Unknown 4	
	Unknown 5	
	Unknown 6	
	Unknown 7	
	Unknown 8	
	Unknown 9	

3.4.3 Species Richness

Each species richness point (circles and diamonds) represents richness values from plots 1-22 and were plotted in sequential order. Amongst 22, 225 m^2 plots, species richness appears to decelerate at 4950 m^2 based on interpretation of plotted species richness values and regressions curves (Figure 3.2). Although deceleration is apparent, identifying whether more species would be found if the sampling area was increased, is not possible at this time. This is due to a lack of information on the actual extent of St. Lucia's dry forests and the number of woody species which reside within it.

Despite the deceleration, evidence of clustering of rare species was observed within plots (section 3.4.7). It is hypothesized that clusters of multiple rare species effects the shape of species area curves such that plateaus are observed where widespread common species are sampled and slight inclines occur when more then one rare species exists within a cluster. If widespread species are common and rare species are clustered, as hypothesized for other dry forests (*Hubbell*, 1979), it is hypothesized that species area curves for St. Lucia would resemble a series of plateaus and inclines if additional widespread sampling strategies were employed; however more data is needed to test this hypothesis.

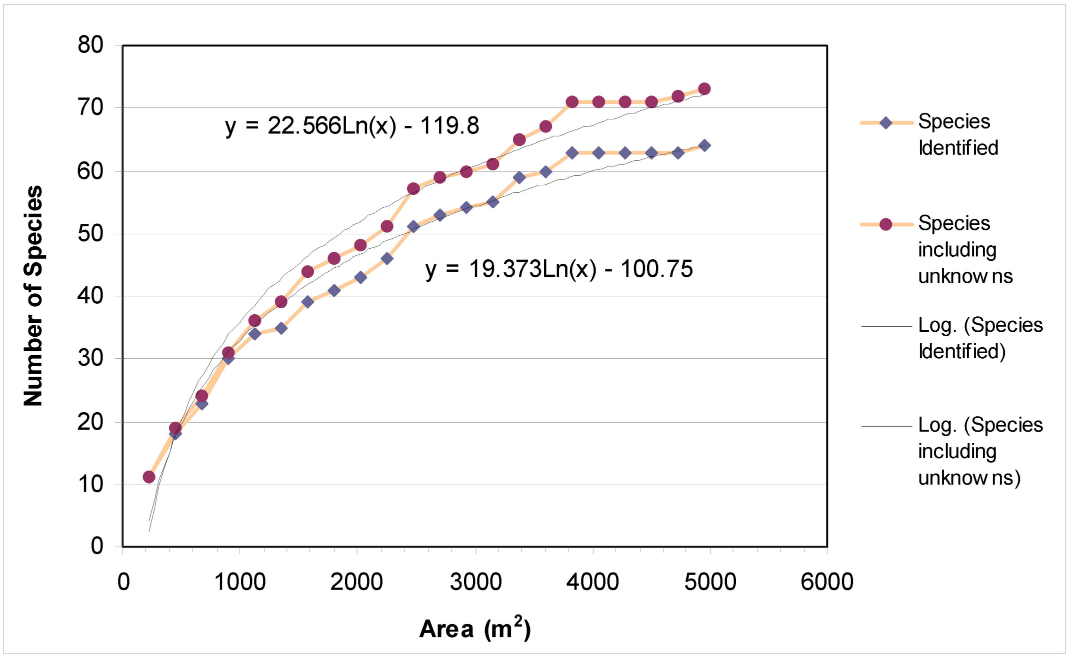

Figure 3.2: Species richness curves for woody stems sampled in 22 225m^2 plots in St. Lucia's "less-disturbed" dry forest

3.4.4 Structural and Floristic Summary

Figures italicized and underlined in Table 3.4 refer to maximum and minimum values for each heading, respectively. Omitting the unknowns, plot species richness ranges from 7 (plot 6) to 20 (plots 4 and 7), while plot family richness ranges from 6 (plots 6 and 21) to 17 families (plot 4). Plot 4 is the richest of the 22 sites having the highest family and species richness overall; average species and familial richness is 13.6 and 10.5, respectively. In addition to having the lowest species and familial richness, plot 6 has the lowest stem density and basal area; plot 6 is regarded as the most disturbed site that was surveyed for these reasons. The number of individual trees censused in each plot ranges from 36 to 127 and the overall average is 67.5, while the number of stems censused is between 42 to 146 and the average number of stems per plot is 89.6. Average plot stem density is extrapolated to 3984 stems ha^{-1} ± 1056 stems ha^{-1} and average basal area is extrapolated to 18.92 m^2ha^{-1} ± 7.94 m^2ha^{-1}. The basal area for the entire study area of 0.495 ha is extrapolated to 19.03 m^2ha^{-1}.

Table 3.4: Taxonomic richness, number of individuals, number of stems, stem density and basal area of woody species $\geq 4cm$ d.b.h. in 22, 0.225 ha plots within St. Lucia's "less-disturbed" dry forest.

Plot	**Sp.**	**Fam.**	**Ind.**	**Stems**	**Stems** ha^{-1}	**BA** (m^2ha^{-1})
1	11	9	69	94	4178	19.82
2	13	8	87	92	4089	41.49
3	12	10	50	82	3644	16.80
4	20	16	77	105	4667	22.76
5	13	10	43	57	2533	18.29
6	*7*	*6*	*36*	*42*	*1867*	*5.82*
7	20	12	52	86	3822	24.87
8	12	7	87	94	4178	20.20
9	11	8	55	106	4711	30.56
10	18	14	71	101	4489	14.52
11	15	14	58	75	3333	10.71
12	13	11	77	82	3644	14.95
13	14	11	47	68	3022	15.53
14	11	7	65	79	3511	12.47
15	19	13	115	137	6089	28.36
16	17	14	127	146	6489	21.94
17	17	12	75	108	4800	21.97
18	16	10	76	100	4444	17.47
19	10	7	49	75	3333	10.49
20	10	9	43	68	3022	8.93
21	8	*6*	58	74	3289	16.43
22	13	10	67	101	4489	21.88
Total	**64**	**32**	**1484**	**1972**	**3984**[3]	**19.03**
Mean	**13.6**	**10.2**	**67.5**	**89.6**	**3984**	**18.98**
Range	**7-29**	**6-16**	**36-127**	**42-146**	**1867-6089**	**5.82-41.49**

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[3] Stem density value for entire study area and does not represent the sum of the Stems ha^{-1} column (1972 stems in 0.495 ha extrapolates to 3984 stems in 1 ha)

Table 3.5: Overall Taxonomic Richness and Structural Characteristics of Study Area

Floristic Composition	
Total no. species/genera	65
Total no. species/genera (including unknowns)	74
Average no. species/genera/plot	13.6
Total no. families	32
Ave. no. families/plot	10.2
Structural Composition	
Total no. stems	1972
Ave. stems/plot	89.6 ±3.71
Total individuals	1484
Ave. individuals/plot	67.5 ±2.97
Total stem density (stems ha^{-1})	3984
Average plot stem density (stems ha^{-1})	3984 ±1056
Total stand basal area (m^2ha^{-1})	19.03
Ave. stand basal area (m^2ha^{-1})/plot	18.92 ±7.94
No. stems >10 cm d.b.h.	238
No. species >10 cm d.b.h.	34 (including unknowns)
Stem density (stems ha^{-1}) >10 cm d.b.h.	480
Basal Area (m^2ha^{-1}) stems >10 cm d.b.h.	9.28
Ave. plot canopy height (m)	7.07 ±1.72

3.4.5 Stem diameter distribution

A large proportion of stems (88%), were identified to be $\leq$ 10 cm d.b.h. in 22 plots of St. Lucia's dry forest (Figure 3.3A). Both the 4-5 and 5.1-10 cm basal diameter classes were rich in species, at least 80% of the species (including unknowns) identified within the study area, were found in both classes (Figure 3.3B). Although only 12% (238) of stems were found above 10 cm d.b.h., the stems were represented by 50% (39) of the species/genera (including unknowns) found within the study area. Interestingly, size class 10.1 - 15 cm basal diameter d.b.h., contains only 8.7% of measured stems, but includes 34 species (47% of all species/genera, including unknowns). Species richness for 15.1-20 cm d.b.h. stems was 19 (26%, including unknowns) and 7 (10%, including unknowns) for stems >20 cm d.b.h.

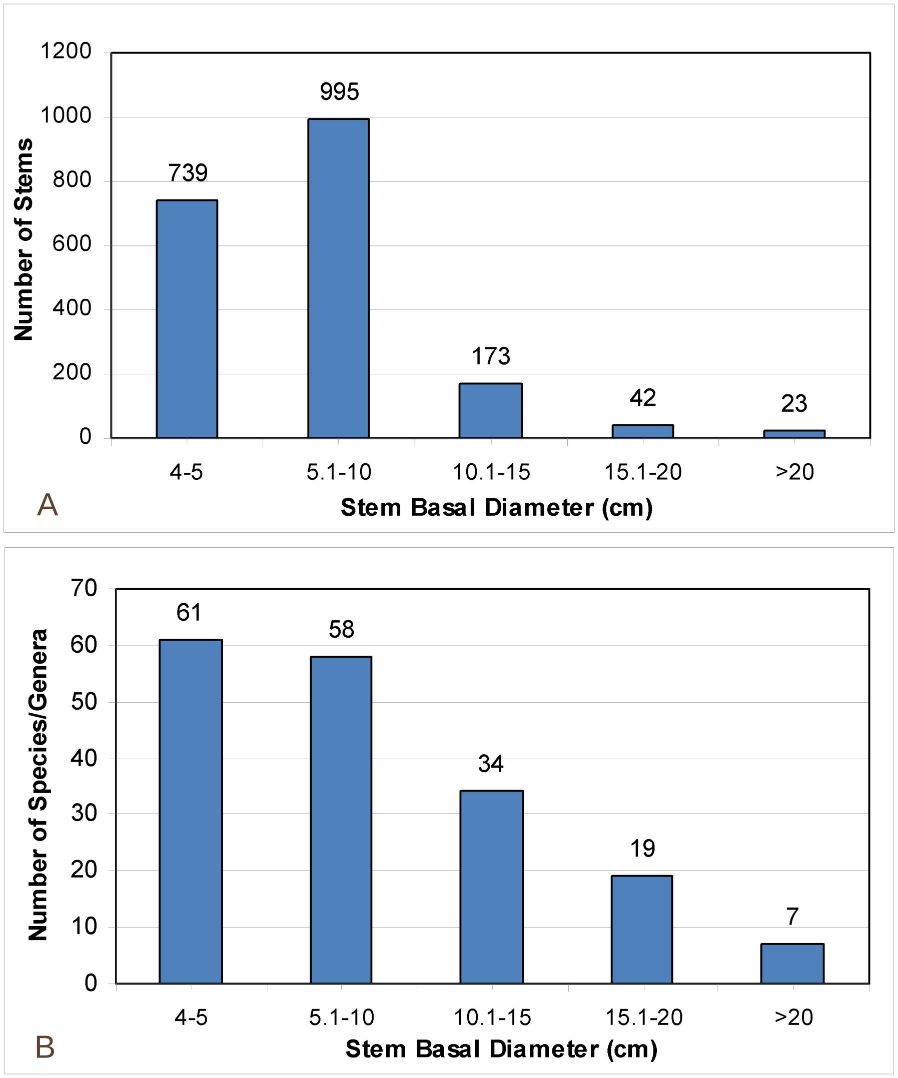

Figure 3.3: Stem and species distribution amongst basal diameter classes.

Table 3.6: Relative density, relative dominance, relative frequency, and importance values for the ten most represented woody species.

