# PART II RELATIONSHIPS BETWEEN THE SOIL AND VEGETATION IN CUBA

## CONTENTS

## PART II

## Relationships between the soil and vegetation in Cuba

11	A brief survey of Cuban soils	117
	11.1 Geological background	117
	11.2 Soil classification of Bennet and Allison	117
	11.3 The genetic concept of Zonn	117
	11.4 The first genetic soil classification by Cuban pedologists	118
	11.5 Correspondence between soil classifications	119
	11.6 Two new classifications of the soils of Cuba	119
	11.7 Remarks on soil classifications in Cuba from an ecological viewpoint	120
12	The main relationships between soil and vegetation types	120
	12.1 Serpentines and soil types	120
	12.2 Soil-vegetation type relationship	121
13	The effect of serpentines on the flora and vegetation	121
	13.1 The serpentines and endemism	124
	13.2 Serpentines as an ecological factor group	124
	13.3 A concept of the serpentine effects on tropical flora and vegetation	127
	13.4 Stages of serpentine flora development and the controlling factors	134
	13.5 Serpentines and vegetation	136
	13.6 Serpentine effects on tropical vegetation	137
	13.7 Xeromorphy as a general adaptive syndrome of vegetation	143
14	Relation of soil and vegetation development	143
	14.1 Climatic pattern	144
	14.2 Soil succession	144
	14.3 Change of vegetation types during succession	144
	14.4 Soil-vegetation relationships	146
	14.5 Some remarks on the climax concept	146
15	Nature and origin of savannas in Cuba	148
10	15.1 Short historical survey	148
	15.2 Cuban grasslands Bennett's concent	151
	15.3 The savanna concent of Beard	153
	15.4 Physiognomic types and genesis of Cuban grasslands	155
	15.4 Physiognomic types and genesis of Cuban grassiands	100

## 11 A brief survey of Cuban soils

### 11.1 Geological background

The richness of the flora and the variability of the vegetation in Cuba are explained by the varied edaphic conditions. The diversity of soils is attributable to the wide variability of rocks on the island (limestones of various age, serpentine, dolomite, basalt, granite, diorite, gabbro, sandstone and slate) on which, as a consequence of the varied geological past, soil developing processes of different duration proceeded. Certain land masses have elevated (Sierra de los Organos) since the Cretaceous, others (Sierra de Nipe, Moa) from the beginning of the Oligocene, whereas the lowlands and coastal regions of considerable areas are of Quaternary origin. It is understandable that the many kinds of bedrock, under rather varied climatic conditions, produced soil development processes of strongly different duration. An extremely wide range of soil types developed, as well reflected by the soil classifications based on various approaches.

### 11.2 Soil classification of Bennet and Allison

Five different comprehensive classifications have appeared on the soils of Cuba. The first is of Bennett and Allison (1928) supplemented by a map to a scale of 1:1 million prepared by Bennett (1932). It is based mainly on morphological features (colour, structure, consistency, more important chemical properties, the presence of ironpan or gley horizon, drainage, bedrock) of the soils.

Only the soils of agricultural regions are studied and discussed, the majority of forest areas are excluded. The soil types are classified into series and these are grouped into families. Bennet's soil system comprises 15 families and 108 series which bear the name of those localities (e.g., families Matanzas, Nipe, Truffin, Bayamo, Esmeralda, Habana, Norfolk, etc.) where the soil types were originally described. The map depicts, with certain simplifications, the distribution of 79 types.

## 11.3 The genetic concept of Zonn

Zonn (1968), Zonn, Vazquez and Cabrer-Mestre (1966), apart from their own analyses. primarily used the results of Hungarian researchers (Klimes-Szmik and Szabédi unpubl.). Their genetic soil system is based on the origin and the developmental stage of soils. This, above all, can be expressed by the characteristic molecular ratios of the soils and in their clay fractions as  $SiO_2/R_2O_3$ ,  $SiO_2/Al_2O_3$ ,  $SiO_2/Fe_2O_3$  and  $Al_2O_3/Fe_2O_3$ . Zonn's system distinguishes 6 soil types and 17 subtypes as follows:

- I. Red ferrallitic soils
  - 1. Limestone red ferrallitic soils
  - 2. Acid red ferrallitic soils
- II. Quartz allitic soils
  - 3. Humic quartz-allitic soils
  - 4. Yellow lessivated quartz allitic soils
  - 5. Yellow pseudogleyic quartz allitic soils
  - 6. Pseudopodsolic laterites
  - 7. Yellow pseudopodsolic quartz allitic ferrallitic soils
- **III.** Soils formed on serpentines
  - 8. Ferritic soils
  - 9. Allitic-ferritic soils
  - 10. Humic magnesio-siallitic pseudopodsolic soils
- **IV.** Humus carbonate siallitic soils
  - 11. Humus carbonate soils
  - 12. Iron carbonate soils
  - V. Cinnamonic siallitic soils
    - 13. Cinnamonic carbonate soils
    - 14. Cinnamonic carbonate-free soils
- VI. Alluvial soils
  - 15. Dark carbonate-sulphate alluvial soil
  - 16. Black, leached alluvial soils
  - 17. Humic gley alluvial soils

No distribution map has been drawn yet of the mentioned soil types.

## 11.4 The first genetic soil classification by Cuban pedologists

Cuban researchers, O. Ascanio (1968) and his team (Jimenez, Hernandez), worked out a detailed system of the genetic soil types of Cuba. This, in principle, is similar to the earlier one but relies to a greater extent on the morphological properties and the origin of the soil (quality of the bedrock). This system consists of 17 main types divided into 100 genetic types according to the origin of the type and the quality of the bedrock. These are the following (the number of genetic types in each main type is in brackets).

- 1. Latosols or ferritic soils (4)
- 2. Latosolic or ferrallitic soils (20)
- 3. Weakly gleyized grey sands (1)
- 4. Tropical black soils (13)
- 5. Tropical brown soils (18)
- 6. Brown and red carbonate soils (9)

- 7. Humus carbonate soils (8)
- 8. Tropical meadow soils (17)
- 9. Alluvial soils (1)
- 10. Mocarrero or hardpan or cuirasses (4)
- 11. Yellow-red montane soils (7)
- 12. Yellow montane soils (2)
- 13. Peat (1)
- 14. Swamp soil (1)
- 15. Coastal swamp (1)
- 16. Salty soils (1)
- 17. Lowland karsts (Piedra hueca, dogtooth on hard limestone).

Two maps were drawn on the distribution of the types in 1968 to the scales of 1:250 000 and 1:1 000 000.

### 11.5 Correspondence between soil classifications

The soil classification categories of the three approaches are partly the same, their agreement is illustrated by Table 4 with several examples of corresponding soil types.

Bennett	Zonn	Ascanio	
Matanzas	acidic red ferrallitic soil	red latosolic or ferrallitic	
Nipe	ferriticsoils	latosols or ferritic soils	
Bayamo	humus carbonate siallitic	tropical black soil	
Guantanamo	cinnamonic carbonate	brown carbonate	
Mocarrero	pseudopodsoliclaterites	mocarrero or hardpan	
Guane	yellow alluvial quartz allitic	yellow latosolic	

#### Table 4 Soil classification

## 11.6 Two new classifications of the soils of Cuba

At the first symposium of the Soil Science Institute of the Cuban Academy of Sciences (1975), two new soil classifications were introduced by G. Tatevosian, A. Hernandez and others. One of them is the second genetic soil classification of Cuba with a more updated approach and has more detailed descriptions than the earlier versions. This is advanced especially in the classification of primitive soils, alluvial and swamp soils, vertisols and tropical brown soils. The other is Ascanio's classification and primarily serves purposes of agricultural practice, starting from diagnostic aspects and providing a soil classification key. This instructive soil classification fully combines the theoretical achievements of the genetic concept with practical aspects and greatly facilitates the rapid recognition of the more important soil types in the field for both farmers and ecologists.

## 11.7 Remarks on soil classifications in Cuba from ecological viewpoint

The soil systems mentioned are based on very detailed investigations and exceptional expertise. They give, however, the impression for ecologists that the majority of the described soil types are based on incomplete profiles which must have been decapitated and modified by the century-old anthropic influences. This is especially striking if we compare the soil profiles prepared in natural ecosystems to those described by Bennett, Zonn, Ascanio and Hernandez. The latter can only rarely be found under natural vegetation. Tatevosian (Conferencia del Instituto de Suelos AC 1975) expressed that Cuban soils are generally aged soils for which a slow water infiltration and small degree of permeability are characteristic as well as a high accumulation, accompanied by slow mineral cycling and a reduced microbiological activity. These phenomena are interpreted by pedologists and ecologists in different ways. In our view the main reason of the mentioned soil features is the intensive erosion and not the age of the soil. The whole of Cuba was originally covered with forest soils of developed A-level, more or less rich in humus. As a consequence of logging and burning of the forests the upper layer of the soils was partly decomposed and its major part was lost due to erosion. The upper layer of the B-horizon reaching up to the surface in this way became reactivated by the effect of the secondary grass cover developed in the course of succession and turned into a secondary thinner A-layer poor in humus. Its physical and chemical properties are worse, the permeability, fertility and biological activity are of course lower than those of the original forest soil, partly due to the lower biomass production of the grass cover, partly due to the harmful pedozoological and soil-microbiological effects of burning. According to our view, the lowland soils of Cuba are spoiled or modified rather than old or aged, and in fact we know very little about the soils of the natural vegetation.

# 12 The main relationships between soil and vegetation types

Comparing the genetic soil map and the vegetation map of Cuba (Inset), numerous differences and agreements can be found. The first difference is that the number of soil types is much higher than the vegetation types so the quality of the soil is not always a decisive factor in the development of vegetation. Climax vegetation types are sensitive to only drastic soil differences, the smaller edaphic differences are tolerated by the climax vegetation.

## 12.1 Serpentines and soil types

It is quite obvious that the serpentine rocks within every soil type produce other vegetation than the similar soils developed on other bedrocks. The effect of serpentines is felt on all genetic soil types perhaps the least on tropical brown soils.

It is striking that in the latosolic soils quite different climax vegetation may develop while certain vegetation types, e.g., semi-deciduous forests and pine-forests, may occur on completely different soil types. The soil-vegetation correlations, summarized in the next paragraph do not always exist but are expected with a rather high probability.

## 12.2 Soil-vegetation type relationship

It can be established that pine-forests and semi-dry, sclerophyllous montane rainforests may occur with high probability on latosols while pine woodlands on quartz-allitic soils and poor white sands. Furthermore, evergreen dry shrub forests live on siallitic or allitic-ferritic serpentine soils while on limestone a similar vegetation can be found on cinnamonic humus carbonate soils. On tropical black soils the original vegetation is alluvial forests similar to the tropical meadow soils originally also covered by forests.

The distribution of the tropical brown soils coincides quite well with the semi-deciduous forest belt while the original vegetation of the ferrallitic red soils signified the seasonal evergreen lowland forests and partly the semi-deciduous forests. We find the submontane tropical rainforests on yellowish red soils while the wet montane rainforest and the cloud forest belt coincides with the area of the tropical yellow soils. In spite of the intensive annual water table fluctuation, the., mocarreros are not savanna soils as Bennett and Allison (1928) suggested. The autochthonous vegetation of these areas was a deciduous or semi-deciduous thorny scrub forest which, as a consequence of burning off, quickly transforms to grassland and is reforested slowly. Accordingly, mainly semi-anthropic Sabal and Copernicia grasslands or secondary *Dichrostachys* thickets can be found on their sites. In the limestone haystack hill regions special deciduous or semi-deciduous small-leaved forests, the so-called "mogote forests", prevail: the lowland dogtooth karsts are covered by dry evergreen forests and semi-deciduous forest mosaics. As expected, the coastal regions comprise sandy and rocky vegetation whereas the muddy swamp coasts are covered by mangroves. The vegetation of flat and undrained basins comprises swamps and marshes. In the salty coastal zone behind the mangroves a halophytic vegetation of extremely salt-tolerant subshrubs predominates.

Table 5 shows the main correlations between vegetation and soil types, according to the three different classifications of Cuban soils.

## 13 The effect of serpentines on the flora and vegetation

The effect of serpentine rocks on the flora has been studied in all climatic belts with the main conclusion that the serpentine zones have particular flora and include special territories of speciation and species conservation. Kitamura (1950), Rune (1953) and Whittaker (1954) consider the richness of serpentine flora to be due to the size of the serpentine area and the abundance of the flora in the surrounding area.

