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Cover Photo: Dr. Lynn Margulis, Symposium Keynote Speaker, describes the structure and ecology of living stromatolites. Some, visible as grayish mounds near her feet, line the shore of Storrs Lake whereas others occur farther out in deep water. (See paper by D. C. Edwards, this volume).

Back Cover Photo: Group photo of the 6th Symposium participants and speakers.

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THE VINES OF PINELAND AND DRY EVERGREEN FOREST (COPPICE) COMMUNITIES ON NORTH ANDROS ISLAND, BAHAMAS: ABUNDANCE AND FLORISTIC COMPOSITION

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ABSTRACT

The vines (including small diameter lianas and herbaceous vines) of pineland and dry evergreen forest (coppice) communities on subtropical North Andros Island, Bahamas were sampled by quadrats. Vine abundance, species richness, and floristic composition were determined for vine assemblages in ten stands. Vines in pineland stands were more abundant and climbed significantly more large trees than did those in coppice stands. Unlike pineland vines, those occurring in the coppice occasionally reached diameters greater than 1 cm. Pineland vine assemblages were more species rich than coppice vine assemblages. Consideration of forest structure and frequency of disturbance is important when interpreting differences in vine abundance in Andros pineland and coppice communities. Canopy structure, vertical stratification, and incidence of surface fires differ between the two community types and possibly determine, in part, vine establishment and climbing success in the two communities.

INTRODUCTION

Herbaceous vines and lianas (woody vines) have traditionally been an understudied growth form. Although vines occur abundantly in tropical forest communities their ecology is little understood (Janzen, 1975; Putz, 1984; Peñalosa, 1984; Whitmore, 1990, and Gentry, 1991). Trends in vine distribution show a decrease in abundance with increasing elevation; similarly, vines decrease in abundance with increasing latitude (Grubb, et al., 1963; Holdridge, et al., 1971; Janzen, 1975; Croat, 1978; Gentry, 1983, 1991; Hara, 1985, 1988; Hegarty and Caballé, 1991; Balfour and Bond, 1993; Young, 1993). Thus, vines are poorly represented in temperate forest communities. Otherwise physiognomically similar, rain forests in the subtropics are also observed to have fewer vines than tropical rain forests (Webb, 1959; Walter, 1971). To date, most ecological studies of vines have dealt primarily with lianas greater than 1 cm dbh occurring in tropical forest communities. Relatively few studies have included vines in smaller diameter classes, although several studies have shown that a high proportion of vine stems occur in the smaller diameter classes (Hegarty and Caballé, 1991). In addition, vine stems are small in diameter relative to the sizes of their crowns; increases in cross-sectional area of vine stems have been found to be associated with proportionately larger increases in leaf biomass than comparable increases in tree stem cross-sectional area (Putz, 1983). As noted by Putz and Chai (1987), consideration of small size class vines is thus important when comparing data on community vine abundance.

This study was undertaken to describe the vine assemblages (including small diameter class lianas and herbaceous vines) occurring in plant communities in a subtropical location. Vine abundance, species richness, and floristic composition are described here for vine assemblages occurring in pineland and dry evergreen forest (coppice) stands on North Andros Island, Bahamas. Vine abundance is described in part in terms of size class frequency distribution and the proportion of trees bearing vines (after Putz and Chai, 1987). In addition, pineland and coppice vine assemblages are compared, and then these results are compared to data on vines from other geographical regions.

THE STUDY AREA

Andros, the largest island of the Bahamas, is located approximately 210 km

southeast of Miami, Florida (Smith, et al., 1991). Essentially, Andros is comprised of a number of islands narrowly separated by channels known as bights (Northrop, 1902). North Andros, separated from the rest of Andros by the northernmost bight, is the largest of the component segments (Figure 1). Taken as a whole, Andros is approximately 165 km long by 65 km wide (Eshbaugh and Wilson, 1990).

According to Sealey (1994), the Bahamas have a maritime subtropical climate characterized by a tropical summer regime, a warm temperate winter regime, and persistent northeast trade winds. As Andros experiences infrequent frosts and freezes (Nickrent, et al., 1988; Campbell, 1978), its climate is clearly subtropical. Mean annual rainfall for Andros is 1140 mm (data collected on Mangrove Cay; Henry, 1974; Little et al., 1977). However, eight years of precipitation records collected between 1976 and 1983 on North Andros show a greater mean annual rainfall of 1488 mm for the northern segment of the island (Block and Wilson, 1994). The entire Bahama archipelago lies within the North Atlantic Hurricane Belt (Little et al., 1977).

The substrate of the Bahamas is almost entirely oolitic and bioclastic limestone. Subject to solution weathering, the rockland plains and ridgelands of the Bahamas are examples of tropical karst landscapes (Sealey, 1994; Little et al., 1977). Soils in the Bahamas are thin and discontinuous. Organic or leaf-mold soils are the most common soils in the Bahamas and are characteristic of the rockland. Such soils accumulate in solution holes and cover in varying depths the irregular limestone surface of the rockland (Sealey, 1994; Little et al., 1977).

Andros, over much of its area, is less than 6.1 m above sea level (Henry, 1974). Ridgeland occurs along the eastern coast of the island; the highest point, Morgan's Bluff (a northeastern promontory), is 18.3 m above sea level (Nickrent, et al., 1988). To the west, the landscape grades into rockland and eventually into tidal flats which occupy the greater area of the west coast of the island.

Plant Communities

Ten plant community types are recognized for Andros and were described by Nickrent, et al. (1988), Eshbaugh and Wilson (1990), and Wilson and Eshbaugh (1991). These communities are based, in part, on those described for Andros by Northrop (1902): beach/strand, coastal rock, coastal coppice, interior coppice, pineland, savanna, scrub, freshwater swamp, saltwater marsh (swash), and mangrove. Brief descriptions of the pineland and interior coppice communities of Andros are provided in the next two sections.

