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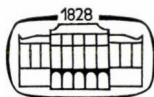
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THE PHYTOGEOGRAPHIC SURVEY OF CUBA

II. FLORISTIC RELATIONSHIPS AND PHYTOGEOGRAPHIC SUBDIVISION

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In the first part (*Acta Bot. Hung.* 31: 1-37, 1985) the main characteristics and the historical survey of the Cuban flora were discussed. The second part deals with the phytogeographical place of Cuba in the Neotropical flora and with its floristic relations to the other floras of the Greater Antilles. Authors consider Cuba as a separate phytogeographic province within the Antillean subregion of the Caribbean region. The phytogeographic province of Cuba can be subdivided into three subprovinces, nine sectors and 36 floristic districts. Each of the floristic units are characterized by describing their geographical, climatological, floristic and geobotanical features.

The geobotanical status of Cuba

Good's phytogeographic regionalization of the Caribbean

Cuba belongs to the Neotropical floristic kingdom whose phytogeographic subdivision is due to GOOD (1954) and, more recently, TAKHTADJAN (1970). According to these authors, the Neotropical kingdom has been divided into seven floristic regions and is characterized by 32 endemic plant families 10 of which occur in Cuba. These are: Marcgraviaceae, Bixaceae, Cochlospermaceae, Brunelliaceae, Picrodendraceae, Calyceraceae, Bromeliaceae, Cyclanthaceae, Heliconiaceae and Cannaceae. The Caribbean floristic region has been divided into four provinces: 1. Southern California-Mexico, 2. Caribbean, 3. Guatemala-Panama, and 4. North Colombia-North Venezuela. Cuba, as a separate subprovince, belongs to the Caribbean province.

A new proposal for the phytogeographic regionalization of the Caribbean area

In the author's opinion the above mentioned phytogeographic classification does not reflect correctly the evolutionary history and the present floristic conditions of the Caribbean. In addition, the early isolation of the Antilles and the rich endemic flora of the archipelago are not considered satisfactorily. For these reasons it seems justified to make a distinction between two equally important sub-regions, continental and Antillean, within the Caribbean floristic region and, further, to modify the regionalization as follows (see Fig. 29).

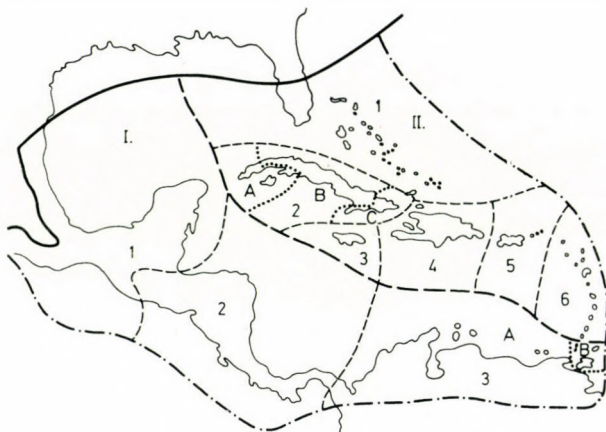


Fig. 29. Phytogeographic subdivision of the Caribbean floristic region according to BORHIDI (1973)

- I. Mexican—Venezuelan sub-region
 Provinces: 1. Baja California—Mexico
 2. Guatemala—Panama
 3. North-Columbia—North-Venezuela
 Sub-provinces: A: Mainland area
 B: Trinidad and Tobago
- II. Antillean sub-region
 Provinces: 1. South-Florida, Bahamas, Bermuda
 2. Cuba
 Sub-provinces: A: Western Cuba
 B: Central Cuba
 C: Eastern Cuba
 3. Jamaica
 4. Hispaniola
 5. Porto Rico
 6. Lesser Antilles

NEOTROPICAL KINGDOM (32 endemic families)

Caribbean region (2 endemic families, Goetzeaceae and Plocospermataceae, and more than 500 endemic genera).

A) Mexican—Venezuelan sub-region (a single endemic family, Plocospermataceae, and approximately 200 endemic genera)

Province:

1. Baja-California—Mexico
2. Guatemala—Panama
3. North Colombia—North Venezuela (incl. Trinidad and Tobago)

B) Antillean sub-region (a single endemic family, Goetzeaceae, and about 200 endemic genera and 7500 endemic species)

Provinces:

1. South Florida—Bahamas—Bermuda (7%, 10% and 8% endemics, respectively)
2. Cuba (51.4% endemics, 74 endemic genera and approximately 3000 endemic species)

3. Jamaica (20–22% endemics, 8 endemic genera)
4. Hispaniola (39.2% endemics, 36 endemic genera, 1797 endemic species)
5. Puerto Rico (13% endemics, 2 endemic genera)
6. Lesser Antilles (10–12% endemics)

Relationships within the flora of the West Indies

In the paper on the vegetation of the Antilles by HOWARD (1973) in fact the relationships between the flora of the islands and the distribution patterns of plants, rather than the vegetation, are discussed. In HOWARD's views the geobotanical relationship between the continent and the islands should be evaluated on the basis of genera, rather than species. The results of this analysis are presented in 30 tables where only those genera are listed which were considered by HOWARD as being free from taxonomic problems. Based on this analysis the following statements were made.

In the Antilles several endemic genera are restricted to one or two islands and there are only two endemic genera with more than 20 species.

Picrodendraceae, including a single genus and three species, is the only family restricted to the Antilles in distribution.

The flora of the Greater Antilles has several genera in common with Central America which are otherwise absent from the Lesser Antilles. Contrarywise, the Lesser Antilles have several South American genera that are missing from the Greater Antilles.

Table 1

*West Indian genera missing in Central and South America
and genera of West Indian evolution center represented only
by a few species in the American continent (*)*

<i>Borrichia</i> (Compositae)	1 species
<i>Calycogonium</i> (Melastomataceae)	33 species
<i>Catesbaea</i> (Rubiaceae)	20 species
<i>Charianthus</i> (Melastomataceae)	2 species
<i>Coccothrinax</i> * (Palmae)	45 species (2 in Yucatan and Fda)
<i>Consouea</i> (Cactaceae)	14 species
<i>Ernodea</i> (Rubiaceae)	3 species
<i>Gesneria</i> (Gesneriaceae)	55 species
<i>Gundlachia</i> (Compositae)	10 species
<i>Hypelate</i> (Sapindaceae)	1 species
<i>Metopium</i> (Anacardiaceae)	3 species
<i>Neolaugeria</i> (Rubiaceae)	5 species
<i>Oplonia</i> (Acanthaceae)	20 species (2 in Peru and 3 in Madagascar)
<i>Oxandra</i> (Lauraceae)	2 species
<i>Petitia</i> (Verbenaceae)	2 species
<i>Reynosia</i> * (Rhamnaceae)	18 species (1 in CA)
<i>Rhytidophyllum</i> * (Gesneriaceae)	21 species (1 in SA)
<i>Rochefortia</i> * (Boraginaceae)	12 species (1 in CA and SA)
<i>Rondeletia</i> * (Rubiaceae)	130 species, only 3 in CA (?)
<i>Sarcomphalus</i> ¹ (Rhamnaceae)	12 species
<i>Scolosanthus</i> (Rubiaceae)	22 species
<i>Strumpfia</i> (Rubiaceae)	1 species
<i>Tetrazygia</i> (Melastomataceae)	15 species
<i>Tetrazygiopsis</i> (Melastomataceae)	13 species
<i>Thrinax</i> (Palmae)	5 species
<i>Wallenia</i> * (Myrsinaceae)	26 species (2 in CA)

¹ I prefer maintain *Sarcomphalus* as a separate genus, because of its type of placentation completely different from that of *Zizyphus* (see VENT 1982).

HOWARD's study suggests that the flora of the West Indies is not uniform and its development is not completely independent, since inner disjunctions are more characteristic than close relationships. This idea has been manifested in KLOTZ's (1978) work in which a northern Caribbean subregion is distinguished within the Caribbean floristic region by excluding the Lesser Antilles. Within this sub-region a Greater Antillean province is delimited.

The regionalization concept described above was developed (BORHIDI 1973) in the year of HOWARD's publication and the studies carried out since then appear to support the author's early view. In the meantime, the Picrodendraceae family, considered earlier as being endemic to this area, was incorporated into Euphorbiaceae, whereas the family status of Goetzeaceae was restored (AIRY SHAW 1965, HUNZIKER 1979, FUENTES 1982). The latter family comprises four genera, all endemic to the Antilles. Several new genera were described from the Antillean area (BORHIDI 1973, 1977, 1981, 1982, AIELLO 1979, A. H. LIOGIER 1981) and new species of West Indian genera were discovered. Following HOWARD's pioneer studies, some problems concerning the floristical relationships between the Lesser and Greater Antilles were clarified. Also, the presence of some South American genera in the Lesser Antilles turned out to be the result of secondary introduction (HOWARD 1982, in litt.).

Table 2

Genera endemic to the Greater Antilles and mostly occurring in the Bahamas as well

Auerodendron (Rhamnaceae) C,J,B, 8 species
Bonania (Euphorbiaceae) C,H,B, 8 species
Grimmeodendron (Euphorbiaceae) C,J,H,B, 2 species
Lasiocroton (Euphorbiaceae) C,H,J,B, 4 species
Leptocereus (Cactaceae) C,H,J,PR, 14 species
Nashia (Verbenaceae) C,H,B, 6 species
Neobracea (Apocynaceae) C,B, 8 species
Neothymopsis (Compositae) C,B, 2 species
Phialanthus (Rubiaceae) C,J,PR,B, 18 species
Picrodendron (Euphorbiaceae) C,J,H,B, 3 species
Pseudocarpidium (Verbenaceae) C,H,B, 8 species
Sachsia (Compositae) C,H,J,PR,B,Fda, 2 species
Spathelia (Rutaceae) C,J,B, 16 species
Tetranthus (Compositae) H,B, 2 species
Triopteris (Malpighiaceae) C,J,H,B, 5 species

Table 3

Genera endemic to Cuba, Jamaica and Hispaniola

Acidocroton (Euphorbiaceae) 10 species
Broughtonia (Orchidaceae) 2 species
Brya (Fabaceae) 12 species
Cameraria (Apocynaceae) 6 species
Gyrotaenia (Urticaceae) 5 species
Haenianthus (Oleaceae) 4 species
Lagetta (Thymelaeaceae) 5 species

Table 4

Genera endemic to Cuba, Hispaniola and Porto Rico

Ditta (Euphorbiaceae) 2 species
Ottoschulzia (Icacinales) 3 species
Torrallbasia (Celastraceae) 2 species

In the sequel some tables will summarize the genera whose distribution is confined to the West Indian subregion (*sensu* BORHIDI). In addition, genera having the evolutionary centre in the West Indies but also represented by as few as 1–2 species in the South or Central American continent are listed, these are indicated by an asterisk (Table 1).

Table 5*Genera endemic to Cuba and Hispaniola*

<i>Ampelocera</i> (Ulmaceae)	2 species
<i>Barleriola</i> (Acanthaceae)	5 species
<i>Bellonia</i> (Acanthaceae)	2 species
<i>Bisgoeppertia</i> (Gentianaceae)	2 species
<i>Chascotheca</i> (Euphorbiaceae)	1 species
<i>Copernicia</i> * (Palmae)	29 species (3 in SA)
<i>Cubanola</i> (Rubiaceae)	1 species
<i>Cubanthus</i> (Euphorbiaceae)	3 species
<i>Ekmanianthe</i> (Bignoniaceae)	2 species
<i>Fuertesiiella</i> (Orchidaceae)	2 species
<i>Isidorea</i> (Rubiaceae)	20 species
<i>Lantanopsis</i> (Compositae)	3 species
<i>Leucocroton</i> (Euphorbiaceae)	27 species
<i>Macrocarpaea</i> (Gentianaceae)	2 species
<i>Margaritopsis</i> (Rubiaceae)	3 species
<i>Mozartia</i> (Myrtaceae)	9 species
<i>Neoregnellia</i> (Sterculiaceae)	1 species
<i>Ottoschmidtia</i> (Rubiaceae)	1 species
<i>Pachyanthus</i> * (Melastomataceae)	24 species (1 in SA?)
<i>Peratanthe</i> (Rubiaceae)	2 species
<i>Picardaea</i> (Rubiaceae)	2 species
<i>Pinillosia</i> (Compositae)	1 species
<i>Plethadenia</i> (Rutaceae)	2 species
<i>Saugetia</i> (Gramineae)	2 species
<i>Scutachne</i> (Gramineae)	2 species
<i>Spirotecoma</i> (Bignoniaceae)	5 species
<i>Suberanthus</i> (Rubiaceae)	7 species
<i>Thogsennia</i> (Rubiaceae)	1 species
<i>Verhuellia</i> (Piperaceae)	3 species
<i>Victorinia</i> (Euphorbiaceae)	1 species

Table 6*Genera endemic to Cuba and Jamaica*

<i>Acrosynanthus</i> (Rubiaceae)	7 species
<i>Calyptronoma</i> (Palmae)	5 species
<i>Cheilophyllum</i> (Scrophulariaceae)	8 species
<i>Cionosicyos</i> (Cucurbitaceae)	1 species
<i>Dinema</i> (Orchidaceae)	2 species
<i>Homalopetalum</i> (Orchidaceae)	1 species
<i>Neo-Urbania</i> (Orchidaceae)	2 species
<i>Pheidonocarpa</i> (Gesneriaceae)	2 species
<i>Stremmeliopsis</i> (Apocynaceae)	2 species
<i>Urbananthus</i> (Compositae)	2 species

Table 7*Genera endemic to Cuba and Porto Rico*

<i>Gaussia</i> (Palmae)	2 species
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In summary, not less than 27 flowering plant genera are considered as being endemic to, or having the evolutionary centre in the West Indies. These genera are represented by a total of 500 species, approximately.

The number of endemic genera common in the Greater Antilles is 15, most of those occurring in the Bahamas as well (Table 2). They include more than 100 species. This figure shows that the flora of Bahamas is closely related to that of the Greater Antilles, in particular, of Hispaniola. The floristic relationships among the islands of West Indies are best illustrated by examining the number of endemic genera found only in the combination of three, or two islands or in a single island.

