PART V THE VEGETATION MAP OF CUBA

PART V

The vegetation map of Cuba

	22 The main vegetation types of Cuba	389
	22.1 Rainforests	389
	22.1.1 Submontane rainforests (Calophyllo – Carapetum guianensis)	389
	22.1.2 Wet montane rainforests (Ocoteo-Magnolietalia)	392
	22.1.3 Semi-arid montane serpentine rainforests (<i>Podocarpo – Sloanetalia</i>)	396
	22.1.4 Cloudforests or mossy forests (Weinmannio-Cyrilletalia)	398
	22.1.5 Semi-arid montane serpentine shrubwoods (Clusio—Ilicetalia)	400
	22.1.6 Elfin thickets (<i>Ilici</i> — <i>Myricion cacuminis</i>)	402
	22.2 Seasonal evergreen forests or seasonal rainforests	404
		404
	22.2.2 Submontane seasonal rainforests (Oxandro-Dipholietum)	405 410
	22.3 Semi-deciduous forests	410
	22.3.1 Semi-deciduous mesophytic forests (Oxanaro—Burseretatia)	410
	22.4 Tropical karstic forests	415
	22.4.1 Species rich karstic forests of western Cuba (Spathelio—Gaussion)	417
	22.4.1 Species poor karstic forests of western Cuba (<i>Thrinacion morrisii</i>)	418
	22.4.3 Karstic forests of eastern Cuba (<i>Tabebuio—Coccothrinacion</i>)	418
	22.4.4 Montane karstic forests (<i>Tabebuio-Garryetum</i>)	
	22.5 Dry forests and shrubwoods	
	22.5.1 Dry evergreen forests (Eugenio-Metopietalia toxiferi)	
	22.5.2 Dry, thorny limestone shrubwoods (<i>Lantano–Cordietalia</i>)	423
	22.5.3 Dry lowland serpentine shrubwoods (<i>Phyllantho–Neobracetalia</i>)	
	22.5.4 Semi-dry lowland serpentine shrublands (<i>Ariadno–Phyllanthetalia</i>)	
	22.6 Semi-desert cactus scrubs (Consoleo – Ritterocereion hystricis)	
	22.7 Coniferous forests	
	22.7.1 Pinus tropicalis forests on sand (Acoelorrapho—Pinion tropicalis)	431
	22.7.2 Pinus caribaea and mixed oak-pine forests on slatey rocks (Pachyantho-	
	Pinion caribaeae)	431
	22.7.3 Pinus caribaea forests on ferritic soils (Neomazaeo – Pinion caribaeae)	433
	22.7.4 Xerothermic Pinus cubensis forests (Guettardo – Pinion cubensis)	435
	22.7.5 Mesophilous and montane Pinus cubensis forests (Andropogono-Pinion	
	cubensis)	439
	22.7.6 Mixed tree fern-pinewoods in the montane rainforest zone (Pinetalia	
	occidentalis—maestrensis)	
	22.8 Savannas and grasslands	
	22.8.1 Roystonea-Ceiba agricultural savannas (Ceibo—Roystonion)	
	22.8.2 Roystonea agricultural savannas (Samaneo-Roystonion)	
	22.8.3 Copernicia agricultural savannas (Andropogono-Copernicietalia)	442
	22.8.4 Dwarf palm agricultural savannas on serpentine (Parvicopernicio-	
	Coccothrinacion)	
	22.8.5 Pine savannas (Pino – Aristidion neglectae)	444
	* 22.8.6 Natural edaphic Sabal savannas (Macrocopernicio – Sabalion)	
	22.8.7 Secondary <i>Sabal</i> savannas	
	- 22.8.8 Acoelorraphe wrightii savannas	
	22.8.9 Deciduous and treeless savannas	
	22.9 Freshwater vegetation formations	
	22.9.1 Alluvial gallery forests	
	22.9.2 Riverside gallery forests and derived types	
	 22.9.3 Swamp vegetation complex 22.9.4 Freshwater weed communities 	440
	22.10 Coastal vegetation	
	22.10 Coastarvegetation 22.10.1 Mangroves (Rhizophoro—Avicennietea)	451 451
	22.10.1 Mangroves (<i>Knizophoro—Avicennietea</i>)	
	22.10.2 The vegetation of sandy beaches (<i>Ipomoeo-manotonieu</i>)	
	23 Classification of major forest types of Cuba (with the contribution of Z. Szőcs)	
<u>`</u>	23.1 The main questions of the classification	
	23.2 Material of the numerical analysis	
	23.3 Results	
		0

23. A Classification of varietation units based on life form composition

22. The main vegetation types of Cuba

The vegetation map of Cuba has been prepared at a scale of 1:1 250 000. 37 different vegetational units are shown, these are primarily distinguished on physiognomic criteria, although floristic composition was also considered in case of karstic forests and pinewoods. Data for 267 relevés taken in 40 different cenological noda representing 22 of the 37 units shown in the map are given in Table 25a and b. (see Appendix) In the sequel the principal structural, floristic, ecological and chorological features of the mapped units will be discussed in brief.

22.1. Rainforests

22.1.1 Submontane rainforests (Calophyllo–Carapetum guianensis)
(Table 25, col. 19)

Forests with three canopy layers occurring on yellowish red mountain soils in the Moa Mts. and in the Toa, Jaguani and Duaba Basins where precipitation is more than 2500 mm and is evenly distributed over the year. The upper canopy layer is 30-35 m high, almost completely closed. As in the Mora forests of Trinidad (Beard 1946b), this layer is composed of a single species, which in Cuba is Carapa guianensis (Fig. 273). It is very rarely mingled with some exceptionally tall specimens of second level constituents. The plank buttresses of Carapa guianensis are frequently entwined by the aerial roots of the strangler Clusia rosea. (Fig. 274). The fully closed middle layer is 20-25 m high, and is composed of numerous tree species, whose leaves are mostly mesophylls. Permanent elements are Calophyllum utile, Sloanea curatellifolia, Dipholis jubilla, Guarea guidonia, Cupania americana, Buchenavia capitata, Ficus wrightii, and Roystonea regia. Of the montane elements Ocotea leucoxylon and Phoebe montana are mentioned. Cecropia peltata, Didymopanax morototoni and Ochroma pyramidalis occur in the cleared habitats. Palms are commonly found between the second and third layers along creeks, e.g., Bactris cubensis, Prestoea montana and Calyptronoma clementis ssp. orientensis.

Such stands rich in palms are popularly referred to as "Manacales" (see León 1946: 61). The third canopy layer is 6-15 m high, and is only up to 50-60% closed.

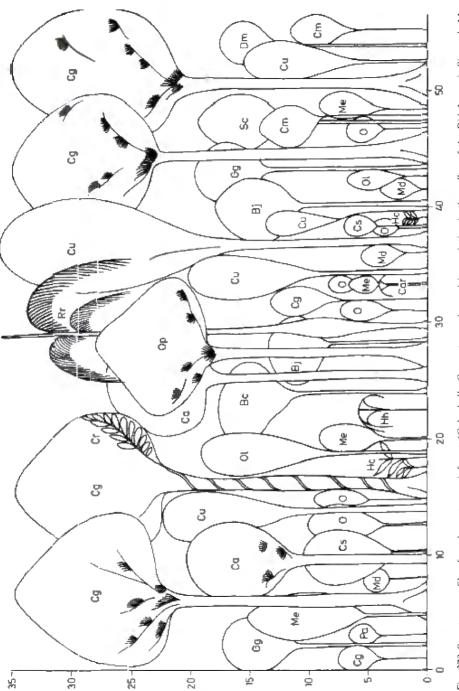


Fig. 273 Structure profile of a submontane rainforest (Calophyllo-Carapetum guianensis) association in the valley of the Rió Jaguani, Sierra de Mor (Borhidi and Muñiz) Cg=Carapa guianensis; Cg|=Cupania glabra; Ca=Cupania americana; Cu=Calophyllum utile; Dm=Didymopanax morototoni $Cm = Cedrela \ mexicana; \ Fb = Ficus berteroi; \ Cs = Cordia sulcata; \ Me = Miconia elata; \ Gg = Guarea guidonia; \ Op = Ochroma pyramidalis \ Bc = Buchenarvii$ capitata; Bj=Bumelia jubilla; Car=Cyathea araneosa; Cr=Clusia rosea; Hc=Heliconia caribaea; Hh=Hemitelia horrida; Md=Miconia dodecandra O = Oxandra lanceolata; O1 = Oxandra laurifolia: Rr = Roystonea regia; Sc = Sloanea curatellifolia



Fig. 274 Clusia rosea L. is one of the most common stranglers in all forest types of Cuba (Photo: A. Borhidi)



Fig. 275 Columnea tincta Griseb (Acanthaceae) a beautiful endemic epiphyte of the Moa range (Photo: A. Borhidi)

It is very rich in species, some characteristic elements being Oxandra lanceolata, O. laurifolia, and the large-leaved Cordia sulcata, Miconia elata, M. dodecandra, and tree ferns, such as Cyathea araneosa and Hemitelia horrida. The tree-sized herbaceous life-form is also typical (Heliconia caribaea). In the sparser shrub layer Cassipourea elliptica, Myrtaceae and Melastomataceae species are abundant. The herb layer is dominated by ferns, Ichnanthus pallens, Scleria pilosissima and S. secans in the moister places. Few macrophyllous lianes occur, e.g., Omphalea diandra and Marcgravia evenia. The double epiphyte layer is rich, the upper being dominated by flowering plants Columnea tincta (Fig. 275), Psychotria guadelupensis, Hillia parasitica (Fig. 276) Maxillaria species, Laelia lyonsii, Reichenbachianthus emarginatus, Aechmea nudicaulis, Hohenbergia penduliflora, Guzmania monostachya and G. lingulata. The lower epiphyte layer is composed primarily of ferns, e.g., Elaphoglossum crinitum, Rhipidopteris peltata, Polypodium, Asplenium and Trichomanes species, and Lycopodium funiculum. Forest communities with similar structure are the Sloanea berteriana — Ormosia krugii association described by Ciferri (1936) from Hispaniola, the Dacryodes—Sloanea community in Dominica (Beard 1949), also reported from Puerto Rico (Dansereau 1966) and Guadeloupe (Stehlé 1945) and the Psidium montanum-Calophyllum jacquinii community described from Jamaica by Asprey and Robbins (1953). Everywhere often transformed into coffee-plantages (Fig. 277)



Fig. 276 Hillia parasitica Jacq. (Rubiaceae) a common dicot epiphyte of the rainforest communities (Photo: A. Borhidi)

22.1.2 Wet montane rainforests (Ocoteo–Magnolietalia) (Table 25, cols 20—21)

This is the climax vegetation zone over 800 m altitude in Sierra Maestra, Escambray Mts and Sierra del Purial, and also in some mesoclimatic spots in Moa, Sierra del Cristal and Baracoa. Annual precipitation is 1700-3000 mm, distributed evenly over the year, the average temperature is 14 – 22 °C. Yellowish red ferrallitic soils and montane vellow allit-ferritic soils predominate. Two canopy layers can be recognized. These rainforests correspond to the "fangales" (León 1946) the "high open forests" (Seifriz 1943) and are called the "montane mist forests" in Jamaica (Asprey and Robbins 1953). They are 20–25 m high and have a closed upper layer consisting of microphylls and notophylls, e.g., Magnolia cubensis, Ocotea cuneata, O. leucoxylon, O. floribunda, Myrsine coriacea, and Cyrilla racemiflora. (Fig. 278) Characteristic trees in the second layer are Clusia tetrastigma, Gomidesia lindeniana, Alchornea latifolia, Garrya fadyenii, Miconia punctata, and Ossaea ottoschmidtii, and tree ferns, such as Cyathea arborea, C. balanocarpa and C. cubensis. The two epiphyte layers are very rich, having orchids and bromelias (e.g., Pleurothallis species, Guzmania lingulata, G. monostachya (Fig. 279) G. ervthrolepis, Tillandsia species, Vriesea species Catopsis species, and Dilomilis mon-



Fig. 277 The last coffee-plantation at the border of the rainforest-virgin forest belt of the Jaguani Reserve (Photo: A. Borhidi)

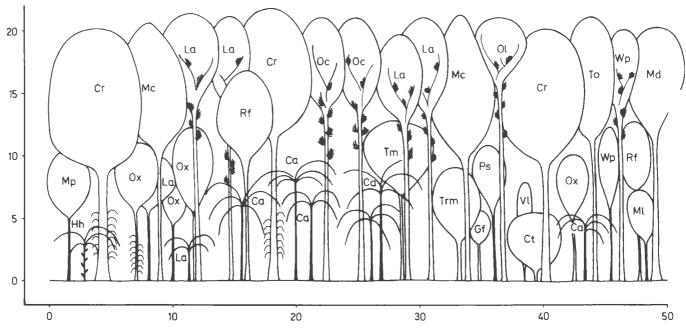


Fig. 278 Structure profile of a montane humid rainforest (Magnolio-Laplaceetum angustifoliae) association in Alto de Cardero, Sierra Maestra, at 1350 m a.s.l. Ca=Cyathea arborea and C. spp.; Cr=Cyrilla racemiflora; Ct=Clusia tetrasperma; Gf=Garrya fadyenii; Hh=Hemitelia horrida; La=Laplacea angustifolia; Lq=Lophosoria quadriradiata; Mc=Magnolia cubensis; Md=Matayba domingensis; Ml=Meriania leucantha ssp. nana; Mp=Miconia punctata; Oc=Ocotea cuneata; Ox=Oxandra laurifolia; Ps=Persea similis; Rf=Rapanea ferruginea; Tm=Talauma minor; To=Tabebuia oligolepis; Trm=Ternstroemia monticola; Vl=Vaccinium leonis; Wp=Weinmannia pinnata



Fig. 279 Guzmania monostachya (L.) Rusby ex Mez (Bromeliaceae) a frequent hygrophilous epiphyte of the submontane and montane rainforest belts (Photo: A. Borhidi)

tana) in the upper, and in the lower epiphyte ferns (Polypodium, Elaphoglossum, Hymenophyllum and Trichomanes species), epiphyllous mosses and liverworts. Terrestrial orchids (Prescottia, Ponthieva, Malaxis and Phaius) and shade-tolerant lianes (Odontosoria, Gleichenia, Peperomia, and Schradera species) are characteristic of the herb layer. The Magnolio-Laplaceetum angustifoliae community developed in Sierra Maestra between 800-1600 m (Column 20 in Table 25) represents a relatively rich rainforest type characterized by *Torralbasia cuneifolia*, Solonia reflexa, Ditta maestrensis, Brunellia comocladifolia, Weinmannia pinnata, Lasianthus lanceolatus, Clevera nimanimae, Graffenrieda rufescens, and Ilex macfadyenii; it has very diverse epiphyte layers (Fig. 280). Secondary communities with Prestoea montana and ferns dominating the herb layer, are typical following deforestation or wind damage between 800-1200 m (e.g., Gran Piedra). A poorer community with a less montane character is the Magnolio-Cyrilletum racemiflorae (col. 21) developed in the Escambray Mountains between 800 and 1100 m, it often occurs as extrazonal stands. Submontane elements and some endemics of the herb and shrub layers, such as Pilea clarana, P. cellulosa, P. clementis, and Psychotria martii, are typical.