Pineland

In the Bahamas, pinelands occur in level rockland landscapes on more or less rugged, honeycombed limestone substrates (Little, et al., 1977). Occupying a large area of central North Andros, pinelands may be considered the most extensive plant community on the island (Nickrent, et al., 1988; Smith, 1991).

Typically, pinelands in the Bahamas are open-canopy woodlands which, in terms of vertical structure, are essentially two-layered. The canopy tree layer consists only of *Pinus caribaea* var. *bahamensis* (Bahamian pine) which, at maturity, may reach 21 to 24 m in height. A shrub layer is present and may be quite variable in height and composition due to the influence of water table level, canopy density, and incidence of fires (Little, et al., 1977). Relatively few herbs occur in this community. With the possible exception of South Andros pinelands (W.H.E., pers. obs.; T.K. Wilson, pers. comm.), stands of pineland in the Bahamas are secondary in nature, having been extensively exploited for sawn lumber and pulpwood (Henry, 1974; Patterson and Stevenson, 1977; Campbell, 1978).

Surface fires are an annual phenomenon in Bahamian pinelands (Henry, 1974). These fires burn the shrub understory back to ground level while the mature pines are rarely seriously damaged. On North Andros, the pinelands nearest the settlements of the eastern coast experience frequent burns; these fires are primarily anthropogenic in origin, resulting from the careless burning of slash on fields cleared for cultivation or to make land crab hunting an easier task. Although not documented, Smith (1991) suggested that a reduction in fire frequency in
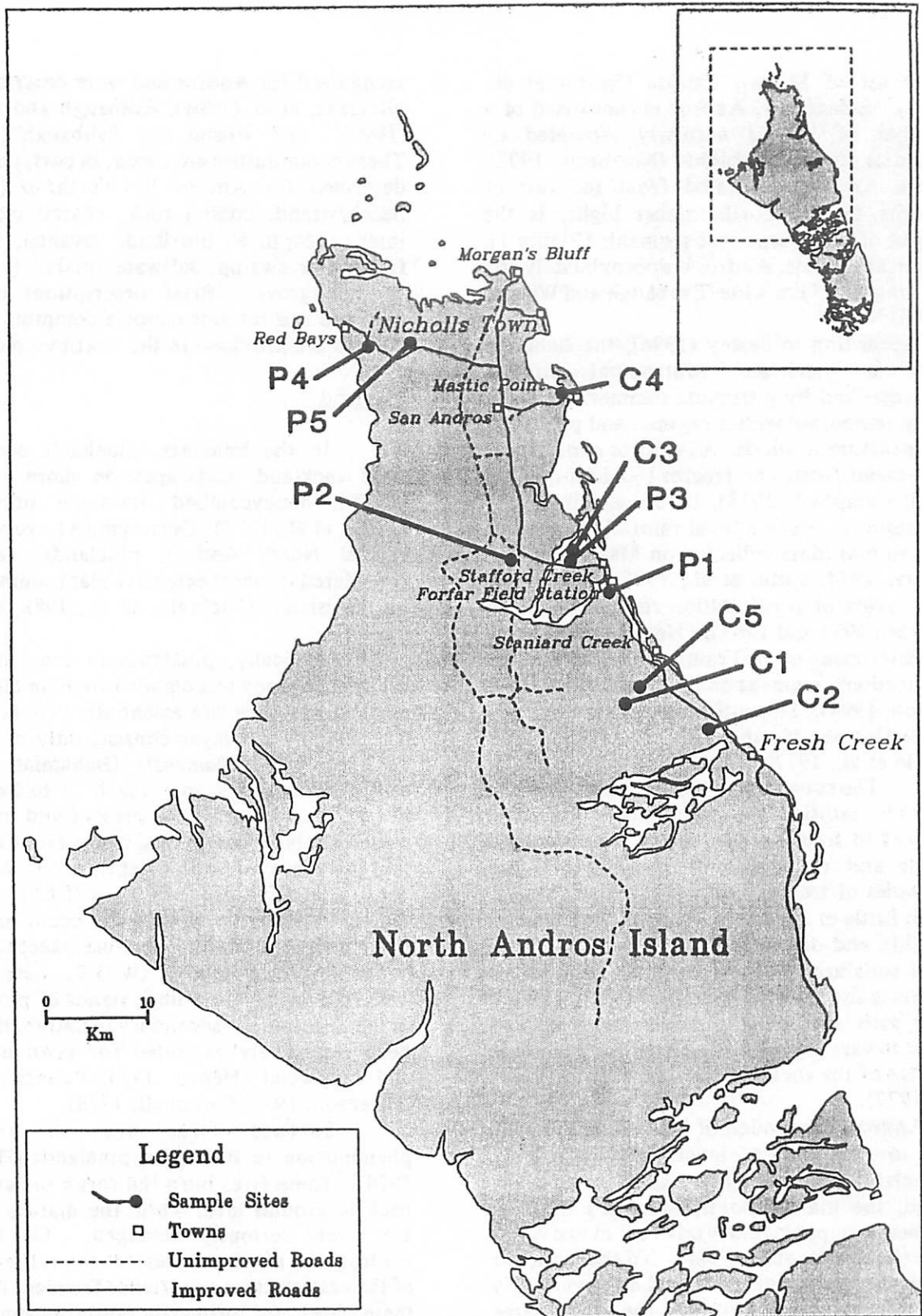
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Figure 1. Map of North Andros Island, Bahamas and locations of the 10 stands sampled. P1-P5 represent sampled pinelands stands; C1-C5 represent sampled coppice stands. Original base map compiled by D. R. McRitchie, 1988; this version by Miami University Geographic Information Systems Laboratory, 1992.

Andros' pinelands may lead to greater height growth of hardwood species in the shrub layer, resulting in eventual conversion to broad-leaved forest as has been described for fire-climax pinelands in south Florida and the Caribbean (Tomlinson, 1980; Campbell, 1978).