Species	$\bar{x}$ **d.b.h.**	**Den.**	**Dom.**	**Freq.**	**IV**	**IV/3**
Bursera simaruba	10.29	8.9	22.1	4.8	35.8	11.94
Tabebuia spp.	9.58	6.19	13.69	5.41	25.29	8.43
Croton bixoides	5.44	11.71	6.05	6.05	23.82	7.94
Guettarda scabra	5.54	8.01	4.65	5.41	18.08	6.03
Erithalis odifera	5.92	6.49	4.04	3.18	13.72	4.57
Coccoloba pubescens	7.48	4.61	4.87	3.82	13.30	4.43
Lonchocarpus heptaphyllus	7.55	4.21	4.53	2.87	11.61	3.87
Bourreria succulenta	5.28	3.8	2.0	3.5	9.3	3.09
Cornutia pyramidata	7.12	2.69	2.62	3.82	9.13	3.04
Pisonia fragrans	6.63	2.74	2.19	4.14	9.07	3.02

3.4.6 Floristic Representation

Species Representation

The top ten species/genera that received the highest importance value ranking are presented in Table 3.6. The ten most important species/genera were each identified in $\geq$ 40% of the plots. They represent 59.4% of all measured stems and encompass 66.8% of the total basal area (BA). The top 8 species/genera encompass half (50.3%) of the total importance value for the study area. Ranked by importance values, *Bursera simaruba* was most important despite having a lower relative frequency than the the 3 succeeding species. This may be attributed to the species high relative dominance (22%), nearly twice that of *Tabebuia* spp. and 3 to 5 times that of *Guettarda scabra* and *Erithalis odifera*.

The most frequently censused (widely dispersed) tree amongst plots was *Croton bixoides* (86% of plots), followed by *Tabebuia* spp. (77%) and *Guettarda scabra* (77%). In 10/19 plots where *C. bixoides* occurred, it was among the top two most abundant species within the plot, most commonly sharing the status of most abundant species with *B. simaruba* (plots 5, 6, 8 and 22). *C. bixoides* is also attributed with the highest stem density overall, having 109 more stems than *Tabebuia* spp. and 55 more stems than *B. simaruba*. Despite the high relative frequency and abundance of *C. bixoides*, it received the third highest importance value ranking. This is due a low relative dominance attributed to the small stem girth (mean d.b.h. 5.44 cm) of this species, relative to the 9 other species in Table 3.6. Overall, *Tabebuia* spp. was found to be among the top two species/genera with the highest relative dominance in 10/22 plots, *B. simaruba* was slightly less dominant (8/22 plots). Both *Tabebuia* spp. and *B. simaruba* were most frequently found to be among the top two species with the highest relative dominance within plots and accounted for 20% of the total importance value ranking, highlighting their overall significance within the study area.

Family Representation

Unidentified individuals were omitted from the FIV calculation, thus the total stems were reduced to 1,958 and the total stem basal area to 93,587.4 cm^2 (from 94,198.9 cm^2). In addition, the Bignoniaceae family is represented by 2 species rather than 1 genera (*Tabebuia*) since both species are known and were observed in samples; this increased the total number of species/genera to 65 for this analysis.

Despite having half the relative dominance as Burseraceae (only represented by *Bursera simaruba*), Rubiaceae had the highest FIV due to its high stem density (17% of stems identified). The majority of families were not speciose, with approximately 25/34 (74%) represented by $\leq$2 species. The most speciose families were Rubiaceae, Fabaceae, Myrtaceae, and Rutaceae, the former two representing 6 species and the latter two representing 5 species and one genera. Additionally, one species of Rubiaceae (*Morinda citrifolia*) is known to be locally cultivated (Table 3.9).

The representatives of the Myrtaceae and Rutaceae families that were only identified to genus level, *Eugenia* and *Zanthoxylom* respectively, may include species that are not listed in this study [4], thus are considered equally as speciose. Although Rutaceae was one of the most speciose families identified, it's individuals were not well represented throughout the island. Only 95 stems were censused and 5 of the 6 species were only found within 1-3 plots. The largest concentration of Rutaceae individuals was observed in plot 9 (40% of individuals within the family).

Table 3.7: Relative density, relative dominance, relative frequency, and importance values for the ten most represented woody families.

Family	**Spp.**	**Stems**	**Σ BA**	**Div.**	**Den.**	**Dom.**	**FIV/3**
Rubiaceae	6	339	9,412.8	9.23	17.31	10.06	12.20
Burseraceae	1	176	20,837.3	1.54	8.99	22.27	10.93
Myrtaceae	6	183	5,588.3	9.23	9.35	5.97	8.18
Euphorbiaceae	3	237	5,972.7	4.62	12.10	6.38	7.70
Bignoniaceae	2	122	12,899.9	3.08	6.23	13.78	7.70
Polygonaceae	2	145	6,979.5	3.08	7.41	7.46	5.98
Rutaceae	6	95	3,002.7	9.23	4.85	3.21	5.76
Fabaceae	6	184	8,869.1	9.23	9.40	9.48	9.37
Nyctaginaceae	3	103	3,775.7	4.62	5.26	4.03	4.64
Boraginaceae	3	104	3,541.7	4.62	5.31	3.78	4.57

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[4] In regards to the genera *Zanthoxylum*, *Z. martinicensis* (Lam.) DC and *Z. caribaeum* have been identified within St. Lucia's dry forests. *E. lambertiana* DC, *E. gregii* (Sw.) Poiret, *E. pseudopsidium* Jacq., *E. trititatis* DC, *E. uniflora* L of the Eugenia genera have also been identified in these forests are considered locally rare by Roger Graveson, especially *E. trititatis.*

3.4.7 Species Distributions

Widespread and Rare Species

Of all individuals censused (including unknowns), the majority of species were not widespread, 77% (56) were identified in $\leqq 5$ plots, (87.5% removing the unknowns) (Figure 3.4). Only 11 species (15% of total) occurred in at least half of the plots (Table 3.8), the most widespread being *Croton bixoides*, followed by *Guettarda scabra* and *Tabebuia* sp.

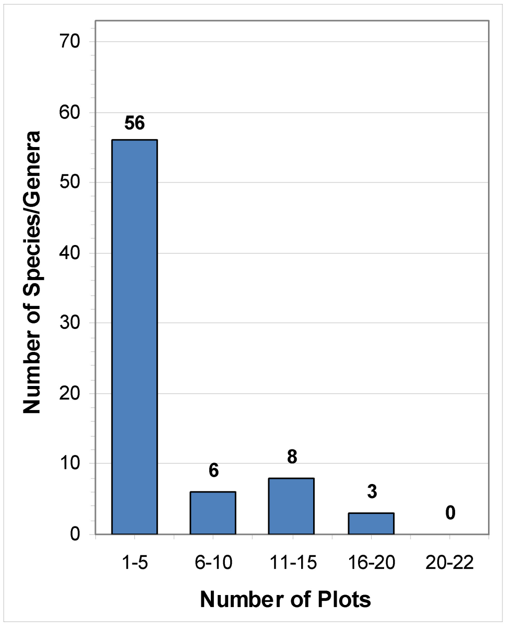

Figure 3.4: Species distribution amongst 22 plots in St. Lucia's dry forest.

Table 3.8: Widespread species occurring in ≥50% of plots within St. Lucia's less-disturbed dry forest.

Species	**No. of Plots**
Croton bixoides	19
Guettarda scabra	17
Tabebuia sp.	17
Bursera simaruba	15
Pisonia fragrans	13
Amyris elemifera	12
Coccoloba pubescens	12
Cornutia pyramidata	12
Myrcia Citrifolia	12
Coccoloba swartzii	11
Bourreria succulenta	11

A large proportion of species were rarely occurring in the study area. Including the unknowns, 56 (77%) species/genera were represented by ≤20 individuals (Figure 3.5). Approximately half (50.6%) of the species/genera were represented by less than 5 individuals. Omitting the unknowns, 26 species and 2 genera were represented by less than 5 individuals and are considered rare in this study area (Table 3.9). Species identified as rare amongst the "less-disturbed" forest and are classified as rare on St. Lucia by Roger Graveson, include *Comocladia dodonaea*, *Krugiodendron ferreum* and *Eugenia tapacumensis*. The conservation status of St. Lucia's flora has yet to be formally assessed, however local botanist and herbarium curator Roger Graveson has made some extensive observations on the presence and status of some of St. Lucia's flora. Based on these observations, the majority of flora identified as rare within this study area are indigenous and commonly found on St. Lucia. None of the species observed in this study are endemic to St. Lucia and none were found on the IUCN Red List of Threatened Species (*IUCN*, 2007b).

Among the 26 rare species and 2 genera, three are known to be cultivated by locals; *Mangifera indica* (Mango) and *Morinda citrifolia* (Noni) are both fruit trees which may have been historically planted or naturally propagated and *Cassia fistula* (Golden shower tree) has naturalized on the island after being introduced as a garden ornamental.

The single palm species *Coccothrinax barbadensus* (Latanye), was represented by two individuals, one located in plot 11, the other in plot 16. This species is reported to be rare by Roger Graveson; Latanye's rarity is likely due to the harvesting of the leaves of the palm for broom making. The brooms are produced for local market and were exported from St. Lucia for a period of ten years (1993 - 2003) until leaf supply couldn't sustain the market (*Gustave et al.*, 2006). Although full grown specimens of *Coccothrinax barbadensus* were rare, saplings were frequently observed in the understory. Given the rarity of Latanye and the market for its

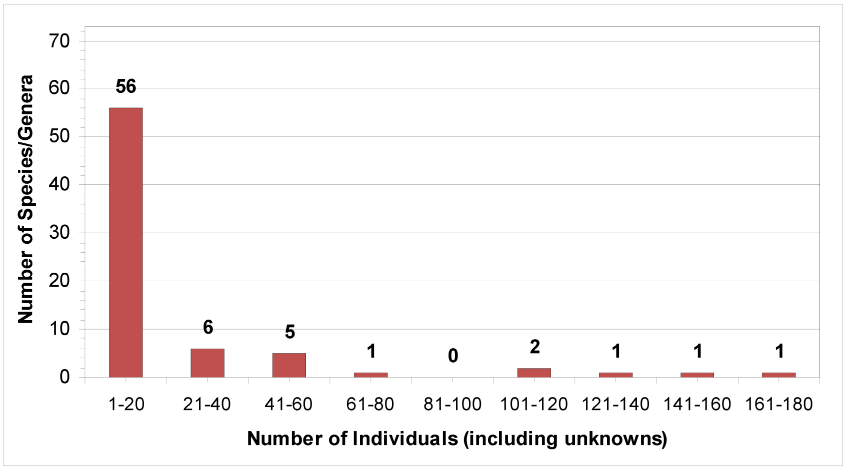

Figure 3.5: Number of individuals of each species/genera (including unknowns) in St. Lucia's "less-disturbed" dry forest.

leaves, selective harvesting may have occurred historically in this study area.

Clustering of Species

Several species were found clustering within a few plots. Clustering amongst species was analyzed by calculating a ratio of the number of individuals to the frequency of occurrence (number of plots). The number of individuals of each species (omitting unknowns) were divided by the number of plots in which they occurred. The mean of the individual/frequency ratio values was 3.5, thus species with an individual frequency ratio >3.5 were considered to be clustering. Species which were identified in ≤5 plots and had an individual/frequency ratio > 3.5 were considered to be heavily clustered. Amongst all clustering species, 54% were identified to be heavily clustered (Table 3.10).

Of the species observed to be heavily clustered, 7 were found to have >50% of their individuals within 1 plot (Table 3.11). Each of these 7 species comprise between 16.9 - 30.43 % of the individuals identified within the plot (including unknowns). Three of these species were identified in plot 9, located on the southern Peninsula of Moule à chiq, namely *Zanthoxylum spinifex*, *Zanthoxulum monophyllum* and *Cordia sulcata*. Approximately 84% of individuals of both *Zanthoxylum monophyllum* and *Zanthoxylum spinifex* were found in plot 9 and each represented at least 18% of individuals within the plot. >50% of individuals representing the species *Cordia sulcata* were also identified in plot 9 and represented at least 18% of the individuals within the plot. The species composition of plot 9 and the evidence of heavily clustered species (Table 3.11) coincides with the observations of *Hubbell* (1979) who noticed clumped patterns amongst rare species and supports the hypothesis that species dominance is never predictable within tropical dry forests (*Hubbell*, 1979). The evidence of species clustering also highlights the need for in-

Table 3.9: Rarely occurring species in study area ($\leqq 5$) individuals, number of individuals, plots where individuals were identified and rarity classification according to St. Lucia herbarium curator, Roger Graveson.