Fig. 280 Structure profile of a montane rainforest of the Cuba Peak of the Turquino group, Maestra range, with two densely closed canopies at 1700 m a.s.l. (Photo: A. Borhidi)

22.1.3 Semi-arid montane serpentine rainforests (*Podocarpo – Sloanetalia*) (Table, 25, cols 14 – 15)

These forests represent the climax vegetation type in the Cristal and Moa Mountains between 400 and 900 m elevation. Extrazonal stands are found in the valleys of Nipe Mts. Climatic requirements are: annual precipitation 1800-3200 mm, with rainfall all year round, and a mean temperature of 18-24 °C. Two canopy layers are recognized, the constituents being sclerophyllous and lauraceous trees and shrubs. The open, 15-22 m (Fig. 281) high upper canopy layer is composed of Calophyllum utile, Podocarpus ekmanii, Hyeronima nipensis, Dipholis jubilla, Cyrilla cubensis ssp. nipensis, Pera ekmanii, Ocotea leucoxylon, O. bucheri, Tabebuia dubia, Byrsonima coriacea and B. orientensis, Matayba domingensis, Bonnetia cubensis, Talauma minor ssp. oblongifolia, and Magnolia cubensis, often mingled with *Pinus cubensis*. The lower stratum is 5-12 m high and more closed. Abundant species are Chionanthus (Linociera) domingensis, Tetrazygia cristalensis, Spathelia pinetorum, Tapura cubensis, Byrsonima biflora, and Ilex berteroi. A constant elements are Bactris cubensis, and the tree fern Alsophila aquilina. In the shrub layer Psychotria moaënsis, Myrcia gundlachii, Rauvolfia salicifolia, Moacroton ekmanii, Baccharis shaferi, Shafera platyphylla, and Eugenia, Lyonia, Ossaea, Calycogonium, Eupatorium, and Vernonia species are typical. Due to the openness

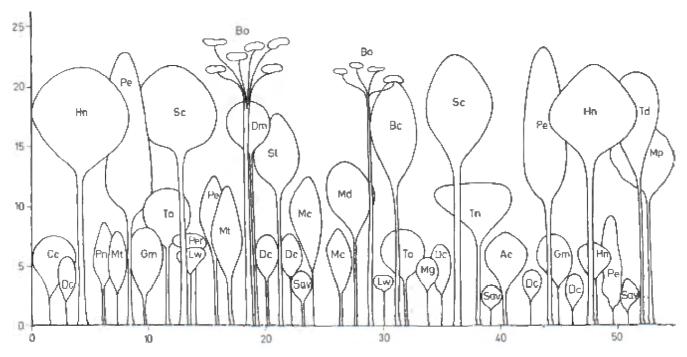


Fig. 281 Structure profile of a montane semi-dry serpentine rainforest (Hyeronimo-Sloanetum curatellifoliae) association in the Sierra del Cristal, Cayo Verde, at 800 m a.s.l. Ac=Annona cristalensis, Bc=Byrsonima coriacea, Bo=Byrsonima orientensis, Cc=Coccoloba costata, Dc=Dipholis cubensis, Dm=Didymopanax morototoni, Gm=Guatteria moralesii, Hn=Hyeronima nipensis, Lw=Leucocroton wrightii, Mc=Myrsine coriacea, Md=Matayba domingensis, Mg=Mozartia gundlachii, Mp=Micropholis polita, Mt=Miconia tetrandra, Pe=Podocarpus ekmanii, Per=Pera ekmanii, Pn=Pachyanthus neglectus, Sav=Savia cuneifolia, Sc=Sloanea curatellifolia, Sl=Simaruba laevis, Td=Tabebuia dubia, Tn=Terminalia nipensis, To=Talauma minor ssp. oblongifolia

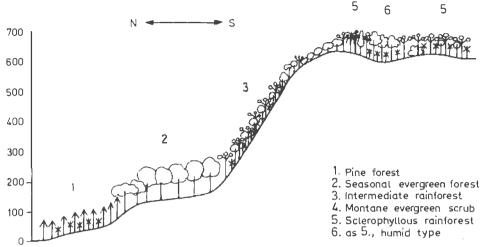


Fig. 282 Vegetation transect of the Sierra de Iberia, Cuchillas de Moa (Borhidi and Muñiz)

of the canopy layers the epiphyte levels are less clear-cut and poorer, with small orchids (Dilomilis elata, D. oligophylla, Polystachya luteola, Dichaea hystricina, Dinema cubincola, Epidendrum globosum, Lanium hiorami, Comparettia falcata, Elleanthus linifolius) predominating. The shade-tolerant epiphytes and epiphyllous bryophytes are absent, the number of ferns is much reduced. By contrast, many lianes grow in these forests, e.g., Morinda moaensis, Vanilla wrightii, Gleichenia flexuosa, G. leonis, Chusquea abietifolia, Arthrostylidium species, Odontosoria species, Schradera cubensis, Marcgravia evenia, Rajania baracoënsis, Eupatorium rhexioides, Lygodium volubile, and Platygyne oboyata, etc. The forests of this vegetation belt (Fig. 282) have been classified into two cenological noda. The broad-leaved climax forests belong to the Podocarpo-Byrsonimion orientensis nodum (col. 15) with several associations. The non-climax woodlands, in which pines are dominant, have been assigned to the Cyrillo-Pinion cubensis alliance (col. 14). The latter one is a more humid community having luxuriant herb and moss strata and relatively rich epiphyte layer. Noted discriminating species are: Senecio rivalis, S. polyphlebius, Hedyosmum crassifolium, Cladium restioides, Rhynchospora marisculus, Scleria secans, Calyptronoma clementis ssp. orientensis, Isachne leersioides, Rondeletia pachyphylla, Gundlachia cubensis, Brya subinermis, and Pilea species.

22.1.4 Cloudforests or mossy forests (Weinmannio—Cyrilletalia) (Table 25, col. 22)

In Cuba this type is confined to the high altitude regions of Sierra Maestra, and to the high mountains of the Pico Turquino and Pico Bayamesa group between 1600—1900 m. In frost-free, evenly cool moist climate it is a climax type, but

extrazonal stands on moist gravel slides may also occur. The annual mean temperature required is 10-14°C, the total rainfall is 2800-3200 mm per year. This type is partly identical with the "monte fresco" described by León (1946:63), but this statement does not hold for the stand shown in Fig. 33. The "alpine thicket" (Seifriz 1943), the "elfin woodland" (Beard 1944, 1955, Asprey and Robbins 1953), the "montane shrub zone" (Dansereau 1967) and, in part, the "foresta montana" (Ciferri 1936) appear to be synonymous. In the Antillean islands mossy forests are found at very different altitudes: in the Lesser Antilles as low as at 300 m (Beard 1949), in Puerto Rico between 1000 and 1200 m (Howard 1969), in Jamaica between 1600-2000 m, and in Hispaniola over 2000 m. The canopy layer is closed, very dense, 6-12 m high. The constituents include small-leaved sclerophyllous and leaf-succulent twisted trees and a variety of tree ferns reaching the canopy level (Fig. 283). The shrub layer is also dense, an almost impenetrable bush tangled by pteridophytic lianes, such as the Dennstaedtia, Odontosoria and Gleichenia, species. Species characteristic of the canopy layer are Myrsine microphylla, Nectandra reticularis, Sapium maestrense, Persea anomala, Symplocos leonis, Eupatorium (Ageratina) paucibracteatum, Cyrilla racemiflora, Weinmannia pinnata, Torralbasia cuneifolia, Garrya fadyenii, Cyathea arborea, C. balanocarpa, C. minor, Alsophila aspera, and Lophosoria quadriradiata. Examples of the abundant



Fig. 283 Elfin mossy forest with crowded dwarf trees covered by thick epiphytic mossy carpet on the Real Peak of the Turquino group at 1900 m a.s.l. (Photo: A. Borhidi)

shrub layer plants are Vaccinium leonis — sometimes tree-sized individuals — Lyonia calvcosa, Ternstroemia monticola and T. leonis, Miconia turquinensis, M. nystroemii, Duranta fletcheriana, Cordia longipedunculata, Tabebuia turquinensis, Hedvosmum cubense, Henriettea ekmanii, and Scolosanthus maestrensis. Ferns and lycopods, such as Cheilanthes harrisii, Diplazium urbanii, Blechnum tuerckheimii, Danaea species, Lycopodium clavatum, L. serrulatum, L. taxifolium, and L. montanum, are dominant in the herb layer. The simple epiphyte stratum is very rich in small endemic orchids (e.g., Lepanthes ekmanii, L. blepharantha, L. fractiflexa, L. fulva, L. acunae, Stelis cubensis, Pleurothallis spp.), in Hymenophyllaceae species (six Trichomanes and four Hymenophyllum species occur), and Polypodium and Elaphoglossum species. The soil surface, the branches and the lower foliage of trees are covered by an unbroken stretch of bryophytes, including nearly 40 mosses, such as Meteoriopsis patula, Mettenothamnium reptans, Macromitrium harrisii, M. jamaicense, M. schwaneckeanum, Hypnum polypterum, Phyllogonium fulgens, Pilotrichella flexilis, Prionodon densus, Rhizogonium spiniforme, and Fissidens weizii, etc. Only one community type in Cuba may be assigned to this cenological category, namely the Myrsino (microphyllae)-Nectandretum reticularis association, which is extremely rich in endemics (they account for 41.15% of the non-zero scores in the data).

22.1.5 Semi-arid montane serpentine shrubwoods (Clusio—Ilicetalia) (Table 25, cols 16 and 18)

Microphyllous evergreen montane shrubwoods have been reported to be present on young lava soils of Central American volcanoes (Lötschert 1959) and on the slopes of the Blue Mountains in Jamaica, in a mesoclimatically arid zone (Asprey and Robbins 1953). These two noda, under the respective names Myrico-Baccharidetalia vaccinioidis and Myrico-Lyonietalia jamaicensis, have been amalgamated into the class Myrico-Baccharidetea (Knapp 1965, see also Knapp 1965:297). However, the montane serpentine shrubwoods of Cuba, often called "charrascals", are completely different from these in floristic composition and seral position. The Cuban shrubwoods are not pioneer communities, unlike those in Central America, and not subclimax types of arid regions, unlike the sclerophyllous montane shrubwoods of Jamaica. The montane shrubwoods in the Nipe, Cristal and Moa Mountanins are edaphic climax communities developed under a humid tropical rainforest climate. Their sclerophyllous character is a mere consequence of the ferritic soils derived from serpentine bedrocks (see Part II chapter 13 for more details). The overwhelming majority of species are endemic so that a separate class, Clusio-Ilicetea, was created to include these communities. It consists of a dense bush of microphyllous and nanophyllous sclerophyll shrubs and stunted trees up to 4-6 m height, with an open layer of emergent trees reaching 7-10 m height. In Moa this community has high species diversity between 600 and 1000 m in altitude. The more moist association group of Moa (Ilici-Laplaceion) is characterized by the following trees and shrubs: *Ilex berteroi*, *I. victorini*, *I. hypaneura*, *I. shaferi*, Laplacea moaënsis, L. benitoënsis, Clusia moaënsis, C. callosa, C. monocarpa,



Fig. 284 Cyrilla cubensis P. Wils. an endemic shrub of North Oriente, characteristic of the evergreen serpentine scrub communities (Photo: A. Borhidi)

Acrosynanthus trachyphyllus, Rauvolfia salicifolia, Byrsonima biflora, Lyonia glandulosa, Cyrilla cubensis (Fig. 284), Tapura cubensis, Myrica shaferi, Antirhea abbreviata, Alsophila aquilina, Jacaranda arborea, Illicium cubense, and Rheedia polyneura, etc. Only a few epiphytes occur (Dilomilis oligophylla, Polypodium duale, Hymenophyllum abruptum). Conversely, the sclerophyllous lianes are numerous (e.g., Arthrostylidium fimbriatum, A. pinifolium, Feddea cubensis, Rajania baracoënsis, Symphyisia alainii, Morinda moaensis, etc.). Ekmanochloa aristata, Paepalanthus pungens, P. riparius, Rhynchospora cernua, R. pruinosa, and R. shaferi are characteristic of the herb stratum in cleared areas. The contribution of endemic taxa to the total of all scores is 77 (cf. Table 25, col. 16). In Nipe and Loma Mensura at 650-1000 m the Myrcio-Bourrerietum association is found, which is similar in appearance but more xeromorphic, having many spinose elements (here the contribution of endemics to the total is 70%, also very high!). Characteristic species are Bourreria pauciflora, Myrcia retivenia, Coccoloba reflexa, Spathelia cubensis, Callicarpa lancifolia, Ariadne shaferi ssp. shaferi, Clusia nipensis, Annona sclerophylla (Fig. 285), Calycogonium rosmarinifolium, Euphorbia podocarpifolia, Jacaranda arborea, Eugenia mensuraensis, and Baccharis shaferi. There are few lianes, the endemic Harnackia bisecta is characteristic. In the herb layer some drought-resistant terrestrial orchids (Bletia purpurea, B. florida, Encyclia atropurpurea) and many cyperaceous species are found.



Fig. 285 Annona sclerophylla Safford, a common shrub of the evergreen montane serpentine scrub communities of North Oriente (Photo: A. Borhidi)

22.1.6 Elfin thickets (*Ilici—Myricion cacuminis*) (Table 25, col. 23)

This vegetation type is represented by extrazonal stands on the southern and eastern bluffs between 1800 and 1970 m in Pico Turquino, the highest mountains of Sierra Maestra (Fig. 286). It corresponds to the "alpine thicket" described by Beard (1944, 1955), the "alpine woodland" of Howard (1969) and is on a par with the Central American alpine shrublands that are rich in Ericaceae species (Knapp 1965:300), the latter being a climax vegetation belt between cloudforests and paramós. Léon's (1946) "monte fresco" term includes this type too (in elfin thicket is illustrated by the photograph in Fig. 33 as "monte fresco"). This vegetation type is much drier than the shrubwoods of the cloudy zone, partly because it is above the condensation belt and partly because water is rapidly drained from the steep rocky surface. This is why many herbaceous leaf-succulents and spinose shrubs are found here. Within this nodum two associations may be recognized. The first is a dense bush composed of 1.5 – 2 m high microphyllous and nanophyllous evergreen shrubs (Illici – Myricetum cacuminis) and is characterized by Ilex turquinensis, I. nunezii, Peratanthe cubensis, Myrica cacuminis, Lobelia cacuminis, Eupatorum (Ageratina) paucibracteatum, Vernonia parvuliceps, V. praestans ssp. cacuminis, Weinmannia pinnata, Persea similis, Lyonia calycosa, Torralbasia cuneifolia, and Viburnum vil-



Fig. 286 Elfin thicket of the main ridge of the Real Peak of the Turquino group at 1950 m a.s.l. with the local endemic Agave pendentata Trel. (Photo: A. Borhidi)

losum, etc. The other association, Agavo—Mitracarpetum acunae, is a 50—100 cm high evergreen thicket on steep rocky slopes. This is rich in lianes, subshrubs and orchids rooted in the moss carpet. Prominent characteristic species are emergent agaves (Agave pendentata Fig. 255) and many small epiphytic orchids living on the ground here (Pleurothallis gelida, P. obliquipetala, P. wrightii, P. testifolia, P. parvula. P. velaticaulis, Lepanthes turquinoënsis, L. pergracilis, L. blepharantha, Lepanthopsis microlepanthes). Typical members of the shrub layer are the dominant Ilex turquinensis, I. nannophylla, Mitracarpus acunae, Cassia turquinae, Micromeria bucheri, Juniperus saxicola, Schoepfia stenophylla, Vernonia praestans ssp. cacuminis, Eugenia maestrensis, and E. lomensis. Of the herbs Chaptalia turquinensis, Pilea micromeriifolia, Peperomia galioides, P. grisebachiana, and Begonia lomensis are to be mentioned. Chusquea abietifolia and Arthrostylidium multispicatum are dominant lianes densely entangling the vegetation.

22.2 Seasonal evergreen forests or seasonal rainforests

Many authors do not make a distinction between the important tropical seasonal forests and the true rainforests. For example, the Spondias-Oreodoxa association of Ciferri (1936:222), thought to be true tropical rainforest, is in fact a seasonal lowland rainforest. The "forêt ombrophile tropicale" category used by many French researchers comprises seasonal forest formation. Others, e.g., Walter (1962) disagree only with the adjective "seasonal". Our vegetation type is indentical with the "seasonal evergreen forest" of Beard (1944), although that type may be more broadly interpreted. The Jamaican equivalent is the "wet limestone forest" (Asprey and Robbins 1953). In Puerto Rico seasonal evergreen forest is called "lowland rainforest" by Dansereau (1966:20). He uses "seasonal evergreen forest" for a drier formation than Beard's community of the same name. Dansereau's seasonal evergreen forest should be called a semi-deciduous forest. Knapp (1965) uses the term "semi-deciduous moist forest", which is obviously unacceptable as these forests are actually evergreen. The reason for this nomenclatural confusion is that these forests are transitional between the rainforests and semi-deciduous forests. They are closer to the rainforests in structure (number of strata, richness in epiphytes). However, the presence of deciduous emergents, the highly developed liane stratum and the absence of shade-tolerant epiphytes and epiphylls emphasize their similarity to the semi-deciduous forests. In the Antilles this formation, the climax type in extensive areas, can be clearly distinguished from both the rainforests and the semi-deciduous forests.

22.2.1Lowland seasonal rainforests

This vegetational zone formerly occupied the most extensive areas in the island and is still widespread in Cuba. It is a climax formation in tropical seasonal climate with 3-5 dry months and 1200-1600 mm annual precipitation, it occurs on calcareous, ferrallitic, and deep red ferrallitic soils. On shallower ferrallitic soils it

may develop only if there are not more than one or two dry months a year, as longer dry seasons are more favourable for semi-deciduous forests. This forest zone is the most suitable for tropical agriculture. Consequently, undisturbed stands are hardly found anywhere in Cuba. Their probable physiognomy is reconstructed from semi-cultivated fragments, and from studying standard trees of agricultural savannas and the shade trees of abandoned lowland coffee plantations. Two canopy levels, both evergreen, are recognized. The upper is more open and 20–25 m high, the lower is closed and 8-15 m high. Typically there are emergent specimens of the deciduous Ceiba pentandra which may be as tall as 30—40 m. Elements of the upper canopy layer are Roystonia regia, Guazuma ulmifolia, Bucida buceras, Mastichodendron foetidissimum, Lonchocarpus domingensis, L. latifolius, Luehea speciosa, Chlorophora tinctoria, Cecropia peltata, Cordia collococca, C. gerascanthus, and Ficus species, and many microphyllous trees, such as Pithecellobium cubense, Samanea saman, and Peltophorum adnatum. In the lower stratum Oxandra lanceolata, Andira inermis, Ateramnus lucidus, Crescentia cujete are characteristic species. Drought-tolerant epiphytes (Tillandsia fasciculata, T. recurvata, T. valenzuelana, T. polystachya, T. tenuifolia) and lianes (Philodendron lacerum, Ph. krebsii, Ph. clementis, Hylocereus undatus, Pithecoctenium echinatum) are commonly found on tall trees. The royal palm-cotton treesamanea agricultural savannas widespread in the northern Caribbean are derived from these forests by logging, burning and grazing.