## Table 5 Correlation between vegetation and soil types of Cuba (after Borhidi 1973, Borhidi and Muñiz 1980, 1984, Capote et Berazain 1984)

Vegetation	Soil types according to the soil classifications of Cuban authors made in					
Physiognomic units	1973	1975	1979			
A. Woody formations						
I. Closed forests						
I.1. Tropical ombrophilous forests						
I.1.1. Submontane rainforests	latosolic yellow tropical	red ferrallitic and yellow ferrallitic	red ferrallitic and yellow ferrallitic			
I.1.2. Montane rainforests						
I.1.2.1. Wet montane rainforests	latosolic yellow tropical	red ferrallitic and leached yellow ferrallitic	red ferrallitic and leached yellow ferrallitic			
I.1.2.2. Semi-dry sclerophyllous rainforests on serpentine	latosols	ferritic purple and ferrallitic yellow	ferritic purple and ferrallitic yellow			
<ul><li>I.1.3. Elfin forests</li><li>I.2. Tropical evergreen seasonal forest</li><li>I.2.1. Broad-leaved evergreen forests</li></ul>	yellow tropical	leached yellow ferrallitic	leached yellow ferrallitic			
I.2.1.1. Lowland type	latosolic and yellow tropical	red ferrallitic and reddish-brown	red ferrallitic and reddish-brown			
	and pardo tropical	fersiallitic and tropical brown	fersiallitic, yellowish-red fersiallitic, not carbonate brown soil			
I.2.2.2. Submontane type	humic limestone	red rendzina and black rendzina	red and black rendzinas			
I.2.2. Needle-leaved evergreen forests						
I.2.2.1. Lowland type	yellow tropical latosol	ferritic purple quarzitic ferrallitic	purple red and quarzitic sandy soil,			
	brown tropical	skeletal	yellow quarzitic ferrallitic, skeletal			
I.2.2.2. Montane type	latosol montane yellow	purple ferritic montane yellowish-red ferrallitici or allit-ferritic	purple ferritic montane yellowish-red allit-ferritic			
I.3. Edaphically humid evergreen or						
deciduous forests						
I.3.1. Alluvial or riverain forests	alluvial	alluvial	alluvial			
I.3.2. Mangrove forests	gley tropical	peatandmud	peat and mud			
I.3.3. Tropical swamp forests	gley tropical	peat	peat			
I.4. Tropical semi-deciduous forests						
I.4.1. Mesophyllous	humic carbonate brown tropical	rendzina red and black carbonated brownsoil	red and black rendzinas carbonated brownsoil			
I.4.2. Microphyllous	skeletal on dog-tooth limestone	skeletal	black protorendzina brown protorendzina and skeletal			
I.5. Tropical deciduous forests	skeletal on dog-tooth limestone	skeletal	black protorendzina skeletal			
II. Shrublands and thickets						

22

II.1. Evergreen broad-leaved thickets			
11.1.1. Montane serpentine	latosol, gravelly	purple ferritic	purple ferritic
I1.1.2. Elfin thicket	montane reddish-yellow	not specified	not specified
II.2. Semi-deciduous broad-leaved	-		
thickets			
II.2.1. Littoral limestone thicket	skeletal on dog-tooth	skeletal and red rendzina, black	skeletal, rendzina red and black,
	limestone, brown soil	rendzina carbonated brown	carbonated brown
11.2.2. Submontane serpentine	latosol, latosolic red	purple ferritic red ferrallitic	purple ferritic red ferrallitic
11.2.3. Lowland with fluctuated water			
table	mocarrero	gravelly reddish yellow pseudogley	gravelly reddish and yellow pseudogley
II.3. Extremely xeromorphic (thorny)			
thicket			
II.3.1. On serpentine	latosol, latosolic	purple ferritic red latosolic	purple ferritic red latosolic
11.3.2. In the subdesert belt		red fersiallitic	reddish-brown fersiallitic
B. Herbaceous formations			
III. Savannas and parklands			
III.1. Tall grass savannas			
III.1.1. with tall palms	latosolic brown tropical	red ferrallitic brownish-red	red ferrallitic brownish-red
	black tropical	fersiallitic dark plastic gleyized	fersiallitic dark plastic gleyized
III.1.2. with evergreen trees	black tropical alluvial	dark plastic gleyized alluvial	dark plastic gleyized alluvial
111.1.3. with deciduous trees	mocarrero brown tropical	reddish-yellow pseudogley	reddish-yellow pseudogley
	yellow tropical	reddish-brown fersiallitic	reddish-brown fersiallitic
111.2. Short grass savannas			
III.2.1. with low palms	dog-tooth limestone, skeletal,	skeletal, red rendzina, quarzitic	skeletal, red rendzina, quarzitic
	quarzitic sand, latosolic,	ferrallitic, red ferrallitic, reddish-brown	ferrallitic, red ferrallitic, reddish-brown
	mocarrero	fersiallitic	fersiallitic
III.2.2. with xeromorphic trees	mocarrero, black tropical	reddish-brown fersiallitic dark plastic	reddish-brown fersiallitic dark plastic
		gleyized	gleyized
III.3. Swamps and marshes			
III.3.1. Sedge swamps and marshes	gley tropical, alluvial	peaty gleyized, dark plastic gleyized, alluvial	peaty gleyized, dark plastic gleyized, alluvial
III.3.2. Wet lowland savannas	black tropical	dark plastic gleyized, dark plastic not gleyized	dark plastic gleyized, neoautomorphic dark plastic, greyish-brown soil
III.4. Herbaceous and half-woody salt		<i>B.ej</i> ( <i>bea</i> )	
swamps			
III.4.1. Half-woody salt marsh	salinesoils	solonetz and solontshak	solonetz and solontshak
III.4.2. Salt meadows	saline soils, black tropical	solonetz, solontshak, dark glevized	solonetz, solontshak dark gleyized,
	· •	soil	

#### 13.1 The serpentines and endemism

Rune (1953) demonstrated that the rocks with high Ca and Mg contents (serpentine, magnesite, dolomite, limestone, gypsum, gabro) favour the formation and conservation of palaeoendemics and relic species while on heavy metal soils primarily neoendemic taxa develop. The serpentines combine both chemical properties, thus they are rich both in palaeoendemics and neoendemics.

#### 13.2 Serpentines as an ecological factor group

Studying the mechanism of action of serpentines, most researchers concede [cf. Krause's review (1958 a)], that the serpentines are effective as several other equally important limiting factors combined in a so-called "serpentine combination". Of these factors the following were studied:

a) Ca/Mg ratio: Blackshaw (1920), Novák (1928), Beckett (1965), Proctor (1971 *a,b*). Lyon *et al.* (1971) consider the low Ca/Mg ratio of serpentine soils to be decisive since it influences the stability or inhibits the development of the Ca/Mg balance of living organisms.

In the young serpentine soils of Cuba, the Ca/Mg ratio varies between 0.01-0.5 and even on the most mature latosols it does not reach one. This factor seems to be rather important and it shows why the serpentines are unsuitable for other Mg plants (dolomite and gypsum plants). At the same time it could be established that neither the high Mg-content nor Mg-excess are constant properties of serpentine soils. Bennett and Allison (1928), as well as Robinson *et al.* (1935), demonstrated for latosols and latosolic serpentine soils that they were completely free of Mg. Without doubt, due to the instability of Ca-balance, the ultrabasic character of young serpentine soils with relatively low SiO<sub>2</sub> content may change quickly and this could make the serpentines ecologically ambiguous: relatively basic and relatively acid at the same time.

**b)** Nutrient deficiency: Gordon and Lipman (1926) emphasized the role of the high pH values accompanying low N and P content. Robinson *et al.* (op. cit.) pointed out the connection between the decline of Si in the course of soil development, the poor Al storage of clay minerals and the reduction in adsorption capacity due to Ca deficiency. Bennett and Allison (op. cit.) demonstrated that the clay of Cuban serpentine ferritic soils was suitable for ten times less adsorptive capacity than the clay fraction of a sandy mud soil. Lipman (1926) pointed out the exceptionally weak microflora of these soils.

c) Ca deficiency: Kruckeberg (1954) and Walker (1954) later considered the role of Ca deficiency to be important and that of Mg to be secondary, whereas in the case of the serpentines the effect of both cannot entirely be separated.

d) Mg toxicity: Proctor pointed out in his excellent study series (1970, 1971b) that Mg is extremely toxic. He proved with water culture experiments that this toxic effect is decisive in the low Ca/Mg ratio. The strongest toxicity was produced by Mg with total lack of Ca and upon the slightest addition of Ca the toxic effect was

reduced. In this way Proctor reinforced Kruckeberg (1954) and Walker's (1954) views with respect to the importance of the lack of Ca. From another aspect Berazain's investigations in Cuba show that the vegetation of the serpentines strive to balance the low Ca/Mg ratio of the soil with a vigorous adsorptive control. She proved by studying six species living in serpentines that in spite of the 0.09-0.17 Ca/Mg ratio in the soil, all investigated plant leaves had a Ca/Mg ratio of about 1.0 or more. Of the studied species the most serpentine-tolerant was *Leucocroton havanensis* Borhidi (*L. flavicans* auct. cub. non Muell. Arg.) which approached the optimal physiological value of the Ca/Mg ratio in the leaves (Table 6).

Table 6 Element content of leaves in plants of serpentine soils: Loma de Galindo, Prov. Matanzas, Cuba (after Berazain 1981b) in % of dry matter

Ni	Со	Mg	Fe	Са	Cu	Zn	Ca/Mg
1.58	0.03	5.81	12.1	1.04	0.00	0.00	0.17
1.29	0.02	11.61	9.9	1.04	0.00	0.00	0.09
11.45	0.05	7.13	0.18	26.58	0.02	0.05	3.72
6.34	0.02	13.75	0.26	18.36	0.02	0.04	1.26
0.89	0.03	12.50	0.50	11.60	0.04	0.03	0.92
0.12	0.01	14.50	0.38	20.78	0.03	0.04	1.43
0.02	0.01	6.25	0.13	13.34	0.02	0.03	2.13
0.05	0.01	2.50	0.18	3.38	0.02	0.06	1.35
	Ni 1.58 1.29 11.45 6.34 0.89 0.12 0.02 0.02	Ni         Co           1.58         0.03           1.29         0.02           11.45         0.05           6.34         0.02           0.12         0.01           0.02         0.01           0.05         0.01	Ni         Co         Mg           1.58         0.03         5.81           1.29         0.02         11.61           11.45         0.05         7.13           6.34         0.02         13.75           0.89         0.03         12.50           0.12         0.01         14.50           0.02         0.01         6.25           0.05         0.01         2.50	Ni         Co         Mg         Fe           1.58         0.03         5.81         12.1           1.29         0.02         11.61         9.9           11.45         0.05         7.13         0.18           6.34         0.02         13.75         0.26           0.89         0.03         12.50         0.50           0.12         0.01         14.50         0.38           0.02         0.01         2.50         0.13	Ni         Co         Mg         Fe         Ca           1.58         0.03         5.81         12.1         1.04           1.29         0.02         11.61         9.9         1.04           11.45         0.05         7.13         0.18         26.58           6.34         0.02         13.75         0.26         18.36           0.89         0.03         12.50         0.50         11.60           0.12         0.01         14.50         0.38         20.78           0.02         0.01         6.25         0.13         13.34           0.05         0.01         2.50         0.18         3.38	Ni         Co         Mg         Fe         Ca         Cu           1.58         0.03         5.81         12.1         1.04         0.00           1.29         0.02         11.61         9.9         1.04         0.00           11.45         0.05         7.13         0.18         26.58         0.02           6.34         0.02         13.75         0.26         18.36         0.02           0.89         0.03         12.50         0.50         11.60         0.04           0.12         0.01         14.50         0.38         20.78         0.03           0.02         0.01         6.25         0.13         13.34         0.02           0.05         0.01         2.50         0.18         3.38         0.02	Ni         Co         Mg         Fe         Ca         Cu         Zn           1.58         0.03         5.81         12.1         1.04         0.00         0.00           1.29         0.02         11.61         9.9         1.04         0.00         0.00           11.45         0.05         7.13         0.18         26.58         0.02         0.05           6.34         0.02         13.75         0.26         18.36         0.02         0.04           0.89         0.03         12.50         0.50         11.60         0.04         0.03           0.12         0.01         14.50         0.38         20.78         0.03         0.04           0.02         0.01         6.25         0.13         13.34         0.02         0.03           0.05         0.01         2.50         0.18         3.38         0.02         0.06

e) Mo deficiency: It has been proved that the serpentine soils were poor in physiologically important trace elements, especially in Mo, as it was pointed out by Johnson, Pearson and Stout (1952).

f) High Fe content: Sarasin (1917), Göhlert (1928) and Minguzzi and Vergnano (1953) showed that high iron concentrations had a major role in dwarfing plants. It is without doubt that one of the most striking features of plants living on serpentines  $\swarrow$  is the dwarf growth, moreover, the Fe<sub>2</sub>O<sub>3</sub> content in serpentine soils may be as high as 80%. Of the six species studied by Berazain, all appear to be major Fe accumulators. Nevertheless, if compared to the related species, none of them showed signs of nanism. Dwarfing in plants, according to my observations, develops in Cuba only in ancient serpentine areas on mature latosols where the \* Fe<sub>2</sub>O<sub>3</sub> content of the soil exceeds 50% and on extremely poor acid white sand.

**g)** Ni toxicity: the high toxicity of Ni has been studied by numerous researchers. Hunter and Vergnano (1952), Crooke and Inkson (1955), Crooke (1956), Soane and Sauder (1959), Proctor (1971 *a*, *b*), Proctor and Woodell (1971), Brooks, Lee and Jaffré (1974), Wiltshire (1974) and Berazain (1981) studied Ni tolerance on materials derived from Scandinavia, Britain, Italy, Rhodesia, Cuba, New Zealand and New Caledonia. All agree that the toxic effect is significant, the plants accumulate Ni in large quantities and the Ni uptake increases in acid soils. Hunter and Vergnano suppose that in the plants which had adapted to Ni (e.g., Alyssum *bertoloni*), Ni has a positive physiological role, perhaps the plant makes up for lacking Ca by Ni. This supposition has not yet been confirmed. Wiltshire proved that Ni tolerance did not depend on the amount of Ni uptake, but on the site of accumulation in the plant. Populations with higher Ni tolerance take up the same amount of Ni as the less tolerant ones, but the Ni level decreases from the root to the stem. Berazain's investigation, however, shows that the narrower the area of a serpentine endemic species the greater the activity of the nickel ion accumulation. At the same time it is striking that heavy metals are hardly accumulated in the leaves of palms. Gregory and Bradshaw (1965), Proctor (1971b) and Wiltshire (1974) established that Ni tolerance is less specific than copper tolerance and that chromium and copper have a greater effect on the mechanism of speciation, as it has been shown by Duvigneaud (1959), Duvigneaud and Plancke (1959), Duvigneaud and Timperman (1959) in Katanga, by Jacobsen (1967, 1968), Wild (1968, 1970) and Wiltshire (1974) in Rhodesia and by Drew and Reilly (1972) in Zambia.

**h)** Dysgeogenic effect: The slow dysgeogenic decomposition of serpentines creates typical geomorphological forms of extreme micro-climate and habitats with reduced competitivity. This is similar to the dolomite phenomenon (Gams 1930, Zólyomi 1942) and to the effect of other dysgeogenic rocks (e.g. quartzite, sandstone, quick sand).

i) Physical properties: Numerous researchers (Novák and Pelišek 1940, Benett and Allison 1928, Robinson *et al.* 1935, Rune 1953, Lam 1927) have stressed the characteristic physical properties of serpentine soils, the hot dry feature of the shallow serpentine rendzina, the flexibility, the lack of rocks, the water-retaining capacity, etc. of the serpentine laterite. It can be established, however, that these physical properties do not explain the low fertility of the serpentines; in the evolution of serpentine soils the physical properties considerably change without changing their effect on the flora.