Species	**Ind.**	**Plot(s)**	**Class**
Mangifera indica	1	4	Common, cultivated
Comocladia dodonaea	1	22	Rare, indigenous
Plumeria alba	1	5	Indigenous
Ilex sideroxyloides	1	5	Very common, indigenous
Diospyros revoluta	1	11	Common, indigenous
Argythamnia polygama	1	16	Uncommon, indigenous
Ocotea cernua	1	4	Common, indigenous
Maclura tinctoria	1	9	Common, indigenous
Krugiodendron ferreum	1	11	Fairly rare, indigenous
Morinda citrifolia	1	17	Common, cultivated
Guazuma ulmifolia	1	17	Common, indigenous
Symplocos martinicensis	1	4	Common, indigenous
Aegiphila martinicensis	1	7	Common, indigenous
Tabernaemontana citrifolia	2	10	Very common, indigenous
Tapura latifolia	2	4	Very common, Lesser Antilles
Ocotea membranaceae	2	11	Common, indigenous
Inga laurina	2	17	Common, indigenous
Coccothrinax barbadensis	2	11, 15	Indigenous, fairly rare
Cassia fistula	3	1	Common, cultivated ornamental
Gyminda latifolia	3	15, 16	Common, indigenous
Zanthoxylum microcarpum	3	15	Unknown
Cordia nesophila	4	2, 3, 9	Locally common
Croton spp.	4	3, 5, 7	Common genera
Ficus citrifolia	4	5, 10, 18	Common, indigenous
Eugenia spp.	4	4, 5, 7	Common genera
Eugenia tapacumensis	4	8	Indigenous, very rare, endangered
Rodeletia parviflora	4	2, 4	Indigenous, common
Zanthoxylum punctatum	4	7, 22	Unknown

Table 3.10: Frequency (number of plots), number of individuals and individual/frequency ratios of clustering and heavily clustered* species within 22 dry forest plots on St. Lucia.

Species	**Frequency**	**Individuals**	**Ratio**
Eugenia monticola *	5	18	3.6
Eugenia tapacumensis *	1	4	4.0
Coccoloba pubescens	12	48	4.0
Myrcia citrifolia	12	53	4.4
Byrsonima spicata	7	31	4.4
*Zanthoxylum spinifex**	3	14	4.7
Pisonia sp.*	2	10	5.0
Daphnopsis americana *	3	15	5.0
*Ouratea guildingii**	3	15	5.0
Zanthoxylum sp.*	2	11	5.5
Lonchocarpus punctatus *	4	22	5.5
Eugenia ligustrina	10	59	5.9
Tabebuia sp.	17	101	5.9
*Canella winterana**	1	6	6.0
*Cordia sulcata**	2	12	6.0
*Zanthoxylum monophyllum**	2	12	6.0
Lonchocarpus heptaphyllus	9	55	6.1
Pisonia suborbiculata	6	37	6.2
*Psychotria microdon**	4	25	6.3
*Ternstroemia peduncularis**	3	19	6.3
Bourreria succulenta	11	70	6.4
Croton bixoides	19	146	7.7
Guettarda scabra	17	134	7.9
*Miconia cornifolia**	2	16	8.0
Bursera simaruba	15	161	10.7
Erithalis odifera	10	109	10.9

Table 3.11: Species, Plot number, number of individuals, proportion of all individuals of species and proportion of all plot individuals of species found heavily clustering within a particular plot (>50% of individuals).

Species	**Plot**	**Ind.**	**% Sp.**	**% Plot Ind.**
Cordia sulcata	9	10	83.3	18.2
Lonchocarpus punctatus	10	12	54.6	16.9
Miconia cornifolia	12	15	93.8	25.9
Psychotria microdon	1	21	84.0	30.4
Ternstroemia peduncularis	21	14	73.7	24.1
Zanthoxylum monophyllum	9	10	83.3	18.2
Zanthoxylum spinifex	9	12	85.7	21.8

creasing sampling ranges if species richness data is used to characterize diversity within a given region.

3.4.8 Structural Heterogeneity

Basal area variation between plots

There were significant differences between the total basal area of each plot within St. Lucia's "less-disturbed" tropical dry forest (Kruskal-Wallis test, $p < 0.05$). Each plot differed significantly with at least 2 other plots in terms of the total basal area amongst stems within each plot (where the standard critical value was $p < 0.05$; some differences were actually significant at $p < 0.01$ or $p < 0.001$ (Table 3.12). Further, plots 2, 7, 10, 11, 19 & 20 all had significantly different plot basal areas versus at least 10 other plots (Table 3.12).

Some inference can be made from stem sizes distributions within these plots. The number of large diameter stems (i.e. >10 cm d.b.h.) largely influences plot basal area and is responsible for the large number (>10) of significant differences ($p < 0.05$) observed between the six aforementioned plots. Plot 2 had an overall basal area significantly different to 19 other plots (Table 3.12). The structural variation of plot 2 can be attributed its high basal area relative to all other plots (Figure 3.6), which was twice the mean for the entire study area. The high basal area is attributed to the ten stems measured >20 cm girth, which account for 35% of all stems measured >20 cm girth. Plot 7 also had a high basal area amongst stems >10 cm d.b.h., which was the third highest overall (Figure 3.6). Conversely, plots 10, 11, 19 & 20 were depauperate in large diameter stems (<5 were >10 d.b.h.) and as a result were amongst plots with the lowest overall basal area and basal area amongst stems >10 cm d.b.h.

This analysis reveals that there is high structural (basal area) variation amongst "less-disturbed" dry forest plots in St. Lucia despite the preferential selection of

Table 3.12: Summary of the number of significant differences in basal area found using a Kruskal-Wallis test amongst 22 plots within St. Lucia's dry forest.

Plot	**$p < 0.05$**	**$p < 0.01$**	**$p < 0.001$**
1	5	1	0
2	19	15	0
3	2	1	0
4	2	1	1
5	5	1	0
6	3	2	0
7	10	7	1
8	5	2	0
9	5	2	0
10	11	3	0
11	12	5	0
12	2	1	0
13	5	0	0
14	2	2	0
15	5	1	0
16	2	2	0
17	3	1	0
18	2	1	0
19	10	2	0
20	10	2	0
21	5	0	0
22	5	1	0

low disturbance sites. It is expected that more variation would be observed if more-disturbed forests were included in this analysis. Given the variation found within this study site, it points to the difficulties in extrapolating general characteristics about dry forest formations and this analysis provides supporting evidence that these forests are complex heterogenous ecosystems. Therefore, if this much variation is found within one island, basal areas reported for larger geo-political regions should only represent the plots that were sampled and not entire islands, groups of islands or the continental Neotropics. Transects or plots representative of small areas of forest, do not represent the structural variability found within complex vegetation formations.

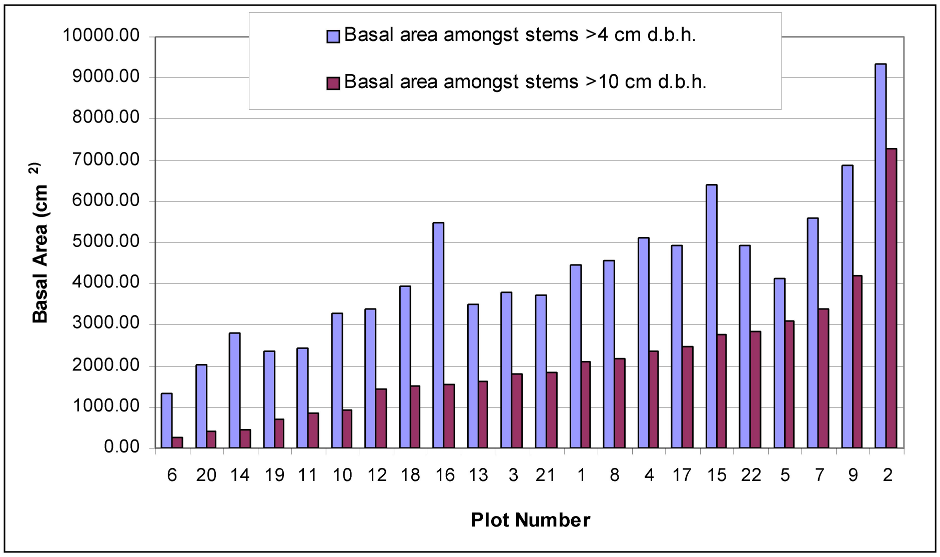

Figure 3.6: Plot basal area (cm^2) of all stems (>4 cm d.b.h.) and stems >10 cm d.b.h.

3.5 Chapter Summary

In 22, 225 m^2 plots widely dispersed amongst "less-disturbed" stands of St. Lucia's dry forest, 59 species, 6 genera and 9 unidentified individuals were found amongst 1972 stems $\geq$4 cm d.b.h. Species area curves appear to decelerate within the study area, but this should not be interpreted as a suitable sampling area for St. Lucia's dry forests as a whole, since the total dry forest area and the number of woody dry forest species that reside within these forests are unknown.

Species diversity was highest amongst stems 4-5 cm d.b.h., despite >200 stems measured between 5.1-10 cm d.b.h. Interestingly, although 88% of stems censused were $\leq$10 cm d.b.h., diversity was still high amongst stems >10 cm d.b.h., since 39 (47%) of species identified in this study (including unknowns) were found in this size class. Species richness decreased amongst large diameter stems, only 7 species (including unknowns) were found >20 cm d.b.h.

Amongst importance value rankings, 8 species accounted for approximately 50% of the importance value ranking and were all found in at least 40% of the plots. The top two most important species/genera (*Bursera simaruba* and *Tabebuia* spp.) have highest mean stem basal areas and were commonly found but were not the most abundant or widespread species found in the study area (*Croton bixoides* and *Guettarda scabra*). Family importance analysis revealed a slightly different situation than species importance analysis. Rubiaceae, which had the highest stem density, was ranked as the most important family, but was followed by Burseraceae (representing only *Bursera simaruba*), Myrtaceae and Euphorbiaceae. Although *Tabebuia* spp. had a high species importance ranking, the family Bignoniaceae was ranked 5th. The most speciose families were Rubiaceae, Fabaceae (Leguminoseae s.s.), Myrtaceae and Rutaceae, all represented by 6 species/genera, however one species of Rubiaceae is known to be locally cultivated.

Similar to observations within other tropical dry forests, few species were found to be widespread and highly clustered distributions of 7 species were observed, particularly within plot 9. No species occurred within every single plot, only 11 species/genera were found in $\geq$50% of the plots and the majority of species (77%) were found in $\leq$5 plots. This evidence supports the theory that species dominance is never predictable within tropical dry forests *Hubbell* (1979) and highlights some of the floristic heterogeneity of St. Lucia's dry forests. A large proportion of individuals identified were rare within the study area, 77% of species were represented by $\leq$20 individuals. It is hypothesized that species area curves will appear as a series of plateaus and inclines if widespread sampling regimes encounter local distributions of rare species and species with restricted ranges.

In addition to evidence for floristic heterogeneity, analysis of structural (basal area) variation between plots revealed a high degree of structural intra-island heterogeneity despite the preferential selection of sites of low disturbance. All plots had significant differences (p ¡0.05) in basal area with at least 2 plots. Plots which had a number and basal area of/amongst stems >10 cm d.b.h. and plots that had a high basal area overall and amongst stems >10 cm d.b.h. were found to have significant differences (p ¡0.05) with >10 plots. The heterogeneity is attributed to the variability in the representation of large diameter stems within each plot, since they have a large effect on total basal area calculations. A greater degree of structural variation is expected between "less-disturbed" and more disturbed stands (where selective harvesting and natural disturbances from hurricanes may reduce the number of large diameter stems within a stand). This analysis also reveals that community basal area from localized plot-based studies, should not be over-extrapolated to larger geo-political regions with high environmental heterogeneity.

These results present a summary of the characteristics of "less-disturbed" stands of St. Lucia's dry forests surveyed in this research. More research is needed to determine how these results compare to other "less-disturbed" forests before these results can be considered as characteristic of St. Lucia's dry forest. How these results compare to other Antillean and Neotropical dry forests previously research are presented in the next chapter.

Chapter 4

Comparative Analysis

4.1 Purpose of Analysis

A comparative analysis of results from the previous section is necessary in order to develop geographical context and perspective to some of the results presented in Chapter 3. The literature on Neotropical dry forests presents some interesting perspectives on the structure and composition of St. Lucia's dry forests, Antillean dry forests as a whole and how they compare to continental Neotropical dry forests. Given comparisons must take into account previous methods employed, this section also draws upon the effects specific methods have on measuring dry forest structure and composition.