Coppice

Coppice is a community type of widespread distribution within the Bahamas (Smith and Vankat, 1992). According to Smith (1991), coppice communities are examples of dry evergreen forests (DEF) primarily consisting of broad-leaved shrubs and trees. The terms coppice and coppet have been used since at least the early 1900's (Northrop, 1902; Coker, 1905) to describe Bahamian DEF probably as a result of the British influence in the islands (Smith and Vankat, 1992). In the literature numerous names have been used to describe the community type: blackland, woodland, bushland, thicket, and hammock (e.g. Correll, 1979; Byrne, 1980; Smith, 1982; Gillis, 1977). Although Byrne (1980) indicated that coppice-type vegetation may be encountered in low limestone environments throughout the New World subtropics, it has been suggested that Bahamian coppice is most similar to the tropical hardwood hammocks of southern Florida and some communities on limestone and coral soils in the Greater Antilles (Smith and Vankat, 1992; Robertson, 1955 as cited in Snyder, et al., 1990; Britton and Millspaugh, 1920).

Two basic types of coppice vegetation, coastal and interior, are generally recognized for the Bahamas. Interior coppice may occur on flatland or ridgeland honeycombed with sinkholes, including the large "banana holes" (so-called because they are often planted with bananas and fruit trees; Coker, 1905; Sauleda and Adams, 1979; Correll and Correll, 1982; Eshbaugh and Wilson, 1990). Interior coppice is considered to be the most diverse community in the Bahamas (Correll and Correll, 1982). The vegetation is typically dense with a closed canopy and, often, a moist microenvironment. Some stands may contain isolated pines. Epiphytic bromeliads and orchids, as well as terrestrial orchids, are often present. Additionally, banana holes may provide habitat for a variety of ferns (Coker,

1905; Campbell, 1978; Correll, 1979; Smith, 1982; Eshbaugh and Wilson, 1990). On North Andros, interior coppices occur interspersed with pineland on the rocky ridges of the east coast, as well as on ridges in the western tidal flats (Sauleda and Adams, 1979; A.M.F., pers. obs.). Three types of interior coppice have been recognized for North Andros by Smith (1991): *Metopium-Coccoloba*, *Metopium-Exothea*, and *Exothea-Bursera-Metopium*. Interior coppice communities were found to be less dense but more diverse in woody understory species than were coastal coppice communities (Smith and Vankat, 1992).

Most, if not all, stands of coppice in the Bahamas are thought to be secondary or even tertiary growth (Patterson and Stevenson, 1977; Campbell, 1978; Smith and Vankat, 1992). Historically, coppices have been sources of forest products extracted and often exported for construction and pharmaceutical purposes (Campbell, 1978). Today, coppices are still disturbed by human activities. On Andros, stands of coppice are cut and the land is cleared for conversion to crop land and home sites. In addition, interior coppices are still sources for economically valuable wood used for carving such as mahogany (*Sweitenia mahogoni*) and horseflesh (*Lysiloma sabicu*; Smith, 1991; Smith and Vankat, 1992).

METHODS

The methods used in sampling North Andros pineland and interior coppice communities were modeled after those of Putz and Chai (1987). Five 20 m x 50 m (0.1 ha) plots were established in stands representative of each community type (Figure 1). In most cases, stands were accessed by road; consequently, plots were located at least 20 meters into the stand from the road in order to avoid edge effect.

Within each plot, the diameter at breast height (dbh) of all trees greater than 10 cm dbh and all vines over 1 cm dbh that were rooted in the plots was measured. In addition, basal diameters were measured for the vines in order to facilitate comparisons to studies in which vine stem diameter was measured at the point of greatest diameter (e.g. Gentry, 1991). All trees which supported a vine were noted regardless of whether the vine originated

inside or outside of the plot. A 20 m x 20 m (0.04 ha) subplot was located randomly at one end of each plot. All vines rooted within the subplot were counted and identified. A 10 m x 10 m (0.01 ha) quadrat was randomly located in one corner of the 20 m x 20 m subplot. In this quadrat, all vines, woody seedlings, and saplings were counted. Individuals smaller than 10 cm dbh with heights above 1.3 m were designated as saplings; shrub stems which met the diameter and height criteria were included in this category. Individuals less than 10 cm dbh but shorter than 1.3 m were designated as seedlings; shrub stems which met the diameter and height criteria were also included in this category. Woody seedlings were counted and the dbh of the saplings was measured. Vines were designated as either climbing or free-standing (non-climbing individuals which may be seedlings, new vegetative offshoots, or mature stems which have fallen from the canopy).

Field work was carried out from June through August 1991, with an additional two week period in March 1992. All vines were identified to species, and voucher specimens were collected and deposited in the Willard Sherman Turrell Herbarium (MU), Miami University, Oxford, Ohio.

RESULTS AND DISCUSSION

Characterization of pineland and coppice vine assemblages

In total, 32 species of vines were sampled. Twenty-eight species occurred in pinelands and 19 species were recorded for coppices; 14 species occurred in both community types. Mean pineland vine richness was 16.2 ± 1.8 species (± standard deviation; range of 14 to 18; Figure 2) in the 0.1 ha plots, while in coppices species richness was 9.6 ± 2.3 (range of 7 to 12; Figure 2). The most abundant vines (in terms of numbers of individuals) are listed in Table 1. Interestingly, the three most abundant species, *Rajania hastata*, *Passiflora suberosa*, and *Galactia rudolphoides*, have not previously been reported as commonly occurring in Andros pinelands. This is probably due to the fact that such small, herbaceous vines typically limit their leafing to the wet season and may

die back to ground level during the dry season (Johnston, 1949; Opler, et al., 1991; Hegarty and Caballé, 1991), thus often escaping detection (Lugo, et al., 1978; Gentry, 1982).