**j) Role of reduced competition:** according to Kruckeberg (op. cit.) this is an important feature in the evolution of endemics on serpentines. The non-serpentine populations of species occurring both on serpentine and non-serpentine soils as a consequence of competition become exhausted earlier and extinct, while those living on serpentines are faced with reduced competition and survive as isolated populations. He supposes that many serpentine endemics come about as a consequence of such biotype exhaustion. The populations adapted to serpentines are not able usually to return to other rocks because they are not able to tolerate the stronger competition prevailing on other soils anymore. It is largely a consequence of this that the serpentines can be regarded as edaphic islands which have their own endemic flora (Cain 1944, Mason 1946).

#### 13.2.1 Conclusion

Based on observations carried out so far, we cannot make general conclusions on the mechanism of serpentine effect. Observations confined to various areas and factors cannot yet be assessed although research in recent years has primarily stressed Mg and heavy metal toxicity. According to Krause (1958a), so much is certain that it is not the omnipotence of a single factor but basically the combination of different serpentine factors that have to be taken as the starting point and each case must be analyzed individually in accordance with the circumstances.

From our observations we may state that, of the serpentine factors, the really acting, limiting ones can be different in dependence of time and place. From the point of view of place the composition of the serpentine rock (the peridotite/augite ratio), as the initial material of soil formation, and the climate, as a factor determining the direction and stages of soil development processes, are important. Time is important because soil evolution proceeds in time, and in different phases of soil development different serpentine factors become decisive in limiting and adaptation mechanisms. The only factor group which remains more or less unchanged irrespective of place and time is nutrient deficiency. Undoubtedly, this factor group has a great effect in that the metabolism of serpentine plants is essentially slower compared to plants living on other rocks. This is an irreversible adaptive property of plants (see 13.3.5). It may be attributed to nutrient deficiency that in spite of the different acting serpentine factors the physiognomy of serpentine vegetation is rather uniform. However, we cannot accept it as a single factor because other nutrient deficient rocks may produce similar physiognomic vegetation but the gene pool similar to serpentines cannot. Nutrient deficiency cannot be disregarded, it is rather important because in different phases of soil evolution processes it reinforces certain soil factor effects since the plant has been forced to take up and tolerate large amounts of toxic material.

## 13.3 A concept of serpentine effects on tropical flora and vegetation

We shall try to assess how and to what extent the different serpentine factors have a role in developing the flora and vegetation of serpentine areas of various age, size and climate under tropical conditions.

#### 13.3.1 Serpentine areas of Cuba

Cuba is an especially suitable region for studying the origin and adaptation of serpentine floras because it has three large serpentine ranges and nine smaller or larger separate lowland colline serpentine territories of 7500 km<sup>2</sup> area altogether. These areas largely differ from one another with respect to age, evolution, orography, soil conditions and climate and are appropriate for multilateral observation.

#### 13.3.2 Endemic serpentine genera in Cuba

The serpentine areas in Cuba have proved to be the most intensive and successful 'workshops' of plant speciation and diversification. This is proved by the fact that one-third of the endemic flora of Cuba (920 species, 31.2%) has developed on serpentine areas covering not more than 7% of the whole country. 14.6% of the total flora is endemic exclusively, to serpentine. Of the 72 endemic phanerogamous genera 24, i.e., 33.3%, live in serpentine areas. Examples are *Ekmanochloa Sauvallella*. *Moacroton, Kodalyodendron, Adenoa*, (Fig. 51) *Tetralix, Phidiasia*,



*Fig. 51 Adenoa*, a monotypic endemic genus of Turneraceae living in the serpentine mountains of the northern Oriente (Photo: A. Borhidi)

Sapphoa, Dasytropis, Acunaeanthus, Ceuthocarpus, Neomazaea, Phyllomelia, Schmidtottia, Ariadne, (Fig. 52) Shaferocharis, Eosanthe, Koehneola, Lescaillea, Harnackia, Shafera, Ciceronia and Feddea, 75% of the endemic Acanthaceae genera (3 genera), 67% of the endemic Rubiaceae genera (8 genera) and 50% of the endemic Compositae genera (6 genera) are exclusively serpentinecolous. Apart from the listed genera, some supraspecific taxa should be mentioned whose species are also exclusively serpentine endemic, such as Phyllanthus sect. Orbicularia, Leucocroton sect. Leucocroton and Spathelia sect. Splendentes (see Table 6).



Fig. 52 Ariadne (Rubiaceae) an endemic genus of the serpentine shrubwoods in the Sagua-Baracoa range (Oriente) (Photo: A. Borhidi)

#### 13.3.3 Causes of taxon-richness of serpentine floras

The richness of serpentine floras (12.1.1), according to our observations, depends on the following factors in order of importance:

- Age of serpentine region
- Size of serpentine region
- Number of climatic changes
- Specialization of surrounding flora
- Richness of surrounding flora

a) The richness of serpentine flora depends above all on the age of the region (not the age of the rock), or more exactly, on the time available for the flora evolution. Of the twelve serpentine regions of Cuba, four are rather old surfaces, the west Cuban Cajalbana collines, the Nipe, Cristal and Moa ranges of Oriente. On these areas as a result of several million years of soil development processes the latosolization is in an advanced state, according to many soil scientists it is predominated by old fossil soils. According to Finko, Korin and Formell (1967), the estimated age of latosols in Moa is about 30 million years. The other eight serpentine territories of Cuba can be found in central Cuban lowlands and collines which are around 1 million years of age or younger. Their soils are young humus magnesium siallitic or allitic ferritic soils of moderate development. The old

Tura of regions	Ar	ea	Ender	nic genus	Endemi	c species
I ype of regions	km²	%	No.	%	No.	%
Old serpentine areas	4800	64	22	91.7	750	81
Young serpentine areas	2700	36	0	0	128	14
Common	0	0	2	8.3	42	5
Total	7500	100	24	100	920	100

Table 7 Comparison of old and young serpentine areas with respect to the flora

serpentine areas cover a 4,800 km<sup>2</sup> area (64% of the total serpentine surfaces) whereas the young serpentine areas correspond to 2700 km<sup>2</sup> (36%). Comparing the flora of the two regions (Table 7) it is striking that of the 24 endemic serpentine-colous genera mentioned in 13.3.2, 22 are exclusive to the old serpentines. Only the *Acunaeanthus* and *Moacroton* are common, for both old and young serpentine regions. The young serpentines have no endemic genus. Of the 920 endemic serpentine species 792, i.e. 86%, are found in the old serpentines. Of these 750, (81%) are exclusive to this area while 42 species (5%) – e.g. *Neobracea valenzuelana* (Fig. 53) – are common in the younger regions. In contrast with this the endemic species of the younger serpentines account for 14%.

b) The extent of the serpentine area from the point of view of flora richness is only important in certain extreme cases, namely when it is so small that it becomes



*Fig. 53 Neobracea valenzuelana* (A. Rich.) Britt. a Pan-Cuban serpentinophilous shrub occurring in all serpentine areas of Cuba. (Photo: A. Borhidi)

a barrier to isolation of newly evolved populations. In serpentine areas of the same age and larger than 500 km<sup>2</sup>, the differences noticeable in orographic variety, habitat of climate may have a much greater effect on the floristic richness than the extent of the region. The size of the region is effective if it is combined with orographic variability, abundance of different meso- and microclimatic habitats. Table 7 can also be interpreted in such a way that in addition to the age of the areas, their extent can also have a major role in the development of floristic richness. In reality, as compared to the age, the importance of the extent of the area is minimal. Our findings are supported by the data of Table 8 where it is seen that in an area of 70 km<sup>2</sup> colline serpentine block of Cajalbana Hill there are twice as many endemic species as in the Camagüey serpentine zone which is younger and ten times larger in area. Moreover, the former has three endemic genera and a number of isolated palaeoendemics while in the latter area, almost without exception, vicarious neoendemics occur only.

Table 8 Comparison the serpentine areas of Cajalbana and Camagüey with respect to local endemics

	Area	Local endemic genus	Local endemic species
Old serpentine area			
Cajalbana	70 km <sup>2</sup>	3	32
Youngserpentine area			
Camagüey	800 km²	0	16

c) The climatic changes have a rather important role in the evolution of flora, especially the frequent changes of longer wet and dry periods. The floras of the Moa and Nipe ranges of about the same age of old regions are good examples. From the latosols and extrazonal rain forests we may justly conclude that this montane region previously had moist tropical climate; in fact in the latosols of the Nipe several hardpan layers can be found as products of alternating dry and wet climatic periods of the Quaternary or upper Tertiary ages. It may be due to this that the relatively lower flora richness approaches that of Moa as seen in Table 9.

Table 9 Comparison of the flora of the Moa and Nipe ranges, with respect to endemic species

Region	Area	Annual mean precipitation	No. of endemic genera	No. of endemic species
Nipe Mts.	500 km <sup>2</sup>	1617 mm	4	151
Moa Mts.	2500 km <sup>2</sup>	2314 mm	4	190
Common			6	263

We have to note that drought in Cuba is a rather stimulating evolutionary ecological factor which is not surprising since the main trend in the evolution of the plant kingdom is its tolerence to drought. Figure 54 demonstrates this effect of dryness well, from which it turns out that 68% of the microphyllous trees and shrubs are endemic, 78% of the nanophyllous trees and shrubs and 75% of the leptophyllous trees and shrubs. On serpentine areas this evolutionary effect is even



*Fig.* 54 The leaf size class pattern of the Cuban trees and shrubs. mg: megaphyll; ma: macrophyll; ms: mesophyll; nt: notophyll; mi: microphyll; na: nanophyll; lp: leptophyll, -a) tropical species, b) Caribbean species, c) Cuban endemic species

more explicit since the physiological drought of serpentine soils, as will be shown later in several examples markedly increases the ecological effect of the climatic aridity.

d) Naturally, the serpentine areas reaching the surface by denudation develop their own flora from the surrounding 'basic' flora, so it is important how rich the basic flora is. A more important factor than species richness is the degree of basic flora specialization. A species-poor basic flora, which has adaptable and genetically flexible taxa, can develop into a serpentine flora of greater variability than a species rich one which has become highly specialized. There are examples of these in Cuba: the Cajalbana hills are surrounded by the conic karst areas of Sierra de los Organos and Sierra del Rosario on which—being in one stretch from the Cretaceous age already by the middle of the Miocene—a probable time for the emergence of Cajalbana serpentines—a very rich but strongly specialized chasmophytic limestone flora developed whose members were mostly unsuitable for colonizing the serpentine region. So Cajalbana obtained its florula not from here but from the species-poor Cayetano sandstone regions. From that developed a highly specialized serpentine flora whose richness is comparable with the older relic flora of Sierra de los Organos.

#### 13.3.4 Importance of Mg and Ca level

With respect to the ecological factors inducing the evolution of serpentine flora and development of special "serpentinomorphoses", we agree with Proctor (1971a, b) in finding low Ca/Mg ratio and heavy metal, especially Ni, toxicity. It should be emphasized that the two factors rarely act combined or simultaneously as the same plant population does not tolerate Mg and Ni generally to the same extent (Proctor 1971b: 839). Kruckeberg (1954) and Walker (1954) consider the Ca deficiency to be the determining ecological effect of serpentines, as well as low nutrient level and finally Mg content and the reduced competition. There are several questions which are difficult to answer:

Why is it that we find the most serpentine endemics in the pioneer shrub vegetation of primary serpentine rendzinas which are not yet poor in Ca?

Why did the flora of serpentine areas remain isolated even when a Ca-free rock area surrounds it, e.g., granite, diorite or sandstone?

Obviously, it is due to the high Mg level. According to our experiences under tropical conditions, Ca deficiency, besides appropriate augite content, appears on mature ferrallitic and ferritic serpentine soils and not in the early phases of soil evolution whereas the decisive moment of the development of endemic serpentine flora takes place just on these young, Ca-rich (CaO content ranges between 3-10%) and Mg-rich soils. Thus, the importance of Ca deficiency has to be considered as a secondary or tertiary factor however spectacular the mature serpentine soils are from the point of view of flora development. Undoubtedly, the plant species which have adapted to Ca deficiency are most suitable to settle in serpentine areas, often without changes in the biotype (e.g., conifers, grasses, *Ericaceae*), but the acidophilous species which have adapted to serpentines in the form of a new biotype are rarely able to return to the original bedrock although the Ca deficiency would not mean a barrier.

#### 13.3.5 Irreversible adaptation to serpentines and effects of fertilization

The specialization of trees and shrubs of Cuba to serpentine rocks results in metabolic changes and is a largely irreversible process. The serpentine species are not able to survive on soils other than serpentine merely on account of the intensified competition. Acuña (personal communication) and my own observations proved that in the Botanical Garden of Santiago de las Vegas, on limestone latosolic ferrallitic soils, the serpentine endemics introduced there disappeared after one or two years without having any competitors. It is also proved by K, N and P fertilization experiments which aimed at greater productivity and growth of serpentine flora and vegetation by reducing nutrient deficiency on serpentine soils. Fertilization accelerated the metabolism of plants which caused growth discrepancies, leaf fall and dieback of serpentine trees and shrubs. Fertilization experiments carried out with grasses proved that raising the low nutrient level does not entail significant yield growth, in fact, it rather spoils the tolerance to toxic materials. The most effective proved to be Ca fertilization (Walker 1954, Proctor 1971b) but in the tropics this could only produce results on young shallow soils still rich in Mg. Crooke (1956) proved that low pH increased heavy metal toxicity and Crooke and Inkson (1955) pointed out that the toxicity of nickel was greater in the presence of high phosphorus and low Ca and K levels. N-fertilization was found to be ineffective on Mg soils (Wiltshire 1974) because the N source had no effect on the Ca/Mg ratio. Negative results of N fertilization were likewise found on Ni soils because ammonium as an N source intensified the acidity of the soil and, together with this, the heavy metal uptake and toxicity (Antonovics *et al.* 1971, Gigon and Rorison 1972). Nitrate addition, however, stimulates the uptake of iron and aluminium even up to a toxic level. It has to be remarked that these plant responses were experienced on grasses of great adaptivity and not on less tolerant tree and shrub species which account for 75% of the serpentine flora of Cuba.