4.2 Components of Analysis

4.2.1 Characteristics of More-Disturbed Antillean Dry Forests

There is a lack of plot based quantitative studies from the Antilles that could be sufficiently compared to the results from this study. Two studies which can be compared may be considerably more disturbed than the "less-disturbed" forests I sampled in St. Lucia. These include the predominately more disturbed forests of St. Lucia sampled by *Gonzalez and Zak* (1996) and the Guánica Forest, Puerto Rico, which is reported to be privy to previous disturbances (*Murphy and Lugo*, 1986b, 1995; *Ramjohn*, 2004) and was sampled by *Murphy and Lugo* (1986b). Therefore, this analysis can be perceived as a comparison between forests effected by different levels of disturbance. Caribbean dry forests have been identified as heavily disturbed ecosystems but disturbances are variable over time and space, therefore forests will exhibit different structural and floristic characteristics depending on the severity of previous disturbances.

Old-growth Caribbean dry forests have been found to have more species, genera and families than more disturbed formations (*Roth*, 1999). Additionally, younger forests have been found to have a smaller average girth and lower basal area than old-growth formations (*Roth*, 1999). Therefore, more disturbed formations than the forests I sampled, would be expected to have a higher density and species richness amongst large diameter stems. Thus the following question is raised:

1. Is there a lower density and diversity amongst large diameter stems in the more disturbed forests?

   Given that importance value rankings can be used to rank species representation within a community and provides indication of the characteristics of species which are well- or under-represented. The following questions are also raised:

2. Is there a difference in the number of species which contribute to 50% of the importance value ranking in more-disturbed forests?
3. Are there structural differences between the species which receive the highest importance value ranking in more-disturbed forests?

4.2.2 Floristic Representation

Previous research on genera and family representation within Antillean dry forests is limited to the study conducted by *Gentry* (1995). It is hypothesized that conclusions drawn from *Gentry* (1995) may not coincide with the results of this study, particularly because only two Antillean islands were used for comparison (Jamaica and Puerto Rico) and plots were concentrated in localized and small samples (0.1. ha) of each island's dry forest. Results of the analysis by *Gentry* (1995) are compared to results in the widespread sample of "less-disturbed" dry forests of St. Lucia, in order to identify whether generalizations made about Neotropical and Antillean dry forests are consistent with the results of this study. The following questions are raised in this comparison:

1. Are the genera under-represented in the Antilles also under-represented in St. Lucia?
2. Are widespread Neotropical species found on St. Lucia and are they widespread?
3. Are the genera over-represented in the Antilles also over-represented in St. Lucia?
4. Is Myrtaceae the preeminent Antillean dry forest family also preeminent in St. Lucia?
5. Is Fabaceae (Leguminosae s.s.) under-represented in St. Lucia's dry forest relative to other families I identified in the "less-disturbed" forests and relative to continental Neotropical forests?

Antillean dry forests have been reported as having a lower species richness than continental Neotropical forests (*Lugo et al.*, 2006). However, this generalization is based on conclusions drawn by *Gentry* (1995) who's results were based on Antillean dry forests averaging fewer species than continental sites. As previously mentioned, Antillean samples were limited to localized samples on two islands. Given the lack of Antillean samples used by *Gentry* (1995), woody species richness between Antillean and Neotropical dry forests is re-evaluated using data from more Antillean sites.

4.2.3 Structural Differences

A general picture of Antillean dry forest composition has been painted from limited studies conducted in small areas of dry forest that have not always recognized the influence of disturbance on the vegetation formation. Antillean dry forests are regarded as having a high density of small diameter stems, a larger proportion of multiple stemmed trees and less basal area at maturity than dry forests in the Continental Neotropics (*Murphy and Lugo*, 1986b; *Gentry*, 1995; *Van Bloem*, 2004; *Van Bloem et al.*, 2005; *Lugo et al.*, 2006). However, the only plot-based quantitative study which has compared Antillean dry forest structure to continental Neotropical dry forest structure using similar methods is *Gentry* (1995).

Results from the "less-disturbed" forests of St. Lucia cannot be directly compared to reported individual density and basal area values in *Gentry* (1995) because different methodologies were employed (see following section). Therefore, this analysis is largely a critique of prior observations by *Gentry* (1995) and draws upon evidence of structural heterogeneity within St. Lucia to support an argument against over-generalizing the structural characteristics of Antillean dry forests.

4.3 Analytical Methods for Comparing Data

Without the availability of raw data from previous studies, data comparisons are difficult to make from literature and several factors must be taken into consideration. The methods employed by different researchers all serve varying purposes and therefore differ from the methods employed in this research. In addition, how the data is analyzed and presented in literature largely effects the ability for comparison. The minimum d.b.h. I employed in this study ($\geq$4 cm) and the exclusion of cacti and lianas, affects my ability to make direct comparisons to other studies. This was a tradeoff that was made so that more plots could be completed in the time available; 0.1 ha plots or transects (as employed by *Gentry* (1995)) would have limited the study to a few select locations and would likely have not accounted for the heterogeneity observed within St. Lucia's dry forest. However, other studies that can be used for comparison have not employed the methods used by *Gentry* (1995), thus this problem would have been encountered regardless of the methods I employed.

Comparative analysis conducted using data reported in literature limits certain comparisons as it depends on how the information is presented; thus, many comparisons could not be made. Where data could be compared, methodologies varied with every study. When different methodologies are employed several questions should be asked. These questions are difficult to resolve in many cases and in some instances the format in which the results are presented inhibits comparison between study areas. How the methods outlined in Chapter 3 and the methods employed by other researchers effected the comparative analysis are discussed throughout. The questions asked in this analysis include:

> What types of vegetation are included as woody vegetation?
>
> What is the minimum size parameter (i.e. d.b.h.) employed by the researcher for including an individual within the study?
>
> What plot size was used? How were the plots dispersed? What was the total area sampled?
>
> Did the author identify a scale or level of disturbance within their study sites?
>
> Was the data extrapolated to a larger scale and how does this vary between all locations?
>
> Was the data presented as total of the area sampled or as a mean due to the use of subplots?

In reference to the last question, data which were presented as mean within sample areas (often due to the use of transects) were not used for this comparative analysis; all results are reflective of the total sample area. While the majority of data comparisons made with results presented in *Gonzalez and Zak* (1996), *Murphy and Lugo* (1986b) and *Gentry* (1995) required only a simple reconfiguration and recalculation of data, a comparative analysis of species richness between Neotropical dry forest sites was slightly more complex.

4.3.1 Species Richness Comparison

Species richness values were gathered from a review of Neotropical dry forest literature. In total, 64 species richness values from 16 studies, dispersed throughout the Neotropics, are presented. The previously mentioned questions (4.3) aided the selection of sites to include in this comparison and the analysis is discussed in the context of the methods employed by the researchers. In total, 16 species richness values from 11 Antillean dry forest sites and 47 values from 47 continental Neotropical dry forest sites are used for comparison (Table 4.1). A large proportion of published species enumeration studies were from the continental Neotropics as there is a lack of published research from the Antilles.

Antillean samples include data reported from studies in the Dominican Republic (*Roth*, 1999), Guadeloupe (*Imbert and Portecop*, 2008), Jamaica (*Kelly et al.*, 1988;

Gentry, 1995), Puerto Rico (*Murphy and Lugo*, 1986b; *Gentry*, 1995; *Lugo and Brandeis*, 2005), and St. Lucia (*Gonzalez and Zak*, 1996) and this study. In regards to continental samples, richness data is reported from studies in Argentina (*Gentry*, 1995), Bolivia (*Gentry*, 1995), Brazil (*Felfili et al.*, 2006), Columbia (*Gentry*, 1995), Costa Rica (*Gentry*, 1995; *Burnham*, 1997; *Gillespie et al.*, 2000; *Kalacska et al.*, 2004), Equador (*Gentry*, 1995), Mexico (*Gentry*, 1995; *Trejo and Dirzo*, 2002; *Segura et al.*, 2003), Nicaragua (*Gentry*, 1995; *Gillespie et al.*, 2000; *Gonaález-Rivas et al.*, 2006), Paraguay (*Gentry*, 1995), Peru (*Gentry*, 1995; *Linares-Palomino and Ponce Alvarez*, 2005) and Venezuela (*Gentry*, 1995). Since a large proportion of the data was already available from 0.1 ha plots and from Mexico, the results from *Trejo and Dirzo* (2002) include only three sites which represent the maximum, minimum and median values reported for species richness. Additional species richness data selections include the highest species value reported for 0.1 ha plots in Brazil (*Felfili et al.*, 2006) and the maximum, minimum and median values from a 1 ha sample in Peru (P) (*Linares-Palomino and Ponce Alvarez*, 2005).

Table 4.1: Neotropical dry forest study sites, plot area and literature used to collate 64 species-richness values for comparative analysis.

	Site	**Area(m^2)**	**Reported**
	Antilles		
	Domincan Republic		
1	Old Growth	6200	Roth, 1999
2	Scrub	11400	Roth, 1999
	Guadeloupe		
3	Grand-Terre	2400	Imbert & Portecop, 2008
	Jamaica		
4	Broom Hall	1000	Kelly et al., 1988
5	Round Hill	1000	Kelly et al., 1988
6	Round Hill	1000	Kelly et al., 1988
	Puerto Rico		
7	Mogotes	1000	Gentry, 1995
8	Guánica	1500	Gentry, 1995
9	Guánica	1500	Murphy & Lugo, 1986b
10	Guánica	1500	Gentry, 1995
11	Island wide	14700	Lugo and Brandeis, 2005
	St. Lucia		
12	Island wide	4950	Hansen, 2008
13	Island wide	4950	Hansen, 2008
14	Island wide	4950	Hansen, 2008
15	East Coast	6200	Gonzalez & Zak, 1996
16	East Coast	6200	Gonzalez & Zak, 1996
17	East Coast	6200	Gonzalez & Zak, 1996

	Continental Neotropics		
	Argentina		
18	Salta, Salta	1000	Gentry, 1995
19	Riachuelo, Corrientes	1000	Gentry, 1995
20	Parque El Rey, Salta	1000	Gentry, 1995
	Bolivia		
21	Chaquimayo, La Paz	1000	Gentry, 1995
22	Sana Cruz, Santa Cruz	1000	Gentry, 1995
23	Quia paca, Santa Cruz	1000	Gentry, 1995
	Brazil		
24	Gama-Cabeca de Veado	1000	Felfili et al., 2006
	Columbia		
25	Galerazamba, Bolivar	1000	Gentry, 1995
26	Tayrona, magdalena	1000	Gentry, 1995
27	Loma de los Colorados, Bolivar	1000	Gentry, 1995
28	Lomas de Santo Tomas, Tolima	1000	Gentry, 1995
29	Coloso, Sucre	1000	Gentry, 1995
	Costa Rica		
30	Guancaste	10000	Burnham, 1997
31	Guancaste (upland)	1000	Gentry, 1995
32	Guancaste (gallery)	1000	Gentry, 1995
33	Santa Rosa	1000	Gillespie et al., 2000
34	Palo Verde	1000	Gillespie et al., 2000
35	Santa Rosa	6000	Kalacska, 2004
36	Santa Rosa	10000	Kalacska, 2004
37	Santa Rosa	10000	Kalacska, 2004
	Equador		
38	Capeira, Guayas	1000	Gentry, 1995
39	Perro Muerte, Manabi	1000	Gentry, 1995
	Mexico		
40	Chamela Reserve	1000	Gentry, 1995
41	Chamela Reserve	1000	Gentry, 1995
42	Chamela Reserve	1000	Gentry, 1995
43	Chamela Reserve	2400	Segura et al., 2003
44	Chamela Reserve	2400	Segura et al., 2003
45	Chamela Reserve	2400	Segura et al., 2003
46	Chamela Reserve	2400	Segura et al., 2003
47	Caleta, Mich.	1000	Trejo and Dirzo, 2002
48	Calipam, Pue.	1000	Trejo and Dirzo, 2002
49	Jocotipac, Oax.	1000	Trejo and Dirzo, 2002
	Nicaragua		
50	Chacocente Reserve	10000	Gonzalez-Rivas et al., 2006
51	La Flor Reserve	1000	Gillespie et al., 2000

52	Chacocente Refuge	1000	Gillespie et al., 2000
53	Ometepe Reserve	1000	Gillespie et al., 2000
54	Masaya National Park	1000	Gillespie et al., 2000
55	Cosiguina Reserve	1000	Gillespie et al., 2000
	Paraguay		
56	Fortin Teniente Acosta	900	Gentry, 1995
57	Fortin Teniente Acosta	600	Gentry, 1995
	Peru		
58	Cerros de Amotape	1000	Gentry, 1995
59	Tarapoto	1000	Gentry, 1995
60	Cerros de Amotape	10000	Linares-Palomino & Ponce Alvarez, 2005
61	Cerros de Amotape	10000	Linares-Palomino & Ponce Alvarez, 2005
	Venezuela		
62	Boca de Uchire	1000	Gentry, 1995
63	Los Llanos	500	Gentry, 1995
64	Blohm Ranch	1000	Gentry, 1995

4.4 Results and Discussion

4.4.1 Comparison to More-Disturbed Antillean Dry Forests

Diversity Amongst Stem Diameter Classes

St. Lucia:

Stem density and species richness I observed in the "less-disturbed" dry forests of St. Lucia is compared to results from predominately more disturbed forests of St. Lucia, reported by *Gonzalez* (1994) and *Gonzalez and Zak* (1996). A higher stem density and species richness was observed amongst stems >4 cm d.b.h. in the "less-disturbed" forests and is mainly attributed the use of sub-plots by *Gonzalez and Zak* (1996), except for large diameter stems. The lower stem density and species richness amongst stems >14.5 cm d.b.h. reported by *Gonzalez and Zak* (1996) is attributed to the placement of 2/3 of the plots within "secondary scrub forest". It may also be attributed to the widespread sampling regime I employed, but further research is needed to verify range restrictions of rare species.