Table 8

*Genera endemic to Hispaniola
and Porto Rico*

<i>Goetzea</i> (Goetzeaceae)	1 species
<i>Piptocoma</i> (Compositae)	1 species
<i>Pleodendron</i> (Canellaceae)	1 species
<i>Stahlia</i> (Leguminosae)	1 species

Table 9

Genera endemic to Hispaniola

<i>Anacaona</i> (Cucurbitaceae)	1 species
<i>Arcoa</i> (Caesalpiniaceae)	2 species
<i>Casabitoa</i> (Euphorbiaceae)	1 species
<i>Coeloneurum</i> (Goetzeaceae)	1 species
<i>Cryptorhiza</i> (Myrtaceae)	1 species
<i>Ekmaniocharis</i> (Melastomataceae)	1 species
<i>Eupatorina</i> (Compositae)	1 species
<i>Fuertesia</i> (Loasaceae)	1 species
<i>Haitia</i> (Lythraceae)	1 species
<i>Herodotia</i> (Compositae)	1 species
<i>Hottea</i> (Myrtaceae)	4 species
<i>Leptogonum</i> (Polygonaceae)	2 species
<i>Manekia</i> (Piperaceae)	1 species
<i>Mattfeldia</i> (Compositae)	1 species
<i>Mommsenia</i> (Melastomataceae)	1 species
<i>Narvalina</i> (Compositae)	1 species
<i>Neobabbottia</i> (Cactaceae)	2 species
<i>Neobuchia</i> (Bombacaceae)	1 species
<i>Pedinopetalum</i> (Umbelliferae)	1 species
<i>Penelopeia</i> (Cucurbitaceae)	1 species
<i>Poitea</i> (Fabaceae)	5 species
<i>Priamosia</i> (Flacourtiaceae)	1 species
<i>Pterocissus</i> (Vitaceae)	1 species
<i>Rhodopis</i> (Fabaceae)	1 species
<i>Samuelssonsonia</i> (Acanthaceae)	2 species
<i>Sarcopilea</i> (Urticaceae)	1 species
<i>Selleola</i> (Caryophyllaceae)	1 species
<i>Selleophytum</i> (Compositae)	3 species
<i>Stevensia</i> (Rubiaceae)	6 species
<i>Theophrasta</i> (Theophrastaceae)	2 species
<i>Tortuella</i> (Rubiaceae)	1 species
<i>Ulbrichia</i> (Malvaceae)	1 species
<i>Vegaea</i> (Myrsinaceae)	1 species
<i>Wunschmannia</i> (Bignoniaceae)	1 species
<i>Ximeniopsis</i> (Olacaceae)	1 species
<i>Zombia</i> (Palmae)	1 species

Table 10*Genera endemic to Jamaica*

<i>Acanthodesmos</i> (Compositae)	1 species
<i>Dendrocousinia</i> (Euphorbiaceae)	3 species
<i>Jacaima</i> (Asclepiadaceae)	2 species
<i>Jacmaia</i> (Compositae)	1 species
<i>Odontocline</i> (Compositae)	6 species
<i>Portlandia</i> (Rubiaceae)	6 species
<i>Salpicantha</i> (Acanthaceae)	1 species
<i>Tetrasiphon</i> (Celastraceae)	1 species

Table 11*Genera endemic to Porto Rico*

<i>Cybianthopsis</i> (Myrsinaceae)	1 species
<i>Rudolphia</i> (Leguminosae)	1 species

The importance of insularity in evolution is emphasized by the fact that the number of endemics occurring in three islands is lower than that in two islands. This number is the highest for the single islands. When Cuba, Jamaica and Hispaniola are viewed together 7 endemic genera with 44 species result (Table 3). Cuba, Hispaniola and Puerto Rico together possess 3 endemic genera with 7 species, so the total is 10 genera with 51 species (Table 4).

If pairwise combinations are taken, the following figures are obtained: Cuba and Hispaniola have in common 30 endemic genera with 168 species (Table 5). Cuba and Jamaica have 10 genera with 32 species (Table 6). There is only a single genus with two species common, to Cuba and Puerto Rico (Table 7). Hispaniola and Puerto Rico have in common four species, each representing a different genus (Table 8). The totals are 45 and 206, respectively, for genera and species.

Finally, the number of genera confined to one island is 121 altogether (237 species) (Tables 9, 10, 11). The number of species per endemic genus is 2.27 in Cuba, 1.4 in Hispaniola,

Table 12*Genera endemic to Cuba — with indication of edaphic conditions*

	Number of species	Lime- stone	Slate sand- stone	Silic. sand	Serpen- tine	Other rocks
<i>Acunaeanthus</i> (Rubiaceae)	1	—	—	—	1	—
<i>Adenoea</i> (Turneraceae)	1	—	—	—	1	—
<i>Amphiolanthus</i> (Scrophulariaceae)	3	+	+	+	—	+
<i>Ancistranthus</i> (Acanthaceae)	1	1	—	—	—	—
<i>Antillia</i> (Compositae)	1	+	—	—	—	+
<i>Ariadne</i> (Rubiaceae)	2	—	—	—	2	—
<i>Asciadium</i> (Umbelliferae)	1	—	—	1	—	—
<i>Behaimia</i> (Fabaceae)	2	+	+	—	+	+
<i>Belairia</i> (Fabaceae)	6	3	1	1	1	+
<i>Bembicidium</i> (Fabaceae)	1	1	—	—	—	—
<i>Caribaea</i> (Nyctaginaceae)	1	1	—	—	—	—
<i>Ceratopyxis</i> (Rubiaceae)	1	1	—	—	—	—
<i>Ceuthocarpus</i> (Rubiaceae)	1	—	—	—	1	—
<i>Chaetium</i> (Gramineae)	1	+	—	—	+	—
<i>Ciceronia</i> (Compositae)	1	—	—	—	1	—
<i>Cubacroton</i> (Euphorbiaceae)	1	1	—	—	—	—
<i>Dasytropis</i> (Acanthaceae)	1	—	—	—	1	—

Table 12 (continued)

	Number of species	Lime- stone	Slate sand- stone	Silic. sand	Serpen- tine	Other rocks
<i>Dendrocereus</i> (Cactaceae)	1	1	—	—	—	—
<i>Doerpfeldia</i> (Rhamnaceae)	1	1	—	—	—	—
<i>Ekmania</i> (Compositae)	1	1	—	—	—	—
<i>Ekmanochloa</i> (Gramineae)	2	—	—	—	2	—
<i>Encopella</i> (Scrophulariaceae)	1	—	—	+	—	+
<i>Eosanthé</i> (Acanthaceae)	1	—	—	—	1	—
<i>Espadaea</i> (Goetzeaceae)	1	+	+	—	+	+
<i>Euchorium</i> (Sapindaceae)	1	1	—	—	—	—
<i>Euleria</i> (Anacardiaceae)	1	1	—	—	—	—
<i>Feddea</i> (Compositae)	1	—	—	—	1	—
<i>Gastrococos</i> (Palmae)	1	+	—	—	+	+
<i>Goerziella</i> (Amaranthaceae)	1	1	—	—	—	—
<i>Grisebachianthus</i> (Compositae)	7	2	—	—	5	—
<i>Harnackia</i> (Compositae)	1	—	—	—	1	—
<i>Hebestigma</i> (Fabaceae)	1	+	+	+	+	+
<i>Hemithrinax</i> (Palmae)	3	2	—	—	1	—
<i>Henleophytum</i> (Malpighiaceae)	1	+	—	—	+	—
<i>Henoonia</i> (Goetzeaceae)	1	+	—	—	+	—
<i>Heptanthus</i> (Compositae)	7	1	1	1	4	—
<i>Herpyza</i> (Fabaceae)	1	—	+	+	—	—
<i>Kodalyodendron</i> (Rutaceae)	1	—	—	—	1	—
<i>Koehneola</i> (Compositae)	1	—	—	—	1	—
<i>Krokia</i> s. l. (Myrtaceae)	11	2	—	—	8	1
<i>Lachnorrhiza</i> (Compositae)	1	—	+	+	+	—
<i>Lepturidium</i> (Gramineae)	1	—	—	1	—	—
<i>Lescaullea</i> (Compositae)	1	—	—	—	1	—
<i>Linodendron</i> (Thymelaeaceae)	3	—	—	—	2	1
<i>Megalopanax</i> (Araliaceae)	1	1	—	—	—	—
<i>Microcycas</i> (Cycadaceae)	1	+	+	—	—	—
<i>Mniochloa</i> (Gramineae)	2	+	+	—	+	+
<i>Moacroton</i> (Euphorbiaceae)	7	—	—	—	7	—
<i>Neomazaea</i> (Rubiaceae)	1	—	—	—	1	—
<i>Nodocarpaea</i> (Rubiaceae)	1	—	—	1	—	—
<i>Notodon</i> (Fabaceae)	4	2	—	—	2	—
<i>Phania</i> (Compositae)	2	+	+	—	1	—
<i>Phidiasia</i> (Acanthaceae)	1	—	—	—	1	—
<i>Phyllacanthus</i> (Rubiaceae)	1	—	—	—	1	—
<i>Phyllomelia</i> (Rubiaceae)	1	—	—	—	1	—
<i>Pinosia</i> (Caryophyllaceae)	2	1	—	1	—	—
<i>Platygyne</i> (Euphorbiaceae)	7	1	1	1	4	2
<i>Rhodogeron</i> (Compositae)	1	—	—	—	—	1
<i>Roigella</i> (Rubiaceae)	1	—	+	+	+	—
<i>Sapphoa</i> (Acanthaceae)	2	—	—	—	2	—
<i>Sauvallella</i> (Fabaceae)	1	—	—	—	1	—
<i>Schmidtottia</i> (Rubiaceae)	16	—	—	—	16	—
<i>Shafera</i> (Compositae)	1	—	—	—	1	—
<i>Shaferocharis</i> (Rubiaceae)	3	—	—	—	3	—
<i>Siemensia</i> (Rubiaceae)	1	1	—	—	—	—
<i>Solonia</i> (Myrsinaceae)	1	—	—	—	—	1
<i>Spaniopappus</i> (Compositae)	5	1	—	—	3	1
<i>Synapsis</i> (Bignoniaceae)	1	1	—	—	—	—
<i>Tetralix</i> (Tiliaceae)	5	—	—	—	5	—
<i>Tetraperone</i> (Compositae)	1	—	1	—	—	—
<i>Triscenia</i> (Gramineae)	1	+	—	—	+	+
<i>Woehleria</i> (Amaranthaceae)	1	+	—	—	—	+
<i>Zonanthus</i> (Gentianaceae)	1	1 (?)	—	—	—	—

2.12 in Jamaica and 1 in Puerto Rico. This ratio is 5.6 for Cuba and Hispaniola taken together, 3.2 for the pair of Cuba and Jamaica, 2 for Cuba and Puerto Rico, and 1 for Hispaniola and Puerto Rico.

The geobotanical subdivision of Cuba

Three proposals for the geobotanical subdivision of Cuba have been published. LEÓN (1946) makes a distinction among three floristic sectors and 9 districts and give a short description of the flora and vegetation of each. VORONOV (1970) also distinguishes 3 sectors within which 11 districts plus 5 sub-districts are differentiated without detailed characterization. SAMEK (1973) elaborated the first comprehensive phytogeographic regionalization of Cuba distinguishing 3 sectors, 7 subsectors and 39 districts and recognizing some of the main characteristics of the Cuban flora. The regionalization presented here is based on the geographical geological and soil conditions and the flora and vegetation, giving equal weight to each. As a result, the suggested geobotanical system distinguishes 3 sub-provinces, 9 sectors and 36 floristic districts (see BORHIDI et MUÑIZ in BORHIDI 1973)

SUB-PROVINCE A: WESTERN CUBA (OCCIDENTO-CUBANICUM)

(Fig. 30)

The western part of Cuba to Bahía Honda, to Cayajabos, River San Juan and Laguna de Piedras the southern swampy coast of the Habana province and the entire Isla de Pinos and the Zapata peninsula plus the adjacent marshland belong to this category. The geological and soil conditions are highly varied, the landscape is characterized by mountains of medium

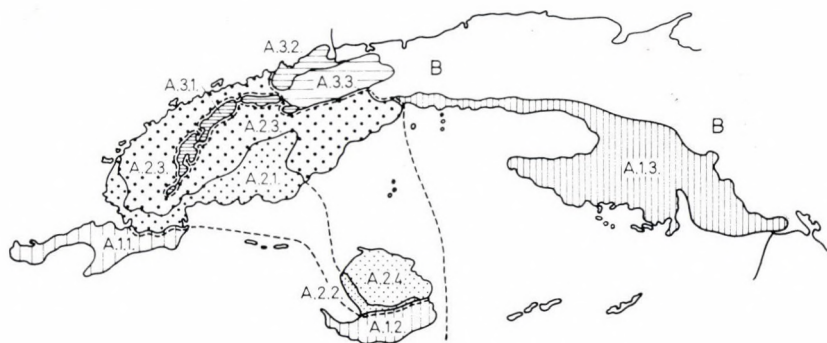


Fig. 30. The phytogeographic subdivision of the West-Cuban sub-province

- A.1. Sector: *Peninsularicum*
 - A.1.1. District: *Guanahacabibense*
 - A.1.2. District: *Sudpineroëense*
 - A.1.3. District: *Zapatense*
- A.2. Sector: *Pinaricum*
 - A.2.1. District: *Sabaloëense*
 - A.2.2. District: *Indiosense*
 - A.2.3. District: *Pinarense*
 - A.2.4. District: *Geronense*
- A.3. Sector: *Rosaricum*
 - A.3.1. District: *Viñalense*
 - A.3.2. District: *Cajalbanense*
 - A.3.3. District: *Rosariense*

height, sandy plains, lagoons, marshes, flat and conical karsts. 16 endemic genera and approximately 500 endemic species occur. Important features of the flora are the high proportion of elements from Florida, southwestern USA and the northern areas, as well as the occurrence of Mexico — Yucatan elements. Several genera, such as *Befaria*, *Kalmiella*, *Chaetolepis*, *Rhexia*, *Pieris*, *Syngonanthus*, *Xyris* and *Eriocaulon* (with one species exception) do not occur elsewhere in Cuba. Coniferous forests of flat and rolling countries and tropical karstic forests are the predominant and characteristic vegetation types. Swamps, marshes and, on the flat karsts, semi-deciduous and dry evergreen forests also cover extensive areas (Fig. 30).

Sector A.1.: Karstic peninsulas (Peninsularicum)

Guanahacabibes, southern Isla de Pinos and Zapata, the three spatially isolated peninsulas that comprise this sector, have similar geological past, vegetation and a relatively monotonous flora poor in endemics. These lands formed a common shoreline at the end of the Pliocene. This land contact has been reflected by the similarity between the forest and shrub vegetation of marshes and flat karsts. The relationship between the flora of Guanahacabibes peninsula and Isla de Pinos is best shown by the presence of some common endemics (*Erythroxylon roigii*, *Allophylus roigii*) and rare floristic elements, e.g., *Bauhinia jenningsii* which is also present in Central America, and *Diospyros tetrasperma*, also occurring in Jamaica. The flora of Zapata peninsula includes some elements common with Guanahacabibes, as *Cissus formosa*, *Pontederia lanceolata* and *Heliotropium antillarum*.