22.2.2 Submontane seasonal rainforests (Oxandro — Dipholietum) (Table 25, col. 24)

These are forest formations in the submontane zone from 200 m to 800 m in altitude. They have a seasonal climate with one to three dry months and an annual rainfall averaging 1400-1800 mm. These forests correspond to León's (1946) "vayales" formation. They are similar to the lowland seasonal rainforests in structure but the megatherm trees differ. Ceiba pentandra, Samanea saman, Guazuma ulmifolia, and Zanthoxylum elephantiasis are absent. Of the emergents Dipholis jubilla occurs in the Oriente whereas Dipholis salicifolia or Cedrela mexicana specimens are found elsewhere. These forests have different composition in the different mountains. In the stands sampled in Sierra Maestra (Table 25, col. 24) Dipholis jubilla is the only buttressed emergent tree (Fig. 287). Calophyllum antillanum, Zizyphus rhodoxylon, Ficus berteroi, Zanthoxylum martinicense, Z. cubense, Didymopanax morototoni, Sapium jamaicense, Faramea occidentalis, Cedrela mexicana, Guarea guidonia, Cupania glabra, C. americana, and Roystonea regia are characteristic of the closed upper canopy, and Oxandra lanceolata, O. laurifolia, Chrysophyllum argenteum, Dendropanax arboreus, Lonchocarpus latifolius, Sloanea amygdalina, Wallenia laurifolia and Ateramnus lucidus, etc., occur in the lower stratum. The herb layer is dominated by terrestrial ferns from the genera Dryopteris, Asplenium, Adiantum, Tectaria, Diplazium, and Dennstaedtia. These ferns, the mesophytic orchids of the epiphyte layer (mostly *Epidendrum*, Encyclia and Oncidium species) and the mesophilous lianes allow a clear distinction

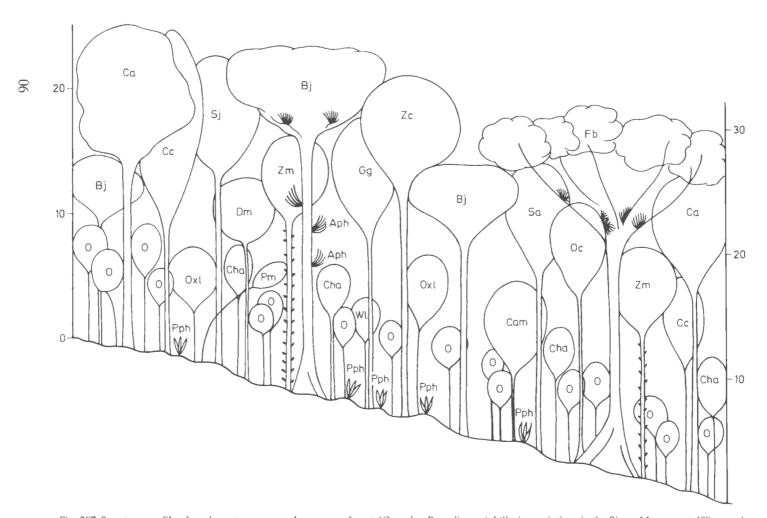


Fig. 287 Structure profile of a submontane seasonal evergreen forest (Oxandro-Bumelietum jubillae) associations in the Sierra Maestra, at 400 m a.s.l. next to Guisa (Borhidi and Muñiz) Aph=Asplenium phyllitidis, Bj=Bumelia jubilla, Ca=Calophyllum antillanum, Cam=Cupania americana, Cc=Calycophyllum candidissimum, Cha=Chrysophyllum argenteum, Dm=Didymopanax morototoni, Fb=Ficus berteroi, Gg=Guarea guidonia, O=Oxandra lanceolata, Oc=Ocotea cuneata, Oxl=Oxandra laurifolia, Pm=Protium maestrense, Pph=Polypodium phyllitidis, Sa=Sloanea amygdalina, Sj=Sapium jamaicense, Wl=Wallenia laurifolia, Zc=Zanthoxylum cubense, Zm=Zanthoxylum martinicense

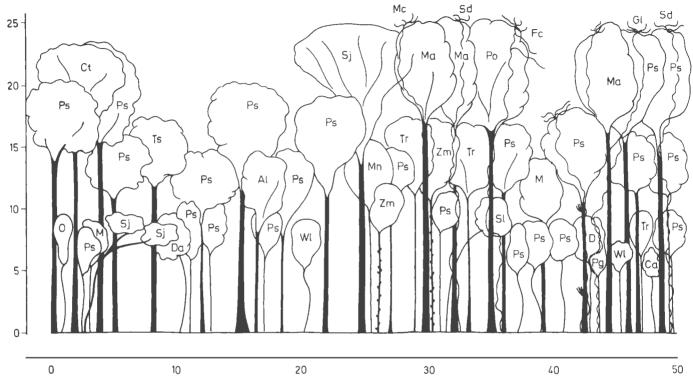


Fig. 288 Structure profile of a submontane seasonal evergreen forest (Mataybaeo-Pseudolmedietum spuriae) association of the Sierra del Rosario, Pinar del Rió province, in the Loma El Salon at 470 m a.s.l. (Borhidi, Capote and Del Risco) Al=Alchornea latifolia, Ca=Calophyllum antillanum, Ct=Cinnamomum triplinerve, D=Drypetes alba, Da=Dendropanax arboreus, Fc=Forsteronia corymbosa, Gl=Gouania lupuloides, Ma=Matayba apetala, M=Mastichodendron foetidissimum, Mc=Merremia cissoides, Mn=Margaritaria nobilis, O=Oxandra lanceolata, Pg=Psychotria grandis, Po=Prunus occidentalis, Ps=Pseudolmedia spuria, Sd=Smilax domingensis, Sj=Sapium jamaicense, Tr=Trophis racemosa, Ts=Tabebuia shaferi, Wl=Wallenia laurifolia, Zm=Zanthoxylum martinicense

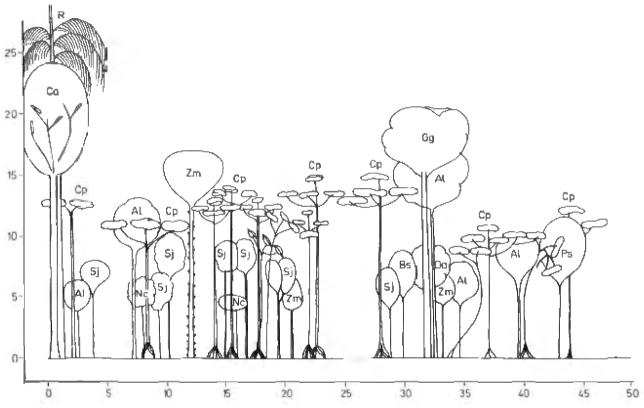


Fig. 289 Structure profile of a second growth forest developed after cutting a seasonal evergreen submontane forest (Mataybaeo-Pseudol-medietum spuriae) in the Sierra del Rosario (R. Capote) Al=Alchornea latifolia; Ca=Calophyllum antillanum; Cp=Cecropia peltata; Bs=Bursera simaruba; Da=Drypetes alba; Gg=Guarea guidonia; Nc=Nectandra coriacea; Ps=Pseudolmedia spuria; R=Roystonea regia; Sj=Sapium jamaicense

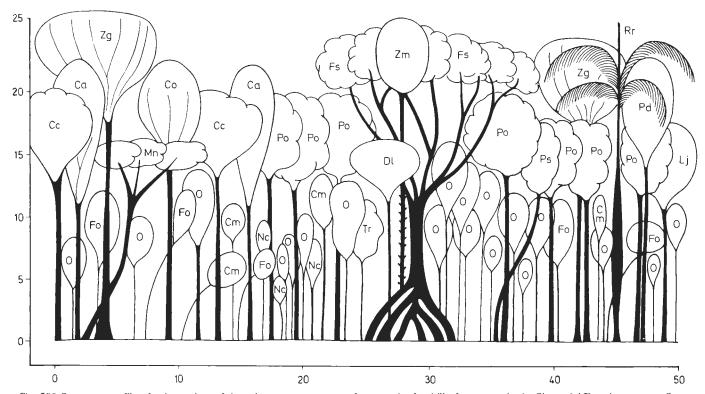


Fig. 290 Structure profile of a dry variant of the submontane evergreen forest at the foothill of a mogote in the Sierra del Faustino, next to San Diego de Los Baños, Pinar del Rio Province, at 200 m a.s.l. (R. Capote and Borhidi) Ca=Calophyllum antillanum; Cc=Cordia collococca; Co=Cedrela odorata; Cm=Cupania macrophylla; Dl=Drypetes lateriflora; Fo=Faramea occidentalis; Fs=Ficus subscabrida; Lj=Licaria jamaicensis; Mn=Margaritaria nobilis; Nc=Nectandra coriacea; O=Oxandra lanceolata; Pd=Pouteria dictyoneura; Po=Prunus occidentalis; Ps=Pseudolmedia spuria; R=Ryostonea regia; Tr=Trophis racemosa; Zg=Zuelania guidonia; Zm=Zanthoxylum martinicense

to be made between seasonal rainforests and semi-deciduous forests. (Figs 288–290). The difference is even more emphasized by the presence of epiphyllous lichens and bryophytes growing on trunks.

22.3 Semi-deciduous forests

22.3.1 Semi-deciduous mesophytic forests (Oxandro—Burseretalia)

Table 25, cols 28—30)

These are natural forests which are widespread especially in the lowlands and hills of western and central Cuba where the annual rainfall is 1200-1700 mm and the dry seasons are of three to six months' duration. In the Antilles this vegetation type is generally distributed. Ciferri's (1935) *Catalpa-Swietenia* association and the "Hammock forests" of Florida (Knapp 1965) are examples, such communities have been described by Dansereau (1967) from Puerto Rico, and by Beard (1949) and Stoffers (1956) from the Lesser Antilles. Two canopy layers occur, the height of the tallest trees ranges from 18 to 25 m. In the upper canopy layer the cover of deciduous trees is not more than two-thirds of the total cover. The 6-12 m high



Fig. 291 Giant Ceiba trees in a semi-deciduous littoral forest in the Zapata Peninsula with Selenicereus boeckelmannii climber on the trunks (Photo: A. Borhidi)



Fig. 292 Strangler fig in a submontane semi-deciduous forest (Photo: A. Borhidi)



Fig. 293 Urera baccifera (L.) Gaud, a horrible shrub of the submontane evergreen forests (Photo: A. Borhidi)

second stratum is composéd exclusively of evergreens, partly of sclerophyllous ones. Deciduous giant trees (Ceiba pentandra Fig. 291, Bombacopsis cubensis) may also be present but are sparsely distributed in any case. Prominent elements of the upper canopy layer are Ficus crassinervis (Fig. 292), Cedrela mexicana, Andira inermis, Bursera simaruba, Mastichodendron foetidissimum, Pithecellobium cubense, Zanthoxylum elephantiasis, Catalpa punctata, Tabebuia shaferi, Zuelania guidonia, Casasia calophylla, and Casearia hirsuta. In the second layer Amyris balsamifera A. elemifera, Trichilia hirta, Picramnia pentandra, Adelia ricinella, Diospyros crassinervis, Krugiodendron ferreum, Ateleia cubensis, Eugenia axillaris, E. rhombea. E. maleolens, Canella winterana, Allophylus cominia, Savia sessiliflora, Cordia gerascanthus, Urera baccifera (Fig. 293), and Ateramnus lucidus are common. The epiphyte level is fragmented, only the emergent trees possess vast numbers of epiphytic plants, especially drought-resistant Tillandsia species. Many lianes, with xerophytic microphylls occur, e.g., Pisonia aculeata, Celtis iguanea, Solandra longiflora, Chiococca alba, Cissus sicyoides, C. formosa, Canavalia ekmanii, Dalechampia scandens, Serjania diversifolia, Abrus precatorius, Securidaca elliptica, Clematis dioica, Passiflora suberosa, P. multiflora, Bauhinia divaricata, (Fig. 294), Pithecoctenium echinatum, Stegnosperma scandens, Platygyne hexandra, and Smilax havanensis, etc. The herb layer is poor or even completely lacking, so are the shade-tolerant ferns. Three closely related associations coming from three different regions of Cuba were studied. The Bombacopsi - Catalpetum (Fig. 295), communi-



Fig. 294 The semi-deciduous forest is rich in climbers; one of them is Bauhinia divaricata L. in the Zapata Peninsula (Photo: A. Borhidi)

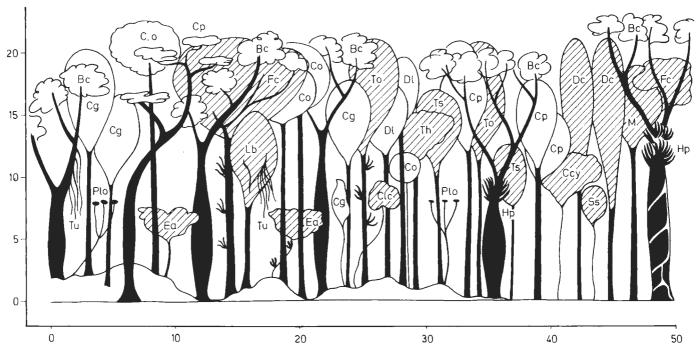


Fig. 295 Structure profile of a semi-deciduous lowland forest on dogtooth limestone in the Guanahacabibes Peninsula, El Veral Reserve Station, 10 m a.s.l. (Borhidi and Capote) white crowns: deciduous trees; hanchured crowns: evergreen trees Bc=Bombacopsis cubensis; Ccy=Capparis cynophallophora; Cg=Cordia gerascanthus; Co=Cedrela odorata; Cp=Ceiba pentandra; Cpu=Catalpa punctata; Dc=Diospyros crassinervis; Dl=Drypetes lateriflora; Ea=Eugenia axillaris; Fc=Ficus crassinervis; Lb=Linociera bumelioides; Plo=Plumeria obtusa; Th=Trichilia hirta; To=Torrubia (Guapira) obtusata; Ts=Tabebuia shaferi; Clc=Clerodenrum calcicola; Hp=Hohenbergia penduliflora; Tu=Tillandsia usneoides

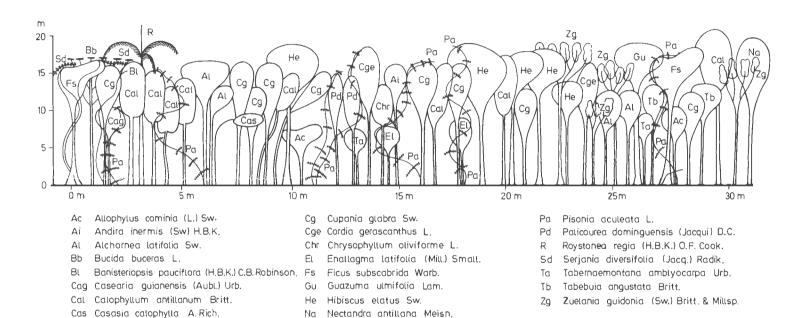


Fig. 296 Structure profile of an anthropically influenced lowland seasonal evergreen forest in the Zapata Peninsula at 5 m a.s.l. (Borhidi and Del Risco)

Na Nectandra antillana Meisn.

ty in the Guanahacabibes peninsula is characterized by emergent giant trees and Mexican elements, the *Coccolobeto-Burseretum* association of Isla de Pinos and the Zapata Peninsula (Fig. 296) has many microphyllous coastal plants, and the *Zanthoxylo-Burseretum* community on the hills in Las Villas and Camagüey has several rainforest trees.

22.3.2 Semi-deciduous xerophytic forests

These are relatively low (12–15 m) forests with a single canopy layer, found in the lowlands and hills of the eastern part of central Cuba, on sandy or rocky, acidic or neutral soils that are poor in nutrients. Annual precipitation is 800–1200 mm, the seasonal climate has 5–6 dry months. The canopy level is up to 80% and is partly composed of deciduous trees. Characteristic trees are, for example, Bursera simaruba, Cordia gerascanthus, C. collococca, C. nitida, Phyllostylon brasiliensis, Gossypiospermum praecox, Manilkara jaimiqui ssp. wrightiana, Maytenus buxifolia, Belairia spinosa, Pisonia rotundata, Ficus laevigata, Eugenia maleolens, Hypelate trifoliata, Piscidia piscipula, Ateleia apetala, Canella winterana, Diospyros halesioides, Tabebuia anisophylla, T. trachycarpa, Carpodiptera cubensis, Copernicia baileyana, C. textilis, and C. sueroana (Fig. 297). The shrub layer consists mainly of spiny sclerophylls, e.g., Brya ebenus s.l., Malpighia, Randia, and Oplonia species. Natural stands are rare, their physiognomy is similar to the cerrado



Fig. 297 Microphyll semi-deciduous forest in the eastern lowland of Cuba, south of Victoria de las Tunas, with Belairia mucronata Griseb. and Copernicia baileyana León (Photo: A. Borhidi)

vegetation of the cerrado forest zone in Brazil, as described by Eiten (1972). As a result of burning and grazing most stands have been replaced by secondary savannas dominated by either *Copernicia* or deciduous trees.