The density of stems >4 cm d.b.h. was higher overall and amongst all size classes in the "less-disturbed" forests, in comparison with predominately more disturbed forests of St. Lucia. Amongst stems >4 cm d.b.h., the extrapolated stem density in "less-disturbed" stands is 3806 stems ha^{-1}, more then twice the density (1437 stems

ha^{-1}) observed by *Gonzalez and Zak* (1996) for this size class. Amongst the four diameter at breast height classes compared (Figure 4.1), stem density was 2.3-2.8 times higher amongst stems 4.1-7.0, 10.6-14.0 and >14 d.b.h. and approximately 6 higher amongst stems 7.1-10.5 d.b.h. in the "less-disturbed" stands.

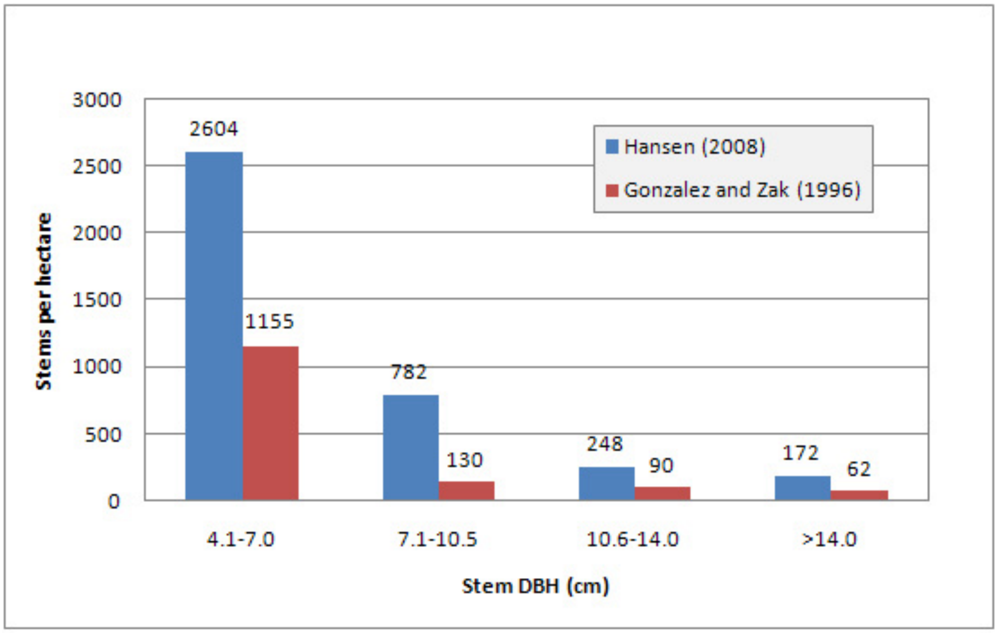

Figure 4.1: Stem density observed in "less-disturbed" stands of St. Lucia's dry forest and predominately more-disturbed forests as reported by *Gonzalez and Zak* (1996).

Species richness was also higher in the "less-disturbed" stands despite the inclusion of stems >1 cm d.b.h. and non-woody species (i.e. vines and cactus) by *Gonzalez and Zak* (1996). *Gonzalez* (1994) and *Gonzalez and Zak* (1996) reported 50 species, genera and families within 6200 m^2 of dry forest while species richness within a smaller total area 4950 m^2 of "less-disturbed" forest was 64 species/genera or 73 species/genera including unknowns. The most notable difference was observed amongst stems >14.5 cm d.b.h.; *Gonzalez and Zak* (1996) report only two species which were measured above this girth, namely *Tabebuia pallida* and *Bursera simaruba*. In contrast, 172 stems represented by 22 species >14.5 cm d.b. were found in the "less-disturbed" forests (Table 4.2).

The lower stem density and diversity reported by *Gonzalez and Zak* (1996) is partially attributed to their use of subplots. The subplot methodology employed by *Gonzalez and Zak* (1996) only provided an area of 3 x 3 m for sampling stems between 1 - 8 cm d.b.h. and a 5 x 5 m area for measuring stems 8 - 15.5 cm d.b.h. within each of the 62 plots. This equates to a total area of only 558 m^2 for stems 1 - 8 cm d.b.h. and 1550 m^2 for stems 8 - 15.5 cm d.b.h., considerably less area than I provided for sampling stems between 4-15.5 cm d.b.h. Given that 80% of the species I identified (including unknowns) had stems between 7.1-10.5 cm d.b.h., the subplots used by *Gonzalez and Zak* (1996) were insufficient at capturing the diversity amongst dry forest flora and may actually be misrepresentative of species diversity within each larger 10 x 10 plot.

The lower stem density and species richness observed amongst large diameter stems (>14.5 cm d.b.h.) by *Gonzalez and Zak* (1996) is not attributed to their use of subplots, since a total area of 6200 m^2 (62, 10x10 m plots) was provided for measuring stems >15.5 cm d.b.h. It is instead attributed to structural and floristic differences between the "less-disturbed" and predominately more disturbed dry forests of st. Lucia; more-disturbed forests appear to have a lower density, thus a lower species richness of large diameter trees. This could be attributed to the early successional stage of the forest, selective harvesting of trees or stems, or high natural disturbance from winds. Worthy of note is the observation made by *Gonzalez and Zak* (1996) who reported only 3 species >10 cm d.b.h. in the "secondary scrub forest" and 8 species >10 cm d.b.h. were identified in the "less-disturbed forest".

The higher species richness amongst large diameter stems in St. Lucia's "less disturbed" forest could also attributed to the wide-spread sampling regime I employed. Amongst the species identified as rare amongst the study area (Table 3.9), 4 species not known to be cultivated (namely, *Inga laurina, Cordia nesophila, Ficus citrifolia* and *Eugenia tapacumensis*) were all found to have stems >10 cm d.b.h., thus are considered trees and were not considered rare in this study due to the minimum d.b.h. employed. These rarely occurring trees (>10 cm d.b.h.) were all found in 5 separate plots (plots 5, 8, 9 $ 17), representing 2 plots from the west coast, 1 from Moule á Chique and 1 from the central-east coast. It is hypothesized that the wide-spread sampling regime was more effective at capturing species with regionally restricted ranges, however more research would be needed to verify whether these species do have restricted ranges.

Guánica Forest:

Similarly, Guánica Forest sampled by *Murphy and Lugo* (1986b) has a lower diversity amongst large diameter stems in comparison to "less-disturbed" stands of dry forest on St. Lucia. *Murphy and Lugo* (1986b) reports only 9/34 (26%) species to be >10 cm d.b.h., where 34/64 (53%) species/genera (omitting unknowns) were identified in St. Lucia's "less-disturbed" stands above this girth. Although this could be attributed to the larger total sampling area (4950 m^2) compared to (1500 m^2) and the widespread plot placement I employed, the low proportional representation (25%) of species >10 cm may be indicative of more disturbance in Guánica Forest but further research is needed.

A more widespread inventory of dry forests throughout the entire island of Puerto Rico (*Lugo and Brandeis*, 2005) revealed the diversity amongst large stems (>12.5 cm) to be >3 times what was found in Guánica. Based on the higher diversity amongst large diameter stems observed in this study and by *Lugo and Brandeis* (2005), it appears that Antillean dry forests have a larger diversity amongst large diameter stems when sample area is increased and dispersed widely across the island.

Table 4.2: Species with stems ≥14.5 cm d.b.h. censused within St. Lucia's "less-disturbed" forest.

Species	No. stems	Percent
Bourreria succulenta	1	1.3
Bursera simaruba	28	35.9
Byrsonima spicata	1	1.3
Canella winterana	1	1.3
Casearia decandra	1	1.3
Coccoloba pubescens	2	2.6
Cordia sulcata	1	1.3
Cornutia pyramidata	2	2.6
Croton spp.	1	1.3
Daphnopsis americana	3	3.8
Eugenia spp.	1	1.3
Ficus citrifolia	1	1.3
Guettarda scabra	3	3.8
Haematoxylon campechianum	4	5.1
Inga laurina	2	2.6
Lonchocarpus heptaphyllus	4	5.1
Mangifera indica	1	1.3
Pisonia fragrans	1	1.3
Tabebuia spp.	17	21.8
Ternstroemia peduncularis	1	1.3
Zanthoxylum spp.	1	1.3
Zanthoxylum spinifex	1	1.3
Totals: 22 Species	78	100.0

Table 4.3: Relative density and basal area results, for first and second ranked species according Importance Value (IV) indices, between this study and results reported by *Gonzalez and Zak* (1996) for Eastern St. Lucia and by *Murphy and Lugo* (1986b) for Guánica Forest, Puerto Rico.

IV Rank	Location	Species	Rel. Dens.	Rel. BA
1	St. Lucia	*Bursera simaruba*	8.9	22.1
2	St. Lucia	*Tabebuia* spp.	6.19	13.69
1	East St. Lucia	*Guettarda scabra*	33.23	11.09
2	East St. Lucia	*Croton* spp.	11.67	8.53
1	Puerto Rico	*Gymnanthes lucida*	21.52	13.84
2	Puerto Rico	*Exostema caribaeum*	7.28	9.12

Species Representation

The number and types of species which received the highest importance value rankings in Guánica Forest, Puerto Rico sampled by *Murphy and Lugo* (1986b) and the predominately more disturbed forests of St. Lucia sampled by *Gonzalez* (1994) and *Gonzalez and Zak* (1996) supports the assumption that structural and floristic differences indicative of disturbance would be identified in this comparison.

Three more species contributed to 50% of the importance value ranking in the “less-disturbed” stands of St. Lucia’s dry forest in comparison with species importance value rankings in predominately more-disturbed forests of St. Lucia and the reportedly disturbed Guánica Forest, Puerto Rico. *Gonzalez and Zak* (1996) and *Murphy and Lugo* (1986b) report 5 species to account for approximately 50% the importance value ranking, while 8 were reported in this study (Table 3.6). This may be due to the larger sampling area I employed which captured more species, however the characteristics of species which dominate the importance value rankings reported by *Gonzalez and Zak* (1996) and *Murphy and Lugo* (1986b) are notably different to what I observed.

While species/genera with the highest relative basal area were found to have the highest IV ranking in the “less-disturbed” dry forests of St. Lucia, first and second ranking species/genera and first ranking species found by *Gonzalez and Zak* (1996) and *Murphy and Lugo* (1986b) respectively, had the highest relative stem density (Table 4.3). Thus, species with large diameter stems received a higher importance value ranking in “less-disturbed” forests, rather than species with multiple small diameter stems. *B. simaruba* and *Tabebuia* spp. were commonly observed in “less-disturbed” stands as tall, large diameter trees with minimal coppicing (personal observation).

Overall this analysis reveals that there are structural and floristic differences between Antillean dry forests, particularly between dry forests of differing levels of disturbance. This supports previous observations by *Roth* (1999) and *Kalacska et al.* (2004) and researchers should attempt to recognize these differences when selecting locations for plot placement if their results will serve to characterize Antillean dry forest structure and composition.

4.4.2 Antillean Dry Forest Floristics

The only analysis of genera and family representation amongst Antillean dry forests is the research presented in *Gentry* (1995), thus comparisons can only be made with generalizations made from this research.