District A.1.1.: Guanahacabibes peninsula (Guanahacabibense)

a. Geography: Flat karsts composed coral limestone originated from neritic medium of the Quaternary. Shallow ferralitic soils.

b. Climate: Seasonal tropical climate with 5–6 arid months, tending to be bixeric in the east.

c. Flora: A single endemic genus, *Goerziella*, occurs. Important endemic species are *Harrisia taetra*, *Piper guanahacabibense*, *Galactia acunana*, *Callicarpa roigii*, *Vitex acunae*, *V. guanahacabibensis*, *Serjania occidentalis*, and *Tabebuia capotei*. *Diospyros anisandra*, *Forchhammeria trifoliata* and *Bumelia retusa* originate probably from the Yucatan peninsula reaching only this part of Cuba.

d. Vegetation: Mangrove on the peaty silt deposits on the northern shore. Dry evergreen shrubwoods on the rocky southern shore. In the inner part of the peninsula semideciduous forests predominate.

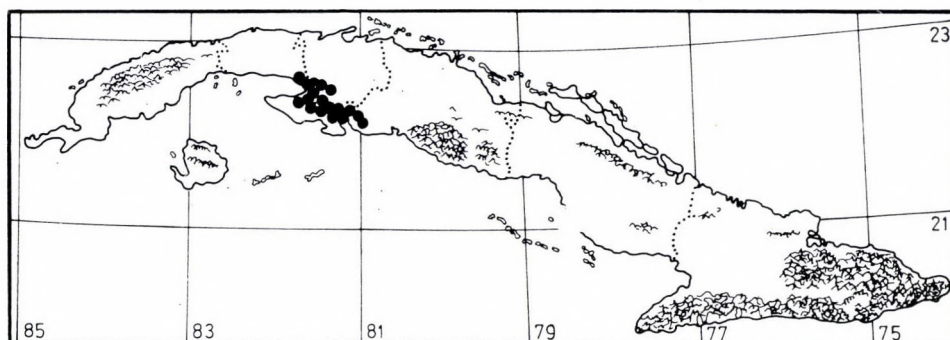
District A.1.2.: Southern Isle of Youth (Isla de la Juventud) (Sudpineroëense)

a. Geography: Marine limestone deposited in the Neogene Shallow tropical brown soils in the west, humic carbonated skeletal soils in the east.

b. Climate: Semiarid monsoon with 5–6 dry months, tending to be bixeric in the west. Annual precipitation is 1200–1600 mm.

c. Flora: One exclusive endemic is *Phialanthus bissei*. The area is characterized by the endemics of western and northern Cuba, as *Allophylus roigii* (common with the Guanahacabibes Peninsula) and *Neobraccia angustifolia*, etc. (Fig. 9).

d. Vegetation: Mangrove and swamp forests and reed vegetation in the Lanier Swamps in the north. In the west semi-deciduous forests, in the east dry evergreen forests predominate. Karstic lagoons are commonly found. An interesting stand of *Pinus caribaea* on limestone grows near Cayo Piedra, in a rather complete community of pine forest.



● *Fraxinus caroliniana* ssp. *cubensis*

Fig. 31. Geographical distribution of *Fraxinus caroliniana* ssp. *cubensis* (after SAMEK 1973, modified)

District A.1.3.: Zapata peninsula (Zapatense)

The Zapata peninsula, the Hatiguanico river basin and the surrounding swamps, Laguna del tesoro, the eastern marchlands of Zapata, the karstic lowland and the marshy mangrove coast of southern Habana province to Majana belong to this district.

a. Geography: Young, mainly peaty and boggy areas with a Neogene limestone ridge of NW–SE direction in the middle. Occasionally, flatland karsts, dissected by lagoons, with shallow, humic carbonated soils.

b. Climate: Seasonal, dry in the winter. 5–6 dry months, 1200–1700 mm annual precipitation.

c. Flora: Very few exclusive endemics (*Acacia zapatensis*, *Phoradendron zapatanum*, *Calyptranthes peninsularis*). *Bucida palustris* is a common endemic to S-Isle of Youth. Furthermore, some species also occurring in the swamps of Florida and Virginia, e.g., *Fraxinus caroliniana* ssp. *cubensis* (Fig. 31), *Vallisneria neotropalis* (MARIE-VICTORIN 1944) and *Polygala carteri*, are characteristic.

d. Vegetation: Extensive mangrove and swamp vegetation, alluvial forests and derived *Sabal* savannas on the northern edge. Semi-deciduous forests, dry evergreen forests and patches of shrubwoods occur on the karsts.

Sector A.2.: The flatland and hill-country of Pinar del Rio Province and North of Isle of Pines (actually Isle of Youth) (Pinaricum)

This sector comprises the northern Isle of Pines (Isla de la Juventud) and the province of Pinar del Rio, excluding Sierra del Rosario, the mogotes of Sierra del los Organos and the serpentine area of Cajalbana. Mainly hills, with sandstone and slate as chief rocks, and flatlands covered by oligotrophic soil with quartz sand underneath. The dominant vegetation types are closed and open coniferous forests and their derived savannas, sandy lagoons and swampy patches with palms. Eight endemic genera occur in this area, one of them *Microcycas*, (also present in Sierra de los Organos), *Colpothrinax*, *Herpyza*, *Nodocarpaea* and *Roigella* live throughout the area, *Tetraperone* is confined to Pinar del Rio, whereas *Lepturidium* is found only in Isle of Pines. In addition, 95 endemic species have been detected, for example, *Pinus tropicalis*, *Colpothrinax wrightii* (Fig. 32), *Phyllanthus junceus*, *Heptanthus ranunculoides*, *Syngonanthus wilsonii*, *Kalmiella ericoides*, *Lyonia myrtilloides*, *Vaccinium cubense* ssp. *ramonii*, *Pieris cubensis*, *Paepalanthus alsinoides*, *Chaetolepis cubensis*, *Miconia adrosemifolia*,

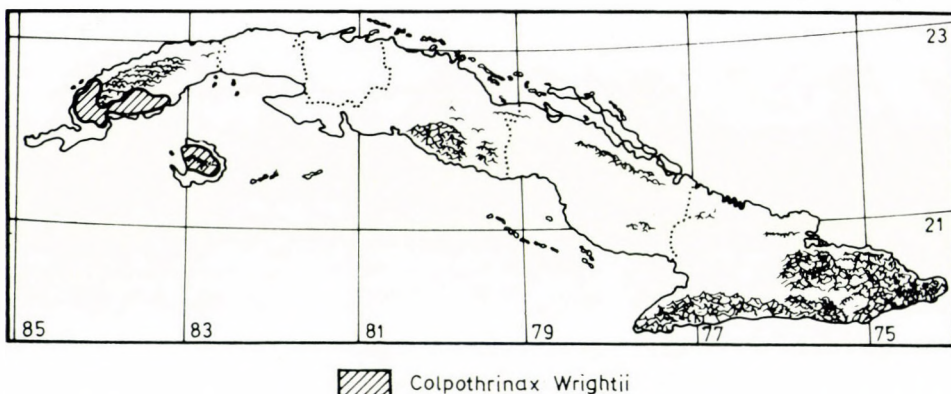


Fig. 32. Geographical distribution of *Colpothrinax wrightii*
(after SAMEK 1973, modified)

Pachyanthus cubensis, *P. angustifolius*, *P. wrightii*. Several vicarious species pairs occur, such as *Lachnocaulon anceps* (Isle of Youth)—*L. ekmanii* (Pinar del Rio); *Lyonia vaccinoides* (Isle of Youth)—*L. ekmanii* (Pinar del Rio); *Galactia jenningsii* (Isle of Youth)—*G. isopoda* (Pinar del Rio); and others in the genera of *Phyllanthus*, *Tabebuia*, *Eugenia* and *Eriocaulon*.

Sub-sector A.2.a.: White sandlands (Sabalo-Indiosense)

Light-colored sandy areas with low nutrient content on the western and southern border of Isle of Youth and South Pinar del Rio from the pre-isthmus of the Guanahacabibes peninsula till Paso Real de San Diego. The open pine woodlands and the swampy sand lagoons have several endemic species in common, for example, *Xyris bicarinata*, *X. grandiceps*, *Paepalanthus seslerioides*, *Aristida brittonorum*, *Eriocaulon sphaerocephalum*, *E. dioecum*, *Amphioranthus arenarioides*, *Micranthemum rotundatum*, *Lindernia alternifolia*, *Bacopa longipes*, and *Colpothrinax wrightii*.

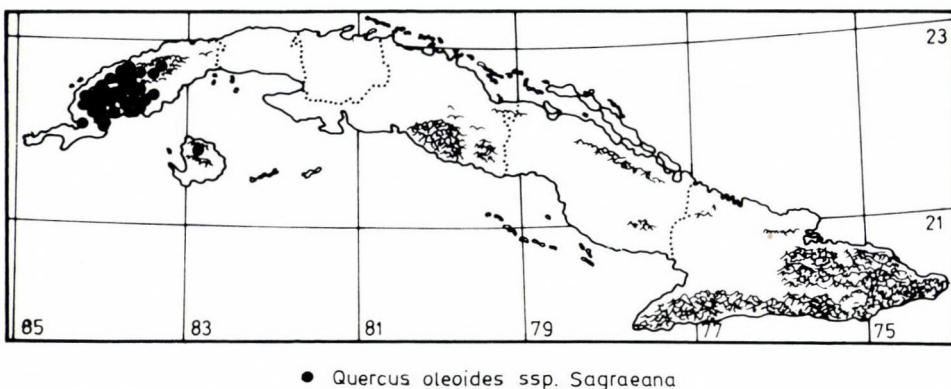


Fig. 33. Geographical distribution of *Quercus oleoides* ssp. *sagraeana*
(after SAMEK 1973, modified)

District A.2.1.: White sandlands of South-west Pinar del Rio (Sabaloëense)

a. Geography: Flatland covered by soils of mild glei character with quartz sand underneath. The area is relatively abundant in oligotrophic lakes.

b. Climate: Seasonal with dry winter, 5–6 dry months. Annual precipitation is 1000–1400 mm on the average.

c. Flora: Several endemics common to this district and the pinewoods of slate areas. These are *Befaria cubensis*, *Gochnatia ekmanii*, *Pinguicula albida*, *Byrsonima pinetorum*, *Quercus oleoides* ssp. *sagraeana* (Fig. 33). Approximately 30 exclusive endemics, for example: *Aristida fragilis*, *Syngonanthus leoni*, eight *Eriocaulon* species, *Hibiscus urbanii*, *Mollugo enneandra*, *M. brevipes*, *Pachyanthus mantuensis*, and *Plinia ramosissima*.

d. Vegetation: Mixed palm-pine woodlands with loose canopy layer (*Eragrosti cubensi*—*Pinetum* Samek) was the original vegetation in which *Colpothrinax wrightii*, *Acoelorrhaphe wrightii* and *Pinus tropicalis* were dominant. Also, derived savannas, wet *Acoelorrhaphe* palm groves, and swampy and freshwater vegetation rich in *Eriocaulaceae*.

District A.2.2.: White sandlands of Isle of Youth (Indiosense)

a. Geography: The area of El Soldado Los Indios, San Pedro and Santa Isabel, is located north of the Lanier swamp and on the western shore of the island. Similarly to the preceding area, it is a humid, acidic, quartz sand plain.

b. Climate: Seasonal with 3–4 dry months in the winter. Annual precipitation is 1400–1600 mm.

c. Flora: A single endemic genus, *Lepturidium*, and approximately 20 endemic species, such as *Eugenia victorini*, *Mollugo pinosia*, *Pectis pinosia*, *Pachyanthus longifolius*, *Kalmiella aggregata*, *K. simulata*, *Phyllanthus selbyi*, *Evolvulus siliceus* and six species of *Eriocaulon* characterize this floristic district. *Bulbostylis paradoxa* is found only here in Cuba, the savanna plant *Byrsonima verbascifolia* occurs here and in Oriente.

d. Vegetation: Open pinewoods on sandy soils (*Paepalantho*—*Pinetum tropicalis* Samek), derived savannas, wet *Acoelorrhaphe* groves. Swampy and freshwater vegetation rich in *Eriocaulons*.

Sub-sector A.2.b.: Silicate heights and their alluvial plains (*Eu-Pinaricum*)

This area includes the silicate heights in the North and South side of Sierra de los Organos, with the adjacent alluvial sites and the northern and north-eastern part of Isle of Youth. Two endemic genera, *Roigella* and *Nodocarpaea*, and about 70 endemic species occur, some of them listed in I.2.

District A.2.3.: The slatey heights and plains of Pinar del Rio (Pinarense)

a. Geography: Gently rolling hill-country, the plains are divided by rivers. The parent material of hills is composed of sandstone and lower Jurassic slate layers (the so-called San Cayetano formation). The quartz-siallitic soils of hills are acidic, yellow in color, and poor in nutrient. In the plains tropical reddish-yellow fersiallitic soils predominate, these are covered by acidic sand.

b. Climate: Seasonal tropical with dry winter. 1–2 dry months and 1600–2300 mm annual precipitation in the hills, 3–4 dry months and 1200–1600 mm annual precipitation in the plain.

c. Flora: Characteristic are the endemics of the sector; these are in common with the other floristic districts. The dominant coniferous vegetation (*Pinus tropicalis* and *P. caribaea*) causes certain floristic uniformity. Additional characteristic elements are *Quercus oleoides* ssp. *sagraeana* (Fig. 33) in the tree layer, and *Befaria cubensis*, *Vaccinium cubense* ssp. *ramonii*,

Lyonia myrtilloides, *Miconia ibaguensis*, *M. splendens*, *Pachyanthus poiretii*, *P. angustifolius*, *Tabebuia lepidophylla*, *Roigella correifolia*, *Rhus copallina* ssp. *leucantha* in the shrub layer. Species in common with Cajalbana, but rare, are *Acunaeanthus tinifolius*, *Hyperbaena columbica* and *Pisonia petiolaris*. *Microcycas calocoma* is common to this district and the limestone karsts. Local endemics are lacking with the exception of *Cassia roigii* in Cerro de Cabras. In the southern plains, however, several local endemics appear, such as *Gochnatia mantuensis*, *G. ekmanii*, *Peperomia nummularia*, *Hyptis cubensis*, *Galactia herradurensis*, *Lyonia ekmanii*, and *Melochia manducata*, usually at the edge of the plain.

d. Vegetation: On the hard crystalline slates a loose pine woodland formed by *Pinus tropicalis* and *P. caribaea* was the original dominant vegetation, but it is mostly replaced by secondary grasslands of *Hyparrhenia rufa* and *Andropogon bicornis*. In the areas of the softer sandstone bedrock (San Cayetano formation) a deeper brownish-yellow soil is developed covered mostly by evergreen sclerophyllous oak forests of *Quercus oleoides* ssp. *sagraeana*, *Buchenavia capitata*, *Pithecellobium cubense*, *Xylopia aromatica*. On the southern slopes and foothills a narrow strip of tropical semideciduous forest is developed frequently transformed into orchards or plantations of vegetables. In the lowland areas *Colpothrinax* palm-pine woodland was extended, but its sites actually are used as rice fields, pastures and secondary grasslands. The district may be subdivided into two sub-districts: the slatey heights (Eu-Pinarensis) and the alluvial plains (Herradurensis).