## 13.4 Stages of serpentine flora development and the controlling factors

Studying the old and richest serpentine flora of East Cuba we consider the following stages of the flora evolution to be the most probable, if we take as an example a simple case where the tropical climate has evenly distributed precipitation and it does not change in the course of soil evolution.

a) The low Ca/Mg ratio and Mg toxic effect The CaO content of primary serpentine rendzina soils may range between 3-8%, the MgO content 10-40%and the Ca/Mg ratio may vary between 0.01 and 0.5. Since these soils are rather poor in nutrients, mainly in phosphorus and the habitat warms up to some extent due to the open vegetation and strong insolation, the plants have to transfer large amounts of water, which makes the uptake of Mg salts unavoidable, in order to take up sufficient nutrients and water for transpiration. As Mg is a poison detrimentally influencing the metabolism of the cell, and the environment does not have sufficient Ca reserves to counteract this, the serpentine plants have to develop an internal mechanism to neutralize Mg, to eliminate it from the metabolism and to accumulate it. The plants colonizing primary serpentine soils are actually shocked by this over-abundant Mg, to which they cannot get adapted, and are either killed or forced to change the biotype. In the development of serpentine flora this has to be regarded as the decisive factor since the number and frequency of endemic elements are the highest in these pioneer evergreen shrubs (see Table 10). It should be noted that the ubiquitous, edaphically indifferent plants are rarely able to survive on pioneer serpentine habitats. For these plants the secondary pioneer habitats resulting from degradation are suitable sites for colonizing as seen in Cuba, in the case of Dichrostachys cinerea, Rhynchelytrum roseum etc.

**b)** In the further development of serpentine soils – siallitization then latosolization – Ca and Mg gradually become leached from the upper levels, the SiO<sub>2</sub> content drops steeply and the soil turns acid. The montmorillonite type of clay minerals is exchanged by kaolinite type and in the adsorption complex  $Al_2O_3$  becomes predominant. Instead of the Mg toxicity, Al toxicity becomes the most dangerous. It is easy to realize that the siallitic, ferrallitic and allitic-ferritic soils formed in this way have completely different ecological features than those to which the serpentine flora was adapted in the first stage of speciation. Soil development therefore necessarily induces newer flora development in the form of a slow differentiation. Largely, the pioneer serpentine flora developed earlier provides the genetic basis, but the plants of neighbouring acid areas (quartz-allitic soils,

yellow montane soils) may also be important. For these leaching process of the surfaces went into effect faster than the adaptation of the serpentine flora. The semi-dry sclerophyllous rainforest flora prevailing on such areas is relatively poor in endemic species compared to pioneer shrubs but it is enriched in fresh genetic material which may serve as a newer starting point of flora development for the next phase of soil evolution, e.g. *Talauma minor* ssp. *minor*  $\rightarrow$  ssp. *oblongifolia*, *Cyrilla racemiflora*  $\rightarrow$  *C. cubensis*,  $\rightarrow$  *C. nipensis* and *Ilex macfadyenii*  $\rightarrow$  *I. moana*, etc.

c) Effect of heavy metals In the last phase or latosolization, as a consequence of vigorous leaching of SiO<sub>2</sub> and Al<sub>2</sub>O<sub>3</sub>, ferritic latosols form which accumulate considerable amounts of Fe<sub>2</sub>O<sub>3</sub>, Ni, Mn and Cr oxides, reaching as much as 60-70% Fe<sub>2</sub>O<sub>3</sub> and 1.1-1.6% Ni content. Undoubtedly, the enrichment of latosols with heavy metals has an added ecological shocking effect on the plants even if the concentration change is not as sudden and intensive as in the primary serpentine soils. Since the latosols are extremely poor in exchangeable bases (in the Nipe clay 1.1%, Bennett and Allison 1928) the uptake, accumulation and neutralization of heavy metal ions in the course of water and nutrient uptake are unavoidable, thus another wave of adaptation is invoked. This process may be well assessed by the fact that the frequency of endemic species in the pine forests prevailing on latosols shows a rising tendency compared to the vegetation type of the previous stage. (Table 10).

		serpentine area		
Serpentine endemisms	Pioneer thickets (4 noda)	Semi-dry rainforests (3 noda)	Pine forests (6 noda)	Degraded pine woodland (3 noda)
Fr %	71.65%	58.29%	63.28%	46.67%

Table 10 Frequency values of the endemic species in different stages of a successional series old serpentine area

Since the latosols are several million years old they may be just as suitable for the evolution of paleoendemics and the survival of relicts (e.g. *Shafera, Koehneola, Feddea, Dracaena cubensis*) as the pioneer habitats rich in Mg. In this sense Rune's (1953) findings on holarctic heavy metal soils were right in that heavy metal soils primarily induce the formation of neoendemics. However, paleoendemisms could arise in large numbers in the tropical belt if there is a much longer process of flora development on heavy metal soils, which was not possible in the north temperate belt due to the glacials.

#### 13.4.1 Serpentines and competition

Studying competition conditions it appears that competition is the least intensive on ferritic latosols. The different anthropic effects influencing the pine forests lead to invasion by weeds and a drop in the number of endemic taxa.

#### 13.4.2 Genetic drift in the evolution of serpentine floras

It should be pointed out that in the development of the serpentine flora, at least under tropical conditions, the exhaustion of biotype is only the first step to the isolation of serpentine endemics. In the further evolution of flora, genetic drift plays an essentially greater role in developing species richness by diversification of the isolated endemics. Since most species are represented by small and strongly dispersed populations pollinated by insects, there is a great chance that the newly derived characteristics become dispersed and isolated. This is indicated also by the fact that in the Nipe mountains every valley has its own florula with different local endemics of the genera *Tabebuia, Gochnatia* and *Leucocroton*. In Moa the different highplains and peaks have their own florula with a number of vicarious *Cordia, Ilex, Buxus* and *Phyllanthus* species.

## 13.5 Serpentines and vegetation

Whittaker (1954) compared the effects of serpentine rocks on vegetation with those of diorite under similar climatic conditions. He found the following.

#### 13.5.1 Characteristic features of serpentine vegetation

**Xeromorphism or pseudoxeromorphism.** This means that the serpentine vegetation physiognomically represents in each case a dryer degree than a vegetation type on another soil. In his opinion this is not merely the consequence of physical properties of serpentine soils, which may often be identical with those of other soils. Serpentine vegetation stands are usually open, which permits the increase of the extreme values of temperature, transpiration, and insolation. Therefore, under identical temperature conditions water loss is greater than on diorite.

**Reduced productivity.** The height and closure of serpentine vegetation and as a concomitant of this, its production is smaller than in the non-serpentine plant communities living under similar climatic conditions.

**Reduced structure.** The diminishing of the vegetation layers results in the transfer of the active surface to lower layers.

**Predisposition to certain growth forms** (Kruckeberg 1954). Grasses have an advantage over forbs, pines over deciduous trees, sclerophyllous evergreen shrubs over deciduous shrubs. Generally, the serpentines favour the vegetation types consisting of pines, evergreen shrubs and grasses.

13.5.2 Serpentines and succession

Serpentine rocks basically influence succession. It can be established that:

• Serpentines have their own succession series and climax which in all respects differ from the non-serpentine, climatic climax.

• The terminal stage of serpentine succession, let us take it as subclimax or edaphic climax vegetation, will never be equivalent to the vegetation of the surrounding, economically more valuable areas.

## 13.6 Serpentine effects on tropical vegetation

Serpentine rocks have their own succession series and edaphic climax which differ from the series developing on other bedrocks and the climatic climax in identical climates. However, there are series and noda developed on other rocks in drier climates which correspond to a given series or is a nodum of the serpentines regarding structure, physiognomy and production. This means that serpentine communities always represent a dryer degree than a community living on another rock, e.g. on limestone or diorite and in a dryer climate on a non-serpentine rock a community of a similar structural physiognomy and production, a serpentine series is equivalent to a limestone series living in a dryer climate of less than 400-500 mm annual rainfall or in a bixeric climate with 2-3 months longer dry period (Fig. 84 and 9.8.4).

The series of acid rocks poor in nutrients are closer to those of the serpentines. The series developing on slate, sandstone or white sand, which have more precipitation, is equivalent to a series of serpentines with more than 100-200 mm precipitation or a one month shorter arid period.

#### 13.6.1 Xeromorphy of serpentines and its climatic equivalence

The xeromorphy of serpentine vegetation or the degree of physiological aridity of serpentine soils can be described exactly by the deficit in precipitation or the length of the dry period.

We have to stress that, the mentioned precipitation amount does not merely express, in a theoretical sense the difference between the habitats mentioned but in reality this amount is able to compensate for the physiological dryness of serpentine habitats. This has been proved by the semi-dry sclerophyllous montane rainforests developing extrazonally in the dryer pine forest belt of the Nipe and Moa mountain regions and the wet montane rainforests occurring in the local climatic humid habitats in the semi-arid sclerophyllous rainforest belt.

With respect to the climatic equivalence and the compensating effect of the edaphic xeromorphy of serpentine plants we investigated the structure, characteristic LAI-s and the ratio of thorny plants in the plant communities of serpentine and limestone areas occurring in different climatic types. In Fig. 84 and from 17.4.2. the climatic differences existing between serpentine and limestone formations of identical structure and biomass can be seen. Studying the leaf size class frequencies expressing the xeromorphism of vegetation we found that the xeromorphism of serpentine vegetation compared to the limestone vegetation under given temperature conditions (24-27 C° annual average) is equivalent to a 500-600 mm annual

precipitation deficit. The increased xeromorphism of serpentine vegetation is evident from the frequency of thorny plants which is more greatly intensified by the drying of the climate here than in the limestone vegetation.

#### 13.6.2 Utilization of space by the serpentine vegetation

It is generally characteristic of the serpentine vegetation that space is not fully used both vertically and horizontally. Whittaker's (1954) findings on tropical vegetation cited in 13.5.1c are supplemented by the following:

- a) Compared to the climatic climax the serpentine climax vegetation is;
- -5-10 m lower,
- the number of tree layers is less by one,
- the canopy is always open,
- the active closed layer is the second one, most frequently, the shrub layer.

b) In the rainforest belt the so-called semi-dry, sclerophyllous types develop. These are called semi-dry because their climate and habitat are wet; only the physiognomy of the vegetation is xeromorphic. The characteristics of semi-dry forests are that their canopy is open and, as a consequence of this, certain layers are missing e.g., the sciophilous, shade-tolerant epiphytic layer is lacking or poor in epiphytic orchids, tree ferns; the epiphytic and epiphyllous liverworts are almost missing and the mossy ground layer is poor; both are replaced by lichens. In contrast with this, the small-leaved shrub layer composed of low trees and shrubs is rather well-developed.

## 13.6.3 Edaphic extrazonality of serpentine vegetation types

As an important conclusion we may say that because of the loose structure, xeromorphism and the reduced production of the serpentine vegetation it is an extrazonal imitation of not only a dryer but, in reality, a cooler climatic and vegetation belt. Certain types of tropical serpentine vegetation, primarily the sclerophyllous scrub forest and the hard-leaved evergreen undergrowth pine woodlands, are very closely related physiognomically to the Mediterranean macchia, chaparral and scrub formations and the Mediterranean pine woodlands.

## 13.6.4 Descending vegetation zones in serpentine mountains

The extrazonal character of serpentine vegetation is manifested more explicitly in the vertical vegetation belt arrangement. Lam (1927) and Bauman-Bodenheim (1955) found that the alpine and montane plant species are prone to settle on the lower belts in the serpentine mountains. Our observations in Cuba proved that it was not merely certain highland elements but entire vegetation belts which descended. In the serpentine highlands certain vegetation belts (in the form of their dryer variants) develop at considerably lower altitude, in Cuba at half that altitude, than in the non-serpentine mountains. Certain extremely humid vegetation zones, such as the cloud or mossy forest belt, are completely missing from the serpentine ranges. This correlation has been supported by the vertical distribution of some life-forms and growth forms as well (Fig. 130). In Table 11 the vertical distribution of the vegetation belts in two east Cuban mountain regions is shown (Fig. 55).

Table 11 Vertical distribution of the vegetation belts in two mountain regions of Cuba

Vegetation belts	Sierra Maestra andesite, limestone, sandstone	Moa serpentine, gabbro
Lowland-submontane belt	seasonal evergreen forest 100—800 m	submontane rainforest 100–400 m
Lower montane belt	humid montane rainforest 800—1600 m	semi-dry, sclerophyllous montane rainforest 400–900 m
Higher montane belt	elfin forest 1600-1900 m	
Subalpine belt	elfin thicket 1900— m	semi-dry montane thicket 900—1100 m



Fig. 55 The serpentine effect on the vertical pattern of the vegetation zones in Cuba. A: Semi-deciduous forest; A': Pine woodland; B: Submontane seasonal evergreen forest; B': Submontane rainforest; C: Montane rainforest; C': Sclerophyllous montane rainforest; D: Mossy elfin forest; E: Elfin woodland; E': Elfin thicket

#### 13.6.5 Serpentine preference of higher plants

Numerous authors have found that serpentine soils favour xero-photophilous oligotrophic elements, such as the genera *Pinus, Vaccinium, Genista, Cytisus* and many species of the *Myrtaceae, Gramineae, Cyperaceae and Caryophyllaceae* families. According to our observations, the serpentinophilous taxa, apart from those mentioned and listed in Table 6 are the following (the brackets indicate the number of taxa and percentage proportions of serpentine plants in Cuba): *Podocarpus* (4 species, 80%), *Harpalyce* (16 species, 94%), *Leucocroton* (26 species, 96%), *Buxus* (26 species, 79%), *Cyrillaceae* (12 species, 86%), *Spathelia* (8 species, 80%), *Ossaea* (27 species, 60%), *Calycogonium* (13 species, 68%), *Ilex* (16 species, 57%).

#### 13.6.6 Serpentine effect on cryptogamic flora

Serpentines have a much less effect on the differentiation of the cryptogamic flora than on that of the phanerogamic flora. In the fern flora the proportion of endemics is considerably smaller, although 30% of them are serpentine plants. Certain fern genera have a greater role in serpentine vegetation, such as *Anemia*, *Lindsaya*, *Pteridium*, *Odontosaria* and mainly hard-leaved and climber ferns. In contrast, the role of hygrophilous ferns is definitely subordinated in serpentine vegetation, for example, the epiphytic and filmy ferns are less represented.