Sixteen families were represented by vines in the ten 0.04 ha subplots. Fourteen families occurred in the pineland, and 12 occurred in the coppice; eleven families were common to both stand types. In terms of numbers of individuals, families found to be common in the pineland were also common in the coppice. Four families, Dioscoreaceae, Leguminosae, Passifloraceae, and Smilacaceae, rank among the five most common families in each community type (Table 2). Three families, Aristolochiaceae, Asteraceae, and Vitaceae, were unique to the pineland stands; however, outside sampled stands, *Vitis munsoniana* was noted in both pineland and coppice. Ranunculaceae and Sapindaceae were unique to the coppice. Five of the 16 families were represented by three or more species. The most speciose family in all stands sampled is Leguminosae (6 species; Table 2, Figure 2). Vines were abundant in the pinelands and a conspicuous component of the shrub layer. This result agrees with observations made by Nickrent, et al. (1988) and Eshbaugh and Wilson (1990) on Andros pinelands, and by Coker (1905) on New Providence. In the 0.1 ha plots, the mean density of climbing and free-standing vines in the pinelands greatly exceeded that of the coppices. On average, there were nearly four times as many climbing vines and free-standing vines in the pinelands compared to the coppices (Table 3, Figure 3). Climbing and free-standing vines contributed a significant proportion (nearly a third) of the total stem density recorded for the pineland (mean of 32%; 20% due to climbing vines and 12% due to free-standing vines; Table 3, Figure 4). In contrast, climbing and free-standing vines only contribute 6.5% of the total stem density recorded for the coppice (3.1% due to climbing vines, 3.4% due to free-standing vines; Table 3, Figure 4). On average, woody seedlings and free-standing vines (self-supporting stems less than 1.3 m tall) account for over 75% of the total stem density in both pineland and coppice plots (77% and 79% respectively); 15.6% of these self-supporting stems occurring in pineland plots are free-standing vines, while only 4.3%

Figure 2. Species richness and family composition of sampled pineland and coppice stands (0.1 and 0.04 ha subplots). Family abbreviations are as follows: ACAN = Acanthaceae, APOC = Apocynaceae, ARIS = Aristolochiaceae, ASTE = Asteraceae, BORA = Boraginaceae, CONV = Convolvulaceae, DIOS = Dioscoreaceae, LAUR = Lauraceae, LEGU = Leguminosae, MALP = Malpighiaceae, PASS = Passifloraceae, RANU = Ranunculaceae, RUBI = Rubiaceae, SAPI = Sapindaceae, SMIL = Smilacaceae, VITA = Vitaceae. Unlabled segments of the P-mean bar represent the mean number of species occurring in sampled pineland plots in the following families (in order from top to bottom): ACAN and ARIS. Similarly, unlabled segments of the C-mean bar should read (from top to bottom): BORA, MALP, SAPI, ACAN, and RANU.
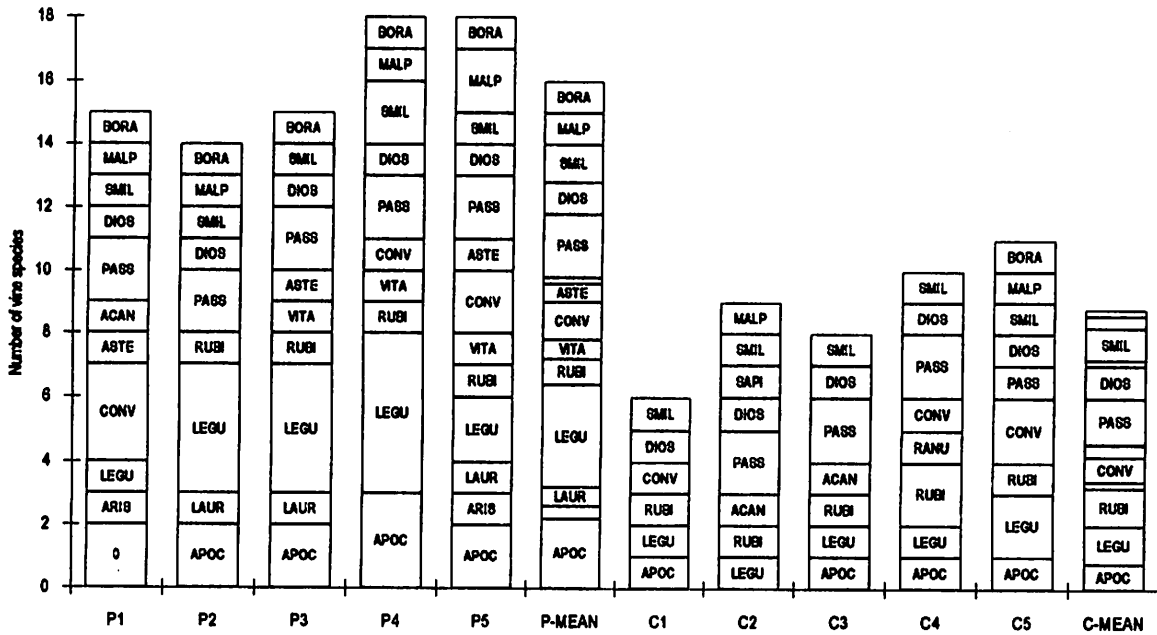
Table 1. The most abundant vine species sampled in Andros pineland and coppice stands. The total number of individuals sampled in the 0.04 ha subplots is also shown.

		Number of individuals	
Vine Species	Family	Pineland	Coppice
Rajania hastata L.	Dioscoreaceae	1409	69
Passiflora suberosa L.	Passifloraceae	597	10
Galactia rudolphoides (Griseb.) Benth. & Hook.	Leguminosae	385	174
Smilax havanensis Jacq.	Smilacaceae	357	306
Stigmaphyllon sagraeanum A. Juss.	Malpighiaceae	304	15
Chiococca alba (L.) Hitchc.	Rubiaceae	0	150
Passiflora cupraea L.	Passifloraceae	0	74

Table 2. The most common families represented by vines in 0.04 ha subplots in sampled pineland and coppice stands on Andros. The number of individuals and the number of species representing each family are also shown.

Family	Number of individuals			Number of species		
	Pineland	Coppice	Total	Pineland	Coppice	Total
Dioscoreaceae	1409	69	1478	1	1	1
Leguminosae	666	184	850	6	2	6
Passifloraceae	752	84	836	2	2	3
Smilacaceae	364	306	670	2	1	2
Rubiaceae	219	181	400	1	2	3
Malpighiaceae	305	18	323	2	2	2

Table 3. The density of trees, woody saplings, woody seedlings, climbing vines and free-standing vines in 0.1 ha plots.