District A.2.4.: North of Isle of Youth (Geronense) (Fig. 30)

a. Geography: Alluvial plain is the most extensive with some karstic limestone mountains (Sierra de las Casas, Sierra de Caballos) and low silicate hills (Sierra de la Cañada, Sierra de La Siguanea, Loma de Mal Pais, etc.). The dominant soil types are yellow quartz allitic or yellow pseudoglei soils.

b. Climate: Seasonal tropical. The dry season is winter. 5–6 dry months, 1400–1700 mm annual precipitation.

c. Flora: Very similar to that of the preceding flora district, although several elements (*Microcycas*) have not reached this area despite the land connection at the end of the Tertiary and during the glacial of the Quaternary. Some characteristic endemic species are *Hyeronima crassistipula*, *Stenandrium pinetorum*, *Machaonia acunae*, *M. pauciflora*, *Miconia perelegans*, *Jacquinia curtissii*, *Hypericum incurvum*, and, on the limestone mountains, *Tabebuia geronensis* and *Eugenia ignota*.

d. Vegetation: Forests of *Pinus tropicalis*, in some places mixed with *P. caribaea*, mostly replaced by pastures. On the limestone hills semi-deciduous forests at the foot hill areas and karstic forests on the steep formations.

Sector A.3.: The mountainous Pinar del Rio (Rosaricum) (Fig. 30)

Three mountainous area of very different geological structure, geomorphology and vegetation have been included: the haystack mountains of Sierra de los Organos, the serpentine area of Cajalbana and vicinity, and the geologically highly varied mountain range of Sierra del Rosario. The main justification for considering these three fundamentally different areas as parts of the same flora sector is that the mountains form an unbroken system, and many species from the limestone flora of Sierra de los Organos and the serpentinophilous flora of Cajalbana are found together in Sierra del Rosario.

Ten endemic genera characterize this sector, these are *Euchorium* (Sapindaceae), *Ancistranthus* (Acanthaceae), *Neomazaea* (Rubiaceae), *Phyllomelia* (Rubiaceae), *Phyllacanthus* (Rubiaceae), *Sauvallea* (Commelinaceae), *Sauvallella* (Fabaceae), *Lescaillea* (Compositae), *Sie-*

mensia (Rubiaceae) and *Ceratopyxis* (Rubiaceae). Genera common to Sierra de los Organos and Sierra del Rosario are *Siemensia*, *Ceratopyxis* and *Gaussia*, whereas *Phyllomelia* is common to Cajalbana and Sierra del Rosario. Here is the chorological centre of the genera *Acunae-anthus* and *Phania* which occur sporadically in the east, in the provinces of Matanzas and Las Villas. In addition to the endemic genera, about 150 endemic species prove the ancient character of the western Cuban mountains and the long, isolated development of their flora.

The vegetation of this area is also characterized by high diversity and intensive mingling. The vegetation of limestone rocks of Sierra de los Organos is also found in several localities in Sierra del Rosario (Pan de Guajabón, Peña Blanca, Monte Toro). Communities similar to the pinewoods and scrubs of Cajalbana occur at several points in Sierra del Rosario (Loma Zambumbia near Rancho Mundito, Rangel, Cuzco, Loma Pelada de Cayajabos). Despite these similarities, the three mountainous areas are sharply different from one another in geomorphology, flora and vegetation.

District A.3.1.: Sierra de los Organos (Viñalense)

a. Geography: Deeply inclined, tower-like karstic hills with narrow and deep gorges hidden cave systems and a long valley separating the mountains in a SW–NE direction. The surface of mountains is usually bare rock or more or less eroded skeletal soils. In the gorges deep humic-carbonated rendzina soils are deposited, whereas in the so-called intercolline valleys tropical brown and red soils predominate.

b. Climate: Seasonal tropical with dry winter. The dry season is shortened in the SW–NE direction. In the west and north 3–4, in the south and east 1–2 dry months. In some centrally situated areas humid rainforest climate may occur mesoclimatically. The annual precipitation is 1500–2200 mm.

c. Flora: The mountains composed of old, very hard upper Jurassic rocks, the so-called blue limestone, emerged in the Cretaceous. They have been dry lands since then. Due to the gradual erosion of soft rocks, free-standing limestone cliffs were formed. On the top of rocks a very ancient and highly specialized flora developed preserving several taxonomically isolated relicts, conditioned by the decreased competition in the extremely unfavourable habitats.

Two monospecific genera, *Euchorium* and *Ancistranthus*, and two other genera common to this district and Sierra del Rosario (*Ceratopyxis* and *Siemensia*), as well as *Microcycas* (which is also present in the slatey heights) illustrate the richness of the flora, likewise the 90 endemic species (e.g., *Gaussia princeps*, *Ancistranthus harpochiloides*, *Ceratopyxis verbenacea*, *Siemensia pendula*, *Ekmanianthe actinophylla*, *Spathelia brittonii* (Fig. 6), *Bourreria polyneura*, *Eugenia galeata*, *Gesneria celsioides*, *Omphalea hypoleuca*, *Annona cascarilloides*, *Malpighia roigiana*, *Anthurium venosum*, *Philodendron urbanianum*, *Bursera shaferi*, etc.).

Important species of karstic woods are the endemic *Bombacopsis cubensis*, *Thrinax morrisii* and *Agave tubulata*. Many local endemics have been discovered here. The most intensively explored area is Viñales where 17 local endemics were found, for example: *Pilea affinis*, *P. simplex*, *Salmea glaberrima*, *S. umbratilis*, *S. caleoides*, *Rhytidophyllum rupicola*, *Clusia brittonii* and *Acalypha mogotensis* (for others, see the list above). Sumidero has 10 local endemics, e.g., *Piper sumideranum*, *Calycogonium saxicola*, *Plinia rubrinervis*, *Cissus dichroa*, and *C. humilis*, Cerro de Guane has 5, e.g., *Eugenia guanensis*, *Peperomia guanensis* and *Caesalpinia guanensis*. *Dorstenia roigii* is an endemic of Mogote la Jagua, whereas *Gouania ekmanii* is endemic to Mogote de la Baliza. Five endemics have been found in the Sierra de la Güira (*Pilea güirana*, *Bourreria mucronata*, *Tetrazygia minor*, *Guettarda amblyophylla* and *Rondeletia susannae*). In the mountains isolated by coombs from one another a number of local vicarious endemics occur, e.g., *Leptocereus assurgens* (Viñales) — *L. prostratus* (Sumidero) — *L. ekmanii* (Cerro de Guane); *Psidium vicentium* (Viñales) — *P. nummularium* (Pan de

Guajaibón); *Pilea hemisphaerica* (Viñales) — *P. sumideroensis* (Sumidero). The mountains of Viñales and Sumidero may be regarded as being the most important centres of speciation.

d. Vegetation: The karstic hills (mogotes or haystack hills) are covered by a unique mogote vegetation including the open *Agave* scrub of sunny cliffs, the veil — communities of shady rock walls and crevices, bromelia-rich open shrubwoods of the eroded tops, and the closed forest on gravel slides and ravines (intrazonal semi-deciduous shrubwoods). On the gravel slides at the foothills semi-deciduous forests, in the coombs seasonal evergreen forests and extrazonal rainforest patches develop. The intercolline valley, formerly covered by seasonal evergreen forests, is a cultivated land with fragments of a *Roystonea* — *Ceiba* secondary savanna.

District A.3.2.: Cajalbana Mountains (Cajalbanense)

a. Geography: Due to the red ferritic soils and the very rich flora, this small (about 70 km²) area of old serpentine mountains extending to the coastal lowland of La Mulata satisfies the criteria of being a separate floristic district. The relief is characterized by wide, flat hilltops and deep valleys with steep slopes. Regarding physiognomy, soil and vegetation, this area is a smaller, vicarious complement of Sierra de Nipe of eastern Cuba.

Loma Preluda to the West, and the range of serpentine hills from Las Pozas to south of Bahía-Honda and the coastal area of Toscano-Morrillo are also included in the district. The adjacent northern coast, composed mainly of serpentine or young sedimentary rocks as the top layer, is also considered here.

b. Climate: Seasonal with dry winter, 3–4 dry months, 1400–1600 mm annual precipitation.

c. Flora: Four monospecific endemic genera: *Neomazaea*, *Sauvallella*, *Phyllacanthus* and *Lescaillea*, and 40 endemic species, including several palaeoendemics characterize the district. Of the endemics of pinewoods *Tetrazygia coriacea*, *Psidium cymosum*, *Phania cajalbanica* (Fig. 25), *Tabebuia leptopoda*, *Plinia dermatodes*, *Rondeletia venosa*, *Coccothrinax yuraguana* (Fig. 34), *Phyllanthus sagraeanus*, *Chaptalia ekmanii*, and *Eupatorium grisebachianum* are

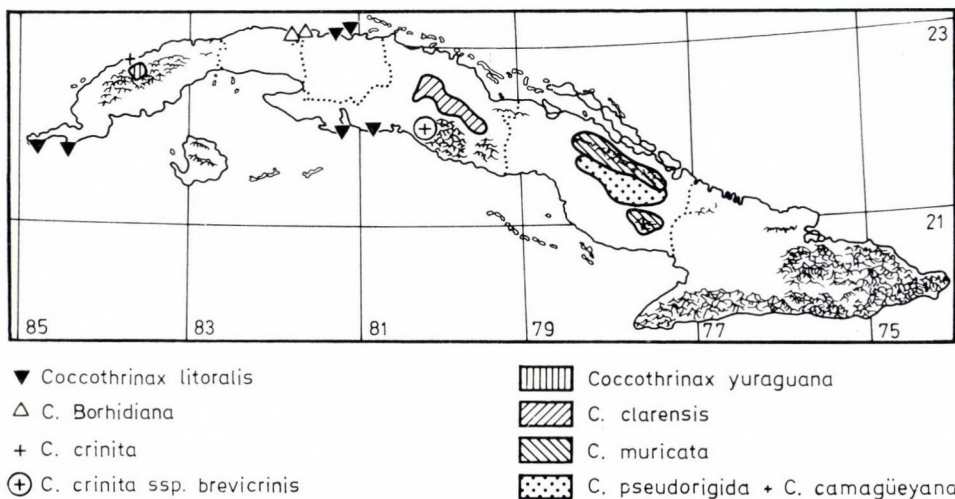


Fig. 34. Geographical distribution of the West- and Central Cuban taxa of the genus *Coccothrinax* (after BORHIDI 1973, modified)

noteworthy. Noted species of the evergreen shrubwoods are *Agave cajalbanensis*, *Moacrotan trigonocarpus* (Fig. 12), *Euphorbia cubensis*, *Zanthoxylum dumosum* s. str. *Gesneria ferruginea*, *Gochnatia intertexta*, *Guapira cajalbanensis*, *Machaonia dumosa*, *Phialanthus rigidus*, and *Scolosanthus acunae*. Several floristic elements are vicariads of Nipe and Moa endemics, for example, *Lescaillea* — *Harnackia* (Fig. 10), *Euphorbia cubensis* — *E. helenae*, *Moacrotan trigonocarpus* — *M. lanceolatus* (Fig. 12), *Anemia cajalbanica* — *A. coriacea* (Fig. 11), and *Helicteres trapezifolia* — *H. nipensis*. Isolated populations of several species may also be encountered in the serpentine areas of central Cuba, e.g., *Ottoschmidtia dorsiventralis*, *Anemia cajalbanica*, *Harpalyce cubensis* (Matanzas), *Acunaeanthus tinifolius*, *Leucocroton revolutus*, *Linodendron venosum*, *Coccothrinax crinita* (Macizo de Guamuhaya).

The coastal belt at Toscano—Playa Morrillo originally had a highly specialized flora. The present vegetation, however, is strongly degraded and an endemic genus (*Phyllacanthus*) and 19 endemic species, e.g., *Maytenus lineata*, *Heptanthus brevipes*, *Ilex ternatifolia*, *Mimosa apleura*, *M. catalinae*, *Calycogonium microphyllum*, *Randia cubana* and *Calyptranthes gracilipes*, etc., have not been collected here for a long time.

d. Vegetation: On the rocky soil of the steep slopes and cliffs evergreen shrubwoods, whereas on the hilltops *Pinus caribaea* forests grow. In the valleys wet coniferous gallery forests with ferns, palms and *Odontosoria wrightiana* are found. In the lowland areas semideciduous forests, serpentine shrub woods, and mangrove vegetation grow.

District A.3.3.: Sierra del Rosario (Rosariense)

a. Geography: Mountainous formations composed primarily of upper Jurassic limestone and, to a lesser extent, of sandstone, gneis and others. Serpentine intrusions often reach the surface forming more or less extensive patches. Two parallel ranges reach the altitude of 5–600 m, some peaks (Monte Toro, Peña Blanca, Piedra Calzada, Pan de Guajaibón) are elevated over 600 m. The relief is highly varied. Tropical brown soils predominate but there are also yellow quartz-allitic soils on sandstone, red ferallitic soils on serpentine and tropical rendzina on limestone.

b. Climate: Tropical climate with 1–2 months long dry winter. In the central basin, particularly in the east, humid rainforest climate occurs, rainy throughout the year.

c. Flora: Rich and diverse, thanks to the high geological variability of the mountains. On the serpentine outcrops the plants of the Cajalbana Mts. and its vicinity occur, for example, *Phyllomelia coronata*, *Malpighia wrightiana*, *Rondeletia chamaebuxifolia*, *Eugenia rigidifolia*. Some species of slatey heights, e.g., *Pinus caribaea*, *Quercus oleoides* ssp. *sagraana* and *Byrsosnima pinetorum*, occur in the sandstone areas, whereas several plants from the karsts of Sierra de los Organos (*Siemensia pendula*, *Gaussia princeps*, *Auerodendron acuminatum*) are found on limestone rocks. The exclusive endemics are relatively few in number, totalling about 25. Examples are *Pilea bullata*, *Zanthoxylum ekmanii*, *Z. organosium*, *Banara acunae*, *Daphnopsis guacocoa*, *Lagetta wrightiana*, *Plinia recurvata*, *Myrtus sagraei*, *Myrcia valenzuelana*, *Pachyanthus tetramerus*, *Mouriri valenzuelana*, *Henriettea granularis*, *Cordia valenzuelana*, and *Gochnatia ekmanii*. Four local endemics are known from Pan de Guajaibón, namely *Gesneria brevifolia*, *Piper perditum*, *Psidium nummularia* and *Tetrazygia lanceolata*.

d. Vegetation: Originally seasonal evergreen tropical forests were predominating. Most of the native vegetation was replaced by coffee plantations in the second half of the last century, but these fields have become abandoned resulting in degraded, secondary forests. Below the peak of Pan de Guajaibón developed a small stand of montane rainforest. On the southern slopes and the foothills semi-deciduous forests grow. The mogotes are covered by deciduous shrubwoods, whereas on the sandstone outcrops pinewoods and mixed pine-oakwoods are found. The serpentine areas are covered by microphyllous thorn scrubs.