At this stage we know little about the effect of serpentine soils on mosses in Cuba. Asiatic studies (Hattori 1955) did not find a correlation between the distribution of bryophyte species and serpentine soils. They established that acidophilous bryophytes live on serpentines and the number of endemics is relatively high but these, in the majority, are not serpentine endemics. It is likely that a similar tendency will be found in Cuba too. Table 12 presents correlation of endemics with serpentine habitats. While serpentine covers not more than 7% of the national territory of Cuba, 30% of the Cuban phanerogamous endemics are found exclusively on these areas. Among ferns 15% of the endemics live on serpentines and only 10% of the endemic mosses. At generic level, differences are even more accentuated. Phanerogamous flora is represented by 24 endemic genera and 920 species, mosses by no endemic genera and only 4 species. All of the endemic mosses are living in old serpentine areas and none on young ones.

Generally, the bryophyte flora of serpentine soils is poorer in species and continuous moss layer in serpentine vegetation rarely develops. Even in the montane rainforests, the role of epiphyllous and epiphytic bryophytes is considerably subordinated in serpentine rainforests, more so than in other non-serpentine rocks, although climate of serpentine areas may be more humid than of other ones (see Tables 13-14).

On the other hand, old serpentine areas can preserve relic elements of extremely disjunct distribution pattern from very early geologic ages. In Cuba, we consider the following serpentine liverworts as relicts: *Calypogeia venezuelana*, *Plagiochila steyermarkii* and *Syrrhopodon elongatus* (Reyes 1982).

In section 13.6.4 an important phytogeographic particularity of the serpentine is discussed, namely the descendence of the montane vegetation belts and montanesubalpine species to lower altitudinal levels. This phenomenon is clearly manifested by the distribution of a number of mosses. Table 14 shows the altitudinal range of some moss species in non-serpentine and serpentine mountains. Eleven selected moss species are listed occurring on serpentines at about half the altitude where they are found on other bedrocks. Pócs explains (Borhidi and Pócs 1985) this by the fact that on serpentines real humid rainforests developed only in the deep valleys while slopes and ridges were covered by more open sclerophyllous evergreen

	National terri	tory of Cuba	Serper	itine areas
Surface	110 92	$2 \text{ km}^2$	7 500 km	2 7%
Flora	No. of species	Flora in %	No. of species	Endemics in %
Phanerogams	6 350	100		
endemics	3 153	50	920	30
Ferns	500			
endemics	53	11	8	15
Bryophytes	723			
Mosses	386			
endemics	39	10	4	10
Hepatics	337			
endemics	cc.17	cc.5	?	?
	Endemics	on old and young s	erpentines	
	old serpent	tine areas	young ser	pentine areas
	*	in bo	th areas	
Endemic phanerogam				
genera	2:	2	2	
species	75	0	42	128
Endemic mosses				
species		4		

 Table 12 Correlation between endemic taxa and serpentine areas in different plant systematic levels (after Borhidi and Pócs 1985)

Table 13 Number of cryptogamic species occurring in serpentine and non-serpentine montane rainforests based on 10 sampling plots on an area of 0.25 ha each (after Borhidi in Borhidi and Pócs 1985)

	Non-serpentine areas Sierra Maestra	Serpentine areas Sierra de Moa
Annual average precipitation	2000-2500 mm	30005000 mm
No. of cryptogamic species	186	95
Treeferns	12	6
Herbaceous ferns	26	16
Epiphyte ferns	28	18
Mosses	75	34
Hepatics	45	21

Table 14 Altitudinal range of some mosses in Cuban serpentine and non-serpentine mountains

	Non-serpentine Sierra Maestra	Serpentine Sierra de Moa
Acroporium pungens Campylopus porphyriodietion C. saxatilis Isopterygium micans Leucobryum giganteum L. polakowskyi Mettenothamnium reptans Philonotis sphaericarpa Pogonatum tortile Schlotheimia torauata	1000 - 1900 (m) 1800 - 1950 (m) 1500 - 1800 (m) 1500 - 1800 (m) 1000 - 1800 (m) 1100 - 1950 (m) 1200 - 1950 (m) 1600 - 1900 (m) 1000 - 1200 (m) 1500 - 1800 (m)	300-470 (m) 600-800 (m) 200-470 (m) 500-800 (m) 600-900 (m) 700-800 (m) 600-800 (m) 400-600 (m) 200-800 (m)
Syrrhopodon tenuifolius	1700–1950 (m)	500-700 (m)

forests or shrub forests conditioned by nutrient-poor and drier serpentine soils. In these communities real hygrophylous rainforest species rarely occur, they are replaced mostly by xero-tolerant elements. Many of them are elements of the elfin forests and thickets of subparamo-character originating from the higher belts, and have been preserved as relics in the lower altitudes. Table 15 contains some species occurring in the Andes and on other Antillean islands between 2000-3000 m, while in Cuba they live as isolated relics at much lower altitudes and only on serpentine bedrock.

Table 15 Altitudinal distribution of some moss specie	s in Latin America (after Pócs in Borhidi and Pócs)
1985	5)
	·

	Antilles + Andes	Cuba only on serpentine
Leskeodon andicola	2000 m →	400— 500 m
Plagiochila stayermarkii	2200 m	1000–1100 m
Drepanolejeunea suchaeta	1000–2500 m	900–1100 m
Leptoscyphus cuneifolius	~ 3000 m	800—1100 m
Calypogeia venezuelana	~ 2000 m	400—1000 m

#### 13.6.7 Serpentine and sclerophyllous vegetation

It is to be stressed that the serpentine rock in tropical climate primarily favours sclerophyllous shrubs and small trees. It can largely be explained by the serpentine effect that 46% of the endemic flora of Cuba is made up of these two life-forms. The role of grasses and sedges is much smaller in the tropical serpentine areas than in the temperate belt. They are commonly abundant mainly in the herb layer of the pine forests and in secondary pine woodlands and dwarf palm savannas. Generally, the extremes of seasonal tropical climates and the compactness of ferritic soils favour their spread. Under tropical conditions they may become dominant only as a consequence of human effects.

## 13.7 Xeromorphy as a general adaptive syndrome of vegetation

On the basis of the above observations and the large number of contradictory findings on xeromorphism we came to the conclusion that although xeromorphism may be attributed to extremely heterogeneous ecological and physiological factors, it may be interpreted only in one way. Xeromorphism can be conceived as a general response of plants to different environmental stresses. It is a general adaptation syndrome, a sort of stress mechanism, which results from an adaptation to different deficiency shocks of the habitat and becomes fixed genetically and morphologically in the plants, and then appears after a long time as a uniform feature in the physiognomy of vegetation.

Vales expressed that in the serpentine plants outer morphological features of xeromorphy are not fully accompanied by inner anatomical characteristics provoked by dry habitat. In many cases (e.g. *Myricashaferi, Bucida ophiticola, Neomazaea phialanthoides*) tissue structure and elements of the vasoductor system show a combination of xeromorphic and mesomorphic anatomical features. Therefore he named this special adaptation form of the serpentine plants as "pseudoxeromorphism" (Vales *et al.* 1982, Carreras and Vales 1986): In some cases the xeromorphic character of serpentine vegetation does not reflect the really existing drought of the habitat but the deficiency of soil in nutrients and indispensable micro-elements, etc. For this reason, xeromorphy of serpentine vegetation can be considered also as "peinomorphy", i.e., a general plant response to the hunger-stress of the habitat at a vegetation level.

## 14 Relation of soil and vegetation development

As indicated earlier, the processes of soil evolution may vary considerably depending on the quality of rocks, the duration of the process and its speed. Eiten (1972) distinguished 9 different soil development series in the Cerrado zone of Brazil, just on the basis of the initial and final phase under identical relief and climatic conditions. In Cuba, we have to count on at least 6 different pedological large series. Of these, we studied the most widespread and studied limestone series and the succession of its vegetation. For the correct interpretation of soil genetic processes we followed Zonn (1958), Zonn *et al.* (1966) and Maul (1973). For characterizing the different soil types the works of Bennett and Allison (1928), Klimes-Szmik in Zonn (1975), Klimes-Szmik *et al.* (1980) and Ascanio *et al.* (1968) were used in addition. The observations on the succession of vegetation types and vegetation-soil relationships during their co-evolution came from the author's field studies. The biomass values of vegetation types were estimated based on structural data according to Basilevich *et al.* (1969).

### 14.1 Climatic pattern

The relationships between soil and vegetation during their coevolution are shown by the simplified scheme in Fig. 56. Here, the complex succession of a lowland limestone region is depicted in the case when the annual mean temperature of the climate is 25 °C and the evenly distributed annual precipitation is 1400-1800 mm with short, moderately dry periods of 1-2 months and in the course of succession it does not change.

#### 14.2 Soil succession

A total of five stages of siallitization and latosolization, which are the main phases of soil evolution, are shown in the diagram. Each of these stages represents a large soil type group: the primary rendzina-like humus carbonate soils, typical tropical carbonate soils, siallitic soils, ferrallitic soils and ferritic soils. The transitional ferritic-allitic and allitic-ferritic soil types formed during the latosolization are disregarded due to the small number of data.

#### 14.2.1 Change of soil features during succession

The two diagrams at the bottom of Fig. 56 illustrate the changes in the adsorption complex in the course of soil succession.

It can be seen that the maturation process of tropical soils is a kind of podsolization whose essence is the leaching of the initially dominant  $SiO_2$  and a simultaneous decline in the  $SiO_2/R_2O_3$  ratio. The limit between siallitization and latosolization processes is set by about 50% of  $SiO_2$  content and where the ratio  $SiO_2/R_2O_3$  is about 2. Simultaneously with the above process, in the course of siallitization the relative amount of  $Al_2O_3$  and the  $Al_2O_3/Fe_2O_3$  molecular equivalent ratio gradually increase and reach their maximum in the ferrallitic soils. During the ferritization process, which is the second phase of latosolization,  $Al_2O_3$  becomes washed out from the soil together with  $SiO_2$  and its amount decreases rapidly. Parallel with this, the relative  $Fe_2O_3$  amount grows continuously; first rather slowly in the phase of siallitization, while in the second phase of latosolization it suddenly rises and thus  $Fe_2O_3$  becomes predominant in the ferritic soils. Its increase results in a decline of the adsorption capacity, thereby implying the re-mineralization of the soil, the regression to rock form.

#### 14.3 Change of vegetation types during succession

In the upper section of the diagram of Fig. 56 the structure profile of each vegetation type is shown. The curves below it show the height of the upper layer and the average biomass values, obtained by extrapolation, for the different vegetation noda.

a) On the rendzina-like humus carbonate soils an evergreen shrub vegetation of 5-6 m height develops in a mosaic-like pattern of scattered individuals of small



Fig. 56 Scheme of the succession of the tropical soils and vegetation types

trees and small grassy patches (scrub woodland). Its biomass could be around  $2000-5000 \text{ t/km}^2$ .

b) On the typical carbonate soils small-leaved evergreen shrub forests grow with a 12-18 m high canopy. Its biomass is estimated to be about  $6000-12\ 000\ t/km^2$ .

c) On siallitic soils, under given climatic conditions, mesophilous evergreen forests or seasonal rainforests may develop with a canopy of 20-28 m height with emerging giant trees; the biomass may surpass 16 000 t/km<sup>2</sup>.

d) On ferrallitic or latosolic soils we can find the most developed vegetation type of the highest production, the real lowland-submontane rainforests whose height in Cuba varies between 30-40 m. Their biomass is probably more than 20 000 t/km<sup>2</sup>.

e) On ferritic soils we may find vegetation types of much less organized structure and lower production: 15-25 m high pine forests and pine woodlands whose biomass is  $9000-15\ 000\ t/km^2$  at most.

#### 14.4 Soil-vegetation relationships

We may read the following relationships from the diagram of Fig. 56.

Of the soil types formed in the course of soil development the ferrallitic or latosolic tropical red soils may be regarded as the most fertile if  $SiO_2/Al_2O_3 = 1$  and  $Al_2O_3/Fe_2O_3 = 1.5-2.0$ .

On these soils grow the most productive natural ecosystems and the yield of crops (e.g. sugar cane) is the highest here. It may be deduced from this that in the course of siallitization and in the early phase of latosolization the fertility of soil increases. In the terminal phase, however, on natural ferritic laterites the fertility suddenly drops. If we compare the curve of the plant biomass with the change in the elements of the adsorption complex we may conclude that the fertility and production of the vegetation within the given tropical soil series vary proportionally to the relative quantity of  $Al_2O_3$ . The two curves imply the same trend showing a high correlation between biomass and  $Al_2O_3/Fe_2O_3$  ratio. Likewise, the importance of  $Al_2O_3$  is proved by the fact that the  $Al_2O_3/Fe_2O_3$  molecular equivalent ratio change shows a similar tendency.

#### 14.5 Some remarks on the climax concept

In connection with the diagram discussed above it would be worthwhile to give a few remarks on the climax question.

In a given soil and vegetation series, which could be of million years scale in duration, we have to consider the latosolic ferrallitic soils and the rainforests developed on these soils as climax. The siallitic soils with mesophyllous evergreen forests can be considered subclimax. The latosolic soils with the pine forests, which have less production and represent a balanced state under the given soil conditions, have to be taken as a paraclimax formation.

#### 14.5.1 Pine woodlands as paraclimax

We have to stress that the role and situation of the soil and vegetation types during succession may be quite different under other climates and, with certain minor modifications, any stage may be even a climax. Under identical temperature conditions with 600-800 mm annual precipitation and 8-9 months of aridity the rendzina-like humic carbonate soils turn into cinnamonic humus carbonate climax soils and the scrub woodland formed on them is the terminal phase of the successional series. Likewise, in the case of 800-1100 mm annual precipitation and with 6-7 dry months the typical humus carbonate soils and microphyllous evergreen forests represent the climax; the siallitic soils and the mesic evergreen forests with 1200-1600 mm precipitation in the case of 3-5 dry months may likewise become stabilized as climax. The latosols and the pine forests developed on latosols cannot in any way be regarded as climax, only as paraclimax or edaphic climax of the post-climatic phase of succession. On other soils depleted of nutrients on account of the nature of bedrock e.g., on the slate-sandstone of the San

Cayetano formation, on quartz-allitic yellow latosolic soils the coniferous forests may develop as optimal edaphic climax vegetation, the peak of a progressive succession series.