Plot	Trees[1]	Woody[2,3] saplings	Woody[2,4] seedlings	Climbing[2] vines	Free-standing[2] vines
P1	134	370	3820	1890	1170
P2	84	240	6060	1070	860
P3	121	200	11590	270	810
P4	108	130	5200	2040	1570
P5	93	120	4890	2260	1430
Mean	108	212	6312	1906	1168
S.D.	20.3	101.3	3057.3	493.7	336.6
C1	67	1960	4010	310	180
C2	52	2720	5160	900	460
C3	68	2510	6220	210	140
C4	76	1290	25940	330	1180
C5	62	2380	5780	180	170
Mean	65	2172	9422	386	426
S.D.	8.8	565.8	9271.1	294.3	440.9

[1]Trees: dbh > 10 cm.
[2]Estimates for climbing and free-standing vines, saplings, and seedlings were based on 0.01 ha quadrats.
[3]Saplings: dbh < 10 cm, height > 1.3 m; includes tree and shrub stems which met the diameter and height criteria.
[4]Seedlings: dbh < 10 cm, height < 1.3 m; includes tree and shrub stems which met the diameter and height criteria.

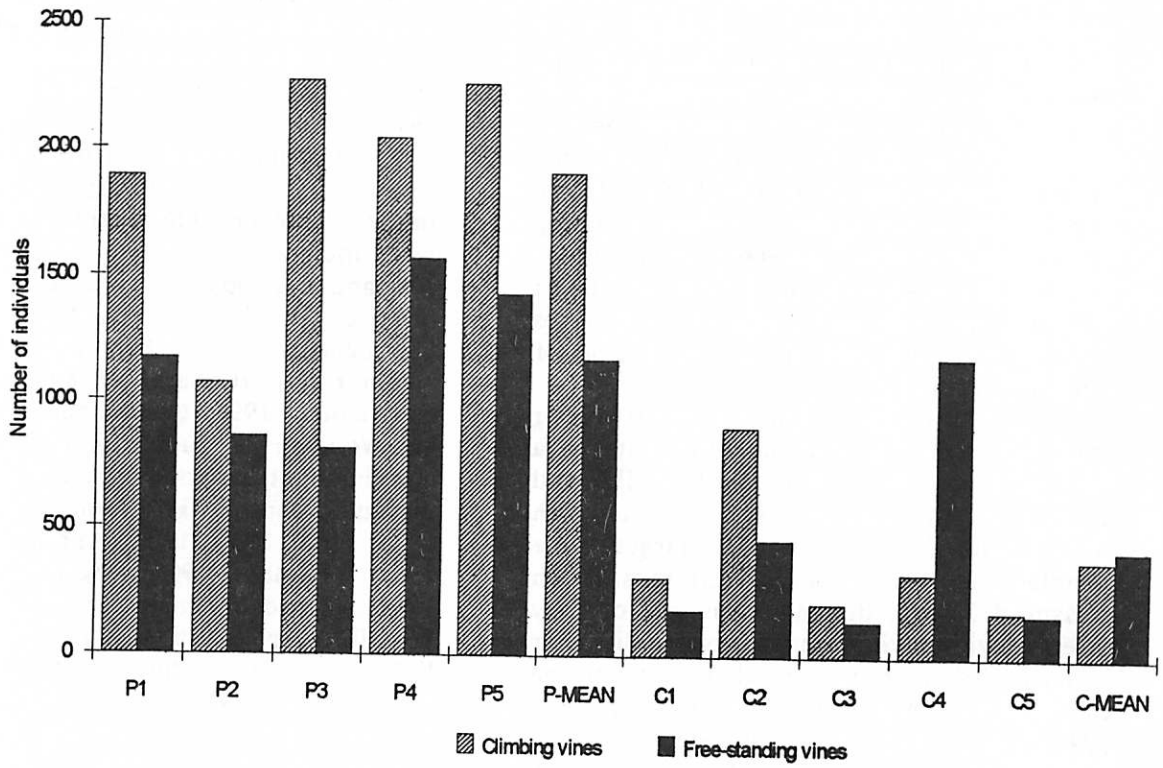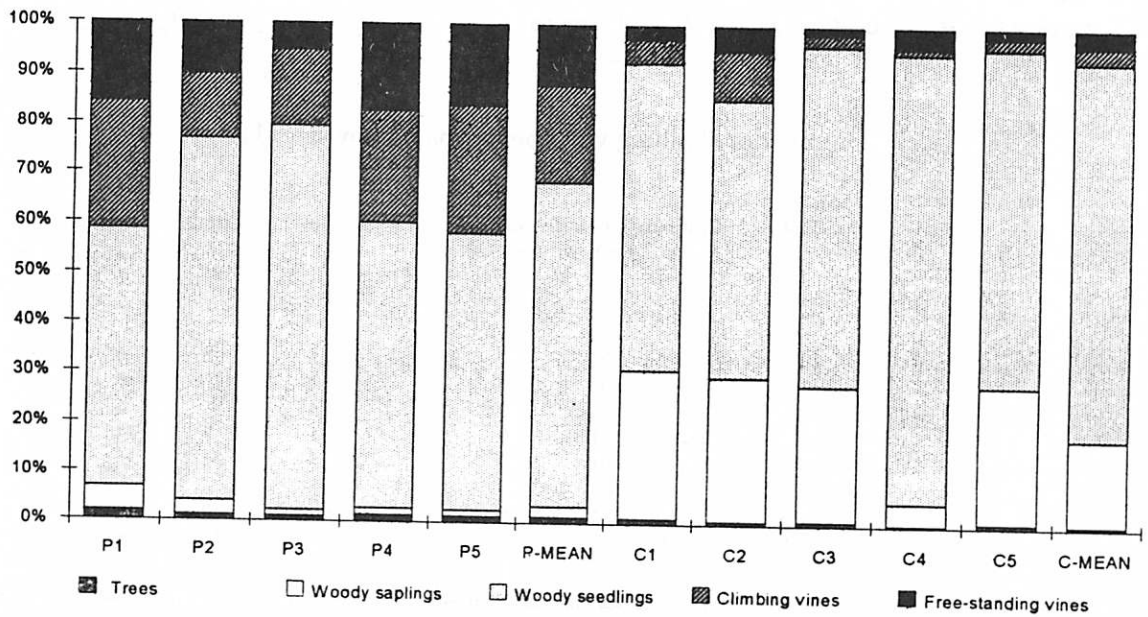Figure 3. The density of climbing and free-standing vines in 0.1 ha plots.