Absent and Widespread Genera

In support of Gentry's observations, the genera *Arrabidaea, Cletis, Capparis, Combretum, Pithecellobium, Peterocarpus* and *Paullinia*, lacking in Antillean samples were not identified within "less-disturbed" forests of St. Lucia. *Gentry* (1995) also observed *Tabebuia* to be the most widespread dry forest genus; *Tabebuia* was represented in every phytogeographic region (including the West Indies, Mexico, Southern subtropics, Northern Columbia and Venezuela and Coastal Equador and Peru). Given *Tabebuia* was represented by two species and was well dispersed amongst study sites (17/22 plots), it is also amongst the most widespread genus within St. Lucia's "less-disturbed" forest.

Other genera found to be among the most widespread in the Neotropics include *Casearia, Trichilia, Erythroxylum, Arrabidaea, Randia, Capparis, Bursera, Acacia* and *Coccoloba* (*Gentry*, 1995); 5 of 9 were identified in this study. *Bursera* and *Coccoloba* were the only genera which were represented by wide-spread species in "less-disturbed" stands of St. Lucia's dry forest (Table 3.8). *Bursera simaruba* was found to have the highest species importance value amongst "less-disturbed" dry forests of St. Lucia and in a widespread sample of Puerto Rico's dry forest (*Lugo and Brandeis*, 2005). The genera has also been identified to be common in Mexico (*Pennington et al.*, 2006) and may be widespread throughout other dry forests of the Neotropics; whether it is more widespread than *Tabebuia* requires further analysis. Of the remaining 7 widespread genera mentioned by *Gentry* (1995), 2 were identified but were not widespread in St. Lucia's "less-disturbed" forests *Casearia, Erythroxylum* & *Randia*) and 4 were absent (*Trichilia, Arabidaea, Capparis* & *Acacia*).

Over-Represented Genera

Based on the species-richness of Genera observed in the 4 Antillean sites (2 in Puerto Rico, 2 in Jamaica) reported in *Gentry* (1995), the genera *Coccoloba, Eu-*

genia, Erythroxylum and to a lesser extent *Drypetes* and *Casearia* were identified to be over-represented in Antilles. The most speciose genera within this study was *Zanthoxylum* (4), followed by *Eugenia* (3), *Pisonia* (2), *Ocotea* (2), *Cordia* (2), *Lonchocarpus* (2) and *Coccoloba* (2). Amongst the genera that *Gentry* (1995) listed as over-represented in the Antilles, *Coccoloba* and *Eugenia* were the only genera in this study that were well represented in terms of numbers of species, however they also had a high relative density, dominance and frequency. *Erythroxylum* and *Casearia* genera were found in this study area, but were only represented by 1 species and *Drypetes* was not identified in this study. This comparison reveals that the genera *Eugenia* and *Coccoloba* are also speciose in St. Lucia, adding support to the observations by *Gentry* (1995). However, since only one species represented the genera *Erythroxylum* and *Casearia* and *Drypetes* was not identified, conclusions generated from *Gentry* (1995) may only be reflective of the area studied and should not be generalized to the entire Antillean Archipelago.

The use of the term "over-represented" in literature is cautioned since the context in which it was used by *Gentry* (1995) only refers to how speciose a particular genus was and is not reflective of the relative density, dominance or frequency of stems or individuals. If I were to use this term, *Zanthoxylum* would be regarded as over-represented amongst St. Lucia's "less-disturbed" forests, since it was the most speciose genera. I would be hesitant to characterize Zanthoxylum as over-represented, since the species only represents 3% of individuals censused in this study, 50% of which were identified in one plot. This observation points to the issues of generalizing plot data from a small localized area to larger landscapes or geo-political units. Overall, it appears a more comprehensive analysis of genera representation within Neotropical dry forests is needed to identify the ecological importance of genera within Antillean dry forests.

4.4.3 Antillean Dry Forest Families

Is Myrtaceae Preeminent in St. Lucia?

The observation that Myrtaceae is the "preeminent" or "predominate" Antillean dry forest family (*Gentry*, 1995; *Lugo et al.*, 2006; *Pennington et al.*, 2006) is only partially supported by results from this research. Myrtaceae was identified to be the pre-eminent family by *Gentry* (1995) based on the family being the most speciose in the Round Hill (top), Jamaica samples, while tying for most speciose with Euphorbiaceae and Rubiaceae in the Mogotes Naveraz, Puerto Rico sample. In regards to this study, Myrtaceae tied with Rutaceae, Rubiaceae and Fabaceae as the most speciose families, each represented by 6 species/genera. In regards to genera representation within these families, Rutaceae is heavily represented by the genus *Zanthoxylum* (5/6), Myrtaceae is represented by 3 genera (*Eugenia*, *Myrcia* and *Pimenta*), while Rubiaceae and Fabaceae are each represented by 6 genera. The majority of individuals identified from the Myrtaceae family were *Myrcia citrifolia* and *Eugenia ligustrina* (72%), both species occurred in approximately half of the plots. A similar situation is observed with Rubiaceae; the family is heavily dominated by the two species *Guettarda scabra* and *Erithalis odifera*, representing 85% of the individuals identified from the family. Individual representation within the Rutaceae and Fabaceae families is more dispersed amongst the species representing the family (Table 3.7). If "preeminence" was based on genera representation and the spread of the family throughout the study area, Rutaceae and Fabaceae would be the preeminent dry forest family in this study.

Using family importance value rankings, the most represented families in this study area was Rubiaceae, followed by Burseraceae, Fabaceae, Myrtaceae then Euphorbiaceae. Interestingly, *Gentry* (1995) identified Rubiaceae, Myrtaceae, and Euphorbiaceae to be unusually prevalent in Round Hill, Jamaica, relative to other dry forests in the Neotropics. It appears that this observation may not be unique to Jamaica.

Is Fabaceae Species-Rich in St. Lucia?

Fabaceae (Leguminoseae s.s.) is regarded as the most species-rich family in the Neotropics, with the exception of the Caribbean (*Gentry*, 1995; *Pennington et al.*, 2006). Interestingly, Fabaceae tied for the most species/genera rich family with Rutaceae, Myrtaceae and Rubiaceae in this study. However, based on results from *Gentry* (1995), 6 species within 0.495 ha of forest is much lower than the average of 12 species per family averaged from 47, 0.1 ha continental samples. Thus, this analysis reveals that Fabaceae is among the most species-rich families in "less-disturbed" stands of St. Lucia's dry forests but is not as species-rich as some continental dry forests.

4.4.4 Species Richness Comparison amongst Neotropical Samples

Richness of St. Lucia's Less-Disturbed Forests

The species/area regression lines from this study (first presented in Figure 3.2) were superimposed on the richness values collected from Neotropical dry forest literature (Figure 4.2). Based on the curvature of the line, it appears that St. Lucia's dry forest sampled in this study are richer than Guánica Forest Puerto Rico and Hog House Hill, Jamaica, which both used a minimum d.b.h. of $\geq$2.5 cm. Data from these study sites (*Murphy and Lugo*, 1986b; *Kimber*, 1988) were used by *Gentry* (1995) to compare Antillean dry forests to continental forests. In comparison with the other 1000 m^2 areas sampled, St. Lucia is lower in species richness than the majority of samples but has a greater richness than dry forests sampled in Paraguay and Argentina, given that a lower d.b.h. ($\geq$2.5 cm) was employed and liana's were included (*Gentry*, 1995). If the regression line was extended further, it would appear that St. Lucia's forests are actually comparable in richness to the widespread sample of Puerto Rico's forest (*Lugo and Brandeis*, 2005); however the 88 species include seedlings $\leq$ 2.5 cm d.b.h. and saplings 2.5-3.9 cm d.b.h, which were not included in this study, thus species richness may be higher amongst St. Lucia's "less-disturbed" forest (if more area was sampled).

Areas of High Woody Stem Species Richness

Among the areas of 1000 m^2 surveyed, continental dry forests in Oaxaca, Mexico (site 54) had the highest species richness, followed by dry forests in Columbia (site 27) and three sites (40-42) in Chamela-Cuixmala Reserve, Mexico. The next richest sites are in Peru, Columbia, and Costa Rica, all of which have 75 species/1000 m^2. Interestingly, 75 species/1000 m^2 is identical to the species richness found on Broom Hill, Jamaica for stems $\geq$3 cm d.b.h. by *Kelly et al.* (1988). This location was not included in *Gentry* (1995), likely because lianas were not censused at this location.

Considering the samples from Peru (site 59), Columbia (site 29) and Costa Rica (site 34) included lianas and a lower minimum d.b.h. was employed (*Gentry*, 1995), the richness of woody trees within the Broom Hill, Jamaica site is considered greater than these continental forests and may be more comparable to the richness observed in Chamela-Cuixmala Reserve, Mexico, if liana's were included. Although dry forests in the Chamela-Cuixmala Reserve were among the richest sites, a study conducted in the same forest by *Segura et al.* (2003), reveals a more variable species richness amongst stems $\geq$5 cm d.b.h. (MX circles). Based on the regression line, this forest has a similar species richness to that reported for "less-disturbed" stands of St. Lucia's dry forest. What this reveals is woody stem species richness reported in this study and by *Kelly et al.* (1988) at Broom Hill, Jamaica, may be similar to one of the richest continental dry forests. This analysis highlights the need for further research and questions the generalization that Antillean dry forests are less species-rich than continental forests, at least amongst tree species.

Other sites which appear to have a high richness are difficult to compare due to the different minimum d.b.h. parameter employed. The richness observed amongst woody stems in old growth dry forests in the Dominican republic (triangle DR(old growth)) appears to be amongst the richest sites and appear to be richer than late successional dry forests in Costa Rica (CR(late)). However, the old growth Dominican Republic sample was measured using a minimum height parameter of 1.5 m (*Roth*, 1999) and the late successional dry forest in Puerto Rico was measured using a minimum d.b.h. of >5 cm.

Amongst other studies which employed a >10 cm minimum d.b.h., species richness in this study (STL(>10)) was much higher than observed in Peru (P) by *Linares-Palomino and Ponce Alvarez* (2005), since only 6 species >10 cm d.b.h. were observed in 1 ha of dry forest. Interestingly, *Gentry* (1995) reports 41 species >10 cm d.b.h in the same Cerros de Amotape region in Peru (but different plot location), in only 0.1 ha of dry forest. This variation again highlights the heterogeneity in species richness observed even between similar dry forest regions and how making extrapolations beyond even the same reserve, let alone political unit (i.e. country), can misrepresent a regions biodiversity.

Species Richness and Disturbance

Both *Roth* (1999) and *Kalacska et al.* (2004) report a difference in species richness amongst forest characterized as "scrub" or "early successional" respectively, in relation to "old growth" and "late successional" forests. Based on a hypothetical extension of the regression lines, species richness in St. Lucia's dry forest would appear to be higher than the "scrub" and "early successional" forests in the aforementioned studies. Given that species richness in this study was also higher than Guánica Forest, Puerto Rico and predominately more disturbed forests in St. Lucia, this observation also supports the argument that there are structural and floristic differences between "less-disturbed" and more disturbed dry forests.

4.4.5 Structural Comparisons

Do Antillean dry forests have a high stem density?

Gentry (1995) reports the number of individuals (>2.5 cm d.b.h) found at each location; extrapolated to the hectare, individual density ranges from 1070-6590 individuals ha^{-1} for all sites except for Guánica Forest, which is reported to have 12170 individuals ha^{-1} (*Murphy and Lugo* (1986b) reports 14, 0007 stems ha^{-1}). The Antillean forests individual density for the three sites outside of Gánica Forest is 4180, 6590 and 5570 individuals ha^{-1}. Individual density amongst continental sites ranged from 1410-4340 individuals ha^{-1}, hence the author's conclusions that Antillean dry forest sites had higher stem density than continental forests.

It is difficult and essentially purposeless to compare any other stem density results to results presented in *Gentry* (1995) since disturbance was not taken into account during site selection and it is unclear if the number of individuals represent the number of stems or individual species. However, worthy of mention is the intra-island variability in stem density found in St. Lucia's "less-disturbed" forests. Stem density (1867-6489 stems ha^{-1}) and individual density (1600-5644 stems ha^{-1}) within St. Lucia's "less-disturbed" forest was found to be just variable as the individual density reported by *Gentry* (1995) for sites located throughout the Neotropics, outside of Guánica Forest. Therefore, any generalizations made about Antillean dry forest stem density from results reported from *Gentry* (1995), Guánica Forest (sampled by *Murphy and Lugo* (1986b) and any other localized plot based study should be avoided.