SUB-PROVINCE B: CENTRAL CUBA (CENTRO-CUBANICUM) (Fig. 37)

The plains, isolated mountains and hills of central Cuba are included in this sub-province which extends from Bahia Honda and the Rosario Mountains in the west to the Cauto basin and the Central Valley of Oriente in the east, reaching the feet of Sagua-Baracoa and Sierra Maestra. This area has been a contiguous land mass since the end of the Pliocene only. Before that period, the terrestrial plants were scattered over the extensive archipelago of limestone mountains and cliffs. The plants of the plain of central Cuba originated primarily from the mountains of Oriente, and also from Pinar del Rio. This view is supported by the fact that the plains are poor in exclusive endemics most of which being local or vicariant endemics. Those distributed all over the area, partly serpentine plants partly coastal elements, are in common with western or eastern Cuba or both nearly without exception. The landscape and the vegetation are characterized by dominant Antillean, Caribbean and Neotropical species that are also found elsewhere. Being most abundant, however, these plants may be considered as the most typical species of the area.

Of the serpentine endemics *Nebracea valenzuelana* (Fig. 9), *Phyllanthus orbicularis* (Fig. 8), *Annona bullata*, *Calliandra pauciflora*, of the mesophilous forest species *Ficus subscabrida*, *F. combsii*, *Coccoloba retusa*, *Tabernaemontana amblyocarpa*, *Espadea amoena*, *Casasia calophylla* and *Guettarda calyptata* are mentioned here.

Pan-Cuban endemics of the dry shrublands and coastal communities are *Belairia mucronata*, *Oplonia tetrasticha*, *Randia spinifex*, *Platygyne hexandra* and *Gastrococos crispa* (Fig. 35), etc.

Further characteristic elements of the landscape are non-endemics, such as *Roystonea regia*, *Ceiba pentandra*, *Bucida buceras*, *Cecropia peltata*, *Samanea saman*, *Croton lucidus*, *Eugenia maleolens*, these are the most common in this area. In addition, species whose dispersal is facilitated by human activity are *Comocladia dentata*, *Glyricidia sepium*, *Dichrostachys cinerea* and *Rhynchelytrum roseum*. In the floristic sub-province of Central Cuba 21 endemic Cuban genera occur, seven being confined to this area. Of these *Megalopanax*, *Euleria* and *Rhodogeron* have a local distribution pattern, and only 4 genera, *Gastrococos*, *Behaimia*, *Henleophytum* and *Chaetium*, have been widely distributed all over the area, although the role of the latter ones in the vegetation is negligible. There are only about 25–30 non-local endemics characterizing this sub-province although their distribution extends a little to the neighbouring areas (e.g., on the southern coast of Oriente). Examples are *Andropogon multinervosus*, *Scleria*

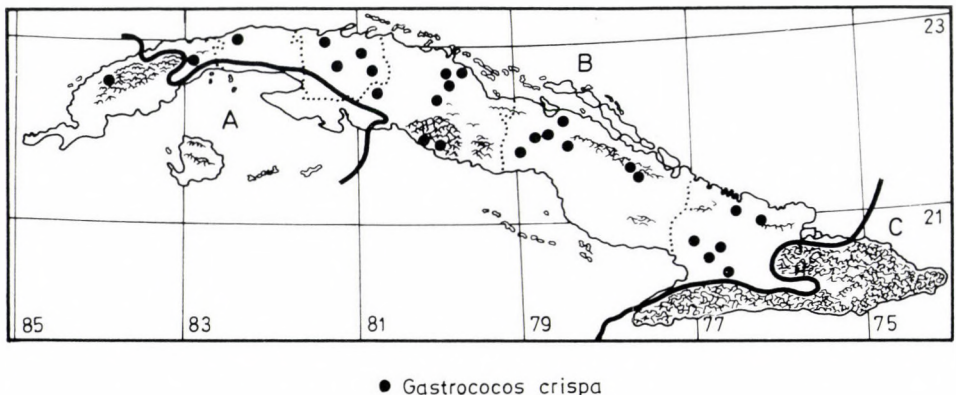


Fig. 35. Geographic distribution of *Gastrococos crispa* (after SAAKOV 1970, modified)

havanensis, *Agave legrelliana*, *Copernicia macroglossa*, *C. baileyana* (Fig. 36), *Coccothrinax miraguama* p. maj. p., *Behaimia cubensis*, *Piscidia cubensis*, *Malpighia nummulariifolia*, *Byrsosima motembensis*, *Leucocroton moncadae*, *L. havanensis*, *Chamaesyce paucipila*, *Tabebuia lepi-*

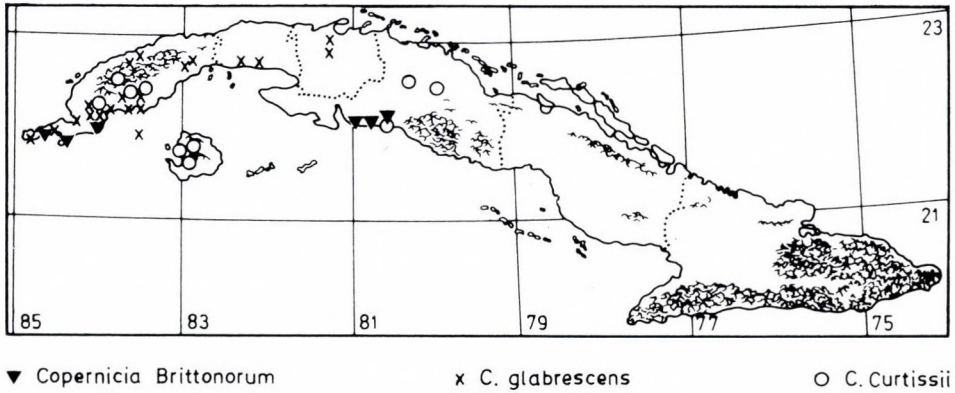


Fig. 36. Geographical distribution of the West-Cuban taxa of the genus *Copernicia* (after DAHLGREN and GLASSMAN 1963, modified)

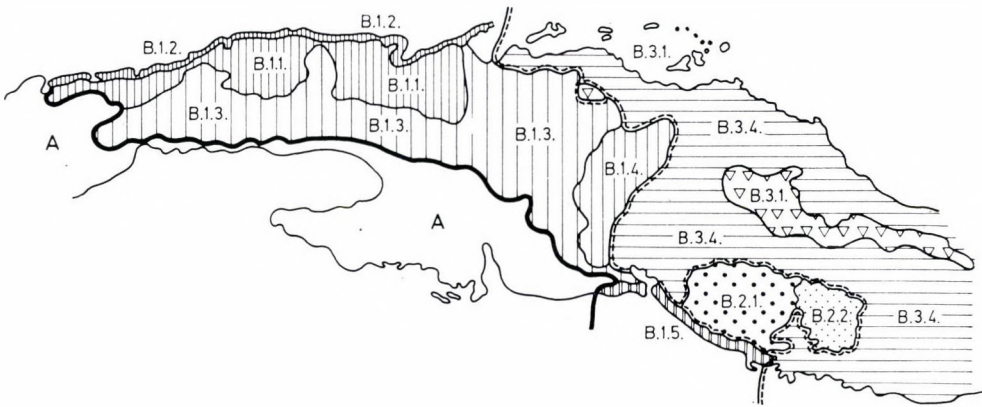


Fig. 37. The phytogeographical subdivision of the western part of the Central Cuban sub-province

B.1. Sector: Western Central Cuba (*Havanicum*)

B.1.1. District: *Jarucoënsë*

B.1.2. District: *Havanensë*

B.1.3. District: *Güinensë*

B.1.4. District: *Cascajalensë*

B.1.5. District: *Casildensë*

B.2. Sector: The Guamuhaya Massif of Escambray (*Trinidadicum*)

B.2.1. District: *Trinidadensë*

B.2.2. District: *Spirituënsë*

B.3. Sector: Eastern Central Cuba (*Camagüeyicum*)

B.3.1. District: *Claraënsë*

B.3.4. District: *Saguënsë*

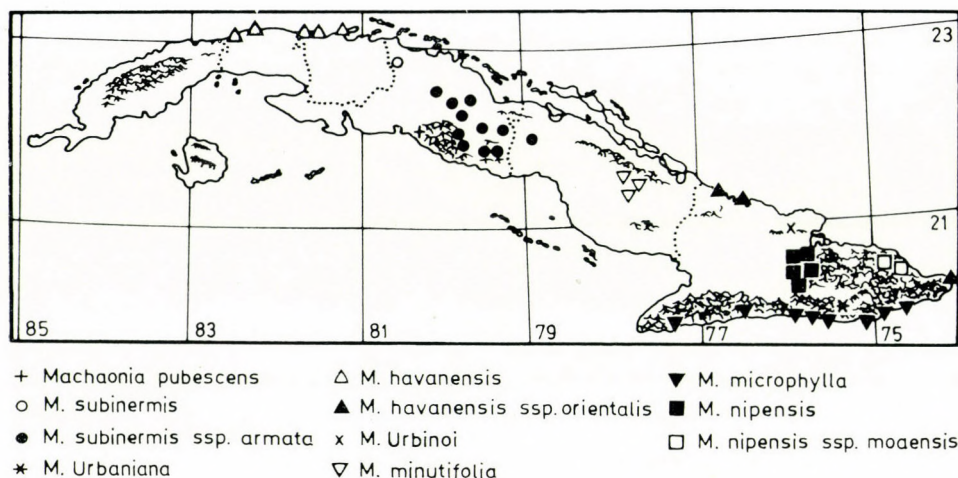


Fig. 38. Geographical distribution of some central and East-Cuban species of the genus *Machaonia* (after FERNANDEZ et BORHIDI 1984)

dota, *Cissus torreana*, *Eugenia camarioca*, *Rondeletia camarioca*, *Machaonia subinermis* s. l. (Fig. 38), *Plumeria cubensis*, *P. keyensis*, *Mesechites minima*, *Scolosanthus crucifer*, *Hyptis armillata*, and *Pectis cubensis*, etc. Recently, more than 75% of this area is a managed or cultivated land. Its original vegetation may be reconstructed only from relict of some fragmental stands. The native vegetation survived in the mountains, on the coast, keys and the less fertile serpentine areas.

Sector B.1.: Western central Cuba (*Havanicum*) (Fig. 37)

This area ranges from Bahía Honda and Artemisa to Cardenas, Cienfuegos and, on the southern coast, as far as Casilda. Coastal zones with rich flora, mountainous and hilly regions of varied bedrocks and diverse plant communities and flatland with monotonous vegetation are included. The plains have been cultivated for centuries. In addition to the few local endemic species, endemic genera [e.g., *Amphiolanthus*, *Acunaeanthus*, *Phania* (Fig. 25)] and species [*Eriochloa setosa*, *Coccothrinax littoralis* (Fig. 34)], *Zephyranthes rosea*, *Crinum oliganthum*, *Bombacopsis cubensis*, *Coccoloba pallida*, *Harpalyce cubensis*, *Phyllanthus discolor*, *Hyeronima havanensis*, *Callitriche occidentalis*, *Comocladia mollifolia*, *Terminalia intermedia*, *Eugenia farameoides*, *Rauwolfia cubana*, *Cordia angiocarpa*, *Brunfelsia nitida*, *Rhytodophyllum wrightianum*, *Oplonia nannophylla* (Fig. 39), *Machaonia havanensis* (Fig. 38), etc. in common with western Cuba are characteristic.

District B.1.1.: Limestone and serpentine areas between Bahía-Honda and Limonar (*Jarucoëse*)

The Las Pozas-Cabañas hilly range at the northern edge of Sierra del Rosario, and Sierra de Anafe, the Habana-Matanzas hills and, south of and parallel to it, the Bejucal-Madruga-Limonar range are included.

a. Geography: This area, being divided into several smaller hilly ranges by valleys, has a varied geological structure. The mosaic-like intermingling of limestone and serpentine rocks is typical. As a consequence, the soil conditions are also diversified. On the Cretaceous limestone (Habana-Matanzas heights) tropical brown soils predominate, often in form of their very shallow, rocky variant. On the Jurassic limestone of Anafe Mountains and the Jaruco karst calcareous soils have developed. Red latosolic, nutrient poor soils cover the serpentine outcrops. On the Tertiary, mainly Oligocene, limestone of the Bejucal-Madruga-Coliseo range calcareous, ferralitic soils of good quality predominate.

b. Climate: Seasonal, dry in the winter. 3–4 dry months and 1400–1600 mm annual precipitation in the western part of the district, 1–2 dry months and an average precipitation up to 1100–2300 mm to the south-southeast of Havana, and 5–6 dry months and 1400–1800 mm annual precipitation east of Jaruco.

c. Flora: Due to the mosaic-like geological and soil structure the number of common endemics is lower than that of the local endemics. For instance, four local endemics occur in the Sierra de Anafe (e.g., *Eugenia anafensis* and *Guapira leonis*). Two vicarious subspecies of *Tabebuia anafensis* occur in the whole limestone range, like *Rhytidophyllum exsertum*. Endemic species of the serpentine of Campo Florido are *Pectis havanensis* and *Psidium havanense*. The richest in endemics is the Canasi serpentine area: *Melocactus matanzanus*, *Coccothrinax miraguana* ssp. *roseocarpa* (Fig. 34). *Myrtus matanzasia*, *Moacroton revolutus* (Fig. 12), *Buxus gonoclada*, *Reynosia microphylla*, *Bucida ophiticola*, *Borreria matanzasia* occur here. Some of them are also found on the serpentine of Camarioca. There are a number of species in common either with Cajalbana (*Anemia cajalbanica*, Fig. 11, *Ottoschmidtia dorsiventralis*, *Harpalyce cubensis*) or with the serpentine areas of Las Villas (*Acacia daemon*, *Buxus flaviramea*).

d. Vegetation: Dominant types are semi-deciduous forests in the northern and middle part of the district and dry evergreen forests in the Sierra de Anafe. The species poor variant of the karstic forests of the Sierra de los Organos predominates on the Jaruco mogotes and other karstic hills, with *Thrinax morrisii* as dominant species. The foothills and the valleys are covered by fragments and derived savannas of seasonal evergreen forests. Dry evergreen forests grow on the serpentine areas, whereas at Canasi evergreen shrubwoods with dwarf palms are found.