Figure 4. Percentage of the total woody plants and vines per 0.1 ha plot comprised of trees, woody saplings, woody seedlings, climbing vines, and free-standing vines.

of the self-supporting stems less than 1.3 m tall occurring in coppice plots are free-standing vines (Table 3).

Although both herbaceous and woody vines were represented, pineland vines consisted entirely of small diameter-class individuals (stems less than 1 cm dbh; Table 4). In the pinelands, vines were common on tree boles; in 0.1 ha plots, 142.4 vines climbed 76% of trees greater than 10 cm dbh (Frazer, 1995). Vines were even more abundant climbing among and stretching between stems within the shrub layer (based on counts within the 0.01 ha quadrats, an estimated mean of 1906 vines climbed on trees and shrubs in 0.1 ha of pineland; Table 3).

A few larger individuals (stems greater than 1 cm dbh) did occur in coppice stands; a mean of 11.6 vines greater than 1 cm dbh, and a mean of 1.4 vines greater than 2 cm dbh were found (Table 4). The largest vine sampled was a *Chiococca alba* individual which measured 3.1 cm dbh and was one of only three individual vines sampled (when diameter is measured at breast height) that can be classified as a liana in the sense of Gentry (e.g. 1991, greater than 2.5 cm diameter). Outside the sample plots, liana-sized individuals of *Chiococca alba* and *Pisonia aculeata* (Nyctaginaceae) were observed in coppice stands. Vines less than 1 cm dbh typically reached canopy height when climbing trees in the coppice. Smaller individuals were restricted to tree boles and sapling or seedling supports within understory tree and shrub

layers. An exception is the slender-stemmed, parasitic *Cassytha filiformis* (Lauraceae), which was restricted to tree crowns in the coppice. Of the trees greater than 10 cm dbh, a mean of 31% supported vines, while a mean of nearly 10% supported vines greater than 1 cm dbh in sampled coppice stands (Frazer, 1995).

Consideration of forest structure and frequency of community disturbance is important when interpreting differences in vine abundance and size classes in Andros pineland and coppice communities. Vines are observed to be associated with high or heterogeneous light habitats within forest communities (Caballé, 1984 as cited in Castellanos, 1991; Castellanos, 1991; Collins and Wein, 1993). Such habitats in which vines are abundant include treefall gaps and forest margins (Johnston, 1949; Walter, 1971; Janzen, 1975; Putz, 1983, 1984; Appanah and Putz, 1984; Whitmore, 1990; Hegarty and Caballé, 1991). Based on this association, vines have been interpreted as a growth form with a high light requirement (Putz, 1984, 1991; Hegarty and Caballé, 1991; Balfour and Bond, 1993). Disturbance to forest structure, particularly to canopy structure, often increases light penetration (Webb, 1958; Hegarty and Caballé, 1991; Teramura, et al., 1991) and may lead to subsequent vine proliferation (Phillips, 1940; Beard, 1946; Johnston, 1949; Webb, 1958; Walter, 1971; Lowe and Walker, 1977; Putz, 1983, 1985; Appanah and Putz, 1984; Putz and Chai, 1987; Hegarty and Caballé, 1991;

Table 4. The number of climbing vines per 0.1 ha plot by size class.

Plot	Climbing vines (dbh)(0.1 ha)$^{-1}$			Plot	Climbing vines (dbh)(0.1 ha)$^{-1}$		
	< 1 cm[*]	≥ 1 cm	≥ 2 cm		< 1 cm[*]	≥ 1 cm	≥ 2 cm
P1	125	0	0	C1	8	6	1
P2	70	0	0	C2	10	8	0
P3	181	0	0	C3	6	4	0
P4	162	0	0	C4	7	24	3
P5	174	0	0	C5	31	16	3
Mean	142.4	0	0	Mean	12.4	11.6	1.4
S.D	45.9	0	0	S.D.	10.5	8.3	1.5

[*]This category includes only those vines < 1 cm dbh that were climbing trees > 10 cm dbh.

Teramura, et al., 1991 and sources cited therein; Balfour and Bond, 1993; Caballé, 1994). Increases in vine density have been linked to defoliation and windthrow from hurricanes and cyclones (Phillips, 1940; Beard, 1946; Webb, 1958; Walter, 1971), canopy die-back due to drought (Bullock, 1990; Hegarty and Caballé, 1991), and increases in treefall frequency due to flooding (Putz and Chai, 1987). Vines also have been observed to dominate forest regeneration after fire (Webb, 1958; Young, 1993) as well as after damage caused by human activities such as logging (Putz, 1984, 1985; Appanah and Putz, 1984). Hegarty and Caballé (1991) have concluded that the invasion of forests by vines is determined almost completely by the structure of the canopy (e.g. the size and frequency of canopy gaps) and by the type and persistence of disturbances. Similarly, Johnston (1949) and Janzen (1975) have noted that in mature forests, new vertical shoots of vines most commonly become established in treefall gaps.