22.4 Tropical karstic forests

These are extremely diverse forests on shallow humic-carbonated rendzina or bare rocks of deeply eroded mountains and solitary cliffs consisting mainly of hard Jurassic and Triassic limestone. Usually a single, 5-10 m high open canopy layer composed mainly of deciduous trees occurs. In Cuba this formation is most similar to the dry deciduous forests. Thanks to the favourable light conditions, the usually epiphytic plants live on the ground forming a closed herb layer on rocks where water balance is just as poor as on the trunk or at canopy level. In extreme habitats which become dry and hot very quickly, succulent agaves, epiphytic, columnar or liane-like cacti (*Rhipsalis*, *Leptocereus*, *Selenicerus*, *Pilosocereus*), and trees with barrel-like trunks capable of water storing (*Gaussia*, *Bombacopsis* (*Fig.* 174)) are found. The thickness of soils, if any, is extremely uneven due to erosion and soil accumulation caused by geomorphological formations. Therefore, the vegetation itself is also of mosaic structure. Lötschert (1958) takes the view that no associations can be distinguished in the mogotes. Of course, associations in the sense applied to

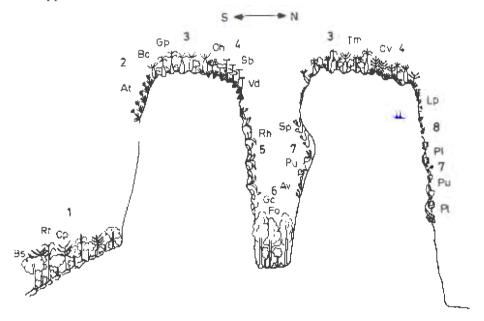


Fig. 298 General scheme of the vegetation types of a "mogote complex" Bs=Bursera simaruba; At=Agave tubulata; Av=Anthurium venosum; Bc=Bombacopsis cubensis; Cv=Ceratopyxis verbenacea; Cp=Ceiba pentandra; Gp=Gaussia princeps; Gc=Gesneria celsioides; Fo=Faramea occidentalis; Lp=Leptocereus prostratus; Oh=Omphalea hypoleuca; Pl=Philodendron lacerum; Pu=Philodendron urbanianum; Rh=Rhytidophyllum rupincola; Rr=Roystonea regia; Sp=Siemensia pendula; Tm=Thrinax morrisii

the temperate zone, especially to Central Europe, cannot be recognized in the tropical vegetation if characterized by a multitude of dominant species (tropical coniferous forests, mangroves, littoral communities and savannas are usually exceptions), but it is possible to define associations. Under favourable conditions seven well-defined vegetational noda may be distinguished in the mogotes: herbaceous communities of the insolated (1) and those of shaded (2) crevices, shrub dominated (3) and bromeliad dominated (4) mogote forests, semi-deciduous forests on rocks (5) and at the foot of hills (6), and seasonal rainforests in the gorges (7) (Fig. 298). The first four communities comprise the "mogote complex" in the wider sense. This complex is hard to subdivide for technical reasons. The shrub and bromeliad dominated mogote forests can be treated as "mogote forests" in a narrower sense. Their composition is shown in Table 25., (col. 26). The mogote forests of the bromeliad type are absent from the soft limestone formations (e.g., Las Villas, Oriente) where only the shrubby variant may develop (cols 25 and 27). The mogote forests have two evolutionary centres with completely different floras, the older in western Cuba (Bombacopsi-Thrinacetalia), another in the central and eastern part of the island (Tabebuio-Coccothrinacetalia). Both vegetation types served as a basis for the flora development on the rocky coasts. Most of the mogotes of eastern Cuba were themselves located on the coastal zone in the Tertiary. Therefore, the connection between the flora of these mogotes and the recent coastal zone had been stronger than that between the coast and the mogotes of Sierra de los Organos that were separated from each other by slatey outcrops.

22.4.1 Species rich karstic forests of western Cuba (Spathelio—Gaussion) (Table 25, col. 26)

These are open forests composed of 5-8 m high, mostly deciduous trees on the steep slopes and the top of the karstic mountains in Sierra de los Organos. Characteristic are Bombacopsis cubensis and Gaussia princeps with barrel-like trunks, and the tree fern-shaped Spathelia brittonii, Thrinax punctulata, Ekmanianthe actinophylla, Omphalea hypoleuca, Bourreria polyneura, Microcycas calocoma, Plumeria emarginata, Colubrina elliptica, Citharexylum caudatum, Erythrina cubensis, Sapium leucogynum, Trichilia havanensis, and Zanthoxylum pimponelloides. In the bromeliad dominated variant (Vrieseo-Bombacopsidetum) Hohenbergia penduliflora, Vriesea dissitiflora and twelve Tillandsia species are typical. Dominant species of the shrubby variant are Ceratopyxis verticillata, Eugenia galeata, Psidium vicentinum, Oplonia purpurascens, Annona cascarilloides, Malphighia roigiana, Guettarda calcicola, etc. Of the succulents Agave tubulata, Leptocereus assurgens, and Selenicereus grandiflorus are worth mentioning. Lianes, such as Siemensia pendula, Philodendron urbanianum, and Cuervea integrifolia, and chasmophytes, e.g., Gesneria celsioides, Rhytidophyllum rupincola, Anthurium venosum, and Peperomia verticillata are also common. The endemic taxa account for 40% of the total of the presence scores in the data, suggesting that among the limestone formations of Cuba these forests are the richest in endemics.

27 417

22.4.2 Species poor karstic forests of western Cuba (Thrinacion punctulatae)

These forests are found in the limestone karsts originated from the Cretaceous and the Eocene in the provinces of Habana and Matanzas, between 200 and 300 m altitude, in a seasonal climate of one to four dry months and 1200 – 1600 mm rainfall per year. In these rocks that are softer than the Jurassic limestone of Sierra de los Organos, the biologically induced karstification process is intensive so these karstic forests are poorer in chasmophytes, most of those being replaced by mesophytic and grophilous elements of canyon forests (Peperomia, Pilea, Rhytidophyllum and fern species). Most typical of these forests is the Bombacopsi-Thrinacetum morrisii association, which was studied in the mogotes of Jaruco. Thrinax morrisi is dominant, its 5-6 m high canopy layer is barley broken by emergent individuals of Bombacopsis cubensis. An additional element characteristic of the Viñales mogotes but also present here, is Agave tubulata. The others are replaced by more common calciphilous species, such as Celtis trinervia, Erythroxylum areolatum, Ficus jacquinifolia, F. aurea, Casearia guianensis, C. hirsuta, Hamelia patens, Bocconia frutescens, Piper umbellatum, Trichilia havanensis, and Cordia globosa. The occurrence of the spiny shrub Leucocroton microphyllus is typical of dry habitats. Rhytidophyllum exsertum occurs in shaded crevices in rocks. The community is strikingly poor in epiphytes.

22.4.3 Karstic forests of eastern Cuba (Tabebuio — Coccothrinacion)

Isolated stands of different size extend from the limestone cliffs of Las Villas as far as the Baracoa area, including the karstic block mountains of Camagüey and the extensive mogote zone of Nipe and Sierra Maestra. They are different from the western mogotes in four respects:

- 1. Trees with barrel-like trunks are absent,
- 2. Thrinax palm is replaced by *Hemithrinax* and *Coccothrinax* species,
- 3. Columnar cacti are customarily found, and
- 4. Deciduous elements are less abundant, being replaced by evergreen sclerophyllous trees and shrubs. The floristic composition differs with various mountain areas.

The isolated mogote floras of Las Villas and Camagüey are poor in species. The most developed stands, that are repeatedly found are representatives of the association *Coccothrinaci—Tabebuietum albicantis*. They were examined in the northern karstic area of Sierra Maestra (Table 25, col. 25). This is in fact a shrubwood with loose canopy layer and dominated by microphyllous evergreen trees, epiphytes and lianes. On the rims columnar cacti *Pilosocereus brooksianus*) and *Agave* occur. Characteristic trees are *Coccothrinax elegans*, *Tabebuia albicans*, *Alvaradoa arborescens*, *Ficus jacquinifolia*, *Plumeria ekmanii* and *P. filifolia*, *Swietenia mahagoni*, *Pithecellobium cubense*, *Zanthoxylum spinosum*, *Colubrina elliptica*, *Catalpa brevipes*, *Hyperbaena cubensis*, *Helietta glaucescens*, *Thouinia trifoliata*, *Cordia alliodora*, *Dendropanax arboreus*, *Savia erythroxyloides*, and

Strempeliopsis strempelioides. In the shrub layer Bernardia dichotoma, Eugenia maleolens and Forsteronia corymbosa are dominant. Additional species are several local endemics (Neobracea susannina, Malpighia acunana, Rhytidophyllum mogoticola, Lunania cubensis), and more than 20 lianes (e.g., Marcgravia rectiflora, Byttneria microphylla, Tournefortia volubilis, Selenicereus grandiflorus, S. urbanianus, Serjania diversifolia, S. crassinervis, Philodendron lacerum, Ph. krebsii, Cissampelos pareira, and Anguria pedata).

22.4.4 Montane karstic forests (*Tabebuio – Garryetum*) (Table 25, col. 27)

These occur in the karsts situated in the montane rainforest zone or at its margin. Annual mean temperature is 19-21 °C, average annual precipitation is 2000 mm, and evenly distributed. A single stand was examined in Pico Potrerillo, Sierra Escambray, at an elevation between 850 and 930 m. It is characterized by a 6-8 m high loose canopy layer composed of drought-tolerant deciduous trees. A highly dense, 2-3 m high shrub layer containing many montane rainforest elements occurs beneath the trees. The rocks, logs and trunks are covered with rich moss assemblages, many rainforest epiphytes (Pleurothallis spp., Lepanthes spp., Guzmania monostachya, G. lingulata, Catopsis nitida), and hygrophilous herbs (Begonia, Peperomia, Pilea, ferns). Characteristic elements are Thouinia clarensis, Garrya fadyenii, Berberis tenuifolia, Dendropanax arboreus, Coccothrinax trinitensis, Terminalia neglecta, and Ocotea floribunda in the canopy layer, and Ilex clementis. Tabebuia sauvallei, Bernardia dichotoma, Savia sessiliflora. Citharexylum matheanum, Erythroxylon clarense, Karwinskia potrerilloana, Sapium leucogynum, and Psychotria martii in the shrub layer.

22.5 Dry forests and shrubwoods

These are the forest communities of arid zones, but are also found elsewhere if edaphic conditions are poor (shallow soils). In the arid zones the climate is seasonal with one dry season in the winter or with two dry seasons; the number of dry months is five to nine, annual precipitations may also develop on serpentines or in the coastal zone even though climate is more humid in these places. Dominant are the microphyllous and nanophyllous trees and shrubs, most of them being sclerophyllous evergreens or having compound leaves (e.g., *Mimosaceae* and *Caesalpiniaceae*). Spinose elements are common, reaching as much as 33% of the presence scores, especially on serpentine. Epiphytes, mosses and cacti are very poorly represented. The liane flora, however, is rich with drought-resistant herbaceous life-forms predominating.

27*

22.5.1 Dry evergreen forests (Eugenio—Metopietalia toxiferi) (Table 25, cols 37—38)

10-18 m high forest with one or two canopy layers. They occur on limestone rendzina and humic carbonate soils or shallow red ferrallitic soils, usually close to the coasts. These forests correspond to the "dry evergreen forests" and "littoral forests" described by Beard (1944), and to the "dry limestone scrub forests" of Asprey and Robbins (op. cit.). Ciferri's (1936) "foresta subxerofitica" associations also belong to this group. The dry evergreen forests are widespread along the rocky coasts of Cuba and even in the higher terraces looking on to the sea in Oriente. especially at Cabo Cruz and Maisi. The height of trees is 15-18 m if two canopy strata occur, or 8-12 m in a single layered canopy. Characteristic constituents are the Mimosaceae and Caesalpiniaceae which dominate the canopy layer, and other sclerophyllous trees. The most widespread community is the 12-18 m high Lysilomo-Burseretum simarubae (Table 25, col. 37) association, the climax stage of the successional sere on littoral rocks. In structure, dry evergreen forest is similar to the semi-deciduous forests. (Fig. 299) Depending on soil depth and human impact the structure and floristic composition of the stands are highly variable. Constant and common species of the canopy layer are Bursera simaruba, Lysiloma bahamense, Thrinax radiata, Ficus aurea (Fig. 300), Capparis cynophallophora, C. flexuosa, Coccoloba diversifolia, Chrysophyllum oliviforme, Tabernaemontana amblyocarpa, Caesalpinia vesicaria, C. bahamensis, Ateleia gummifera, Pithecellobium lentiscifolium, Carpodiptera cubensis, Hypelate trifoliata, and Hippomane mancinella. Prominent elements of the shrub layer and the lower canopy level are Amyris balsamifera, Ateramnus lucidus, Eugenia maleolens, E. axillaris, Bourreria succulenta, Croton lucidus, Cordia globosa ssp. humilis, Plumeria emarginata, Lantana involucrata, Exostema caribaeum, Erythroxylon areolatum, E. rotundifolium, Caesalpinia pauciflora, Solanum bahamense, Adelia ricinella, and Schaefferia frutescens. Of the 25 liane species Caesalpinia crista, Pisonia aculeata, Morinda royoc, Solandra longiflora, Smilax havanensis, and Jacquemontia jamaicensis are shallow and rocky soils, the forest canopy is uneven rather open and 6-10 m high. (Fig. 301) An example is the *Krugiodendro-Drypetetum* association described by Ciferri (1936) from Hispaniola, which is similar to the communities found at Maisi and in the Guanahacabibes Peninsula. The Swietenio-Metopietum brownei association (Table 25, col. 38) is of similar distribution to the former community and it is found in the southern part of Isla de Pinos, in the Zapata Peninsula and the nearby southern coasts. Characteristic trees are Swietenia mahagoni, Metopium brownei, Picrodendron macrocarpum, Krugiodendron ferreum, Pithecellobium cubense, Terminalia neglecta, Bucida spinosa, Nectandra coriacea, Elaeodendron attenuatum s.l., Acacia farnesiana, Peltophorum adnatum, Linociera ligustrina, Belairia ternata, Pseudocarpidium wrightii. Manilkara jaimiqui, Capparis and Erythroxylon species, Gyminda latifolia, Chrysobalanus icaco, and Canella winterana. Of the palms Coccothrinax litoralis and Sabal parviflora are common, the latter occurring in habitats with stagnant water in the summer. The shrub layer is rich in species, the commonest plants being spiny shrubs and lianes, such as Coccoloba armata, Jacquinia aculeata and J. stenophylla, Malpighia cubensis, Zanthoxylum fagara,

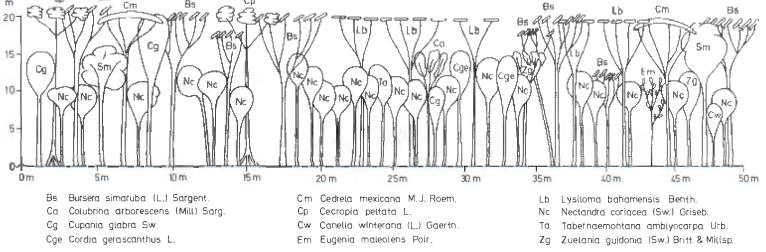


Fig. 299 Structure profile of an anthropically influenced dry variant of a deciduous lowland forest on limestone, (Lysilomo-Burseretum simurubae association) at 10-12 m a.s.l. the Zapata Peninsula, near Soplillar (Borhidi, Del Risco and Ovideo)



Fig. 300 Strangler fig (Ficus aurea Warb.) on a well developed Lysiloma bahamense tree in a semi-deciduous sublittoral forest at Punta del Este (Photo: A. Borhidi)



Fig. 301 Semi-deciduous sublittoral limestone forest in the Zapata Peninsula near Playa Girón (Photo: A. Borhidi)

Caesalpinia crista, C. bonduc, Leucocroton microphyllus, Comocladia dentata, Randia aculeata, Brya ebenus, etc. The dry coastal forests of northern and southern Oriente may also be assigned to this vegetation type. These are rich in Acacia species (A. roigii, A. curbeloi and A. cupeyensis between Puerto Padre and Banes; A. lutea and A. seifriziana at Maisi, and A. cowellii at Santiago de Cuba). The floristic composition of these communitites is not known exactly, but there is an obvious similarity to the Phyllostylon-Acacia and Acacia-Krugiodendron associations reported from Hispaniola by Ciferri. The 'thorn scrub' of Asprey and Robbins also overlaps the dry evergreen forests (Acacia-Prosopis).