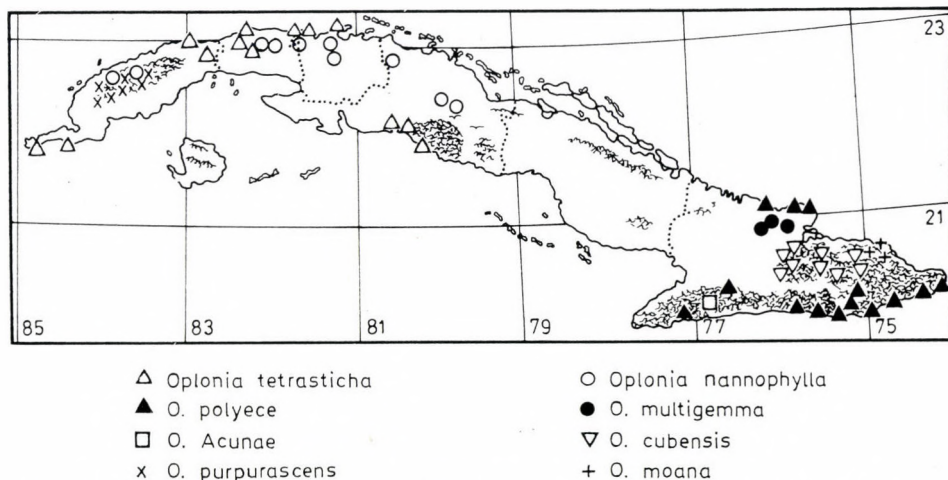


Fig. 39. Geographical distribution of some species of the genus *Oplonia* (Acanthaceae) (after BORHIDI et MUÑIZ 1979)

District B.1.2.: Seashore of the Bahia Honda-Hicacos zone (Havanense)

a. Geography: The coast ranging from Bahia-Honda to Varadero consists mainly of Pliocene limestone which is seldom broken by muddy or sandy beaches. Flat karsts and cliffs (Seboruco) are most usual but rocky hills may also be seen. Mainly shallow, rocky, humic-carbonated soils cover the area.

b. Climate: Seasonal with dry winter, the annual precipitation is 1000–1400 mm with a distribution similar to that in the preceding district. The dry season gets longer eastward, reaching a duration up to 5–6 months.

c. Flora: The area abounds in drought-tolerant endemic species. *Coccothrinax borhidiana* (Fig. 34), *Piper cojimaranum*, *Gochnatia sagraeana*, *Croton litoralis* ssp. *rugelianus*, *Pilosocereus robinii*, *Leptocereus wrightii*, *Eugenia mollifolia*, *Rhytidophyllum crenulatum*, *Borrichia cubana*, *Rondeletia rugelii* and *Guettarda undulata* are worth mentioning.

d. Vegetation: Coastal thickets, dry evergreen forests and shrubwoods, fragments of semi-deciduous forests on the slopes, small stands of mangrove.

District B.1.3.: The plain Artemisa—Colón (Güinense)

a. Geography: Gently rolling denudated plain. Fertile, calcareous red ferrallitic soils predominate.

b. Climate: Seasonal with dry winter. Usually 5–6 dry months. 1200–1800 mm annual precipitation.

c. Flora: Monotonous, no local endemics occur. The influence of the human impact of centuries is obvious.

d. Vegetation: Originally, this is the zone of seasonal evergreen and semi-deciduous forests which have been replaced by culture savannas and agricultural fields. Native vegetation occurs only in the mangrove and gallery forest belt on the seashore.

District B.1.4.: Yaguaramas—Cascajal plain (Cascajalense)

a. Geography: On the border of Matanzas and the old Las Villas province is this completely flat area at an altitude of about 100 m. The soil is mocarrero having an impermeable layer close to the surface.

b. Climate: Seasonal with 5–6 dry months in the winter. The annual precipitation is 1200–1400 mm.

c. Flora: A single endemic monospecific genus (*Rhodogeron coronopifolius*) and nearly 10 endemic species (e.g., *Bucida subinermis*, *Brunfelsia clarensis*, *Eriocaulon echinospermum*, *Lachnocaulon cubense* and three *Cheilophyllum* species) characterize the flora. The eastern limit of the distribution of western "savanna" plants may be drawn here. Eastward the flora becomes completely different: on the mocarrero soil shrublands and secondary savannas with *Copernicia* palms exist.

d. Vegetation: Thorny shrublands and savannas with *Sabal* palms on poorly drained hardpan soils. This is one of the largest edaphic savanna area in Cuba. It may have turned to marshes several times during the Quaternary, and then dried up.

District B.1.5.: Coastal area between Cienfuegos—Casilda (Casildense)

a. Geography: This zone begins at Juragua, east of Playa Giron and extends to the Casilda peninsula. Flat karsts consisting mainly of coastal coral limestone alternate occasionally with sand beaches. It is the ecological equivalent of floristic district II.1.2. on the southern coast, with shallow, humic-carbonated soils.

b. Climate: In the western part seasonal with dry winter of 5–6 months duration. In the east two arid seasons occur and the annual precipitation is 1000–1200 mm.

c. Flora: Strongly xerotherm flora containing large succulents, for example, *Dendrocereus nudiflorus*, *Leptocereus silvestris*, *Rhodocactus cubensis*, and *Pilosocereus brooksianus*. Widespread endemics are *Pavonia calcicola*, *Acalypha hutchinsoni*, *Rondeletia pedicellaris*, *Pectis ritlandi* and *Cassia clarensis*. A local endemic at Cienfuegos (*Acacia polypyrogenes*) and nearly ten further ones at Casilda (e.g., *Cordia intricata*, *Ipomoea flavopurpurea*, *Hyptis rivularis*, *Myrtus crenulata*, *Chrysophyllum clarensense*, *Casearia formosa*, *Rhacoma ekmanii*, etc.).

d. Vegetation: Rocky and sandy coastal communities, evergreen scrubs on the flat karsts, dry evergreen forests and semideciduous forests on deeper soils.

Sector B.2.: The Guamuhaya Massif or Escambray (Trinidadicum) (Fig. 37)

Isolated mountains above the southern coastal zone of central Cuba, divided into two smaller mountains: the more elevated Trinidad Mountains and the lower Sancti Spiritus and Banao Heights. A peculiarity of the flora is its double origin. The montane elements came from the mountains of Oriente, the plants of karsts are partly originated from Pinar del Rio. An endemic monospecific genus (*Euleria*) and approximately 20 regional endemics [e.g., *Miconia ancistrophora*, *M. wilsonii*, *Pachyanthus lunanus*, *Rondeletia leonis*, *R. pedicellaris*, *Tabebuia arimaoensis*, *T. glaucescens*, *Neobracea howardii* (Fig. 9), *Lunania elongata*, three *Calyptranthes* species, *Pithecellobium trinitense*, *Guettarda urbaniana* and *Gesneria clarensis* ssp. *clarensis*] characterize the area. Noted endemics in common with the mountains of Oriente are *Magnolia cubensis* s. l., *Hedyosmum grisebachii* (Fig. 7), *Coccoloba wrightii*, *Ossaea ottoeschmidtii*, *Clidemia wrightii*, *C. capituliflora*, *Meliosma oppositifolia*, *Ocotea ekmanii*, etc. Also, many Caribbean — Neotropical elements of montane rainforests occur, e.g., *Ocotea cuneata*, *O. wrightii*, *Guatteria blainii*, *Oxandra laurifolia*, *Garrya fadyeni*, etc. Some elements of the limestone forest communities of western Cuba reaching eastward this sector are *Tabebuia sauvallei*, *Sapium leucogym*, *Rhytidophyllum wrightianum*, *Karwinskia rocana*, *Rondeletia odorata*, and *Miconia cubensis*.

District B.2.1.: Trinidad Heights (Trinidadense)

a. Geography: Steeply inclined mountains with the highest point at 1156 m and a central plateau at 700 m. The parental rocks are mainly limestone or crystalline slate. Extensive limestone and dolomite karsts in the central and south-eastern part, and a granodiorite zone with scattered serpentine outcrops (San Blas) in the west. Humic carbonated soils on the southern slopes, tropical brown soils on the northern sides, acidic yellowish-red soils in the montane zone.

b. Climate: Seasonal with dry winter of 3–4 months duration up to an altitude about 400 m. One or two dry months up to 700 m and moist rainforest climate further up. The annual precipitation is 1200–2300 mm.

c. Flora: In addition to the regional endemics mentioned above, a number of local endemics occur, particularly in the montane rainforests, e.g., *Calyptronoma microcarpa*, *Pilea clarana*, *P. cacuminum*, *Rhytidophyllum lomense*, *Calyptranthes lomensis*, and *Spaniopappus iodostylus*. The montane karsts of Pico Potrerillo — the contact area of montane rainforests, semideciduous forests and karstic forests — is especially rich in local endemics (*Vernonia potrerilloana*, *Rondeletia potrerilloana*, *Karwinskia potrerilloana*, *Daphnopsis alainii*, *Banara glaberrima*, *Psychotria martii*, etc.). The Hanabanilla area (*Psidium celastroides*, *Erigeron capillipes*, *Cardamine porphyrophylla*) and the karsts of Buenos Aires (*Pinguicula jackii*) (Fig. 40) may also be mentioned. On the dry southern slopes several endemics with point-like geogra-

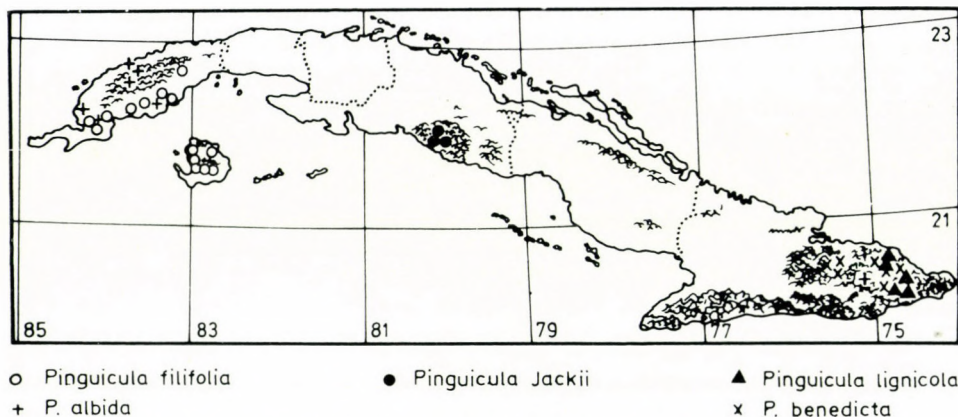


Fig. 40. Geographical distribution of the Cuban taxa of the genus *Pinguicula* (Lentibulariaceae) (after BISSE, LIPPOLD and CASPER 1975)

phical distribution occur, for instance, *Machaonia pubescens* (Fig. 38) and *Guettarda nervosa*.

d. Vegetation: Dry evergreen shrubwoods on the southern slopes up to 200 m, dry evergreen forests up to 550 m. In Pico Potrerillo occurs the semi-deciduous forest at the highest altitude in Cuba (900 m). In the interior of the mountains and on the northern slopes the seasonal evergreen forest belt occurs at an elevation as low as 400 m. At about 800 m the vegetation turns into montane rainforests. In the high parts of the valleys montane rainforests may occur downwards to 5–600 m some montane elements may descend along the watercourses even to the plains (e.g., *Calyptronoma dulcis*). In many valleys secondary forests of the introduced *Syzygium jambos* predominate.

District B.2.2.: Sancti Spiritus Heights (Spirituense)

a. Geography: Mountainous area east of the Agabama river, similar to the preceding district in geology, although much less karstic formations occur. The highest point is 843 m at the Banao Peak. Humic-carbonated soils predominate.

b. Climate: Seasonal with dry winter; 3–4, or at the higher altitude 1–2 dry months. The annual precipitation is 1600–1800 mm.

c. Flora: Due to the drier climate and lower altitude the montane rainforest belt is lacking although some montane elements occur, as *Meriania leucantha* ssp. *nana*, *Torrallbasia cuneifolia*. Yet, this area possesses about ten local endemics, such as *Tetrazygia aurea*, *Pachyanthus clementis*, *Rondeletia bicolor*, *R. convoluta*, *Hyperbaena acutifolia*, *Pilea clementis*, *Dorstenia rocana*, and *Psychotria banaoana*.

d. Vegetation: Less diverse than the vegetation of the preceding district. Semi-deciduous forests and, at a higher altitude, seasonal evergreen forests represent the dominant types.

Sector B.3.: Eastern central Cuba (Camagüeyicum) (Fig. 41)

Mainly young plains formed at the end of the Tertiary and in the Quaternary. Emergent, strongly eroded Cretaceous block mountains (Cubitas, Chorrillo, Jatibonico) and denuded serpentine ridges make the geology of this area more diverse. The limestone flora is originated mainly from the southern slopes of the Baracoa Mountains via the karsts of Sierra Maestra

and Sierra de Nipe. The serpentine elements came directly from Nipe and reached the serpentine hills around Holguin. An evidence of this is the recent distribution of three endemic genera in common with Oriente (*Hemithrinax*, *Doerpfeldia* and *Henoonia*). The colonization of the plains by plants was influenced by the relatively early rise of the northern coast in central Cuba: in the north the Oriente flora migrated to the farthest whereas on the southern coasts the most intensive migration was exhibited by the western elements. This discrepancy is expressed by the well-marked recent boundary of the two sectors.

The descent of plants to the lowlands resulted in a significant change of both the serpentine flora and the xerotherm forest flora. In this regard, the secondary speciation within two young palm genera of high genetic plasticity, *Copernicia* (Figs 36, 42) and *Coccothrinax*, was particularly intensive producing several taxa of hybrid origin (*Copernicia* × *textilis*, *C. × sueroana*, *C. × verpertilionum*, *C. × burretiana*, *C. × shaferi*). In addition, *Copernicia gigas*, *C. hospita*, *C. rigida*, *C. yarey*, *C. molineti*, *C. curbeloi*, *Coccothrinax salvatoris* and *C. clarensis* may be mentioned. Typical are the endemic species in common with southern Oriente, e.g., *Doerpfeldia cubensis*, *Henoonia brittonii*, *Eriochloa ekmanii*, *Mimosa fagaracantha*, *Jatropha tupaifolia*, *Sarcomphalus acutifolius*, *Croton myricifolius*, *Ravenia clementiana*, *Picetia marginata*, *Tabebuia trachycarpa*, *Brya chrysogonii*, *Polygala guantanamana*, and *Antirhea aristata*.