Vine success after establishment may also be determined by forest structure (Putz, 1984; Putz and Chai, 1987; Hara, 1987, 1988; Putz and Holbrook, 1991; Hegarty and Caballé, 1991; Balfour and Bond, 1993), particularly by the horizontal and vertical distribution of small diameter stems and branches that serve as trellises (supports) for climbing vines (Putz, 1984). Trellis availability and trellis structure (the distribution of supports) constrain height growth (the probability that a vine will successfully climb to the canopy) as well as the abundance and distribution of climbing vines within a community (Putz, 1984; Putz and Chai, 1987; Putz and Holbrook, 1991; Hegarty and Caballé, 1991; Balfour and Bond, 1993). Often trellises are abundant at forest edges and in disturbed forest, for example, at edges of treefall gaps (Putz, 1984) and where there is regeneration of young vegetation following disturbance (Balfour and Bond, 1993). The availability of suitable supports is typically limited in the understory of mature forests; however, Putz (1984) found that when free-standing vines in the forest interior were experimentally provided with artificial trellises, they displayed marked height growth (climbing) responses. Further, control individuals failed to find trellises on their own, thus providing additional support for the idea

that trellis availability primarily determines the abundance of climbing vines at the community level.

Canopy structure and vertical stratification differed significantly between pineland and coppice stands; it is likely that these structural features have a role in determining the relative abundance of vines in the two community types on Andros. The pineland community is an open-canopy woodland with strikingly discrete vertical strata. Canopy, shrub, and ground layers are present, while an understory tree layer is absent. In contrast, the coppice is a closed-canopy, relatively low-statured forest community. Vertical stratification is less pronounced than in the pineland, but canopy, understory tree, shrub, and ground layers may be recognized. Ready access to light and the abundance of small diameter stems and branches in the shrub layer probably contribute to the large numbers of vines in Andros pinelands. Although relatively small diameter saplings may be dense in coppice stands, the over-all distribution of small diameter supports is probably more diffuse in the understory of the coppice (A.M.F., pers. obs.). Also, lower light levels under a closed canopy and lack of treefall gaps may contribute to the smaller number of vines in coppices sampled on Andros.

Frequency of community disturbance is probably the most important factor determining the relative abundance as well as the diameters attained by vines in pineland and coppice communities. Pinelands on Andros are subject to frequent surface fires. Typically, these fires burn the shrub layer back to ground level and remove climbing vines from tree boles. After a fire, regeneration is relatively rapid; some shrub stem regrowth is visible during the second week post-burn, and vine regrowth is profuse within the first year or so after a fire (A.M.F., pers. obs.). A significant effect of these fires on the pineland is the maintenance of a forest structure that favors the establishment and growth of vines through abundant access to light and trellis availability. In addition, fire periodicity appears to limit the diameters attained by vines in this community. This is suggested by the finding that all vines sampled in pineland stands with regrowth of at least 15 months

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were under 1 cm dbh. Young (1993) also found an abundance of small diameter class vine stems (1-2 cm diameter) dominating regrowth in burned stands of Andean timberline forest. He attributes the predominance of these small diameter individuals to the presence of stems that survived past fires and then resprouted. Such resprouting of surviving vine stems as well as resprouting from underground tubers (e.g. *Rajania hastata*) may account for a number of the vines in regenerating pinelands on Andros.

Fire does not represent a significant agent of disturbance in coppice communities on Andros. When surface fires occur in pinelands, adjacent coppices do not burn, experiencing only minor damage to marginal vegetation through scorching of exposed foliage (A.M.F., W.H.E., pers. obs.). It may be that coppice vine stems are able to attain greater diameters because they are not periodically destroyed by fire.

One of the coppice stands (C4) may have been exposed to disturbance caused by relatively recent human activity. This stand may once have been the site of an *Agave sisalana* plantation where exposed rock would have been removed (Smith, 1991). In fact, Smith (1991) found that this area was indeed less rocky than sites where other coppice stands were sampled. Other evidence for such disturbance is the great abundance of seedling-sized stems and free-standing vines sampled in this stand; it is possible that this is a response to altered forest floor microenvironment as suggested by Teramura, et al. (1991). There is no evidence that disturbance has promoted climbing vine success in this stand; despite apparently adequate trellis availability, climbing vines are not remarkably abundant here in comparison to other coppice stands sampled. It may be that trellis structure is not conducive to vine attachment.

No evidence of significant disturbance (except that noted above for C4) was observed in sampled coppice stands. However, since hurricanes are known to damage coastal vegetation on Andros (W.H.E., pers. obs.), coppices may experience some amount of wind damage as well. Although not seen in sampled stands, disturbance in the form of defoliation, as suggested by Webb (1958), could influence the establishment of vines in coppice

communities. Phillips (1940) observed vine proliferation in areas of windthrow after hurricane winds damaged a south Florida hammock. Presumably, similar damage to coppice could lead to relatively large scale invasions of the community by vines.

Regional Comparisons

Due to the relative scarcity of quantitative studies of vines, particularly in plant communities outside the tropics, comparisons of vine abundance and diversity across major geographical regions are necessarily limited. Such comparisons may also be complicated by heterogeneity in sample composition, plot areas, and methods used (Hegarty and Caballé, 1991; e.g. Table 11.1). Inclusion or exclusion of certain climber types (e.g. Young, 1993 includes scandent forbs; Putz, 1983 excludes epiphytic and hemi-epiphytic climbers), and differences in minimum stem diameters required for inclusion (Hegarty and Caballé, 1991), contribute to a lack of uniformity among samples. Additionally, standard methods are not followed in measuring the diameters of vine stems, thus confounding comparisons of vine size-class frequency distribution (Frazer, 1995). Finally, there is difficulty in determining genetic or physiologic individuals among vines due to clonal extension and adventitious rooting of stems that have fallen from the canopy (Bullock, 1990; Hegarty and Caballé, 1991). Methods of delimiting individuals may vary among studies; however, ramets and genets are typically not distinguished (e.g. Putz and Chai, 1987 and Balfour and Bond, 1993). Despite these limitations, comparisons (e.g. Gentry, 1991; Hegarty and Caballé, 1991; Frazer, 1995) can be made if interpreted with caution.