Do Antillean Dry Forests have a Low Basal Area?

Gentry (1995) reports Antillean dry forest basal areas to range from 17.8-48.1 m^2ha^{-1} and continental samples ranged from 13.1-57.2 m^2ha^{-1}. Interestingly, both

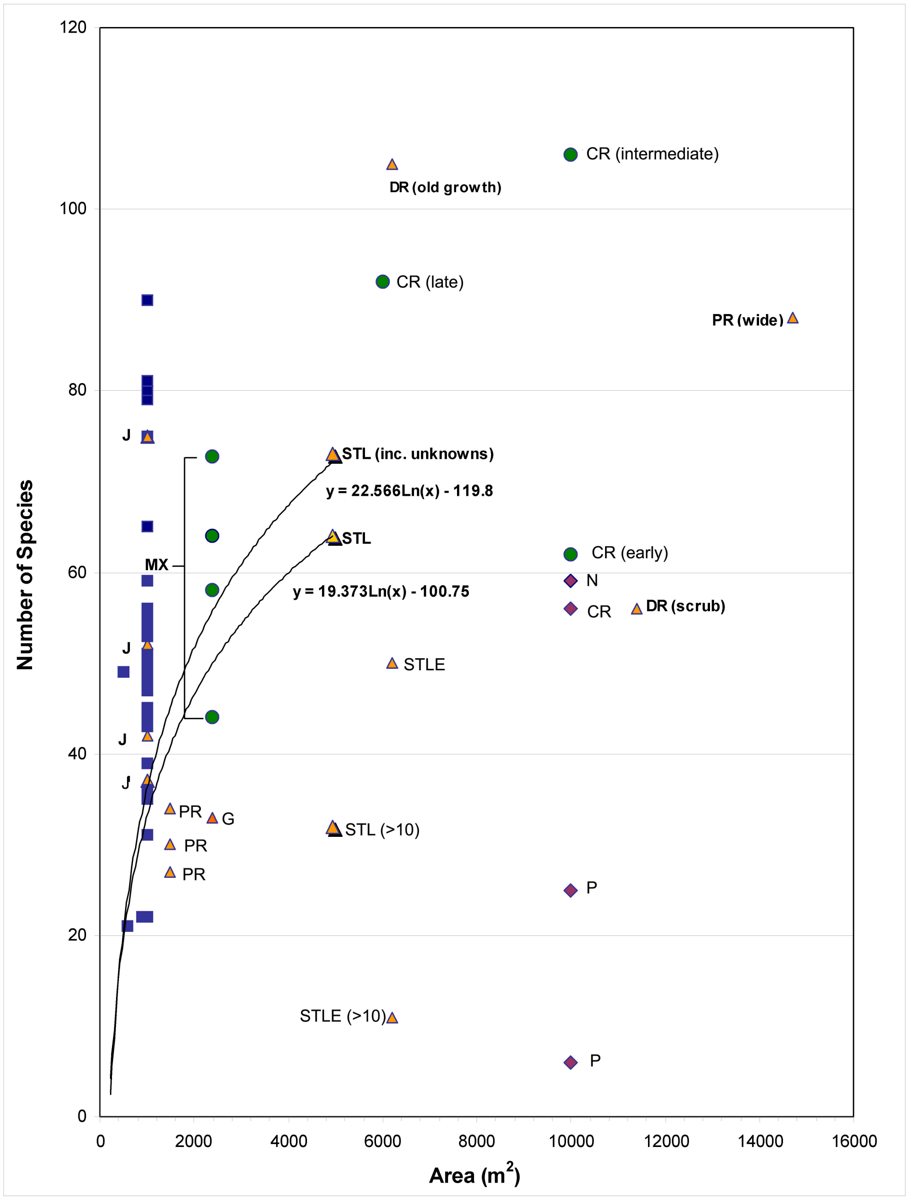

Figure 4.2: Log of species/area curves for from 22 samples of woody flora ≥4 cm d.b.h. in 4950 m^2 dry forest in St. Lucia and 64 species richness values reported from 11 Antillean and 47 continental Neotropical dry forest sites (including this study). △ = Species vs. area reported for woody plants in Antillean dry forests. The minimum d.b.h. reported for each location is: ≥2.5cm, >5 cm and > 10 cm in Puerto Rico (PR), ≥2.5 cm in the Dominican Republic (DR), ≥3 cm in Jamaica (J), ≥10 cm in Guadeloupe (G), ≥1 cm and >10 cm in Eastern St. Lucia (STLE), and ≥4 cm and >10 cm from this study (shadow triangle). ☐ = Species vs. area for woody plants ≥2.5 cm d.b.h. in continental Neotropical forests. ○ = Species vs. area for woody plants ≥5 cm in dry forests in Costa Rica (CR) and Mexico (MX). ◇ = Species vs. area for woody plants ≥10 cm d.b.h. in Costa Rica (CR), Nicaragua (N) and Peru (P).

the minimum and maximum basal area values reported for the Antilles were from Puerto Rico, highlighting evidence of intra-island variability in dry forest structure. The basal area range reported in this study (5.82-41.49 m^2ha^{-1}) is also large and the analysis of basal area variation between plots (section refbasalvar) also supports the argument that Antillean dry forests have a high degree of intra-island variability. Given these observations of intra-island variability, it is also recommended that generalizations made about Antillean dry forest basal area from localized plot-based inventories be avoided.

In comparison to wet forests, dry forest basal area is reportedly lower based on the analysis presented in *Murphy and Lugo* (1986b). However this analysis is also based on ranges developed from results reported from research that employed different methodologies. Comparing basal area and stem density between study sites is very complex and several factors should be considered. Firstly, stem density and basal area is often extrapolated to 1 ha, thus smaller total sampling areas require larger extrapolations. Also important are minimum d.b.h. parameters, how forests are defined, whether the reported number of individuals refers to the number of stems or individual species, what types of species are included, and how stems area measured. Lastly, stem density and basal area are often reported as means in a set of transects for a given area, as opposed to totals. Given that one must consider these factors when interpreting this range and that larger ranges were observed in this research, inference about the structure of dry forests in comparison to wet forests should not be made from this range. Additionally, this range should not be used to identify whether dry forest basal area within a given region is considered high or low. More research is needed where consistent methodologies are employed in formations indicative of the disturbance regime so that we can improve our standards of what is considered high stem density or low basal area.

4.5 Chapter Summary

Given a higher basal area, stem density and species richness (particularly amongst large diameter stems) was observed amongst “less-disturbed” forests of St. Lucia in comparison with dry forests of St. Lucia (*Gonzalez and Zak*, 1996) and Guánica Forest, Puerto Rico (*Murphy and Lugo*, 1986b), these two forests exhibit structural and floristic traits indicative of more disturbance. “Less-disturbed” dry forests of St. Lucia had a higher number of stems and species >10 cm d.b.h. and species which receive the highest importance value ranking are those that have a higher relative dominance, as opposed to species that have a high relative stem density.

There were two observations made by *Gentry* (1995) regarding Neotropical dry forest genera that were consistent with this research. *Tabebuia*, the most widespread Neotropical dry forest genera (*Gentry*, 1995), was also widespread on St. Lucia and genera which were absent from Antillean samples (*Arrabidaea, Cletis, Capparis, Combretum, Pithecellobium, Peterocarpus* and *Paullinia*), were not identified in this study. Other observations were less consistent. Five of nine other genera reported to be widespread in the Neotropics were also found in this study on St. Lucia, however only two were widespread within the study area (*Coccoloba* and *Amyris*. Of the five genera (*Coccoloba, Eugenia, Erythroxylum, Drypetes* and *Casearia*) that were identified to be over-represented (speciose) in Antillean samples by *Gentry* (1995), only *Eugenia* and *Coccoloba* were found to be amongst the most speciose genera in this study and *Drypetes* was not identified. The genera *Bursera* has been found to be widespread and ecological important within "less-disturbed" dry forests of St. Lucia and the Dominican Republic (*Lugo and Brandeis*, 2005). How well the genera *Tabebuia* sp. is represented in Neotropical dry forests in comparison with *Bursera* requires more research.

The generalization that Leguminoseae is the most species-rich family at all areas in the Neotropics, with the exception of the Caribbean where Myrtaceae predominate, made by *Gentry* (1995) and since supported by *Lugo et al.* (2006) and *Pennington et al.* (2006), appears to only be partially correct. Leguminoseae (Fabaceae s.l.) tied as the most species/genera rich family with Myrtaceae, Rutaceae, and Rubiaceae, they were all represented by 6 species/genera. However, in reference to the analysis by *Gentry* (1995) an average of 12 Fabaceae species/0.1 ha sample were found in continental dry forests. This is much larger than the 6 species from this family identified in this study, supporting the observation that the family is under-represented in Antillean forests relative to continental dry forests, however more research in Antilles is needed to support this observation.

Comparisons of species richness results from "less-disturbed" forests to other Neotropical sites, revealed that St. Lucia's "less-disturbed" forests had a higher species richness than two Antillean sites, but was lower in richness to the majority of continental samples with the exception of sites in Paraguay, Argentina and Peru. Based on a hypothetical extension of the regression lines, St. Lucia's "less-disturbed" forests are also richer than the scrub forests in the Dominican Republic and early successional forests in Costa Rica, further supporting the typification of my study sites as "less-disturbed".

In regards to Antillean dry forest diversity, this analysis revealed that some Antillean dry forest sites had a similar species richness to some continental forests; particularly notable was the Broom Hill site on Jamaica, which had a similar species richness to one of the richest continental sites (Chamela Mexico). The most interesting observation from the species richness comparison was the variability in richness reported by different researchers amongst forests of the same reserve or region (i.e. Chamela Mexico and Cerros de Amotape Peru). This is evidence of high variability in species richness within the same forest, let alone the entire country or continent. Overall, the comparison of species-amongst dry forest sites reveals that data from more Caribbean dry forests is needed and that species-richness data can only be reflective of the exact plot that was sampled and should not be extrapolated into broader geo-political regions unless plot sampling methods are sufficiently representative of the area.

The same conclusions regarding the extrapolation of localized plot data are made in regards to characterizing the structure of dry forests. High intra-island variability in stem density in basal area was observed in St. Lucia and is comparable to the variability seen amongst all Neotropical dry forest sites (except for the stem density of Guánica Forest) compared by *Gentry* (1995). Given that *Gentry* (1995) did not account for disturbance, which is expected to influence the density of large diameter stems, the the values presented are unsuitable for comparison to other studies. Lastly, the commonly referenced basal area range for dry forests (17-40 m^2ha^{-1}) as presented in *Murphy and Lugo* (1986b), should not be compared with any dry forest study to infer structural characteristics, since methods used to develop this range were variable.

Chapter 5

Conclusions

5.1 Dry Forest Heterogeneity

Tropical dry forests have been recognized as having a high degree of phenological complexity (*Holbrook et al.*, 1995) are influenced by differential spatial gradients in moisture, often induced by topography and soils, as well as local rainfall intensity, cloudiness, latitude and elevation (*Mooney et al.*, 1995). Seasonally dry forests of the Caribbean are regarded as heavily disturbed environments affected by biotic and abiotic stressors which are variable over time and space. These disturbances affect the structure and composition of dry forest formations; in regions where dry forests are expected to arise, variants of a less disturbed form will be found.

5.1.1 Intra-Island Heterogeneity

Evidence of structural and floristic heterogeneity was observed amongst 22 plots of seasonally "less-disturbed" dry forest in St. Lucia, despite the effort made to select locations of similar form. Three main results observed amongst these "less-disturbed" stands add support to the characterization of St. Lucia's seasonally dry forests as highly complex heterogenous ecosystems that exhibit high variability in structural form and species richness.

1. All plots exhibited significant differences ($p < 0.05$) in basal area with at least 2 plots and 6 plots had significant differences ($p < 0.05$) with 10 or more plots. It is expected that greater variation would be observed if efforts were not made to select locations of similar structural form.
2. The stem density range observed amongst St. Lucia's dry forest plots is just as variable as the stem density range reported amongst all Neotropical dry forest sites (with the exception of Guánica Forest) compared by *Gentry* (1995).