#### 14.5.2 Dry season and succession

It may be concluded from all these that the length of the successional series, i.e., the number of its stages from the pioneer stage to the climax formation on identical bedrock is inversely proportional to the length of the dry season. Under identical climates, however, the length of the series depends on the quality of the parent material, more exactly on, the nutrient content of soils and on the capacity of the adsorption complex.

#### 14.5.3 Climax ecosystem concept

Regarding climax, it seems necessary to mention that in agreement with the concept of Whittaker (1953) and Odum (1962), the climatic vegetation, that is a system in dynamic balance with the climate and soil and endeavouring to maximize its resources, is in a relative stable state. In this self-regulating energy and matter cycling system vegetation has to be considered as the basic compartment for the energy uptake and primary production. Its structural and production stability is maintained at a certain high level by the dynamic balance of the populations.

#### 14.5.4 Monoclimax or polyclimax

In my experience every version of monoclimax theory, even the climax-group theory (Tüxen and Diemont 1937), which appears to be acceptable in the temperate climatic belts, is unacceptable for tropical conditions. In identical climates different successional series develop conditioned by different bedrocks. The convergence of these series however, even at formation level, does not lead to the climax of identical structure and production. Therefore, several edaphic climaxes of different structure and composition may develop under the same climate in the areas of different geological substrate (limestone, serpentine, slate, sandstone, granite, diorite, quartz sand, etc.) which all have the characteristics of the climax ecosystem on their sites. Among these edaphically modified climaxes there is a climax of highly organized structure and maximal production which, using Clement's term (1936), can be considered as an optimal or climatic climax. In most cases, as in Cuba also, this climatic climax corresponds to the climax developing on limestone.

#### 14.5.5 Non-seral factors

I consider all vegetation types to be excluded from the climax concept whose existence is conditioned by edaphic factors of non-bedrock character and by other environmental limiting effects (high water table, shallow hardpan, salt spray, erosion, human influences, etc.) which are able to stabilize the early stages of succession. In this sense I do not accept the concept of the "natural edaphic savanna climax" (Beard 1943) which will be discussed at length in the following.

## 15 Nature and origin of savannas in Cuba

## 15.1 Short historical survey

The literature on the origin of the ecological causes for the existence of savannas comprises divergent and contradictory views. The contradictions can be deduced partly from the inconsistent nomenclature, namely from the term savanna which has been interpreted in various ways. Geographers, pedologists, botanists and ecologists interpret this term in different and sometimes incorrect ways, as the numerous examples by Beard (1953), Walter (1962, 1970a) and others have shown. Furthermore, contradictions stem from the fact that studies discussing the ecological causes of the origin of savannas on the whole disregard the obvious possibility that the xero-mesophyllous tropical tree- and treeless grasslands, called savannas, originate from different vegetation types and are influenced by ecological causes in different ways. Thus, researchers consider the climate, others the bedrock, still others the different soil properties and many consider the fire, grazing and other human interventions to be responsible for the formation of savannas.

#### 15.1.1 Climatic grassland concept

Special soil conditions and seasonally dry climate are attributed to the formation of savannas in Warming's (1892) opinion. This kind of climate is suitable for forest formation, too. However, he rejects the theory as "completely unpermittable" which claims that savannas are caused by cutting and burning of forest areas. Schimper (1898), however, considered savannas to be climatic formations. He qualified the climate of the Venezuelan "llanos" as antiforestal and entirely rainless because of the 5 dry months. Later, under his influence, Warming (1909) thought that the cause for savannas was to be found in dry seasons and did not mention the soil. Schimper's opinion was criticized by Troll (1935). Later, Walter (1962: 254-255) demonstrated that there are zonal savannas in dry regions with less than 500 mm annual rainfall on fine textured alluvial soils and not rocky or gravelly soils. Warming and Graebner (1918) referred to savannas as tropical grassland regions of rainy summers and dry winters which could have been treeless partly for geological, partly for climatic reasons. Havek (1926) approached the question also from a climatic aspect. He considered the savannas to have developed on dry tropical regions where the rainy season coincides with the vegetative period of grasses.

#### 15.1.2 Low nutrient level concept

The main cause of savanna formation was considered by Pulle (1906, 1936), Lanjouw (1936) and Hardy (1945) to be in the leaching of soils. On such nutrient deficient soils only low loosely structured forests can occur which are prone to catching fire in the dry season and turn into a savanna. Ijzerman (1931) exposes that savannas must have been created by pedological factors because the climate of savannas does not differ in any way from that of surrounding forest areas. Jones (1930) and Waibel (1948) found that on certain geological formations particularly poor soils develop on which only savanna vegetation can survive; namely that the existence of the savannas is to be deduced purely from geological reasons. Jones found a definite correlation between sandstone and savannas as well as volcanic rocks and forests. This correlation was reinforced by Walter (1970: 84) in connection with the savannas of the Guyana plateau and the Brazilian sandstone sheath. He stressed the importance of white sand which is a primary product of sandstone decomposition and is extremely nutrient-deficient and is mainly lacking in phosphorus and trace elements.

#### 15.1.3 Drainage concept

On the basis of their soil investigations in Cuba, Bennett and Allison refuted (1928) the concept stating the geological origin of savannas. They established at first that savannas were conditioned by unfavourable drainage which generally is associated with an unpenetrable ironpan layer (mocarrero) close to the surface. As a consequence of this, the habitat in the wet season becomes swamp and in the dry season dries out like a desert, thereby making the otherwise shallow fertile layer unsuitable for forest vegetation. Likewise the "bowal", the tropical grasslands of the African forest belt has developed by reaching to the surface of the lateritic hardpan layer (Schnell 1970, 1971). The same factor was considered by Charter (1941) to be the essential cause of natural savannas in Honduras, by Hills (1969) in South America and by Beard (1944, 1953) in entire tropical America (see Hills and Randall 1968). More recently, Walter (1970: 81-83) reinforced this opinion based on his investigations carried out on the "Ilanos" of the Orinoco valley. In East-Africa, Vesey-FitzGerald (1963a, 1970) came to a similar conclusion, he considered valley grasslands only to be natural grass vegetation. Fanshave (1969) is of the same opinion with respect to the south-east African savannas.

#### 15.1.4 The fire concept

Extensive literature is available on the effect of fire on vegetation. In Africa, Busse (1908), Gradman (1916) and Obst (1923) pointed out that a large part of open grasslands appearing as climax vegetation must have been formed through fire. Bews (1929) in his great work found that the tropical tall grass savannas were derivates of burnt forests while the short grass savannas develop mainly in areas

with climate unsuitable for the survival of closed forests. Bouiellenne (1930) and Myers (1936) represent ambiguous standpoints. They regard the savannas of the Guyana highland to be caused by climatic drought and maintained by fire. Thus, the term fire climax was coined by Myers for savannas. Later this concept became widespread and numerous African ecologists regard a major part of the African savannas as fire climax. Although it has been shown that in certain regions, e.g., Africa, the atmospheric electric activity is especially high, Komarek Snr. (1971) excellent article indicates that this factor should not be overestimated. According to Penzhorn (in Komarek Snr. 1971), between 1957 and 1970 there were 29 fires each year caused by lightning. However, this is only 11% of all fire caused during the same period. Besides, it should be remembered that fires caused by lightning rarely occur repeatedly at the same area during the same period. Therefore, it appears that the role of fires caused by lightning is only decisive in critical situations, for example, in the struggle zone of the grassland-forest ecotone. In this way we can speak of real fire climax only for relatively small areas.

#### 15.1.5 Fire ecology

With respect to clarifying the ecological role of fire, Phillips' works (1930, 1931, 1938, 1965) are outstanding. He demonstrated that fire is the basic cause for creating African grasslands and for destroying the original forest vegetation. He pointed out the economic advantages of applying fire control and the terrible destruction caused by irresponsible burning. On his initiative a scientific network was devised which endeavours to determine by experimentation the scientific ecological bases of the economic use of fire. Of these, Charter and Keay's (1960) comparative investigations are regarded as pioneering with respect to early burning, late burning and protected grassland sites. Several researchers in their works have been reporting the effect of many kinds of treatments in similar experiments (Trapnell 1958, West 1965, 1971, Glover 1968, Innes 1971, Rensburg 1971, Kennan 1971, van Wyk 1971, Scott 1971). They found that the so-called early burning carried out at the beginning of the dry season does less damage to the ecosystem, protects the trees more, including the fire-sensitive species and the zooedaphon, too. This relatively "cool" fire applied regularly leads to the development of savanna woodlands or parklands. In contrast with this, the so-called late burning at the end of the dry season results in hot and intensive fires and regular application of these promotes treeless grasslands with sparsely scattered tree groups. All this is true only for areas where burning is not accompanied by intensive grazing.

#### 15.1.6 Holocenotic concept

Lately, other authors (Cole 1960, Eden 1964, Hills 1965, 1969, Goodland 1970, Monasterio 1971, Monasterio and Sarmiento 1971, Eiten 1972) refer to the interaction and concurrence of several factors in the origin and maintenance of

savanna ecosystems. Some may be simply conditioning or predisposing factors, others may be necessary but not sufficient determinants while others may be important in the genesis of the ecosystem but not in its maintenance. Since this concept includes a set of simultaneous and/or successive agents, it is called holocenotic by Sarmiento and Monasterio.

#### 15.1.7 Anthropic grassland concept

We saw above that ecologists consider fire to be the fundamental cause for the occurrence of grassland also for their maintenance. It would be an illusion to say that savannas are brought about by climatic fires. Christoffel (in Aguerrevere et al. 1939) showed that in the Guyana highland the Indian aborigines destroyed forests by burning as early as  $8-10\ 000$  years ago. Clark (1959), on the basis of the radiocarbon dating, found that man used fire more than 53 000 years earlier in Zambia and Tanzania. Bantu tribes keeping cattle in the first century used fires to gain areas for grazing, for cultivating crops, for supplying fresh grass and for charcoal burning which they used for melting iron. Fire thus became a vegetation modifying means in man's hands and the formation of large grassland areas is above all a result of human activity of combining fire and grazing. While in the neotropics the destruction of forests became extensive especially after the discovery of America, but in Africa, which looks back at a much longer cultural history (Richards 1973), anthropic savannization or desertification (Aubréville 1949) is in a much more advanced state than in the tropics of other continents. In the last decades more studies dealing with the anthropogenic origin of savannas have appeared (Johannenssen 1963, Taylor 1963, Puig 1972). The anthropogenic origin of savannas for Africa was demonstrated by Phillips (1930), Scott (1934), Burtt (1942), Thomas (1946), Aubréville (1947, 1949), Welch (1960), Cole (1963), Hopkins (1965a, b), Trapnell and Langdale-Brown (1971), Lind and Morrison (1974), for Laos by Vidal (1960), for Vietnam by Jeanplong (1968) and Pócs (personal communication). Central and South American savannas were likewise qualified as anthropic ones (Budowski 1956a, b, Aubréville 1965a). Of the latter, Blydenstein (1962, 1963), Vareschi (1960, 1962) and Tamayo (1961, 1962) proved their anthropic origin. The south Brazilian savannas of the Cerrado zone were also considered by Rawitscher (1948) and Cole (1960) as of anthropic origin.

## 15.2 Cuban grasslands. Bennett's concept

In Cuba, ecological research on savannas was commenced by Bennett and Allison (1928) and their findings are reported in 15.1.3. These, in theory, were basically correct and the cited authors strove to use the vegetation as an indicator and to maintain that the savanna should not be determined simply from pedological or geographical aspects but in correlation with the vegetation. So, those soils in which there was a compact water locking layer at 25-35 cm and where grasses and

herbaceous plants prevailed, the Esmeralda, Estrella and Mocarrero soils (altogether 15 soil types) were classified as natural savanna soils. This would have meant that almost one third of the area of Cuba was covered by natural savannas.

#### 15.2.1 The influence of Bennett's concept

Bennett and Allison were outstanding soil scientists but they did not have the necessary botanical and ecological experience to be able to recognize the often hardly conspicuous difference between the natural and secondary savannas. Their authority and the thoroughness of their pedological study influenced greatly the view of the botanists, based on their suggestions León (1946), León and Marie-Victorin (1942, 1944), Seifriz (1943), Carabia (1945b) and later Beard (1953) and Knapp (1965) considered the grassland areas with scattered palms and pines in Cuba as original natural savannas. Carabia (1945) even considered the secondary grassland formed on the site of the cut and burnt pine forests of the Nipe highland as original montane savannas, and Beard adapted this erroneous assumption (1953).

#### 15.2.2 Seifriz's interpretation

Seifriz's study should be particularly mentioned as it is regarded in the literature as the only comprehensive work on Cuban vegetation using an "ecological approach" and which most authors take as the basic source. Seifriz's study has really a geographical view and not an ecological one. During his brief stay in Cuba he could only have got an impression of the vegetation and he probably did not have a comprehensive knowledge of the flora. Thus, his observations are superficial and often faulty. His finding that the most important feature of the Cuban landscape was that it is a savanna, gives the impressions of a traveller. However, his statement is erroneous from an ecological point of view. He mentions, however, that the royal palm savannas probably came about anthropically from some kind of forest vegetation, but the grasslands growing on sandstone and serpentine were definitely considered by him as original savannas. He lists more than twenty-five palm species characteristic for savannas whereas more than half of these does not occur in grassland areas at all but are species of scrubs and shrub forests. The savannas are discussed by him according to the administrative provinces disregarding their ecology, physiognomy, floristic composition and origin. So, Seifriz's savannas are rather heterogeneous even at formation level and in his species lists the most divergently occurring species are listed together.

#### 15.2.3 Anthropogenic savanna concept in Cuba

The anthropogenic origin of Cuban savannas has hardly been mentioned until recently. Muñiz (1959) reports the tremendous destruction of lowland forests but he regards 25% of the country to consist of natural savannas.

Numerous Cuban botanists are of the opinion (Acuña, Muñiz, pers. comm.) that Cuba originally was a forest region but special studies on this have not been carried out. Waibel (1943) tried to reconstruct the original vegetation on the basis of the names of Cuban localities but he was not successful because the word savanna in Cuba is used in rather varied interpretations (Samek and Duek 1967). For example, the Sabana village in the Baracoa region is still surrounded by original seasonal rainforests.