22.5.2 Dry, thorny limestone shrubwoods (*Lantano—Cordietalia*) (Table 25, col. 39)

This is the dense vegetation composed of thorny, sclerophyllous, small-leaved trees and shrubs occurring on bare rocks of dry limestone terraces and the lowland karstic "dogtooth" formations. The 2-3 m high shrubs and the emergent individuals or groups of 5-6 m high "rod like" trees form an unpenetrable vegetation mosaic described under various names in the literature. In Cuba these are usually called the "manigua" or "manigua costera", the latter used for coastal shrubwoods. (It is noted that "manigua" is the more correct term in the sylvicultural and geographical usage. It means secondary shrubwood, mainly degraded ones developed after logging in forest communities described in 22.1.5. This corresponds to the "thorn woodland" of Beard. These woodlands are best developed under a



Fig. 302 Deciduous thorn scrub forest in the littoral limestone belt of Daiquiri (Photo: A. Borhidi)

climate of two dry seasons which together are 7-8 dry months and an average annual precipitation of 600-800 mm. Columnar or tree-shaped cacti may also occur under a loose canopy layer or intermingled with shrubs in some closed fragments of the community. Cacti, however, are never dominant in this vegetation. Smaller stands of this vegetation type are found in the northern coastal zone of Habana and Matanzas and is southern Matanzas and Las Villas. Extensive unbroken stands occur in Oriente between Puerto Padre and Gibara, and in the southern terraced coast between Cabo Cruz and Maisi. The latter was examined at several localities, the relevés taken are summarized in col. 39 of Table 25. This formation is very rich in species. A number of noda, one gradually transformed to the other, may be defined (Fig. 302). Characteristic trees are Picrodendron macrocarpum, Cordia leucosebestena, Colubrina elliptica, Maytenus buxifolia, Polygala cuneata, Auerodendron cubense, Erithalis fruticosa, Cassia emarginata, Ateramnus lucidus, Pseudocarpidium wrightii, P. avicennioides, P. multidens, Diospyros grisebachii, Spirotecoma spiralis, and Thouinia pseudopunctata. Main elements of the shrub layer are Croton lucidus, C. rosmarinoides, C. myricifolius, Jacquinia berteroi, J. maisiana, Eugenia cowellii, Exostema spinosum, Grimmeodendron eglandulosum, Polygala guantanamana, Erythroxylon minutifolium, Bellonia spinosa, Pithecellobium hystrix, Calliandra colletioides, Randia spinifex, Oplonia polyece, Tabebuia myrtifolia, T. polymorpha, Cordia globosa, C. pulverulenta, C. brittonii, C. leptoclada, Bunchosia linearifolia, Plumeria and Savia species, Coccothrinax fragrans, C. munizii, C. microphylla, and Lantana involucrata. Of the succulents Agave underwoodii, Melocactus harlowii, M. borhidii, Harrisia fernowii, and in some places Dendrocereus nudiflorus and Ritterocereus

hystrix occur. The number of herbs and drought-tolerant epiphytes (e.g., Tillandsia circinnata, T. balbisiana, T. recurvata, T. flexuosa, T. pruinosa) is low. Of the 30 lianes more common are Mesechites rosea, Aristolochia clementis, Helicteres semitriloba, Stigmaphyllon spp., Passiflora santiagana, P. cuprea, P. suberosa, P. multiflora, Distictis rhynchocarpa, D. gnaphalantha, D. lactiflora, Gayoides crispum, Jacquemontia jamaicensis, and Morinda royoc etc.

22.5.3 Dry lowland serpentine shrubwoods (*Phyllantho—Neobracetalia*) (Table 25, cols 31—34)

These communities occur on red ferrallitic soils derived from serpentine in several isolated spots from the Cajalbana Hills to the Holguin serpentine area in Oriente. The climate is characterized by a single dry season (or two in the east) with 1-2 to 5-6 dry months and annual precipitation averaging 1000-1600 mm a year. Aridity tends to increase towards the east. This vegetation type, called the 'cuabales' in Cuba, corresponds to Beard's 'dry evergreen scrub forest' or 'scrub woodland', which is a zonal community on limestone with an annual precipitation of 600-1000 mm. It is characterized by a dense, 2-4 m high, closed shrub layer, smaller emergent palms, dwarf palms and 4-6 m high microphyllous evergreen trees. Contrary to the limestone shrubwoods, the physiognomy of serpentine scrub woodlands is quite uniform despite the great differences in climate, soil and floristic composition. The proportion of microphylls and spiny elements is even higher than in the limestone formation. The only major difference is the absence of cacti (except of *Melocactus* species) that usually cannot tolerate the high water retention power (osmotic pressure) of soils derived from serpentine. Another structural characteristic of serpentine scrubs is that the stands alternate with small grassy clearings, these can be transformed into dwarf-grass savannas later by human interference and grazing. Common characteristic species of the lowland serpentine scrubs are Neobracea valenzuelana, Phyllanthus orbicularis, Annona bullata, Rondeletia camarioca, Eugenia camarioca, Zanthoxylum dumosum s.l., Cynanchum ophiticola, Passiflora cubensis, Ipomoea carolina ssp. ophiticola, Tabebuia lepidota, Coccothrinax miraguama, and Malpighia nummulariifolia, etc. Two vegetational noda, differing in their past flora development, may be distinguished. The serpentine scrubs of western Central Cuba are included in the Coccothrinaci-Tabebuion lepidotae alliance (Table 25, col. 31) containing Coccothrinax miraguama ssp. roseocarpa, Ottoschmidtia dorsiventralis, Leucocroton havanensis, Anemia cajalbanica, and Eugenia sauvallei, etc. (see also phytogeographic district B.1.1.). Those of the eastern part of Central Cuba belong to the Guettardo-Jacarandion cowellii nodum which includes three local associations, Rondeletio-Guettardetum clarensis (col. 32) in Las Villas, Copernicio-Tabebuietum trachycarpae (col. 33) in Camagüey, and Acacio belairioidi-Spirotecometum holguinensis and related communities, (col. 34) at Holguin, all these occur solely in sites not disturbed by grazing. (Most of the common and vicarious character species have been listed in the discussion of phytogeographic subsector B.3/a and districts B.3.1-B.3.3.).

22.5.4 Semi-dry lowland serpentine shrublands (*Ariadno—Phyllanthetalia*) (Table 25, col. 17)

Evergreen shrublands developed almost exclusively on the ferritic latosols of the coastal zone north of the Moa Mts, and on the semi-humid serpentine rendzinas in the hilly and lower montane zones of the Sagua-Baracoa range. Precipitation averages 1400 – 1900 mm a year, one or two dry months occur in the spring or early summer. These communities are rather similar to the dry lowland serpentine shrubwoods in physiognomy. However, while the latter are characterized by equal proportions of microphylls and nanophylls, more than 30% of spiny plants, and the occurrence of grassy clearings, in the semi-dry lowland serpentine shrubwoodland microphylls are dominant, the percentage of spiny species is hardly over 10%, and no clearings are present. The ancient endemic flora has originated from Moa, and moved along the coast in both direction. In the dry vegetation type the proportion of endemics reaches 35 – 40%, in the semi-dry type endemics account for as much as 75-85% of the flora. In Cuba this formation is the richest in endemics. Main constituents are several species of small trees and shrubs (Fig. 303). Common or abundant elements are Hemithrinax savannarum H. rivularis, Acrosynanthus minor, Tabebuia linearis, Antirhea abbreviata, A. orbicularis, Phyllanthus comosus, P. chryseus, Purdiaea velutina, Shaferocharis multiflora, S. villosa, Kodalyoden-



Fig. 303 Evergreen sclerophyllous shrub on the serpentine of Yamanigüey river, with Thrinax rivularis (León) Borhidi palms (Photo: A. Borhidi)



Fig. 304 Paepalanthus brittonii Mold. an endemic herbaceous plant of the coastal pine forests of the Yamanigüev river (Photo: A. Borhidi)

dron cubense, Ceuthocarpus involucratus, Exostema purpureum, Neobracea valenzuelana, Spirotecoma apiculata, Jacaranda arborea, Coccoloba shaferi, C. nipensis, C. acuna, Cassia bucherae, Byrsonima bucheri, Suberanthus stellatus, Casasia jacquinioides, C. nigrescens ssp. moaënsis, Dipholis cubensis, Moacroton leonis, Pachyanthus moaënsis, and Miconia javorkaeana (Graffenrieda cordifolia). In the herb layer Paepalanthus brittonii (Fig. 304), Machaerina cubensis and Rhynchospora species are found. A special feature of this plant community is that only very few lianes and epiphytes are present. This fact also emphasizes the difference between the dry and semi-dry lowland serpentine shrubwoods.

22.6 Semi-desert cactus scrubs (Consoleo—Ritterecereion hystricis) (Table 25, col. 40)

The cactus scrubs form an unbroken stretch along the coast from the Guantánamo Bay to Imias. From Imias to Maisi smaller fragments occur, especially on the sand deposits of the coastal areas. The small trees and shrubs constitute an open vegetation. Succulents, mainly cacti, are co-dominant or even dominant in both the shrub and canopy layers. This vegetation type is identical with Beard's 'cactus



Fig. 305 Dry cactus scrub at Baitiquiri, with old individuals of Ritterocereus hystrix (Haw) Britt. and. Rose (Photo: A. Borhidi)



Fig. 306 Guayacum officinale L., a characteristic tree of the dry thorn scrubs and forests in the southern coastal belt of Baracoa (Photo: A. Borhidi)

scrub', the 'cactus-thorn scrub' described by Asprey and Robbins, and partly with Ciferri's 'foresta iperxerofitica'. According to Knapp (1964, 1965) and Hueck (1966) Hueck and Seibert (1972) these scrubs belong to the semi-desert formations and constitute an integral part of coastal semi-deserts in the Caribbean. Several geographically separated associations occur depending on whether the soil is rocky or sandy and on the duration of dry periods. On sandy soils Rittereocereus hystrix, (Fig. 305), Opuntia dillenii, O. militaris, Cylindropuntia histrix and Rhodocactus cubensis are dominant, the sparse herb layer is composed of grasses. Most of the sporadically distributed trees and shrubs are members of the families Caesalpiniaceae and Capparidaceae, e.g., Caesalpinia pinnata, C. pauciflora, Capparis flexuosa, C. cynophallophora, and also Guajacum officinale (Fig. 306). Dominant species of rocky habitats are Consolea macracantha (Fig. 307) Dendrocereus nudiflorus, Pilosocereus brooksianus, Harrisia fernowii, Agave albescens, and Melocactus acunae, the latter two in the herb layer. The shrub flora is very rich, in addition to those mentioned above the Jacquinia, Gochnatia, Cordia, Guettarda, and Lantana species, and emergent Coccothrinax palms (C. hiorami, C. munizii, C. alexandri) are abundant.



Fig. 307 Consolea macracantha (Griseb.) Berger, a tree shaped endemic cactus of the cactus-scrub communities of Cuba (Photo: A. Borhidi)

22.7 Coniferous forests

The primary production and complexity of coniferous forests is lower than those of the climax forests expected under the given climatic conditions. They occur only on nutrient-poor acidic soils, either on quartz sands, slates and sandstones as subclimax communities, or as paraclimax communities on ferritic soils. The geographical range of coniferous forests is bipolar, being restricted to the eastern and western ends of the island, where, at the same time, they are the dominant vegetation type.

22.7.1 *Pinus tropicalis* forests on sand (*Acoelorrapho—Pinion tropicalis*) (Table 25, col. 1)

This type is found in the western coast of Isla de Pinos, in a narrow strip north of the Lanier Swamp, in the Guanahacabibes Peninsula and the southern plains of Pinar del Rio. The soil is light gray quartz sand with low nutrient content and marked seasonal fluctuation of moisture. The natural pine forests, 'clear pine forests', had a loose canopy layer. As a result of logging they have been replaced by 'pine woodlands' with an even looser canopy (less than 30%), or by srub and savannas. Contrary to the general view, expressed in Beard (1953) following the soil surveys of Bennett and Allison (1928) and other sources, the original vegetation was by no means a sort of pine savanna (cf. Samek, 1969). Samek distinguishes between two vicarious associations: the Eragrosti cubensi-Pinetum tropicalis community (ined.) in Pinar del Rio, and the Paepalantho seslerioidi-Pinetum association (see col. 1) in Isla de Pinos. Characteristic elements of the canopy layer of both types are Pinus tropicalis, Colpothrinax wrightii, Acoelorraphe wrightii, Tabebuia lepidophylla, Chaetolepis cubensis, Byrsonima crassifolia, B. wirghtiana. In the latter association Syngonanthus insularis, Cladium jamaicense, Panicum longiligulatum, Kalmiella aggregata, K. simulata, Pachyanthus longifolius, Xyris longibracteata, and Lyonia vaccinioides are typical. The canopy layer of both associations is closed up to 10-30%, the cover of shrubs is similar. The herbs may cover as much as 40-100% of the ground, and some sparse lichen assemblages also occur.

22.7.2 *Pinus caribaea* and mixed oak-pine forests on slatey rocks (*Pachyantho—Pinion caribaeae*) (Table 25, cols 2—37)

These are lowland and hill forests on yellow, quartz—allitic soils derived from slatey rocks. The canopy is 60-70% closed, some palms and evergreen trees are intermingled with the pines. The cover of the rich shrub layer may be as much as 50%. The cover of herbs is close to 100% in the drier, convex orographical formations. The Isla de Pinos representative of this vegetation type is the *Pinetum cariba etropicalis* association (Samek 1969). Characteristic species are *Pinus tropicalis*, *Pinus caribaea*, *Acoelorraphe wrightii*, *Coccothrinax miraguama*,



Fig. 308 Purdiaea cubensis (A. Rich.) Planch. a characteristic endemic element of the West Cuban pine woodland (Photo: A. Borhidi)

Curatella americana, Byrsonima crassifolia, Tetrazygia delicatula, Roigella correifolia, Croton craspedotrichus, Chamaesyce pinariona, Clitoria laurifolia, Evolvulus sericeus, Phyllanthus junceus, Zamia silicea, Panicum aciculare, Lyonia myrtilloides, Xylopia aromatica, Desmodium barbatum, Eriosema crinitum, Herpyza grandiflora, Trachypogon filifolius, and Leptocoryphium lanatum. In Pinar del Rio this community is replaced by mixed oak-pinewoods, Querco sagraenae—Pinetum (Table 25, col. 3), that become oak gallery forests in the moist habitats of valleys. Typical species are Pinus tropicalis, P. caribaea, Quercus sagraeana, Rhus copallina ssp. leucantha, Xylopia aromatica, Roigella correifolia, Tabebuia lepidophylla, Befaria cubensis, Vaccinium cubense ssp. ramonii, Tetrazygia delicatula, Miconia ibaguensis, Conostegia xalapensis, Byrsonima crassifolia, B. pinetorum, Davilla rugosa, Psidium salutare, Clidemia neglecta, Hypericum styphelioides s. str., Lygodium cubense, Pachyanthus poiretii, Chrysobalanus pellocarpus, and Odontosoria wrightiana.

22.7.3 *Pinus caribaea* forests on ferritic soils (Neomazaeo—Pinetum caribaeae) (Table 25, cols 4—5)

This is the original paraclimax coniferous forests in the Cajalbana Hills. The canopy layer is fairly closed, a 70-80% cover is usual. Some degraded stands are of a loose 'woodland' character. On ridges and slopes the shrub layer is usually poor, the herb layer is dominated by grasses. On flat areas a vegetation type with shrubs and tall grasses develops. In the valleys the shrub layer is very dense and many fern species occur. All these are variants of the Neomazaeo-Pinetum caribaeae climax association (Table 25, col. 4). Its characteristic species are *Pinus* caribaea, Coccothrinax yuraguana, Purdiaea cubensis (Fig. 308), Eugenia rosariensis, Vaccinium cubense ssp. ramonii (Fig. 309), Sauvallella immarginata, Neomazaea phialanthoides, Acunaeanthus tinifolius, Psidium cymosum, Tabebuia leptopoda, Anemia cajalbanica, Mitracarpus glabrescens, Phania cajalbanica, Tetrazygia coriacea, Rondeletia longibracteata, Lescaillea equisetiformis, Andropogon gracilis, Aristida refracta, and Rhynchospora tenuis, etc. On steep rocky slopes the more open Agavo cajalbanensi—Pinetum caribaeae community (Table 25, col. 5) is found. This is rich in agaves, palms and spiny shrubs. Of the many serpentine endemics Agave cajalbanensis, Eugenia rigidifolia, Brya ebenus, Jacquinia brunnescens, Malpighia horrida, Buxus wrightii, Zanthoxylum dumosum s. str., Plinia dermatodes, Machaonia dumosa, and Rheedia fruticosa are characteristic here.