3. No species was observed within all plots and only 11/73 (including unknowns) were identified in 50% of the plots. Additionally, evidence of clustering amongst uncommon species was found. These results coincide with observations in other Neotropical dry forests and support the theory that species dominance is never predictable (*Hubbell*, 1979). This may be due to regional restrictions of species due to dispersal mechanisms, disturbance regimes and regular environmental conditions, but may also be brought upon by selective harvesting and planting of certain species.

Evidence of heterogeneity was also observed within continental dry forests of the same reserve or region. While *Gentry* (1995) reports species richness for Chamela Reserve Mexico to be amongst the most diverse sites, four 0.24 ha plots within the same forest sampled by *Segura et al.* (2003) had a much more variable species richness and is comparable to the diversity observed in St. Lucia's "less-disturbed" dry forests. Additionally, dry forests of Cerros de Amotape region in Peru reported to be depauperate of species >10 cm d.b.h. (*Linares-Palomino and Ponce Alvarez*, 2005), were found to have nearly 7 times the species >10 cm d.b.h. by *Gentry* (1995).

Given the intra-island heterogeneity, the inter-region heterogeneity in species richness and the high richness observed in Broom-Hill Jamaica, the generalization that Antillean dry forests are depauperate in species (at least among woody trees) relative to continental Neotropical dry forests, warrants further investigation and should only be considered as an over-extrapolation and broad generalization, rather than a characteristic of Antillean dry forests.

5.1.2 Defining Formations of Varying Disturbances

The dry forests of Guánica Forest, Puerto Rico and St. Lucia that I compared to the "less-disturbed" forests of St. Lucia, exhibited structural and floristic traits which indicate they are more disturbed overall than the forests I censused. Given that a large majority of Antillean dry forest research is conducted within the Guánica Forest and the St. Lucia location was the first of it's kind, these findings are significant in regards to how we perceive Antillean dry forests. Evidently, not all Caribbean dry forests are as heavily disturbed as Guánica Forest or the forests in St. Lucia sampled by *Gonzalez and Zak* (1996).

Through comparative analysis, several observations revealed that there were structural and floristic differences between the "less-disturbed" dry forests of St. Lucia in comparison to relatively more disturbed forests in St. Lucia, Puerto Rico, the Dominican Republic and Costa Rica. These included:

1. A higher density and species richness amongst all stem classes >4 cm d.b.h. in comparison to predominately more disturbed forests in St. Lucia; differences in diversity were particularly high amongst stems >14.5 cm d.b.h., despite the

larger sampling area employed by *Gonzalez and Zak* (1996) for stems >15.5 cm d.b.h.

2. A higher overall species richness, especially amongst stems >10 cm d.b.h. was observed in comparison with Guánica Forest, Puerto Rico.
3. Three less species accounted for 50% the importance value ranking in both predominately more disturbed forest in St. Lucia and Guánica Forest, Puerto Rico.
4. Species with the highest importance value ranking in Guánica Forest and St. Lucia's predominately more disturbed forest were those that had the highest relative stem density, rather than the highest relative dominance.
5. Species-richness was higher in St. Lucia's less-disturbed forests in comparison to forests characterized as "scrub" in the Dominican Republic and "early successional" forest in Costa Rica.

Research which fails to account for disturbance, can misrepresent less-disturbed formations of tropical dry forest. Overall, the more-disturbed Antillean forests were less species-rich particularly amongst large diameter stems. Stem breakage from wind and culling can affect the number of large diameter stems within a region. Dry forests also have a slower growth rate than wet forests, thus recovering secondary vegetation is also expected to have low numbers and diversity of large diameter trees. Previous research which characterizes the structure and composition of Antillean dry forests should be interpreted in this regard. Future research within the Antilles that could serve to characterize dry forests of this region, should better define the vegetation association or formation being studied. Clearly there is a need for developing a standard methodology to delineate shorter shrub dominated ecosystems (remnant or recovering) from taller tree-dominated (remnant or recovering) ecosystems.

Studies of forest structure and composition only provide a snapshot of the characteristics of a specific landscape. These generalizations provide us with a shopping list of possible phenomena that have influenced the characteristics of vegetation associations in a specific landscape (*Crome*, 1997). While we have a general understanding of the types of disturbances that influence Caribbean dry forests, our knowledge of the effects of disturbances on forest structure and composition is less developed. Disturbances effect vegetation over varying spatial and temporal scales and as a result, forests of varying structure and form are found within plant associations that are delineated by bio-climactic characteristics. While the various factors which constitute the total environment of a plant or plant association can be separated, measured and diagrammed, no one has succeeded at reducing to a single statement or single equation the total environment of a plant (*Gleason*, 2000). Resultantly, plant associations based on bio-climactic parameters are likely to have multiple formations. How we recognize (typify) these formations and whether we should divide them up into separate pieces is a much larger philosophical debate (see *Gleason* (2000)).

5.2 Broad generalizations

Floristic data on genera and family representation within 0.1 ha plots used by *Gentry* (1995) were extrapolated to broad geo-political regions, despite intra-island and inter-region heterogeneity in forest structure and composition. As a result several inferences made in regards to genera and family representation within Antillean dry forests were inconsistent with the results of this study.

1. Only 5/9 genera identified to be widespread in the Neotropics were identified in "less-disturbed" dry forests of St. Lucia and among these, *Bursera* and *Coccoloba*, were the only genera which were widespread within the study area.
2. Amongst the 5 genera that were identified to be over-represented in the Antilles, only *Coccoloba* and *Eugenia* were found to be over-represented in the "less-disturbed" dry forests of St. Lucia.
3. The family Myrtaceae identified to be the pre-eminent (most speciose) family in Antillean dry forests was no more pre-eminent than Rutaceae, Rubiaceae and Fabaceae (Leguminoseae s.s.) in the 'less-disturbed" dry forests of St. Lucia.
4. The family Fabaceae (Leguminoseae s.s.) identified to be under-represented in Antillean samples was not under-represented relative to other families in this study but in agreement with *Gentry* (1995) is under-represented relative to the continental sites he compared.

5.2.1 Issues with Terminology and Methodologies

The terms over-represented genera and pre-eminent families used by *Gentry* (1995) represent the number of species and is not indicative of their relative frequency, density or dominance. The methodology employed by *Gentry* (1995) was heavily localized (10, 10x10 m transects) within each study site and is not representative of the geo-political regions which were sampled. If there is a high degree of clustering amongst rare species in dry forests as suggested by *Hubbell* (1979), sampling a small region of forest can make certain species appear to be over-represented within a given area if they are clustered. How well represented they are throughout the area where study results are extrapolated to requires a wider sampling regime. This discussion is supported by evidence of clustering of the genera *Zanthoxylum* in plot 9.

Zanthoxylum was identified to be the most species-rich genera overall, however 50% of the genera were identified within one 15 x 15 m plot (plot 9). None of the species were among those with the highest importance value rankings, two were rare within the study area and the genera only represented 3% of individuals censused. Thus, if I were to identify *Zanthoxylum* as the most over-represented genera in this study it would only be because I sampled a clustering population in plot 9. Therefore, the use of the term over-represented is cautioned for future researchers and it is recommended that analysis of genera representation to be based on the relative frequency, density, dominance or importance value ranking.

Leguminoseae (Fabaceae s.l.) has been identified to be under-represented within the Antilles and Myrtaceae was touted as the pre-eminent dry forest family. This generalization has since been supported by *Lugo et al.* (2006) and *Pennington et al.* (2006). However, results of this study revealed that both families were represented by 6 species/genera in "less-disturbed" stands of St. Lucia's dry forest. Thus, in St. Lucia's dry forests both families would be classified as pre-eminent.

Comparisons of species representation within genera or families should be based on floristic inventories better representative of an islands flora, rather than data from plots either localized or widespread. Species-lists better serve this type of analysis and it is recommended that such generalizations made by *Gentry* (1995) be re-evaluated. To better understand species, genera, or family representation within Neotropical dry forests, plot based methods are suitable; however, representation should be based on frequency, dominance or density. It is recommended that future researchers use importance value rankings (as employed in this study) to better our understanding of how flora is distributed spatially within and amongst dry forest plots. Those that have access to the data-set used by *Gentry* (1995) could re-evaluate species-representation in dry forests genera and families using more then species-richness information. Species, genera and family abundance and dominance (based on basal areas) within each site could be calculated. In addition, importance values could be used to compare the entire Neotropical data-set so that relative frequency, abundance and dominance of dry forest species is better understood.

5.3 Implications and Recommendations

The spatial and temporal scales at which we extrapolate snapshots of dynamic systems is an arduous challenge for all environmental scientists and our conclusions can have direct implications to how landscapes are managed. This research has revealed several issues regarding the extrapolation of forest traits to broad spatial scales, particularly amongst tropical regions of high diversity and high topographic and climactic variability, which are prone to varying degrees and types of disturbance. If we are to manage these ecosystems sufficiently long-term research widespread throughout the Caribbean is critical. We need more then snapshots to better our understanding of their dynamics on varying spatial and temporal scales.

The results from this study reveal that St. Lucia's dry forests have a higher species richness and diversity amongst trees >4 cm d.b.h. than previously identified. This is largely attributed to the sampling methods employed in this study; a replicate sample area was provided for all stem classes inventoried, I defined and attempted to minimize forests indicative of disturbance, and plots were more widely dispersed amongst St. Lucia's dry forests. Given the high degree of heterogeneity, more sampling is required to better classify the structure and composition of St. Lucia's dry forests so that we can improve our understanding of their dynamics and better their overall management.

While broad biogeographical comparisons of forest structure and composition are interesting and may serve to reveal trends in species distributions over large areas, these comparisons should always be recognized as generalizations. It is the opinion and fear of this author that these generalizations can influence policy making and the distribution of funding amongst Neotropical dry forests. These generalizations can provide justification for the lack of conservation efforts in regions identified as depauperate or degraded, especially in geo-political regions (i.e. Caribbean islands) that are lacking research to expand upon generalizations.

The lack of research and previous characterization of St. Lucia's (and Antillean) dry forests as highly disturbed ecosystems depauperate of species, misrepresents the ecological diversity and complexity throughout the various dry forest forms. This research has shown several inconsistencies regarding these broad generalizations and thus prior perceptions of Antillean dry forests should not be used as a justification for lack of conservation efforts. Additionally, it has shown that St. Lucia's and Antillean dry forests may contain stands that are equally as species rich in woody stems as some of the most species-rich continental forests, many of which have received protected status (i.e. Chamela Reserve, Chacocente Reserve). Given that the regions of dry forest which have some protected area status on St. Lucia, are difficult to access and pursue research, it is recommended that a region easier to conduct research be given protected area status (i.e. Mont Gaic Region in the North East).

This research does not attempt to dispute that Antillean dry forests are heavily disturbed ecosystems, but shows that disturbance is variable over time and space. Given the lack of conservation effort directed toward protecting St. Lucia's and Antillean dry forests as a whole (*Lugo et al.*, 2006), I fear that the term disturbance is used synonymously with degraded, despite the different meanings. Degradation is caused by disturbances and given that disturbances are variable over time and space, so is degradation. As *Lugo et al.* (2000) reveals, coral reefs and rainforests in the Caribbean are also highly disturbed ecosystems with great diversity, which co-exist and flourish in spite of the recurring intense destruction of hurricanes. However, they are only regarded as a degraded ecosystem when they pass a certain threshold, where they can no longer support the species that exist within them and an ecosystem hits the point of collapse. Identifying this threshold is one of the major challenges in ecology. Given the lack of information on long-term successional dynamics of Caribbean dry forests (*Roth*, 1999) one cannot assume that these ecosystems have passed a certain threshold if we do not understand what that threshold looks like.

In the past, St. Lucia's dry forests were heavily impacted by woodcutting and land clearing for agriculture, today these forests are primarily threatened with fragmentation and degradation imposed by clearing patches or large expanses of forest for resort and vacation home development. Given that St. Lucia is a signatory to the UN Convention on Biodiversity (*GOSL and UNEP*, unknown), it is recommended that such development within this region is halted until areas of significant habitat for rare and endemic species, of both flora and fauna are identified and plans are made to prevent or compensate for biodiversity loss on the island. This could be facilitated through a nation wide inventory of flora so that we can better identify those species that are locally rare. This is the first step in a series of steps that will be required to sustain the existence of certain dry forest flora and fauna on the island. It is not recommended that this inventory be conducted solely in "less-disturbed" formations and instead should represent the varying structural and floristic forms of dry forest (no particular classification scheme is recommended at this time).

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