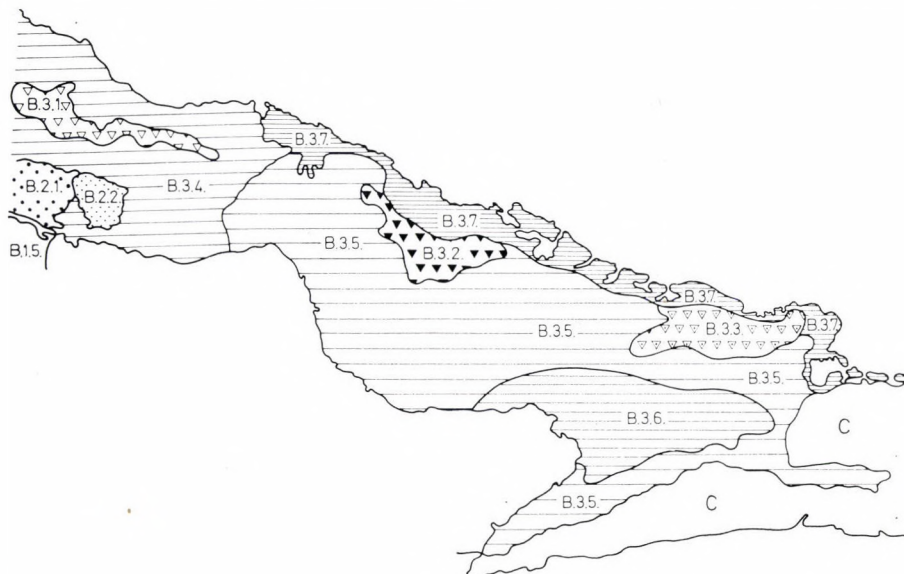


Fig. 41. The phytogeographical subdivision of the eastern part of the Central Cuban sub-province

- B.2. Sector: Guamuhaya Massif (*Trinidadicum*)
 - B.2.1. District: Trinidad Heights (*Trinidadense*)
 - B.2.2. District: Sancti Spiritus Heights (*Spirituense*)
- B.3. Sector: Eastern Central Cuba (*Camagüeyicum*)
 - B.3.1. District: *Claraense*
 - B.3.2. District: *Camagüeyense*
 - B.3.3. District: *Holguinense*
 - B.3.4. District: *Sagüense*
 - B.3.5. District: *Guaimareense*
 - B.3.6. District: *Cautoense*
 - B.3.7. District: *Gibareense*

Sub-sector B.3.a.: Isolated serpentine areas of Motembo—Holguin (Eu-Camagüeyicum) (Fig. 41)

Four serpentine outcrops of different area 100–200 kilometers apart from one another. The smallest one is Motembo having an area of about 50 km², the others are of 500–800 km² area each. Despite the isolation, the flora is unexpectedly uniform. The presence of Pan-Cuban endemics and the absence of *Moacroton* and the *Anemia coriacea* aggregate (Figs 11 and 12) characterize all areas. Some exclusively local endemics also occur, e.g., *Jacaranda cowellii*, *Zanthoxylum nannophyllum*, *Myrtus anomala*, and *Coccoloba geniculata* (Fig. 22).

Numerous serpentinophilous species occur only in two neighbouring areas. For instance, common endemics of the Las Villas and Camagüey serpentines are: *Croton nephrophyllus*, *C. camagüeyensis*, *C. heteropleurus*, *Daphnopsis oblongifolia*, *Machaonia subinermis* (Fig. 38), *Gochnatia cowellii*, *Thymopsis thymoides*. The number of Camagüey—Holguin endemics is much larger, e.g., *Platygyne parvifolia* (Fig. 14), *Jacquinia shaferi*, *Stenandrium crenatum*, *Cordia grisebachii*, *Myrtus cabanasensis*, *Karwinskia orbiculata*, *Ginoria microphylla*, *Polygala ambigens*, *Notodon savannarum*, and *Coccoloba cowellii*.

District B.3.1.: The serpentine of Santa Clara (Claraëense)

a. Geography: Hilly serpentine area with emergent ridges, in Sierra de Agabama up to 450 m, with gabbro and limestone outcrops. Red ferralitic soils, occasionally with pseudoglei character, and brown soils cover the first, humic carbonated soils the second. The isolated serpentine area around Motembo also belongs to this district.

b. Climate: Seasonal with 5–6 (or 3–4 in the north) dry months in the winter. The annual precipitation is 1100–1600 mm.

c. Flora: In addition to those mentioned above, about 15 local endemics occur. For example, *Eugenia clarensis*, *E. subdisticha*, *Guettarda clarensis*, *G. roigiana*, *Xylosma acunae*, *Karwinskia oblongifolia*, *Hypericum ophiticola*, *Xylosma claraense*, *Melocactus actinacanthus*, *Dorstenia lanei*, *Harpalyce macrocarpa*. To the Motembo area *Paspalum edmondi*, *P. motemboense*, *Cheilophyllum sphaerocarpum* and *Scleria motemboensis* are endemic.

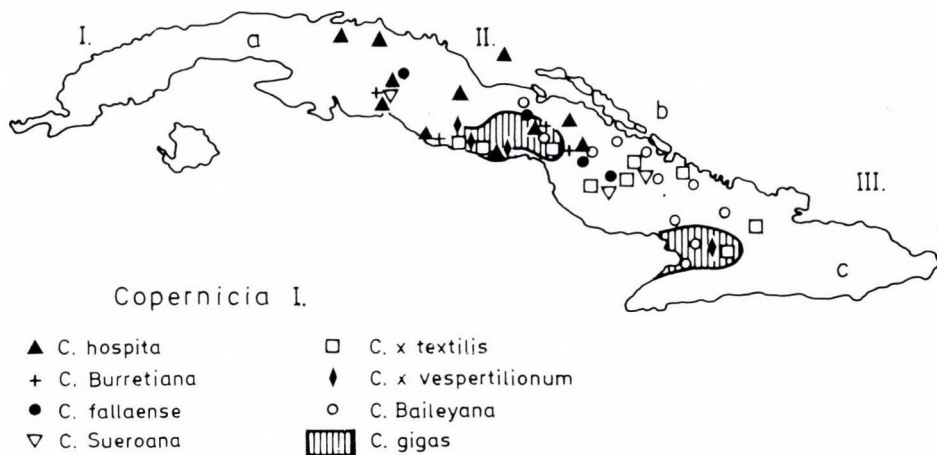


Fig. 42. Geographical distribution of some Central and East-Cuban taxa of the genus *Copernicia* (after DAHLGREN and GLASSMAN 1963, modified)

d. Vegetation: Dry evergreen thorny shrublands. Evergreen shrubwoods and forests on the brown soils. In many places forests and shrubwoods are replaced by secondary dwarf grass savannas and secondary *Brya* and *Dichrostachys* scrubs.

District B.3.2.: The serpentine of northern Camagüey (Camagüeyense)

a. Geography: Low, gently rolling flatland. Different allite-ferritic soils derived from serpentine, magnesium humic-carbonate soils, in the northwest ferritic latosols. Here and there granite, porphyrite and diorite intrusions occur.

b. Climate: Seasonal with dry winter of 5–6 months duration and 1200–1400 mm annual precipitation.

c. Flora: In addition to the common serpentinophilous endemics listed above, this district has 15 local endemic species. In particular, the palms (*Copernicia cowellii*, *Coccothrinax camagüeyana*, *C. pseudorigida* (Fig. 42) are famous. Further endemics are *Reynosia camagüeyensis*, *Randia acunae*, *Waltheria ovalifolia*, *Eugenia shaferi*, *E. malanadenia* ssp. *santayana*, *Cameraria microphylla*, *Nashia variifolia*, *Cheilophyllum macranthum*, *Justicia stenophylla*, *Rondeletia insularis*, *Guettarda camagüeyensis*, and *Wedelia urbanii*.

d. Vegetation: The primary vegetation of this district is evergreen thorny shrubwoods with dwarf palms and shrublands with small grassy clearings. The latter type became gradually predominant due to burning and grazing. The formerly widespread view that the "serpentine savannas" are original is not supported by the comparative taxonomic-phytogeographic-phytosociologic studies of the author (see BORHIDI and HERRERA 1977, BORHIDI 1973, 1974, 1976).

District B.3.3.: The serpentine of Holguín (Holguinense)

a. Geography: A diversified hilly landscape with wide ridges and inclined conical serpentine hills with isolated limestone terraces and cliffs. On the SW and NE border of the area there are red allitic-ferritic soils. Elsewhere tropical brown soils derived from serpentine predominate.

b. Climate: Seasonal with two dry seasons. 5–6 dry months, 800–1200 mm annual precipitation.

c. Flora: Rich in endemics. The flora, especially in Cerro Galano, is closely related to that of Sierra de Nipe and Sierra del Cristal with several endemics in common, for example, *Spirothecoma holguinensis*, *Piper holguinianum*, *Ateramnus revolutus*, *Moacrotan lanceolatus*, *Jacquinia robusta*, *Brya hirsuta*, *Leucocroton saxicola*, *Salacia nipensis*, *Antirhea ophiticola*, *Euphorbia podocarpifolia*, *Antirhea minutifolia*, *Coccoloba nipensis*, *Guettarda shaferi*. Approximately 20 local endemics have been indicated, e.g., *Agave anomala*, *Coccothrinax garciana*, *Acacia belairioides*, *Pithecellobium savannarum*, *Caesalpinia hermeliae*, *Acidocroton trichophyllus*, *Chamaesyce filicaulis*, *Buxus heterophylla*, *Neobesseyia cubensis*, *Justicia tomentulosa*, *Rondeletia savannarum*, *R. shaferi*, *Gochnatia parvifolia*, *Cassia holguinensis*, *Croton acunae*, *C. holguinensis*, *Melocactus holguinensis* (Fig. 45), *Machaonia urbinoi* (Fig. 38), *Oplonia multigemma* (Fig. 40).

d. Vegetation: The conical serpentine mountains, the rocky ridges and the plains were formerly covered by thorny solerophyllous evergreen shrubwoods containing dwarf palms. These have been replaced by secondary savannas with short grasses and palms. The microphyllous semi-deciduous forests in the valleys were cleared and then turned to agricultural lands.

Sub-sector B.3.b.: The lowlands, limestone hills, south-coastal zones and keys of eastern central Cuba (Guaimaricum) (Fig. 41)

Mainly farmland with unvaried vegetation. The points made in B.1 and B.3 are relevant here, too. The flora is characterized by relatively few endemics, in particular, *Copernicia*

hospita, *C. gigas*, *C. vespertilionum*, *C. textilis*, *C. sueroana*, *C. baileyana* (Fig. 42) and *Hildegardia cubensis* (reaching to the northern coasts and keys too and the xerotherm endemics in common with southern arid zone of Oriente. Its phytogeographic division is based primarily on the characteristics of lands because the phytogeographical boundaries have been obscured as a result of human impact. Many important elements of the Neotropical xerotherm flora, such as *Phyllostylon brasiliensis* and *Prosopis juliflora* have reached this sub-sector from the east.

District B.3.4.: The hilly and flat areas and the northern coastal zone in Las Villas (Saguense)

a. Geography: Diversified landscape. The coastal zone is covered by peaty and meadow soils developed on Quaternary sediments. On the Jurassic limestone of the northwestern heights and the Cretaceous limestone of the northeastern heights (including Sierra de Jatibonico) there are humic-carbonated soils. In the valleys ferrallitic soils are predominant. In the lowlands and hills of the west and southwest the tropical brown soils derived from young Tertiary sediments cover extensive areas.

b. Climate: Seasonal bixeric with two dry season (3–4 months) on the northern coast. Elsewhere monoxeric seasonal with dry winter (5–6 months). At the northeastern heights only 3–4 dry months. Annual precipitation is 1200–1600 mm on the average.

c. Flora: It is characterized by the forest elements of limestone rocks, these are in fact typical of the whole country. The Caguaguas mogotes at Sagua la Grande possess a special flora, including the representatives of two rare endemic genera [*Hemithrinax ekmaniana* (Fig. 13), *Megalopanax rex*]. Endemic palms of the savannas are *Copernicia burretiana*, *C. textilis*, *C. molineti* (Fig. 42). *Caesalpinia savannarum* and *C. glaucophylla* are also endemic species of the savannas.

d. Vegetation: The coastal zone is lined with a broad mangrove belt. On the meadow soils moist and treeless secondary savannas predominate taking the place of the former woodlands. In the hills some fragments of semi-deciduous forests represent the natural climax vegetation. Most part of this area is agricultural land, all the tropical brown and red ferrallitic soils are utilized for agricultural purposes. On the mocarrero soils in the southeast semi-culture savannas with *Copernicia* palms occur, probably in the place of microphyllous semi-deciduous forests.

District B.3.5.: The Ciego de Avila—Alto Cedro—La Maya plains (Guaimarensis)

The central and southern parts of Camagüey and the western lowlands in Oriente, except the northern coastal zone and the low Cauto Basin are included.

a. Geography: Mainly denuded plains with a gentle inclination towards the southern coast. Along the shore a wide swamp belt occurs. In western Camagüey, on the plain of Ciego de Avila-Morón, mainly calcareous and fertile red ferrallitic soils are found. In the Camagüey-Tunas-Holguin denuded plains in the interior of the island except the area of districts B.3.3.–B.3.4. tropical brown soils predominate. The karstic limestone mountains (Sierra de Najasa) are covered with humid-carbonated soils. In the lowlands parallel to the coast alluvial soils are the most common. Tropical brown soils with mocarrero mosaics are also found here. The only sandy area of central Cuba is located south of Victoria de las Tunas with a peculiar flora and fauna.

b. Climate: Seasonal tropical which is dry in the winter. 5–6 dry months occur per year. In southern Camagüey persists a more humid climate with 3–4 dry months in the winter. East of Holguin and in the northern foothills of Sierra Maestra there are two dry seasons of 5–6

months duration. The annual precipitation is 1800 mm in the west and gradually decreases eastward to a level of 800 mm/year.

c. Flora: Similar to that of the preceding district. Strongly affected by human impact and quite uniform. Some local endemics occurring in certain places, e.g., *Cleome tenuifolia* (Galbis), *Caesalpinia hornei* (Ciego de Avila). *Rondeletia gamboana*, *Catesbaea gamboana*, *Cleome gamboensis* and *Copernicia longiglossa* is found on the sands at Victoria de las Tunas, the latter also at Dumañuecos (!). At the edge of the Cauto valley *Ateleia parvifoliola* (Mir), *Crotalaria urbaniana* and *Bergia sessiliflora* (Bayamo), *Coccothrinax savannarum* and *C. pauciflora* (Miranda) occur.

d. Vegetation: The natural vegetation of the ferrallitic soils in the central Cuban denuded plains are seasonal evergreen forests, semi-deciduous forests and gallery forests along the rivers on alluvial soils and black tropical soils. In the brown soil zone of the Camagüey-Tunas-Holguin plains extensive semi-deciduous forests with *Sucietenia mahagoni* were found even at the turn of this century. This species is still present as a standard tree in the recent deciduous tree-savannas. On sand and mocarrero microphyllous semi-deciduous forests with *Copernicia* palms, remnants of open forests with loose canopy layer (foret claire) and their derived savannas are found. The shoreline is covered by broad mangrove vegetation. On the rocks of Sierra de Najasa the eastern versions of karstic forests occur in which *Coccothrinax* palms and cacti are typical.