Fig. 309 Vaccinium cubense (A. Rich.) Griseb. ssp. ramonii (Griseb.) Borhidi a frequent shrub of the West Cuban pine woodlands and pine forests (Photo: A. Borhidi)



Fig. 310 Pine forest of Pinus cubensis Griseb. with Coccothrinax orientalis (León) Muñiz and Borhidi in the Nipe mountains Anemio-Pinetum cubensis (Photo: A. Borhidi)

22.7.4 Xerothermic *Pinus cubensis* forests (*Guettardo—Pinion cubensis*) (Table 25, cols 6, 9, 11, 13)

These are xerothermic coniferous forests on the ferritic soils of lowland and hilly serpentine areas and the more elevated, open rocky places of Sagua-Baracoa. These communitites are very rich in endemics (67.74% of the presence scores). The ratio of regional and Cuban endemics is high: RE/CE=4.2. The Greater Antillean species outnumber the Neotropical elements, their ratio being GA/Nt=1.4. The microclimate in the relatively open stands is xerothermic. The highly developed shrub layer is microphyllous; many more phanerophytes occur than hemicryprophytes (P/H=2.6). The percentage of spiny elements is over 10 %. Four associations are distinguished. Anemio-Pinetum cubensis (Fig. 310) includes the climax pinewoods in the foothills and submontane belt of Nipe and Cristal. Characteristic species are Pinus cubensis, Anemia coriacea, A. nipensis, Coccothrinax orientalis, Casearia crassinervis, Rondeletia myrtacea (Fig. 311), Ouratea striata, Clerodendron nipense (Fig. 312), Lyonia macrophylla, L. nipensis, Vernonia urbaniana, Guettarda monocarpa, G. calyptrata, Bletia purpurea, B. floribunda, Plumeria clusioides, Pachyanthus reticulatus, Paepalanthus brittonii, Tabebuia shaferi, Vaccinium cubense ssp. cubense, Andropogon spp., Rhynchospora spp., Galactia rudolphioides, Rajania howardii, and Heptanthus cordifolius. The foothills north of Moa and the hill-country of Baracoa are covered by very rich Dracaeno - Pinetum



Fig. 311 Rondeletia myrtacea Standl., a characteristic element of the pine forest and serpentine scrub communities of the Sagua–Baracoa (Photo: A. Borhidi)



Fig. 312 Characteristic endemic species of the Pinus cubensis forests: Clerodendron nipense Urb. (Photo: A. Borhidi)

28* 435



Fig. 313 Open rocky pine woodland on the serpentine of the Nipe Mountains (Agavo shaferi Pinetum association), with the Loma Mensura in the background (Photo: A. Borhidi)

cubensis forests to about 400 m in altitude. The 72.4% of endemism is higher than all other Cuban coniferous forest communitites. Beneath the closed canopy there is a dense shrub layer of 40—50% cover, and a usually tall herb layer. Characteristic species are Pinus cubensis, Dracaena cubensis, Schmidtottia, sessiliflora, Psidium parvifolium, Casearia bissei, C. moaënsis, Guettarda crassipes, Cyrilla cubensis, Ossaea pauciflora, Phyllanthus myrtilloides ssp. erythrinus, Jacquinia roigii, Myrtus ophiticola, Bumelia cubensis, Suberanthus stellatus, Rhynchospora lindeniana, Eugenia pinetorum, Guettarda ferruginea, Callicarpa oblanceolata, and Anemia coriacea ssp. moaensis.

Two of the rocky coniferous forest communities (Fig. 313) may be classified into the group of the xerothermic pine forests. The Agavo shaferi—Pinetum association develops on the cliffs and even on the eroded mocarrero surfaces of the Nipe and Cristal mountains. Its canopy layer is loose (30–50%), the cover of shrubs is between 30 and 60%. Characteristic species are Pinus cubensis, Coccothrinax orientalis, Agave shaferi, Ariadne shaferi, Aristida laevigata, Oplonia cubensis, Clusia nipensis, Cyrilla nipensis, Callicarpa nipensis, C. lancifolia, Eupatorium nipense, Euphorbia podocarpifolia, Gesneria nipensis, Ossaea acunae, Paspalum breve, and Platygyne triandra, etc. On the eroded rocky ridges of Moa occur the Euphorbio helenae—Pinetum cubensis forests with dwarf palms, sometimes loose canopy, and a shrub layer of 70–80% cover. The characteristic species of this type are Pinus cubensis, Coccothrinax yuraguana ssp. moaënsis, Euphorbia helenae (Fig. 314), Scaevola wrightii (Fig. 315), Croton monogynus, Coccoloba oligantha,



Fig. 314 Euphorbia helenae Urb., a beautiful shrub of the serpentine scrubs of the Sagua-Baracoa range, with bright scarlet bracts (Photo: A. Borhidi)



Fig. 315 Scaevola wrightii (Griseb.) Maza (Goodeniaceae), an isolated endemic shrub of the East Cuban serpentine mountains, characteristic of the rocky pine woodland and scrub communities (Photo: A. Borhidi)



Fig. 316 Hypericum styphelioides ssp. styphelioides, a characteristic element of the West Cuban grasslands (Photo: A. Borhidi)

Eupatorium lantanifolium, Guettarda ferruginea, Gochnatia recurva, Hypericum styphelioides ssp. moaënsis (Fig. 316), Linodendron aronifolium, Malpighia cnide, Neobracea valenzuelana, Rheedia ophiticola, Senecio trichotomus, Tabebuia pinetorum, Byrsonima minutifolia, Vaccinium alainii, and Vernonia wrightii.

22.7.5 Mesophilous and montane *Pinus cubensis* forests (*Andropogono—Pinion cubensis*) (Table 25, cols 7, 8, 10 and 12)

These are natural and semi-cultured stands of the paraclimax coniferous belt between 600–900 m on the ferritic latosols of the Sagua-Baracoa serpentine mountains. The proportion of endemics (52.4% of the total of presence scores) and the ratios of regional and Cuban endemics (RE/CE=2.9) are lower than in the xerothermic *Pinus cubensis* forests. The Neotropical elements outnumber the Greater Antillean species (GA/Nt=0.8). The natural stands are more closed than those abandonned by agriculturalists and, furthermore, the herb layer is tall and dense, the phanerophyte hemicryptophyte ratio is low (P/H=1.3), the spiny elements are absent in most cases (their frequency being lower than 5%). Two climax associations are distinguished. The *Rhynchosporo-Pinetum* association includes the montane pinewoods of the Nipe and Cristal mountains. It is characterized by eight *Rhynchospora* species and the abundance of *Baccharis scoparioides*, *Pteridium caudatum*, *Andropogon reinoldii*, and *A. nashianus*. Three types are recognized within this community.



Fig. 317 General view of the Sierra de Moa from the valley of the Jiguani river, with banana plantations; pine forests in the foreground and sclerophyllous evergreen rainforest in the background (Photo: A. Borhidi)

Type a) panicetosum (col. 7), is found on flat and moderately sloping areas and contains Clidemia capituliflora, Sauvagesia brownei, Panicum aciculare, P. fusiforme, P. scoparium, and Paspalum alainii.

Type b) rhynchosporetosum (col. 8), occurs in hollows and valleys is a moister formation and has Rhynchospora diodon, R. tenuis, R. shaferi, R. nipensis, R. lindeniana, Ternstroemia flavescens, and Turnera diffusa, etc.

Type c) euphorbietosum (col. 10), is found on the shallow soils of mocarrero ridges, some of its species are Euphorbia helenae, Croton borhidii, Lyonia macrophylla, Guettarda ferruginea, and G. calyptrata. Type c) not recognized as a separate association, unlike the analogous situation in the Moa Mts.

In the high interior plataeux of Moa Mts (Cupeyal, upper Toa Valley) is the much richer Shafero—Pinetum (Fig. 317) community. The 20—25 m high closed canopy layer is a mixture of pines and many evergreen trees. A second canopy layer composed of smaller trees, such as Bactris cubensis and Alsophila aquilina, is found underneath. Characteristic species are Pinus cubensis, Spirotecoma apiculata, Miconia cerasiflora, Shafera platyphylla, Vaccinium alainii, Lyonia glandulosa, Eupatorium ayapanoides, E. grandiceps, Clethra cubensis, Ficus wrightii, Gomidesia lindeniana, Gundlachia cubana, Hyeronima nipensis, Ilex macfadyenii, Lisianthus glandulosus, Linociera domingensis, Mettenia oblongata, Miconia spp., Mecranium spp., Ossaea navasensis, O. ferruginea, Schmidtottia multiflora, Scolosanthus lucidus, and Vernonia calida.

22.7.6 Mixed tree fern-pinewoods in the montane rainforest zone (*Pinetalia occidentalis—maestrensis*)

This vegetation type has been studied only in Hispaniola Stands are formed by *Pinus occidentalis* and develops between 1500–2000 m in the rainforest zone (Urban 1923, Ekman 1930, Ciferri 1936, Marie-Victorin 1943b). Accompanying species are *Weinmannia pinnata*, *Garrya fadyenii* and many montane endemics. In Cuba such communities are represented by some isolated stands on the northern slopes of Sierra Maestra between 800–1300 m, on acidic yellow montane soils developed mainly on sandstone outcrops. In Pico Turquino there are stands reaching an elevation as much as 1800 m. In Grand Piedra, too, pinewoods occur in the montane rainforest zone. These have been considered *Pinus cubensis* stands, although the constituent trees may just as well be introgressive hybrids of *Pinus cubensis* and *Pinus occidentalis*. These morphologically rather diversified populations were united under the name of *Pinus maestrensis* Bisse. The variability range of its populations has been studied by A. Lopez. For the structure and composition of this vegetation type see Fig. 318 and Table 139.

22.8 Savannas and grasslands

The map shows both the original and the derived savannas and, in the latter case, indicates the original vegetation type. Based on physiognomy, two main groups of savannas can be distinguished: tall palm-tall grass savannas (Sabalo-Roystonietea)

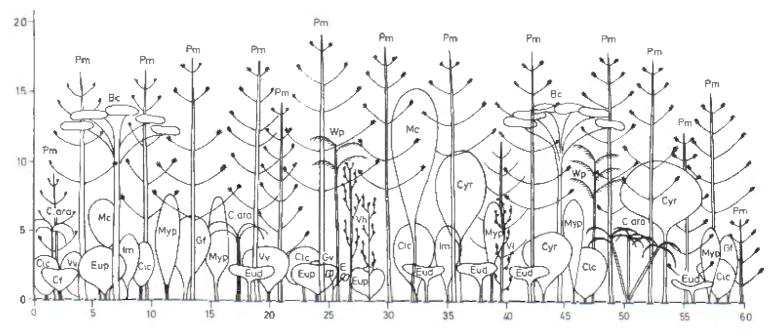


Fig. 318 Structure profile of a montane pine forest of Pinus maestrensis in Alto La Francia, Sierra Maestra at 1300 m a.s.l. (Borhidi 1976) C. ara=Cyathea araneosa; Clc=Clethra cubensis; Bc=Brunellia comocladifolia; Cyr=Cyrilla racemiflora; Eud=Eupatorium dalea; Eup=Eupatorium paucibracteatum; Gf=Garrya fadyenii; Hu=Heterotrichum umbellatum; Myp=Myrica punctata; Pm=Pinus maestrensis; Rf=Rapanea ferruginea; Vl=Vaccinium leonis; Wp=Weinmannia pinnata; Cf=Callicarpa ferruginea; Im=Ilex macfadyenii; Mc=Myrsine coriacea; Vv=Viburnum villosum

and small palm-dwarf grass savannas (Coccothrinaci—Copernicietea). The floristic composition has not yet been the subject of extensive studies in Cuba, only lists containing 'savanna trees and grasses' of each province have been published (Seifriz 1943). These lists, however, cannot characterize adequately the flora of physiognomic units. Furthermore, Seifriz's floristical data are occasionally erroneous and species never found together are often given in the same list. As these lists should be treated with caution, only the structure and ecology of savannas will be described here.

22.8.1 Roystonea—Ceiba agricultural savannas (Ceibo—Roystonion)

Cultivated lands on the rich ferrallitic latosolic soils on the lowlands of central Cuba, especially Matanzas and Habana clays where seasonal rainforest was the original vegetation. Characteristic trees are large specimens of Ceiba pentandra and Spondias mombin, loaded with epiphytes, and Ryostonea regia, Chrysophyllum oliviforme, Genipa americana. The herb layer is rich in species, e.g., Andropogon virginicus, A. pertusus, Paspalum notatum, P. distichum, P. fimbriatum, Panicum caespitosum, P. reptans, P. boliviense, P. adspersum, P. dichotomiflorum, Cyperus iria, C. haspan, C. ligularis, C. flavus, C. surinamensis, Cuphea melanium, C. parsonsia, Borreria ocimoides, Setaria geniculata, S. tenax, Sporobolus indicus, Reynaudia filiformis, Dichromena ciliata, Gomphrena decumbens, Rhynchelytrum roseum, and Macroptilium lathyroides, etc.

22.8.2 Roystonea agricultural savannas (Samaneo – Roystonion)

These are savannas of the semi-deciduous forest zone on moderately rich siallitic lowland soils, in a seasonal climate with 4–8 dry months. Characteristic phanerogams are *Roystonea*, *Samanea*, *Peltophorum adnatum*, *Pithecellobium cubense*, *Cordia gerascanthus*, *C. dentata*, *Psidium guajava*, *Anacardium edule*, and *Bursera simaruba*. The components of the herb layer are mainly those of the previous type, although most *Cyperus* species are replaced by *Sclerias*. Tall savanna grasses not native to Cuba (e.g., *Panicum maximum*, *Hyparrhenia rufa*) are commonly planted and became established.

22.8.3 *Copernicia* agricultural savannas (*Andropogono—Copernicietalia*)

These are secondary savannas of the semi-deciduous dry forest and dry evergreen forest zone. Small fragments developed as a result of edaphic conditions, may be natural. These stands were extended by logging and burning the neighbouring forests. The secondary savannas are usually found on poor sandy or mocarrero

soils, the latter may be secondarily developed after deforestation in wet gallery forests. Characteristic species are Copernicia baileyana, C. gigas, C. vespertilionum, C. sueroana, C. molineti, C. rigida, C. burretiana, C. textilis, C. hospita, in some places also C. roigii, C. clarkii, and C. humicola, (The dwarf Copernicia of serpentine shrublands occur in the savannas discussed in 22.8.4). Here and there spiny trees with loose canopy, such as Belairia mucronata and Acacia species, may occur intermingled with the phanerogams. The herb layer is composed of a great variety of plants, mainly Andropogon and Rhynchospora species (Andropogon virginicus, A. bicornis, A. brevifolius, A. reedii, Rhynchospora diodon, R. tenuis, R. cyperoides) and Panicum chrysopsidifolium. Fimbristylis annua, Bulbostylis setacea, Buchnera elongata, Anisantherina hispidula, Pterocaulon alopecuroideum, Cassia rotundifolia, C. insularis, Schultesia guianensis, Stylosanthes hamata, Zornia diphylla, Sebastiania corniculata, Borreria ocimoides, and B. thymocephala, etc.

22.8.4 Dwarf palm agricultural savannas on serpentine (*Parvicopernicio—Coccothrinacion*)

These communitites are considered by most authors as natural savannas which rapidly spread following the degradation of the original dry shrublands of serpentine zones with seasonal arid climate. Small, 1—4 m high palms are common as standard trees, for example the vicarious serpentinophilous ecotypes of *Copernicia macroglossa*, *Coccothrinax miraguama* and *Copernicia glabrescens* (Fig. 195),



Fig. 319 Coccothrinax moaensis (Borhidi et Muñiz) Muñiz a peculiar dwarf palm of the montane serpentine scrub of the Cupeyal Reserve (Photo: A. Borhidi)

Matanzas, C. hospita ssp. clarensis in Las Villas, C. yarey in Camagüey and Oriente, C. cowellii and Coccothrinax garciana C. nipensis and C. moaensis (Fig. 319) in Oriente. The relatively high Gastrococos crispa savannas of wetter or richer serpentine soils are also included here. The herb layer is dominated by dwarf grasses, namely Andropogon and Aristida species Andropogon hirtiflorus, A. multinervosus, Aristida neglecta, A. refracta, A. vilfifolia, which also occur in the shrublands. Other species to be mentioned are Imperata brasiliensis, Diodia rigida, D. teres, Solanum aculeatum, Byrsonima crassifolia, Sachsia polycephala, Ayenia euphrasifolia, Croton nummulariifolius, Leptocoryphium lanatum, Polygala saginoides, Stylosanthes hamata, Angelonia pilosella, Thymopsis thymoides, Evolvulus sericeus, and Zamia kickxii, etc.

22.8.5 Pine savannas (Pino – Aristidion neglectae)

These secondary communities replace degraded pinewoods on yellow allite-ferritic soils on quartz and slate substrates, or on red ferrallitic soils. Scattered individuals of pine are still present, the herb layer is the same as in the previous type. (The pine savannas are not indicated as a separate category in the map, because their distinction from sandy pinewoods is less obvious and the aim is to show the potential vegetation wherever possible).

22.8.6 Natural edaphic *Sabal* savannas (*Macrocopernicio* – *Sabalion*)

These savannas usually develop on mocarrero soils containing an impermeable layer close to the surface and having a strong seasonal fluctuation of the water table. Most stands are found in the provinces of Pinar del Rio, Matanzas and Las Villas. The floristic composition of these formations is not sufficiently known. Characteristic elements are the dominant *Sabal parviflora*, and in the herb layer *Rhynchospora*, *Scleria* and *Setaria* species. Notable plants are the endemic *Cheilophyllum* species.

22.8.7 Secondary Sabal savannas

The wide-spread Sabal palm swamp meadows and moist pastures have been derived from the wet gallery forests of coastal zones and from the fenwood stages of the vegetational succession in boggy hollows. The floristic composition is determined by the former quality of habitats, the methods of land use and the intensity of land exploitation. Tropical black or alluvial soils, and occasionally peaty soils are typical. The secondary *Sabal* savannas are not distinguished from the gallery forests and bogs in the map.