## 15.3 The savanna concept of Beard

Beard's (1953) comprehensive study summarized the characteristics of savannas as follows:

a) Savanna is a more or less xeromorphic grassland vegetation conditioned by the unfavourable water economy of the natural soil developed in the old eroded land forms. Its life pattern is controlled by regular alternation of flooded and dry periods.

b) Savannas occur in extremely different climates ranging from a 500 mm of annual precipitation and 7-8 dry months to 2500 mm of annual precipitation and negligibly short dry period.

c) The lowland climates of tropical America are suitable everywhere for growing some kind of forest vegetation. Savanna climate does not exist.

d) All savanna types may be regularly damaged by fire and vegetation is adapted to it. Grassland vegetation however, is not maintained by fire but by the soil and habitat as an edaphic climax.

Beard's basically correct findings need a few comments and modifications.

a) It may be debated that natural savannas would be restricted to edaphic, poorly drained though climazonal savannas also exist (Walter 1962).

b) It is not particularly appropriate to consider drainage savannas as edaphic climax. Only Walter's climax savanna can be regarded as edaphic climax because it is conditioned climatically on certain fine grained sedimentary soil types. There it is replaced equivalently by the semi-desert shrub or shrub forest vegetation in other rocks. The drainage savanna can only perhaps be regarded as a paraclimax where it has attained a senescent stage of soil development occurring in over-mature soils. On the whole, however, the natural savannas are edaphically stabilized pre- or subclimax associations and cannot be considered as climax vegetation.

c) Generally, it can be accepted that soils with impermeable layer formed near the surface favour the development of savanna vegetation, but two important aspects were not noticed by Beard. The mocarrero or hardpan soils are not a necessary condition for the formation of savannas. For example, on the latosols of Oriente highlands we can find numerous ironpan outcrops covered by scrub, shrub forest or semi-dry rainforest vegetation or even closed pine forests and only the anthropogenic effects may turn them into savannas. Guerra (1953) studied original lowland rainforests growing in the Amazons on 10 inch (25.4 cm) deep soil with a 1 m thick laterite hardpan layer underneath. Eiten (1972) studied the effect of laterite ironpans on the vegetation of the cerrado zone and found scrub woodland vegetation on them in 90% of the cases.

d) Beard failed to take into account that cutting and burning of vegetation effectuate radical changes not only in the vegetation but in the soil, too. In fact these operations promote the formation of impermeable layers and their thickening and the erosion and thinning of the permeable layer. Samek (1969), in the course of vegetation mapping in the Isle of Pines, came to the conclusion that a major part of the actual natural-like drainage savanna areas was covered originally by mesophyllous tropical forests which are able to balance the water table fluctuation of dry and wet seasons by their own water utilization, by shading of the soil, reducing the transpiration of the soil, and regulating the trend of soil moisture changes. After destroying the forests the fluctuation of ground water table extremely increases in the wet season due to the insufficient utilization of water surplus and in the dry season on account of the extreme evaporation loss, these movements could considerably accelerate the process of ironpan formation. Soil degradation can be intensified by wind erosion of the unprotected upper soil level that desiccates in the dry season. This process eventually leads to the loss of the permeable soil layer. In this way not only the secondary sayannas are anthropogenic but often the habitats of natural-like savannas are also products of anthropic influences.

e) It can be misleading to over-estimate the soil conditions with respect to the nature of savannas as well as the inaccurate interpretation of vegetation and certain life-forms. Many authors call shrub forests and scrub vegetation as savannas just because the patchy herbaceous layer is also present. León's (1946) serpentine savanna, for example, in reality is a scrub or shrubwoodland (Grudzinskaya 1975).

f) It is an unfortunate misbelief of Beard that palms rarely exist together with broad-leaved trees and that the fan palms are mainly typical savanna elements. All of the nearly 100 palm species in Cuba live also in closed forests or shrub vegetation and, in fact, half of the species do not occur in open grasslands (Borhidi *et al.* 1979). Palms are esteemed useful plants that are carefully preserved when forest and scrubs are cut. Most palms tolerate fire well and the early burning used widely in Cuba favours their spread. So, they can easily adapt to grassland conditions. However, this does not mean that savannas can be regarded as natural or original just because of the presence of palms.

#### 15.3.1 Vesey-FitzGerald's grassland classification

Vesey-FitzGerald (1963, 1971), in the course of studying east African grasslands, distinguished three main categories:

1. Natural grasslands are under edaphic or climatic control. They occur prevalently where the drainage or under soil drainage is impeded or seasonal. Swamps, bogs, river valleys, flood plains and other sites in the lower part of the catena are characteristic of their distribution (Vesey-FitzGerald 1970). Seasonally arid flat plains with shallow soils also support natural grasslands. The component species and associations are relatively few and often exhibit a zonal or mosaic form of distribution. The composition and state of natural grasslands may be modified by fire, but fire exclusion will not cause the grassland formation to be replaced by a woody formation. 2. Secondary grasslands are seral. The majority are induced and maintained by fire. In the place where fire is eliminated the course of succession proceeds to a woody sere. A large variety of species occurs, and they tend to have a random distribution. However, in certain circumstances, where a degree of stability is established, a few species may occur as dominants or co-dominants.

3. Derived grasslands are a special type of secondary grasslands. They more or less permanently replace a previously existing type of vegetation as a result of attendant changes occurring in the environment at the time when the original vegetation was replaced. They may conform to the catena, because the original vegetation did so. They may also alternate with relict stands of the preexisting vegetation. Examples are the upland and montane grasslands. Derived grasslands are frequently maintained by grazing if there is an animal community available to occupy them.

## 15.4 Physiognomic types and genesis of Cuban grasslands

One of the main objectives of our vegetation mapping project was to distinguish between natural and secondary savannas and to theoretically reconstruct the latter. The potential productivity of cultivated lands can only be estimated objectively based on the original climax vegetation. For land use plans it is extremely important to know whether a savanna of 4000 t/km<sup>2</sup> biomass, or a forest of 15 000 t/km<sup>2</sup> should be considered, i.e., the distinction between the actual and the potential is essential. In addition to the "landscape surveys" and the "soil studies" carried out by the mentioned authors cited above, our interest was focused on the exploration of intact forest and shrubwood patches and on a comparative phytosociological and floristic analysis of lignosa communities and savannas.

The bioclimatic map of Cuba (Borhidi 1974, Borhidi and Muñiz 1980, 1984) clearly shows that on the lowlands and hilly regions of Cuba a seasonal tropical climate prevails along the whole island which is considered as savanna climate. Although actually only 8% of the national territory of Cuba is covered by natural forests, most of the authors considered (Bennett and Allison 1928, Seifriz 1943, Marie-Victorin and León 1942, 1944, Carabia 1945, León 1946, Beard 1953, Knapp 1965) that originally 25-50% of Cuba was covered by natural grasslands. But when we mapped the natural vegetation and studied its correlation to the clima tic and soil types we found that the country must have been fundamentally a natural forest land and not more than 5-8% of the Cuban territory would have been covered by natural grasslands (Borhidi 1973, 1976, Borhidi and Herrera 1977, Borhidi and Muñiz 1980, 1984).

Almost all the actually existing grasslands of Cuba have developed under a long-term human impact of combined logging/cutting-burning-grazing patterns, (Figs 57-59).



Fig. 57 Recently logged plot of a seasonal evergreen forest stand (in the background) with remaining royal palms

#### 15.4.1 The physiognomic types of Cuban savannas

A classification of the Cuban savannas based on physiognomic criteria was developed by Borhidi and Herrera (1977). The following units of savanna vegetation were distinguished:

#### A) Tall grasslands with tall palms

- a) Royal palm-cotton tree savannas
- b) Royal palm savannas
- c) Copernicia savannas
- d) Sabal savannas
- B) Short grass savannas
  - a) Dwarf palm savannas on serpentine with *Coccothrinax* and low *Copernicia* palms
  - b) Savannas with pines and Colpothrinax palms
- C) Sedge-savannas
  - a) Humid savannas with Sabal and Acoelorrhaphe palms
  - b) Seasonally flooded savannas with broad-leaved trees
- D) Treeless grasslands

#### 15.4.2 Genesis and savannization processes of Cuban grasslands

The Royal-palm savannas are without exception secondary savannas derived from different forest vegetation types.

Roystonea-Ceiba-Samanea savannas are derivatives of seasonal tropical evergreen forests living on fertile red ferrallitic soils (Fig. 57). All stages of their evolution processes have been studied by us in the Guanahacabibes Peninsula where the forest was cut with bulldozers in 1954-1955 and where the royal palms and cotton trees were left only. Then, the area was burnt several times and grazed. In this way the characteristic Roystonea-Ceiba savanna of the Cuban landscape developed in a few years (Figs 58-59). As of 1959, however, after the revolution and the redistribution of lands, burning and grazing stopped on one part of the area and the return of shrubs and forest trees began from the forest edge where every stage of a spontaneous reforestation process from the appearance of the first shrubs to the closure of the shrub layer can be observed, the scattered appearance of pioneer low trees, later their collective penetration, to the formation of forest clumps around the tall left trees could be observed on a 3-5 km wide strip.

Cases of savannization processes were studied in seven different habitats.

#### a) Royal-palm savannas

In the seasonal evergreen lowland forest belt on fertile deep ferrallitic red soils (Matanzas clay), after having logged the valuable timber trees—as *Swietenia*, *Cedrela*, *Hibiscus elatus*, *Calophyllum*—a *Roystonea–Ceiba* woodland develops which is converted into a *Roystonea–Ceiba* tall grassland by repeated burning and into a pasture by an intensive grazing combined with burning (Fig. 60).



Fig. 58 Royal palm savanna on deep fertile red latosolic soil after cutting, burning and grazing of the area at the foot of the Cubitas range, north of Camagüey (Photo: A. Borhidi)



*Fig. 59* Giant *Ceiba* tree a remainder of the original seasonal evergreen lowland forests of Cuba at Perico, Matanzas province. The lower branch indicates the general height of the first canopy (Photo: A. Borhidi)



Fig. 62 Redevelopment of a lowland seasonal everyreen forest from tall grass savannas

In the belt of the semi-deciduous forests a similar process went on passing through the stages of a *Roystonea–Samanea–Spondias* woodland and a *Roystonea-Samanea* tall grassland ending in a pasture with scattered *Roystonea* palms (Fig. 61).

Redevelopment patterns of the mentioned forest types were also studied. The process is going on by a frontal invasion of the colonizing species starting from the edge of the still existing forest patches and also by scattered colonizing centres developing around the left palms and trees. In the invasion of the colonizing plants N-fixing shrubs as *Cassia, Myrica, Caesalpinia, Belairia, Behaimia* and *Brya* species, further fast-growing deciduous soft-wood trees, like *Bursera, Zuelania, Casearia, Trema,* in the hilly regions *Muntingia* and *Cecropia* play a dominant role. (Fig. 62)

In the colonizing centres evergreen shrubs and deciduous trees distributed by birds, like Myrtaceae (*Eugenia*), Borraginaceae (*Cordia, Bourreria*), Spondias-species, palms, and by wind-like Compositae shrubs e.g. *Eupatorium* and Vernonia species plays an important role. Around the Ceiba trees the colonizing process usually starts by settling of royal palms distributed by both birds and mammals.

In the submontane evergreen forest belt savannization process starts with logging of timber trees,—like *Cedrela*, *Swietenia*, *Calophyllum*, *Terminalia*, *Bumelia*, *Micropholis*, *Manilkara*, *Ocotea* etc.—and a second growth forest develop dominated by fast growing soft woods,—*Cecropia peltata*, *Roystonea regia*, *Trichilia hirta*, *Spondias mombin*, *Muntingia calabura*—with a loose canopy which permit the abundant growth of tall grasses forming a rather dense herb layer. *Olyra latifolia*, *Pharus glaber*, *Pavonia fruticosa*, *Panicum glutinosum* and other forest weeds are the most common elements of this layer. After repeated burning a *Roystonea* grassland develops which is grazed intensively provoking heavy erosions and local landslides. At last the eroded bare slopes are artificially repopulated with introduced grasses, mostly with guinea grass (*Panicum maximum*) (Fig. 63).

#### b) Sabal savannas

The savannization process of the swamp forest starts by logging of timber species and fuel woods as Bucida, *Rhizophora* and *Avicennia* and *Tabebuia* species used for charcoal-burning. After logging a *Sabal* palm, swamp woodland develops and by burning and grazing it is converted into a *Sabal* wet grassland and lastly into a wet pasture with scattered *Sabal* palms (Fig. 64).

Hardpan soils or mocarrero soils are largely considered as habitats of natural grasslands. In spite of this we found that the original vegetation of these soil types was a thorny scrub-woodland consisting of endemic palms and trees. This vegetation, without having any economic value, had been very soon converted by burning into *Sabal* palm grasslands, or in eastern Cuba, into *Copernicia* palm grasslands and intensively used for pastures centuries ago. Recently these pastures are invaded by extremely aggressive alien shrubs and colonized within a few years,







*Fig. 64* Scheme of the evolutionary process of the *Sabal* wet savannas from alluvial and swamp forests in Cuba

like the African *Dichrostachys cinerea* introduced for its ornamental flowers some decades ago (Fig. 65).

#### c) Dwarf palm savannas

Savannas are more obviously expected on dry, nutrient-poor soils, e.g. in the serpentine and white sand areas, where several determinant factors listed above, as long dry period, low nutrient level, eventual fires and occasionally also deficient drainage are simultanously present. In spite of this, the original natural vegetation of these dry, nutrient-poor habitats are different woody plant communities and not grasslands.

In the serpentine areas on deep mature ferritic soils the climax vegetation as a dense pine forest of *Pinus caribaea* in West Cuba and of the *Pinus cubensis* in the east. On shallow or gravelly serpentine soils a very dense, thorny evergreen thicket is the original vegetation, which is transformed by burning and grazing into short grass savannas with scattered dwarf palms of the *Coccothrinax* and *Copernicia* genera (Fig. 66).