The vine assemblages of sampled stands of pineland and interior coppice on Andros are similar floristically to those of pineland, interior coppice, and coastal coppice communities occurring elsewhere in the Bahamas (Frazer, 1995). In addition, Andros pinelands and coppices are similar in vine composition to south Florida and Caribbean pineland, scrub, dry evergreen forest, and shrub communities on limestone (e.g. Asprey and Robbins, 1953; Snyder, et al., 1990; Borhidi, 1991).

Small diameter vines (those less than 1 cm dbh) make the greatest contribution to vine species richness in both the pineland and coppice stands on Andros. A similar situation can be inferred for temperate mixed hardwood forests sampled by Collins and Wein (1993), as well as for the vegetation on coastal limestone studied by Howard and Briggs (1953) in Cuba. Other Caribbean forest, shrub, and scrub communities on limestone are reported to be rich in species represented by small vines (Beard, 1946; Asprey and Robbins, 1953; Kelly, 1985; Borhidi, 1991). Subtropical dry forest in Mexico (Lott, et al., 1987; Bullock, 1990), tropical dry, moist, and wet forest in Ecuador (Gentry and Dodson, 1987), timberline forest in Peru (Young, 1993), and tropical dry forest in Madagascar (Sussman and Rakotozafy, 1994) also exhibited significant contributions to vine richness by small vines, particularly at the dry sites. Based on the limited comparable data available, values for vine richness most similar to that of the Andros pineland and coppices occur in timberline forests of Peru (Young, 1993), and primary dipterocarp forest in Malaysia (Putz and Chai, 1987). However, large diameter vines (those greater than 2.5 cm diameter) in Andros coppices had a species richness comparable to that of north temperate forests sampled by Gentry (1991).

Although Gentry (1982, 1983) noted an average ten-fold difference in species richness of vines greater than 2.5 cm diameter between temperate and lowland tropical forests, he also found a positive correlation between vine species richness and precipitation where differences in richness between tropical dry and wet forests are even greater than that between temperate and tropical forests of similar precipitation levels (Gentry, 1982). Similarly, in tropical communities, species richness of vines greater than 2.5 cm diameter has been reported to decrease with decreasing soil fertility (Gentry, 1982; Gentry and Emmons, 1987; Gentry, 1991) and with increasing altitude (Gentry, 1991).

Interestingly, vine species in Andros coppices represent 19% of the woody flora (Frazer, 1995), a value identical to that of the tropical average noted by Gentry (1991). Similarly, for the three sites in Jamaica, Gentry (1991) also noted that while vine species richness is similar to temperate zone values, climbing species "constitute a near tropical average of 14% of these depauparate insular floras." In contrast, vines comprise a greater than tropical average of 24% of each flora at two dry tropical forest sites (Lott, 1985, as cited in Gentry, 1991; Gentry, 1991) while vine species represent an average of 6% of temperate zone floras (Hara, 1985; Gentry, 1991). The comparatively low value of vine richness in Andros pinelands and coppices may possibly be explained by the depauperate nature of their floras, as well as by the relatively low average annual rainfall and frequent droughts experienced on North Andros (Correll and Correll, 1982).

For vines of all diameters, mean density in pineland stands was most similar to that of subtropical dry forest in Mexico (arroyo site at Chamela, Bullock, 1990), tropical dry forest in Madagascar (Sussman and Rakotozafy, 1994), and alluvial forest in Malaysia (Proctor, et al., 1983). Coppice vine density was found to be most similar to that of subtropical dry forest in Mexico (hillside site at Chamela, Bullock, 1990), tropical dry forest in Ecuador (Gentry and Dodson, 1987), timberline forest in Peru (Chochos Valley, Young, 1993), and primary dipterocarp forest in Malaysia (ridge plots, Putz and Chai, 1987). For vines greater than 2.5 cm diameter, the mean density for coppice stands was comparable to that of north temperate forests sampled by Gentry (1991). Gentry (1982, 1983, 1991) found an order of magnitude difference in the density of large vines between north temperate and lowland neotropical forests. Gentry (1991) also noted that tropical islands that received their floras through over-water dispersal tend to have low liana densities, possibly resulting from the "prevalence of wind-dispersed seed in lianas, whereas most long-distance island colonizers are bird-dispersed."

Vine abundance has been reported to be associated with altitude (Grubb, et al., 1963; Janzen, 1975; Hara 1985; Balfour and Bond, 1993; Young, 1993). Despite the drop in density of vines found with increasing altitude, Young (1993) reports high vine densities for timberline forest in Peru relative to other forest types studied (as reviewed in Hegarty and Caballé, 1991). Soil fertility has been

related to vine abundance (Emmons and Gentry, 1983; Gentry and Emmons, 1987; Putz, 1985; Putz and Chai, 1987). Vines have been reported to be abundant in seasonally flooded forests (Proctor, et al., 1983; Putz and Chai, 1987; Gentry, 1991; Hegarty and Caballé, 1991) where river water enriches the soil. However, in alluvial forests, flooding also increases treefall frequency and it is possible that vine success in these forests may be influenced by treefall disturbance (Putz and Chai, 1987). It has also been noted that vines are abundant at sites with pronounced dry seasons (Gentry, 1991; Hegarty and Caballé, 1991).

Factors such as latitude, altitude, soil fertility, temperature, and seasonal rainfall are not independent, and thus it is difficult to relate regional vine abundance to any single environmental variable (Hegarty and Caballé, 1991; Balfour and Bond, 1993). For forest communities in Africa, Balfour and Bond (1993) suggest that the gradient in climber abundance associated with altitude is best explained by a gradient in host tree architecture (mean height to base of crown). This idea was supported in sample plots controlled for altitude. On Andros, vine abundance at the community level may be explained by forest structure and frequency of disturbance (in particular, frequency of surface fires). However, beyond the suggestion that there is a paucity of large vines in island floras due to dispersal complications (Gentry, 1991), it is not clear how other factors may influence the density of vines in pineland and coppice stands on Andros compared to other regions.

ACKNOWLEDGEMENTS

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