Fig. 320 Overgrazed Colpothrinax wrightii savanna at Consolación del Sur (Photo: A. Borhidi)

22.8.8 Acoelorraphe wrightii savannas

These are either degraded forms of *Acoelorrapho-Pinion* pinewoods on sands, secondary communities derived from deforested fenwoods, or, in some cases, stages of the natural reforestation of bogs (meadows with palms and tall sedges). Being relatively small, these are included in the categories of sandy pinewoods and bogs in the map. (Fig. 320)

22.8.9 Deciduous and treeless savannas

These stands are usually the result of the complete transformation of the wet alluvial forest belt found parallel to the coasts. The origin of these savannas was revealed by the study of soils and geomorphology. Voronov (1970) describes many such areas from Camagüey and Oriente, but they are of heterogeneous origin and their separation is doubtful. These stands are shown as areas of potential alluvial forests on the map.

22.9 Freshwater vegetation formations

22.9.1 Alluvial gallery forests

These forests occur in the wide valleys of lowland rivers, especially along the Cauto, on the coastal alluvial banks of smaller rivers, and in flatlands bordered by small rivers and the coast. The soils are rich tropical black soils or tropical meadow soils (term 'meadow' refers merely to soil type and not vegetation) they are under water in the wet season and do not dry out even in the dry season. The forests, with a single canopy layer and emergent Roystonea palms, are 20-25 m high. In places covered by water for a longer time the height is 10-15 m and emergent Sabal palms occur. Most trees are partially deciduous, e.g., Bucida subinermis, Tabebuia angustata, and Erythroxylon confusum. The diverse epiphyte layer is composed mainly of drought-resistant heliophytic Tillandsias. Contrary to the epiphytes, the lianes are macrophyllous hygrophilous species (e.g., Philodendron krebsii, Vanilla articulata). Characteristic species are Roystonea regia, Sabal parviflora, S. japa, Acoelorraphe wrightii, Bucida buceras, Hibiscus elatus, Calophyllum antillanum ssp. rivularis, Tabebuia angustata, Swietenia mahagoni, Guettarda combsii, Ficus subcabrida, Myrsine cubana, Tabernaemontana amblyocarpa, Crescentia cujete, and Conocarpus erecta. In the herb layer Cladium jamaicense, Acrostichum danaifolium, Nephrolepis biserrata, Enhydra sessilis, Bacopa spp., Hemianthus spp., Paspalum vaginatum, Dichromena colorata, Cyperus acicularis, C. articulatus, Fimbristylis annua, F. spathacea, and Aster spp. occur. Following the removal of gallery forest trees Roystonea groves and savannas, second-grown Sabal groves and savannas, various mixed deciduous savannas (with Bucida, Swietenia, etc.) and tree-less savannas may develop, depending on the type of habitat and intensity of land exploitation.

22.9.2 Riverside gallery forests and derived types

The gallery forests along rivers and creeks (Fig. 321) are rich in lianes, palms and tall grasses and have only a single canopy layer. Characteristic elements are Roystonea regia, Calyptronoma dulcis, Lonchocarpus domingensis, Lysiloma bahamense, Dalbergia ecastophyllum, Bucida buceras, Ginoria americana; of the lianes Arthrostylidium cubense and A. capillifolium, and of the tall grasses Gynerium sagittatum, the latter forming dense stands like reeds. Most natural stands have been replaced by secondary vegetation, such as Roystonea lines, Bambusa vulgaris bushes, and Arundo donax stands. The Calyptronoma galleries along mountain streams have been almost completely removed. They are succeeded by dense stands of the introduced Syzygium jambos and by second-growth marginal stands of Pennisetum purpureum and Cyperus alternifolius.



Fig. 321 Evergreen tropical gallery forest in the valley of the Jauco river, near Baracoa (Photo: A. Borhidi)

22.9.3 Swamp vegetation complex

Just like in the temperate zone, the vegetation of bogs and swamps is a mosaic of several noda with dissimilar structure and composition which is determined by the quantity of accumulated litter. Therefore, all uliginal vegetation types are included in a single category in the map of 1:1 250 000. But in more detailed map swamp-mosaic may be divided into several units, as it is shown in Fig. 322. The succession starts with floating plants followed by submersed and rooted weeds of ponds. Then, Eleocharis interstincta, E. cellulosa, Scirpus validus, S. olneyi and later Typha domingensis associations follow. Skipping the Scirpus stage, Typha domingensis may directly form small floating stands ('marsh islets'). Along watercourses Typha may be replaced by Cyperus giganteus. The next stage of the successional sere is occupied by Cladium jamaicensis which grows to a height of 1.5-2 m. In sites always covered by water the Crino-Cladietum association is found, otherwise Pontederio-Cladietum develops. This is the earliest stage in which fenwood elements may be encountered, e.g., Acoelorraphe wrightii, Chrysobalanus icaco and Annona glabra (Fig. 323) and then tall Sabal parviflora palms (Chrysobalano-Annonetum Ciferri, 1936). Subsequently, high fenwoods (Tabebuio – Bucidetum) with Bucida palustris, Tabebuia angustata, Hibiscus elatus, Fraxinus caroliniana ssp. cubensis, and Salix longipes develop. In the meantime Sabal is gradually replaced by Roystonea. Logging and grazing result in boggy meadows or wet Sabal (or Roystonea) cultured savannas. On limestone substrate, bogs are succeeded by low karstic fenwoods (Osmundo-Annonetum) with many ferns and epiphytes. On sandy beaches of lagoons fern-palm shrubwoods (Blechno-Acoelorraphetum Hadač and Hadačová, 1971) represent the subsequent stage. The latter association occurs in the zone of sandy pinewoods.

22.9.4 Freshwater weed communities

Extensive stands, large enough to show in the map, are associated with the major lakes (Ariguanabo, Laguna del Tesoro). In deep water a floating layer of duckweed (Lemno-Azolletum carolinianae, Salvietum auriculatae) and floating mats of water-hyacinth and water-lettuce (Eichhornietum crassipedis and E. azureae Pistietum stratiotidis Ciferri, 1936) develop. Submerged floating bladderworts are also present forming communitities, of the Aldrovando-Utricularion alliance. In the ponds and slow streams of the Zapata Peninsula the submerged and rooted Vallisneria forms a community (Vallisnerietum neotropicalis). Extensive aquatic communities of other localities are composed of Cabomba piauhiensis and Myriophyllum sparsiflorum. In Laguna del Tesoro Chara mats, submerged Najas populations, then Vallisneria neotropicalis, Potamogeton nodosus and P. illinoënsis are found in large multilayered stands (Fig. 324). Rooted mats of water-lily, lotus and fringed water-lily are also significant. Major constituents of freshwater weed communities are Brasenia schreberi, Nymphaea ampla, N. odorata, Nuphar advena, Nymphoides grayanum, Nelumbo lutea, Polygonum portoricense and Limnocharis flava. In the shallow coastal zone of sandy lagoons a very special floating community formed by the moss-like Mayaca wrightii is found.

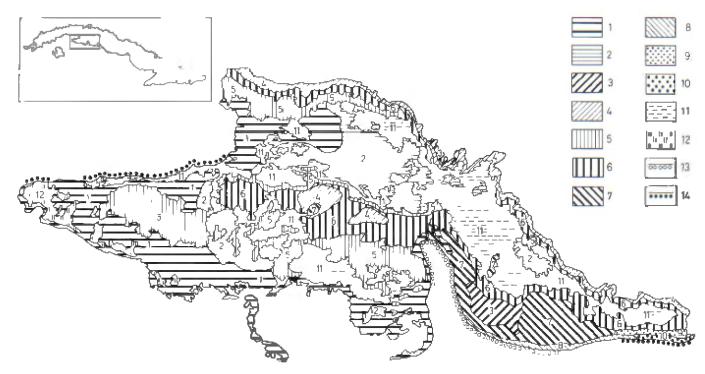


Fig. 322 The vegetation map of the Zapata-Peninsula (Del-Risco and Borhidi 1975) Legend: 1=mangroves of salt water; 2=mangroves of low salinity water; 3=tropical evergreen seasonal forest; 4=alluvial forest; 5=swamp forest on peat; 6=swamp forest on flooded limestone; 7=tropical semi-deciduous forest; 8=dry littoral forest; 9=tropical deciduous forest; 10=thorny dry limestone forest; 11=herbaceous swamp (Typha, Cladium); 12=salt marsh; 13=littoral sand vegetation; 14=littoral rock pavement vegetation. Scale: 1:450 000



Fig. 323 The pioneer bush vegetation of the swamp succession is formed by Bucida palustris Borhidi et Muñiz, Acoelorraphe wrightii Wendl., Myrsine cubana A. DC. and others, surrounded by the herbaceous swamp vegetation of Cladium jamaicense (Photo: A. Borhidi)

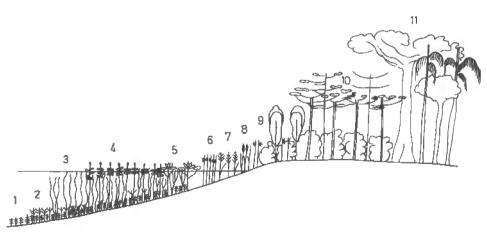


Fig. 324 Zonation of the fresh water communities in the Laguna del Tesoro, Zapata Peninsula (Borhidi and Muñiz). 1. Chara domingensis, 2. Najas minor, 3. Vallisnerietum neotropicalis, 4. Potamogeton illinoësensi-nodosus, 5. Nymphaeetum amplae, 6. Scirpetum americani, 7. Paspalidietum vaginati, 8. Typhetum domingensis, 9. Cladietum jamaicensis, 10. Tabebuio-Bucidetum, 11. Guazumo-Ceibetum

22.10 Coastal vegetation

22.10.1 Mangroves (Rhizophoro – Avicennietea)

The Caribbean mangrove vegetation, composed only of four tree species, has been studied in several localities (Ciferri 1936, Asprey and Robbins 1953, Stehlé 1945, Holdridge 1940, Dansereau 1966, Dansereau and Buell 1966, Loveless 1960, and Davis 1940, 1942). Besides floristic surveys, some reports on the growth and regeneration (Wadsworth 1959), ecology (Davis 1940) and nutrient cycling (Golley, Odum and Wilson 1962) of mangrove communities are also available. In Cuba, as elsewhere, mangrove vegetation occurs along shallow muddy beaches protected by coral reefs (Fig. 325). Here mangroves may form zones 2—3 km wide. In estuaries

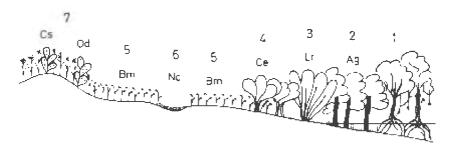


Fig. 325 Zonation of the mangrove at La Isabela, Las Villas Province, (Borhidi and Muñiz) 1. Rhizophora mangle belt, 2. Avicennia nitida belt, 3. Laguncularia racemosa belt, 4. Conocarpus erecta belt, 5. Batis maritima belt, 6. Nostoc commune belt, 7. Chloris sagraeana sand dune vegetation

with a shallow gradient (Hatiguanico, Cauto) mangroves penetrate deeply into the island following water from high tides. In the intertidal zone Rhizophora mangle forms a belt between the low tide and normal levels, whereas Avicennia nitida is dominant between the normal and high tide levels (Fig. 326). In some Avicennia stands Laguncularia racemosa individuals are intermingled. The Rhizophoretum community is usually free from accompanying species. In contrast, the Avicennia mangrove has many special elements, such as Acrostichum aureum, A. danaifolium, Rhabdadenia biflora, Cynanchum salinarum, Lycium carolinianum, and Batis maritima. In the uppermost section of the intertidal zone an extremely salt-resistant species, Conocarpus erecta, forms pure stands or it may be mixed with Laguncularia and Avicennia mixed stands (Fig. 326). Salt deposit zone up to 1 km wide is commonly found in the landward edge of the Conocarpus belt. This area is under water only during the equinoctial periods. The vegetation of salt deposits is composed of Batis maritima, and occasionally also of Suaeda linearis and Salicornia perennis. Due to its small size, this saltwort vegetation is included in the mangroves on the vegetation map.

29* 451



Fig. 326 Mangrove forest of the tidal belt formed by Avicennia germinans, at La Isabela (North of Las Villas) (Photo: A. Borhidi)



Fig. 327 Young mangrove forest destroyed completely by sinking of water table in the Zapata Swamp. (Photo: A. Borhidi)

22.10.2 The vegetation of sandy beaches (*Ipomoeo—Mallotonietea*)

The plant communities of sandy beaches are found to be particularly well developed between Habana and Varadero, and also in the Guanahacabibes Peninsula, in the southern part of Isla de Pinos, and in several short sections of the southern coast of Cuba (Fig. 328). Two noted pioneer plants of the strand line are Ipomoea pes-caprae and Canavalia maritima. They are common in the open strand communities such as Sesuvio-Ipomoeetum, Ipomoeo-Philoxeretum, and Philoxero-Unioletum virgatae. The community type actually occurring in a site is determined by the hardness of ground, angle of slope and water supply. The next successional stage is the horse-bush scrub (Borrichio-Mallotonietum) with various combinations of Borrichia arborescens, Mallotonia (Tournefortia) gnaphaloides, Spartina juncea, Turnera diffusa, Ernodea maritima, Suriana maritima, Baccharis halimifolia, and Sporolobus virginicus. The primary dunes are covered by sea-grape (Coccoloba uvifera) scrubs. Towards the interior of the island this successional sere is terminated by dry coastal evergreen scrubs ('manigua costera'). The vegetation of sandy beaches is only shown on the map where extensive continuous stands are found.

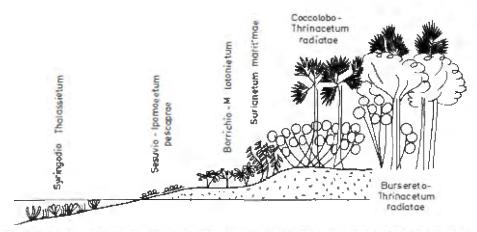


Fig. 328 Zonation of the vegetation of the sandy shores in the Casilda Peninsula, near Trinidad (Borhidi and Muñiz)

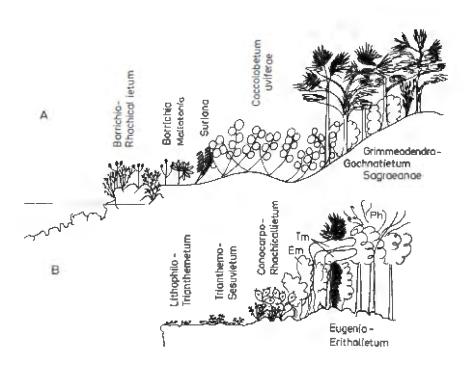


Fig. 329 Zonation of the coastal rock pavement vegetation. A: Arroyo Blanco near Jibacoa and B: Punta Guanal near Matanzas Em=Eugenia maleolens; Ph=Piscidia havanensis; Tm=Tabebuia myrtifolia

22.10.3 The coastal rock pavement vegetation (Sesuvio—Rachicallietea)

The communities of coastal rocky slopes are especially widespread along the southern coast of eastern and Central Cuba and at Habana and Matanzas. In contrast to the sandy vegetation, which is primarily of pan-tropical character, the vegetation of coastal rock pavements is mainly of Antillean and Caribbean elements. Most constituents of the open pioneer community (Trianthemo-Sesuvietalia) are succulent creepers (Lithophila muscoides, Trianthema portulacastrum, Sesuvium portulacastrum, S. maritimum). (Fig. 329). The next successional stage is the coastal rocky scrub (Borrichio-Rachicallietalia) containing Rachicallis americana, Borrichia arborescens, Erithalis fruticosa, Strumpfia maritima, Conocarpus erecta, Flaveria linearis, Heliotropium humifusum, Pectis spp., Opuntia dillenii, and Agave legrelliana. Many scrub associations may be distinguished. On cliffs exposed to salt-spray and winds Rachicallis and Conocarpus form a community, which is similar to some alpine creeper communities in appearance (Fig. 330). Further up these stands may reach a height of 1.5 m. Then, low sea-grape scrub follows on shallow sand. Elsewhere, e.g., in north-western and south-eastern Oriente, this sea-grape stage is skipped and thorn scrubs occur. These thorn scrubs are rich in Mimosaceae species.



Fig. 330 Rough dogtooth limestone area in the coastal belt of the Guanahacabibes Peninsula, near Punta del Holandés partly covered by creeping individuals of Rachicallis americana and Conocarpus erecta severely controlled by salt spray and sea winds (Photo: A. Borhidi)

23. Classification of major forest types of Cuba (with the contribution of Z. Szőcs)

23.1 The main questions of the classification

The classification of forest and shrubwood communities of Cuba, based on objective criteria, may answer several important questions:

- Is the choice of mapped vegetation units correct?
- What relationships are there between the structure and floristic composition of vegetation types?
- What conclusions may be drawn from the present day floristic composition of vegetation types about the past flora and vegetation development?