The degradation of the pine forests growing in ferritic soils can be seen in Fig. 67, that shows examples derived from the Cajalbana hills and the Nipe Mountains. The



*Fig.* 65 Scheme of the evolutionary process of the *Sabal* pastures and *Dichrostachys*-thicket on the mocarrero soils of Cuba



*Fig. 66* Scheme of the successional process of the serpentine pastures ("savannas") from serpentine scrub-woodland in Cuba



*Fig.* 67 Scheme of the successional process of the serpentine short grass pastures ("savannas") from the latosol pine woodland in Cuba



Fig. 68 Scheme of the evolutionary processes of the white sand savannas from pine woodland under different land use and control

originally closed pine forests after a deforestation become at first a woodland vegetation and after burning they turn into a pine *Coccothrinax* wooded grassland and lastly by overgrazing into a short grass pasture.

#### d) Savannization on white sand

In the white sand areas, in very nutrient poor acid soils the optimum of the vegetation is a pine-woodland with well-developed herb layer and scattered *Colpothrinax* palms of barrel-shaped trunk mixed into the canopy.

When palms are logged, which is uncommon in other communities and with other palms, —but *Colpothrinax* is often exploited for several uses, —a pine-dwarf palm savanna develops first and by burning and grazing, it is converted into an *Acoelorraphe* palm savanna, and at last, into a white sand pasture with scattered pines and dwarf palms (Fig. 68), as it was explained by Samek (1969).

When pine is logged as it is usually, a *Colpothrinax* woodland develops which is converted by burning into a *Colpothrinax* pasture (Fig. 68).

## 15.4.2 Phytogeographic approach of the genesis of the short grasslands of Cuba

Special attention was devoted to the serpentine savannas with short grasses and dwarf palms and to the pine savannas which the earlier authors all unequivocally regarded as natural savannas. Only Samek (1969) claimed that the pine savannas were the derivates of sandy pine forests. In these communities we used fractionated phytosociological analysis in such a way that the herb layer was sampled separately from shrubs and trees living in savannas; these samples were examined in separate chorological analyses.

We started out from the idea that:

a) In an original savanna vegetation, being a natural formation, the existing trees and shrubs had to be such species which do not occur in closed forests or shrublands.

b) Since the original plant communities of Cuba are rich in endemic species, it is to be expected that the savannas, as far as they are original, should be similarly rich in endemics, especially the serpentine savannas.



Fig. 69 Participation of the geoelements in two pine-savanna ecotones: a) Paepalantho–Pinetum on white sand and b) Pinetum tropicalis–caribeae on slate of Isle of Pine in four "serpentine savanna" communities (c) Coccothrinaci-Tabebuion lepidotae in Havanna and Mantanzas provinces, d) Rondeletio–Guettardetum clarensis in Las Villas Province e) Copernicio–Tabebuietum trachycarpae in Camagüey Province and f) Zanthoxylo Jacquinietum shaferi in Oriente Province) based on the relative cover values of species. Lined columns: forest elements, black columns: savanna elements. Abbrevia-tions: El=local endemics, Er=regional endemics, EOCu=West-Cuban endemics, EECu=East-Cuban



endemics, ETCu=Pan-Cuban endemics (occurring in the whole territory of Cuba); AM=species of the Greater Antilles, Antillean species, AB=species of the Antilles and the Bahamas, B=species of the Bahamas and Cuba, CuFU=species of Cuba. Florida and the SE States of the USA. NC=North Caribbean species, SC=South Caribbean species, C=Caribbean species. CuSA=species of Cuba and South America, NTr=Neotropical species, PTr=Pantropical species. Am=American species, Csm cosmopolitan and adventive species

c) Whittaker (1954) demonstrated that in the temperate serpentine forest associations the ratio of endemic hemicryptophytes and phanerophytes is 6:1. If we consider that the tropical flora is richer in woody plants than the flora of the temperate zone, but the savanna predominantly consists of herbs, it is to be expected that in the original savannas the ratio of the endemic herbaceous and woody plants will not be less than 1:1.

d) Finally, even by taking into consideration the more favourable dispersal characteristics of herbaceous plants (e.g. wind pollination), it is expected that in an island flora and in the original native savannas the dominant herbaceous species have smaller distribution areas and that the accidentally occurring trees and shrubs in the savanna communities should belong to the geoelements of greater distribution patterns.

## 15.4.3 Partial chorographical analysis of the pine savannas and serpentine grasslands

Our investigations were carried out on two pine savanna communities (Fig 69a-b) and 4 serpentine grassland associations (Fig 69c-f). The results of the chorological analysis are integrated in Fig. 70. The black columns show the frequency of savanna plants (mostly herbs) within the different chorological groups. The dashed lines running vertically separate the groups of the endemic elements from the Caribbean distribution groups and from those of widespread areas. It can be established that:



Fig. 70 Integrated diagram showing the participation of the geoelements in different pine woodland and serpentine scrub-savanna communities or ecotones, based on the relative cover values of the forest or scrub species (lined column) and savanna species (black column). 1. Paepalantho-Pinetum, 2. Pinetum tropicalis-caribaeae, 3. Coccothrinaci Tabebuion lepidotae, 4. Rondeletio-Guettardetum clarensis, 5. Copernicio-Tabebuietum trachycarpae, 6. Zanthoxylo-Jacquinietum shaferi, Abbreviations: End=endemics of Cuba, Car=Caribbean species, Tr=tropical and other widely distributed species

a) The shrubs, palms and trees existing in the savannas have almost without exception a major role in the forest and shrubland communities, that is, they cannot be considered as savanna elements.

b) The overwhelming majority of endemic species living in savanna communities are trees and shrubs which are alien to savannas. Among the endemic species the ratio of herbaceous to woody plants is 1:4 to 1:7 which does not prove the original character of the pine savannas and the serpentine grasslands.

c) At the same time, 80-90% of the savanna elements are herbs and shrubs of neotropic, pan-tropic and cosmopolitan distribution, a fact which especially in the case of an island flora implies the secondary character of savannas. These two features are demonstrated in the combined diagram of six plant associations (Fig. 70).

#### 15.4.4 Process of the pine savannas

The degradation of pine forests and the process of the origin of savannas on their habitats were studied in several biotopes. The typical elements of the white sand pine woodland (Fig. 71) are the dominant *Pinus tropicalis* and the populations of the palms *Colpothrinax wrightii* and *Acoelorraphe wrightii*. This is why their stands are used in several forms. If the *Colpothrinax* palms are cut together with the pines, an open Pine-*Acoelorraphe* wooded grassland develops which changes by regular burning into an *Acoelorraphe*-grassland and with grazing turns into a rather poor sandy pasture. *Byrsonima crassifolia* is a common shrub of these pastures (Fig. 72). In contrast with this in the wet valleys after cutting the *Colpothrinax* palms renew better than other trees and a *Colpothrinax* woodland develops and from this with burning a *Colpothrinax* grassland evolves which very often is overgrazed.

#### 15.4.5 Grasslands and relict serpentine shrublands

The natural original character of serpentine savannas was suggested by the fact that the primary shrubland vegetation of the serpentine areas, which have had low productivity for centuries of burning and grazing, have turned into short grass savannas. The initial and final stage of this process are demonstrated in Figs 73-74. In the serpentine regions of Camagüey and Holguin we can only find original shrubland remnants of a few hundred km in area. Their original character is reflected undoubtedly by the floristic composition, with 30-40 local endemic species and, at the same time, with the presence of all palms and shrubs of the savannas as well as many herb species.

#### 15.4.6 Conclusion and ecological classification of Cuban grasslands

Summarizing our studies on the nature of Cuban savannas we found that on the basis of the origin of grasslands we may allocate them into the following groups:



*Fig.* 71 Pine woodland of *Pinus tropicalis* in the white sand area of the southern lowland of Pinar del Rio Province, near to La Coloma, with young *Colpothrinax* and *Coccothrinax miraguama* ssp. arenicola palms (Photo: A. Borhidi)



Fig. 72 Byrsonima crassifolia (L.) HBK., a common shrub of the pine-woodlands and the secondary savannas in West Cuba (Photo: A. Borhidi)

#### Natural or original grasslands

Fire is a modifying but non-controlling factor (Vesey-FitzGerald 1963a, 1970) which can change the floristic composition but the grassland itself is not induced or maintained by it. The role of fire is mainly manifested in the flora selection and the control of nutrient cycling. It can be attributed to this selective effect that after a longer period of time the florulas and the phytosociological composition of the natural and derived grasslands may become similar and the differences between them may diminish.

#### a) Climatic grasslands

These develop under rather dry climates (Walter 1962, 1970) with 300-600 mm annual precipitation and 9-10 dry months. These ecological conditions characterize practically the semi-desert shrubland and thorn woodland belt. In contrast with this, the alluvial clays of valleys favour the development of climatic grassland vegetation.



Fig. 73 Remaining original dry evergreen serpentine scrub woodland at Cromo, north-east of Camagüey, with Copernicia hospita and many endemic shrubs (Photo: A. Borhidi)



*Fig.* 74 Secondary, overgrazed serpentine savanna with scattered *Copernicia* and *Coccothrinax* palms at the same place seven years later (Photo: A. Borhidi)

Thus, we consider them as the alternative edaphic climax of the semi-desert belt. Climatic grasslands are less widespread in America, they are mainly common in the semi-desert belt of south and south-western Africa (Walter 1968). In Cuba, they occur in the alluvial valleys of the coastal regions of South-Baracoa in very small areas (Guantanamo, San Antonio del Sur, Imias).

#### b) Edaphic grasslands

These are identical with Beard's (1953) drainage savannas and Vesey-FitzGerald's (1963a, 1970) edaphic valley grasslands. These savannas are controlled by unfavourable water drainage which in consequence of the seasonal climate creates drastic changes in water management. In Cuba, such areas of valley grasslands can be found in the valleys of the Zaza, Cauto, Yara, and Jatibonico del Sur rivers.

#### c) Swamp grasslands

They develop in constantly flooded or undrained basins mainly in the vicinity of sea coasts. Thus, in these areas in consequence of the high and low tides fresh and salt waters often mix. Swamp grasslands in Cuba in some areas become extensive (Cienaga de Zapata, Laguna del Leche, coastal area of La Fe and Los Arroyos de Mantua etc.). They are largely used for animal breeding and rice cultivation.

#### Anthropic, secondary or derived grasslands

It is characteristic for the grasslands that their origin and existence is the result of human activity. The extent of human interference and its intensity may be distinguished at three levels.

a) Semi-anthropic grasslands

It is characteristic of these grasslands that their floristic composition developed from the herbaceous flora of their own habitat or the surrounding natural plant communities. These grasslands were brought about by the less intensive and not regularly repeated human intervention (accidental burning, extensive grazing). In these grasslands the flora matches the habitat but the ecosystem does not correspond to it. They mainly occur in such areas which, although they were not grasslands originally, could potentially be converted easily into savanna even by a single drastic human intervention (Borhidi and Herrera 1977, Borhidi and Muñiz 1980). For their savannization it is sufficient to burn the plants only once or only a few times, depending on the organization level of the vegetation. In the sites of such grassland originally there were dry shrublands, thorny woodlands, pine woodlands, mainly on oligotrophic soils or on hardpans of bad water management on which in consequence of the small biomass and the slow nutrient cycling they have reduced accumulative capacity and regeneration. In Cuba the hardpan areas (mocarrero), the young serpentine belts and sand regions, especially the white sand areas (Fig. 75) possess these ecological characteristics.

#### b) Anthropic or derived grasslands

These are grasslands on fertile clays of lowlands and submontane belts, collines, as well as alluvial areas flooded for only short periods of time induced and maintained by regularly repeated intensive human intervention (deforestation, burning, grazing). In the case of these grasslands neither the flora nor the ecosystem correspond to the habitat, although in the course of degradation the derived community is in direct successional connection with the flora of the original ecosystem. In Cuba, these are actually the most extensive savannas and the best examples of these are the royal palm and broad-leaved tree savannas.

#### c) Artificial grasslands

These are intentionally planned and artificially created grasslands that follow the total destruction of the earlier, even anthropic, vegetation. In this case not only the grassland flora and ecosystem are completely alien to the original habitat but there is no continuous successional connection to the previous flora and vegetation. In Cuba, these kinds of grasslands include the artificial monocultural pastures of the Guinea grass, elephant grass, Bermuda grass, *Dichanthium caricosum* and *Digitaria decumbens* etc.

#### 15.4.7 Historical and actual grassland pattern

To understand the anthropic process of savannization we studied the vegetation and examined the historical bibliography and archive materials of economic and land history (Borhidi and Herrera 1977). On the basis of these studies we tried to get approximately precise estimates on the size of grassland areas and their extent at the

	Flora		Ecosystem		Spatial pattern in Cuba cover in % of the national		
			~				
					terntory		
	frite as contro lung factor	indigenous ( anthropic ( -	adequate ( • non-adequate to the entena	Successional pattern	in original state	ın 1492	in 1976
Natural grasslands		-+	+	progressive	3-5	3-5	<1
Semi-anthropic grasslands	Ŧ	+		regressive seral	⟨2	5-7	7-10
Anthropic or derived grasslands	+			regressive seral		5-10	20-25
and cultivated belts	+			non-seral		(2	58 - 60
Total grasslands					3-6	15 - 22	90-92
Forests					94-97	78-85	8-10

Table 16 Savanna types and their distribution in Cuba



*Fig.* 75 The hypothetical distribution of the savannas of Cuba in 1492 (after Borhidi and Herrera 1977). Legend: 1. Original wet, periodically flooded tall grasslands; 2. Original marsh and swamp meadows, steadily flooded areas; 3. Easily savannizable ecosystems on nutrient poor soils; 4. Other vegetation types (forests, shrublands)



Fig. 76 The actual distribution of the savannas and the important crop fields in Cuba (after Borhidi and Herrera 1977).

time of the discovery of America, and to compare these estimates with the present state values (Table 16). In our estimation, at the time of Columbus' first landing, grasslands covered 15-20% of the whole area of the island. Of these 2-3% were natural grasslands, whereas the semi-anthropic grasslands accounted for 7% and the anthropic and derived grasslands 5-10% (see Fig. 75). Our viewpoint is in agreement with the opinion of Cuban researchers (Acuña, Muñiz) in that 95-97% of Cuba was originally covered by forests. From historical data, however, we may presume that in the pre-Columbian period the Indian cultures had brought about changes which cannot be disregarded. At present 87-90% of Cuba is a forestless land. The natural grasslands make up 1-2%, the semi-anthropic grasslands account for 7-10%, the anthropic savannas 20-25% and cultivated lands 50-60% of these areas (see Fig. 76).