23.1.1 The vegetation categories to be classified

The based on structural features (height, number of levels, per cent closure, life forms and growth types) following the works of Davis and Richards (1933, 1934), Richards, Tansley and Watt (1940), Richards (1952, 1959, 1961), Beard (1944, 1955), Küchler (1949), Fanshave (1954), Dansereau (1958), Webb (1959), Aubréville (1965b), Ellenberg and Mueller—Dombois (1966a) and Eiten (1968). Most resulting categories proved to be identical with the Neotropical forest types established and clearly characterized by Beard (1955). The semi-arid serpentine formations, was studied by Borhidi (1973, 1974, 1975, 1976; 1979, in Borhidi *et al.*, 1980, in Borhidi and Muñiz), and Berazain (1978, 1981a,b) discussed and their recognition and present description provides new phytosociological findings.

23.1.2 Problems of classifying tropical forest communities

Mapping and classifying tropical forest communities are difficult for several reasons. For example, it is doubtful if they can be characterized by any means as associations, if their objective separation is possible, and if the tropical vegetation is continuous or discontinuous (Walter 1962). The discussion of these problems is beyond the scope of this book, only a few points relevant to the topic will be made to summarize my personal experience. Ciferri's (1936) and Knapp's (1964, 1965) work seemed to suggest that a cenological approach to the analysis of tropical vegetation might be plausible. I also made an effort not only to study the structure of formations but also to reveal principles determining floristic composition and to recognize and describe associations. Such a treatment of aquatic and uliginal vegetation, coastal sandy and rocky communities, mangroves, salt prairies and most coniferous forests presents no difficulties. The situation is completely different, however, in case of tropical forests and shrubwoods dominated by a multitude of species. The floristic richness of these communities causes high diversity, making the determination of minimum areas and the recognition of

characteristic species combinations extremely difficult. As far as classification is concerned, the richness in local endemics is also a disadvantage. Having the large number of exclusive 'characteristic species' in mind, one tends to establish too many categories with a result overemphasizing geographic differences. Furthermore, the presence of many local endemics conflicts with the final goal of classification, i.e., the recognition of relationships and common features.

23.1.3 Continuity or discontinuity of Cuban vegetation

In Cuba there are relatively few synbotanical objects supporting the continuity theory of vegetation. The recognition of vegetation types and associations is usually facilitated by the great variety of reliefs, substrates and soils. For example, a sharp vegetational boundary results wherever limestone and serpentine substrates meet. However, the delimitation of associations in zonal stands of semi-arid rainforests, semi-arid serpentine shrubwoods and xeric limestone scrubs is always difficult. In these formations only higher phytosociological categories were established since results of more detailed surveys were not available.

23.2 Material of the numerical analysis

In order to answer the questions raised in 23.1. data from 267 relevés taken in 40 lignosa noda (forest and shrubwood communities) usually dominated by many species were summarized in the matrix of the Table 25. (in the Appendix.) Accidental species have been omitted from this list. The frequency or constancy values of all other species, the life-form and growth type of each taxon (38 categories altogether) and 36 chorological types are indicated. The data matrix contains nearly 85 000 entries in more than 2 000 rows (taxa) and 40 columns (communities). This matrix was analyzed from three aspects:

- Floristic composition,
- Life-form spectrum, and
- Chorological spectrum.

First, traditional tabular sorting was done and then, to avoid the problems mentioned in 23.1.2. computer techniques were used. The ordination of the 40 vegetation units was obtained by principal components analysis (PCA) with VARIMAX rotation (Lawley and Maxwell 1963, Harman 1967) using floristic data. The classification of the same set of data was based on physiognomic and chorological variables. The method was sum of squares agglomeration clustering (SSA, Orlóci 1967). The computations were performed on a CDC 3300 computer using the clustering program developed by Goldstein and Grigal (1972a).

The numerical analysis was not operational in a sense that its purposes were to justify or reject the hypothesized classification and to indicate possible corrections to be made. The results, with an exception, support the hypotheses. The only major discrepancy arises in the case of Oriente pinewoods, possibly as a result of sampling error. The hypothesized classification was corrected accordingly, and the interpretation of modified results proved fairly easy.

23.3 Results

23.3.1 Component analysis based on floristic composition data

The first five components account for 45% of the total variance. The ordination in the first three dimensions is shown by Figs 331—333. The ecological and phytosociological interpretation of these components is as follows:

- a) On PCI the communities of the montane serpentine zone in Oriente, being characterized by ferritic soils and the most unique flora, are separated from the others.
- b) On PCII the broad-leaved forests growing mainly on limestone or neutral soils form a separate group.
- c) The lowland serpentine shrubwoods and pinewoods, i.e., communities with few strata and many hemicryptophytes, have high positive loadings on PCIII. At the opposite end of this axis relevés from extremely xeric limestone thorn scrubs are located. These communitites have also few layers and are very poor in terrestrial herbs.
- d) The ordination results suggest that the floristic diversity of the vegetation of Cuba is primarily due to edaphic factors.

These are:

- Latosols, rich in heavy metals, in old serpentine areas,
- Limestone karsts and connected young limestone flatlands and coastal rocky formations.
- Younger lowland areas, poor in nutrients, on serpentines, slates and quartz sands.

It is noted that rainforests determined merely by climate (19-23) are not affected by these edaphic factors.

23.3.2 Relationships in floristic composition depicted by PCA

Relationships depicted by PCA are summarized as follows:

- a) In the plane of PCI and PCII (Fig. 331) the pinewoods and serpentine shrubwoods occur in quarter I; the montane rainforests (with semi-arid and wet types clearly separated) in quarter II; the submontane rainforests in quarter III; and the broad-leaved forests of lowlands and hills of the seasonal climatic zone in quarter IV.
- b) In the plane of PCI and PCIII (Fig. 332) the coniferous forests of lowlands and hills and the serpentine shrublands are found in quarter I; the montane communities in quarter II, and the forests and scrubs of the seasonal climate belt in quarter III.
- c) In dimensions II and III (Fig. 333) the first quarter contains the same communities as in case b) The rainforests occur in quarter III, while the others are grouped in quarter II.

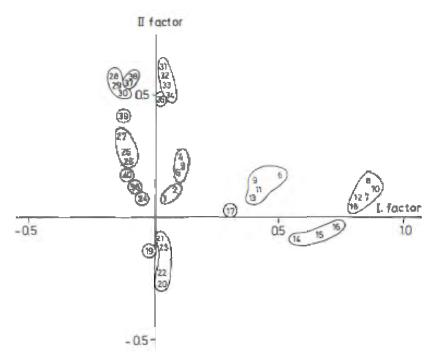


Fig. 331 PCA ordination of Cuban Lignosa-communities in the plane of components I and II (Borhidi and Szócs)

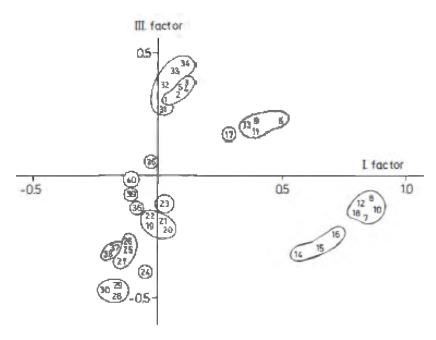


Fig. 332 PCA ordination of Cuban Lignosa-communities in the plane of components I and III. (Borhidi and Szőcs)

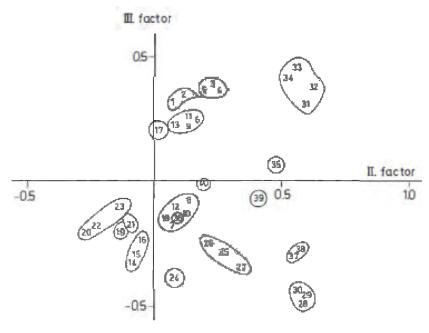


Fig. 333 PCA ordination of Cuban Lignosa-communities in the plane of components II and III. (Borhidi and Szőcs)

23.3.3 Grouping of the communities by PCA

The PCA results suggest that 15 lignosa groups be distinguished based on floristic composition. These are:

- 1. Coniferous forests of western Cuba (1-5) subdivided into two sub-groups, namely the forests of Isla de Pinos (1.2) and Pinar del Rio (3-5).
 - 2. Lowland coniferous forests of eastern Cuba (6, 9, 11,13).
- 3. Montane coniferous forests and serpentine shrublands of eastern Cuba (7, 8, 10, 12, 18).
 - 4. Semi-arid serpentine montane rainforests and shrubwoods (14-16).
 - 5. Semi-arid serpentine shrubwoods of lowlands (17).
- 6. Rainforests (19–23), with the submontane rainforest (19) and high montane wet shrublands (23) quite well-separated from each other.
 - 7. Seasonal rainforests (24).
 - 8. Karstic forests (25-27).
 - 9. Semi-deciduous forests (28—30).
 - 10. Arid serpentine scrubs of lowlands (31-34).
 - 11. Evergreen oakwoods (35).
 - 12. Alluvial forests (36).
 - 13. Dry evergreen forests and scrubs (37, 38).
 - 14. Arid limestone thorn scrubs (39).
 - 15. Semi-desert scrubs (40).

23.3.4 Relations between physiognomic and coenological units

In practice, these units correspond to those indicated in the field and used in the sampling and mapping project. This fact allows for the conclusion that the physiognomic units of the vegetation in Cuba are mainly identical with the major phytosociological groups, that is, there is a close relationship between structure and floristic composition (see next paragraph).

23.4 Classification of vegetation units based on life-form composition

The classification of 40 lignosa noda was obtained using structural variables and sum of squares agglomeration clustering (Orlóci 1967). Two types of starting data matrix were used, one containing presence/absence scores for 38 life-form categories (Fig. 334) and the other with frequencies of life-forms (Fig. 335).

23.4.1 Relations between structure and composition

The cluster analysis results suggest the following:

a) The presence and frequency of life-forms, i.e., the structural attributes of vegetation, and the floristic data yielded quite similar classifications of the lignosa noda. It also means that the different formations are composed of dissimilar floras developed as a result of long isolation and long periods of adaptation and speciation.

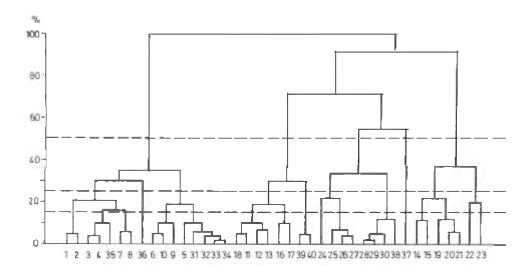


Fig. 334 Classification of Cuban Lignosa-communities obtained by Orlóci's sum of squares agglomeration method using the presence scores of the life-form types (Borhidi and Szőcs)

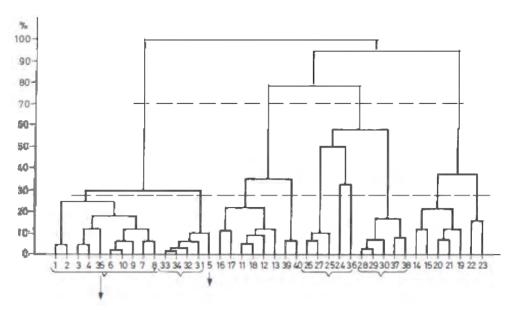


Fig. 335 Classification of Cuban Lignosa-communities with sum of squares agglomeration based on the frequency of life-form types (Borhidi and Szócs)

- b) The results of cluster analysis are more straightforward, more informative and easier to interpret than the PCA ordination.
- c) The structural relationships of tropical forests are better reflected in life-form frequencies than in the presence/absence data. Nevertheless, the alternative classifications differ only in the positions of three noda. The clustering based on life-form frequencies is in the best agreement with the field observations, so the correct positions of the misclassified noda are easily found: the alluvial forests (36) should be removed from the group of coniferous forests and placed among the seasonal rainforests and semi-deciduous forests; the pinewoods of Nipe Mts (7, 8 and 6, 9, 10) are closer to one another than to the serpentine shrubwoods and to the western pinewoods, although the genetic relationship is obvious; the dry evergreen scrubs (37) and dry evergreen forests (38) are more similar than suggested by Fig. 335.

23.4.2 The physiognomic classification of the forest noda

The physiognomic classification of forest noda may be interpreted according to Fig. 335 as follows:

- a) At the highest hierarchic level communitites with few strata, diverse herb layer and very few or no epiphytes and lianes (group A) are separated from those composed of several strata, rich in shrubs, lianes and epiphytes but having a poor herb layer (group B).
- b) Within group A the forests and shrubwoods form distinct clusters. Smaller forest groups are the pinewoods of Isla de Pinos and the adjacent evergreen

oakwoods, and the pinewoods of Nipe. In the shrubwood group the presumed evolutionary relationship between the pine-mixed shrubwoods of Cajalbana (5) and the xeric evergreen serpentine shrubwoods of lowlands in Central Cuba (31-34) is justified.

- c) In group B first the rainforests (14-15, 19-23) separate from the others: the semi-arid serpentine rainforests (14, 15), the submontane and montane wet rainforests (19-21) and the mossy forests and elfin thicket (22, 23) form smaller clusters.
- d) At lower lever in group B the broad-leaved seasonal forests form a separate group. Four smaller physiognomic categories are distinguished within this: karstic forests (25-27), seasonal rainforests (24), alluvial forests (36) and semi-deciduous and xeric evergreen forests (28-30) and (37, 38, respectively). The latter two are separated at an even lower level.
- e) The last subcluster of group B is very heterogeneous floristically. All communities included are characterized by few strata, rich shrub layer and reduced or missing herb and epiphyte strata. This cluster is subdivided into three fairly homogeneous groups, the lowland and montane semi-arid serpentine shrubwoods (16, 17), the Oriente latosol pinewoods with rich shrub layer (11, 18, 12, 13) and the limestone thorn scrubs and semi-desert scrubs (39-40).

23.5. Classification of the forest noda based on chorographical patterns

The 40 lignosa noda were also classified based on the frequency of flora according its different chorographical patterns. However, instead of creating a new syntaxonomical system, the goal of this analysis was to gain ideas, free from subjectivity, regarding the hypotheses on flora evolution and migration outlined in chapters 16-18 in connection with some representative distribution patterns or chorographical types.

23.5.1 General conclusions

General conclusions drawn from the classification results are:

- a) The classification hierarchy of 40 noda, resulted from the frequency data of chorographical elements, is in a good agreement with the dendrograms obtained based on floristic or structural variables. The only major difference is that geographic similarities are more emphasized due to the increased importance of local and regional endemics.
- b) The high similarity among the classifications reflecting different aspects in the data suggests that the vegetation types in Cuba are not only typical physiognomic categories but also phytosociological and ecological units and, in many cases, centres of flora development.
- c) It is concluded that the classification shown in Fig. 336 supports my hypotheses on the development and migration of endemic flora, (see chapters 19-20).

23.5.2 The chorographical relationships among the floras of forest noda

The relationships among the floras of forest noda are summarized using Fig. 336 as follows:

a) The serpentine forests on latosol of northern Oriente have an old and unique flora if compared to other parts of the country. Within these the pinewoods and shrubwoods of Nipe (with a flora containing 45-70% endemics), and the pinewoods, shrubwoods and semi-arid rainforests of Moa (with the percentage of endemics up to 50-80% represent distinct types. It is an important point that all vegetational formations of Moa are primarily characterized by endemics. In Nipe only the pinewoods and shrubwoods can be mentioned in this regard, since the extrazonal montane rainforests are identical with the forests of Moa.

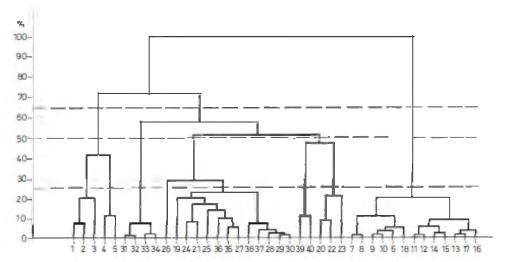


Fig. 336 Classification of Cuban Lignosa communities with sum of squares agglomeration based on the frequency of phytogeographic elements (Borhidi and Szőcs)

- b) The flora history of all other noda is largely independent of northern Oriente, Most links to the flora of northern Oriente are indicated in the pinewoods of western Cuba (1-5), which are subdivided into three groups of flora development. Isla de Pinos, Pinar del Rio and the Cajalbana forests.
- c) Regarding flora development, the serpentine shrubwoods of Central Cuba (31-34) are closely related to the pinewoods of western Cuba and even to the Oriente latosol zone.
- d) There are weaker relationships between the montane rainforest noda of Sierra Maestra (20, 22, 23) and the forest noda of northern Oriente. Nevertheless, definite floristic relationships exist between the fairly dissimilar vegetation of the mountains and the coastal arid zone in Oriente.
 - e) Most different from the serpentine vegetation are the forest noda of limestone

areas, whose flora is usually much younger. Due to the relatively low number of local endemics, the geographic differences among these noda are less pronounced. Within this group the species rich karstic forests of the mogotes in western Cuba form a fairly distinct class. The others are divided to two groups. The first (19–27) is rather heterogeneous phytosociologically and floristically, being constituted by submontane and seasonal rainforests, karstic forests and gallery forests. These are all characterized by a young, somewhat uninteresting flora containing few endemics and many species of Neotropical and Caribbean distribution pattern. The relatively wetter habitat and the more heterogeneous flora distinguish these noda from the similarly characterless semi-deciduous and xeric evergreen forests, which are also composed of widely spread species.

30 465