District B.3.6.: The Cauto Basin (Cautoëense)

a. Geography: The alluvial area and the delta of Rio Cauto are among the youngest areas on the surface of Cuba. The delta is covered by peaty soils containing brackish water. On the alluvium tropical black soils and alluvial soils are found. These tend to become alkaline soils in some places.

b. Climate: Seasonal with dry winter in the west. Two dry seasons in the eastern part of the area with a total of 5-6 dry months. The annual precipitation is about 700-1200 mm.

c. Flora: Depauperated upon human influence, monotonous, species poor. *Chamaesyce biraensis* is an endemic of the marshes in the delta area.

d. Vegetation: Only a few degraded stands of the extensive rainforest-like gallery forests remained. The natural vegetation is replaced by treeless marshy meadows and moist savannas. As a result of deforestation, erosion is intensive.

District B.3.7.: Littoral terraces and islands of the northern coastal area; the Cayo Francés—Turiguanó—Cebolla zone (Gibareense)

a. Geography: The flat coastal area and the archipelago are composed of young Tertiary and Quaternary limestone sediments and subfossil peat layers. There are, too, some small limestone outcrops (Turiguanó, Cayo Romano). For phytogeographic reasons, the higher limestone hills and karstic mountains, Loma Cunagua, the upper Cretaceous-Eocene blocks of the Sierra de Cubitas and the limestone mountains of the Mariabón group at Gibara and Banes are also assigned to this district. Salt marshes and flat karsts covered by shallow humic-carbonated soils alternate in this area. Occasionally, smaller serpentine, gabbro and diabase outcrops increase the geological variability (Puerto Padre, Bahía de Naranjo). The hills and mountains are covered by tropical brown soils and brown carbonated soils. In the valleys of Sierra de Cubitas red ferrallitic soils occur.

b. Climate: Seasonal bixeric climate with two dry seasons. In general, 5-6 dry months occur, 7-8 in the islands and only 3-4 in the east at Banes. The annual precipitation is 700-1100 mm on the average. The precipitation is low in the Puerto Padre-Gibara area where climate is

similar to that of South-Oriente and sometimes years of extreme drought may also occur.

c. Flora: Local xerotherm endemics. The close relationship to the flora of Bahamas is indicated by many species shared by the two regions, e.g., *Guapira bracei*, *Pithecellobium millsbaughii*, *Eugenia lucayana*, *Cordia bahamensis*, *Auerodendron northropianum* and *Phialanthus myrtilloides*. Relatively few indigenous species are typical of the whole district, for example, *Coccothrinax salvatoris*, *Trichilia pungens*, *Sarcomphalus obovatus*. On the contrary, many local endemics are found in the islands and peninsulas e.g., *Chamaesyce paredonensis*, *Heliotropium myriophyllum* (Cayo Paredon Grande), *Selenicereus brevispinus*, *Nashia cayensis*, *Isocarpha glabrata*, *Notodon cayensis* (Cayo Guayaba), *Crescentia mirabilis* (Cayo Sabinal). *Guettarda lanuginosa* and *Argythamnia microphylla* are in common with Sierra de Cubitas and the coast. *Coccothrinax muricata* is an endemic palm species of the Cubitas and Najasa mountains. A local endemic of Sierra de Cubitas is *Guettarda munizii*. *Copernicia oxycalyx* occurs in the savannas of Manati. The Puerto Padre-Playa Herradura area is the richest in endemics, e.g., *Ximenia roigii*, *Acacia cupeyensis*, *A. curbeloi*, *A. roigii*, *Zanthoxylum curbeloi*, *Banara wilsoni*, *Tabebuia truncata*, *Xylosma roigii*, *Randia costata*, *Baccharis orientalis* ssp. *orientalis*, *Galactia rotundata* and *Casasia clusiifolia* var. *hirsuta* are endemic to Gibara and surroundings, whereas *Pictetia arborescens* is endemic to Playa Pesquero Nuevo. *Eugenia pteroclada* is an endemic species of Banes. In the very dry coastal area between Puerto Padre and Banes some elements of the southern Oriente semi-desert zone also occur, for instance, *Lemaireocereus hystrix*, *Bonania microphylla*, *Amyris diatrypa*, *Samyda ramosissima*, *Cordia curbeloi*, *Eupatorium littorale*, *Thouinia pseudopunctata*, *Pseudocarpidium avicennioides*, *Oplonia polycece*, and *Doerpfeldia cubensis*.

d. Vegetation: Besides the extensive mangroves, the most attractive types are the dry evergreen forests and xerotherm evergreen scrubs of flat karsts. The former gallery forests grown on alluvial soils have been replaced by secondary savannas. The natural vegetation on brown soils is the semi-deciduous forest as seen in Loma Cunagua and the valleys of Sierra de Cubitas. The eastern Cuban karstic mogotes with *Coccothrinax* palms have been even less intensively studied.

SUB-PROVINCE C: EASTERN CUBA (ORIENTO-CUBANICUM) (Fig. 43)

This phytogeographic unit includes two big massifs in Oriente, the Sierra Maestra and the Nipe-Baracoa range, the basin in between and the adjacent coastal lowlands. This area is considered to be the cradle of the Cuban flora and, together with western Hispaniola, the most prominent centre of speciation in the Antilles. In addition to the 13 Pan-Cuban and 5 central-eastern Cuban endemic genera, there are 24 genera and more than 1500 species exclusively endemic to this sub-province. Approximately 1950 endemic taxa, including western and Pan-Cuban elements, occur in this area of about 18 000 km². The close relationship to Hispaniola is indicated by ten other endemic genera (*Plethadenia*, *Spirotecoma*, *Bellonia*, *Barleriola*, *Picardaea*, *Isidorea*, *Margaritopsis*, *Peratanthe*, *Fuertesella*, and *Victorinia*) and 103 species present in both islands. Furthermore, this sub-province is the evolutionary centre of 22 Caribbean genera, such as *Roystonea*, *Spathelia*, *Leucocroton*, *Bonania*, *Reynosa*, *Auerodendron*, *Neobracea*, *Pseudocarpidium*, *Gesneria*, *Rhytidophyllum* and *Acrosynanthus*, and the largest or one of the largest evolutionary centres for additional 32 Neotropical and Pantropical flowering plant genera, e.g., *Coccothrinax*, *Lepanthes*, *Metopium*, *Buxus*, *Purdiaea*, *Calypttranthes*, *Pimenta*, *Eugenia*, *Pachyanthus*, *Ossaea*, *Lyonia*, *Tabebuia*, *Dorstenia*, *Coccoloba*, *Schoepfia*, *Pilea* (shared with Hispaniola), *Harpalyce*, *Amyris*, *Rondeletia* and *Gochnatia*. It may be concluded from this list that this area is in fact one of the richest gene reserves of the world. Its exploration, however, is by no means complete.

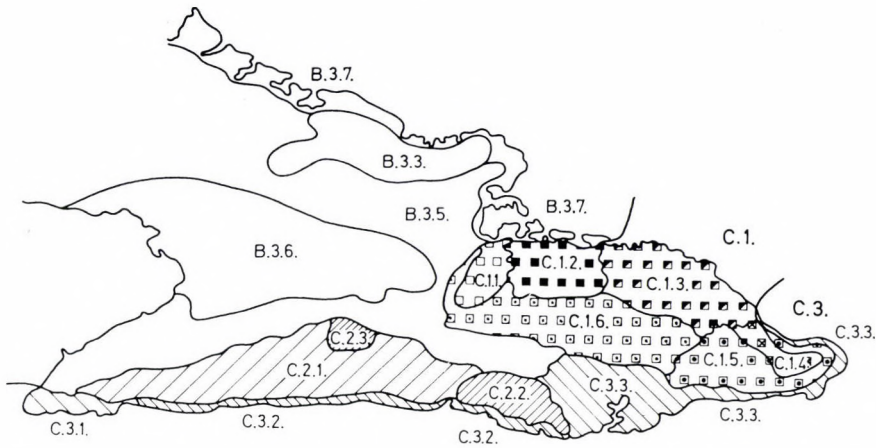


Fig. 43. The phytogeographical subdivision of the East-Cuban sub-province

- C.1. Sector: Sagua-Baracoa massif (*Moanicum*)
 - C.1.1. District: Nipe Mountains (*Nipense*)
 - C.1.2. District: Cristal Mountains (*Cristalense*)
 - C.1.3. District: Moa and Toa Mountains (*Moaëense*)
 - C.1.4. District: Serpentine of Baracoa (*Baracoëense*)
 - C.1.5. District: *Purialense*
 - C.1.6. District: *Yaterense*
- C.2. Sector: Sierra Maestra (*Maesticum*)
 - C.2.1. District: Western Maestra (*Turquinense*)
 - C.2.2. District: Eastern Maestra (*Piedraëense*)
 - C.2.3. District: Mogotes of the Maestra (*Bairense*)
- C.3. Sector: South-eastern coasts (*Santiagicum*)
 - C.3.1. District: *Pilonense*
 - C.3.2. District: *Uveroëense*
 - C.3.3. District: *Guantanamoense*

Two humid mountainous areas (Sierra Maestra and Nipe-Baracoa) and an arid coastal plain is included in this phytogeographical category. The mountains have three endemic genera (*Synopsis*, *Zonanthus*, *Triscenia*) and more than 325 endemic species, mainly orchids (e.g., *Pleurothallis*, *Lepanthes*, *Epidendrum*, *Maxillaria* species). Furthermore, many species of *Lyonia*, *Coccoloba*, *Clusia*, *Pilea*, *Peperomia*, *Ossaea*, *Miconia*, *Calycogonium*, *Eupatorium* and *Vernonia*; and several montane species, such as *Clethra cubensis*, *Magnolia cubensis*, *Purdiaea nipensis*, *Euphorbia helenae*, *Calyptrotrichia clementis*, *Ilex macfadyenii*, *Myrica punctata*, *M. shaferei*, *Cleyera nimanima*, *Guatteria moralesi*, *Illicium cubense*, *Laplacea ekmanii*, *L. wrightii*, *Dalbergaria cubensis* and *Bumelia jubilla* may be mentioned. Contrarywise, the arid coastal plain has many species in common primarily with the limestone karsts of mountains, e.g., *Hyperbaena cubensis*, *Calliandra orientalis*, *C. colletioides*, *Alvaradoa arborescens*, *Bursera glauca*, *Stigmaphyllon lineare*, *S. sericeum*, *Plumeria stenophylla*, *Rochefortia stellata*, *Tabebuia arenicola*, *T. hypoleuca*, *T. libanensis*, *T. simplicifolia*, *Gesneria gibberosa*, *Rhytidophyllum intermedium*, *Agave underwoodii*, *Rondeletia lomensis*, *R. baracoensis*, *Eupatorium* (*Grisebachianthus*) *carsticola*, *Aristida laevigata*, *A. pradana*, *Rajania baracoensis*, *Pitcairnia cubensis*, *Aristolochia lindeniana*, *Coccothrinax gundlachii* and *Gochnatia maisiana*. Particular attention should be paid to two isolated ancient relicts of this area, namely *Dracaena cubensis*, which has its closest relatives in the Canaries and Honduras, and *Cneorum trimerum*, the only Neotropical species of the Cneoraceae which includes merely 3 species, the other two being native to the Canaries and the European Mediterranean.

Sector C.1.: The Nipe—Baracoa Massif (Moanicum) (Fig. 43)

Extensive serpentine ranges and large, bordering limestone karsts. The flora development of this area has been continuous since the upper Eocene. This region is characterized by high relief energy and diversified edaphic, macro- and microclimatic conditions. The richest flora of the Caribbean, and one of the richest floras of the World is found here and, too, this area is the most significant evolutionary centre of the Cuban flora and a starting point for the dispersal of species groups with different ecological requirements (serpentinophilous, montane and karstic elements). Eighteen endemic genera occur, five confined to this sector, namely *Tetralix*, *Phidiasia* (Fig. 44), *Schmidtottia* (16 species!), *Ariadne* and *Ekmanochloa*. The majority of species belonging to highly polymorphic genera, such as *Podocarpus*, *Gochnatia*, *Vernonia*, *Guettarda*, *Rondeletia*, *Purdiaea*, *Phyllanthus*, *Moacrotan* (Fig. 12), *Coccoloba*, *Casearia*, *Spathelia* (Fig. 6), *Siphocampylus* and *Hemithrinax* (Fig. 13), etc., have a limited geographical range restricted to this sector. The number of regional endemic species is about 200. However, if the local endemics are also considered this number reaches 725. Some typical species are *Podocarpus ekmanii*, *Pinus cubensis*, *Dracaena cubensis*, *Guettarda ferruginea*, *Phyllanthus myrtilloides*, *Cyrilla cubensis*, *Rauwolfia salicifolia* and *Clerodendron nipense*.

Sub-sector C.1.a.: The serpentine mountains of the Nipe—Baracoa Massif (Eu-Moanicum)

Four mountains or mountain groups have been distinguished from a phytogeographic point of view. These are the Nipe, Cristal, Moa and the Baracoa-Jauco zone. The first two, just as the second two, represent more closely related units. Nipe and Cristal are separated only by a narrow limestone strip, the valley of Rio Mayari. The boundary between Moa and Baracoa is a narrow gabbro zone. However, Cristal and Moa fall far apart, there is in between the wide Sagua de Tanamo depression lined with Tertiary limestones. This area, with its mesophilous tropical forest, must have acted as an important barrier of migration for the serpentine floras. Within the East-Cuban sub-province this area has the richest flora. Of its eighteen endemic genera sixteen are confined to this sub-sector, including all regional endemic

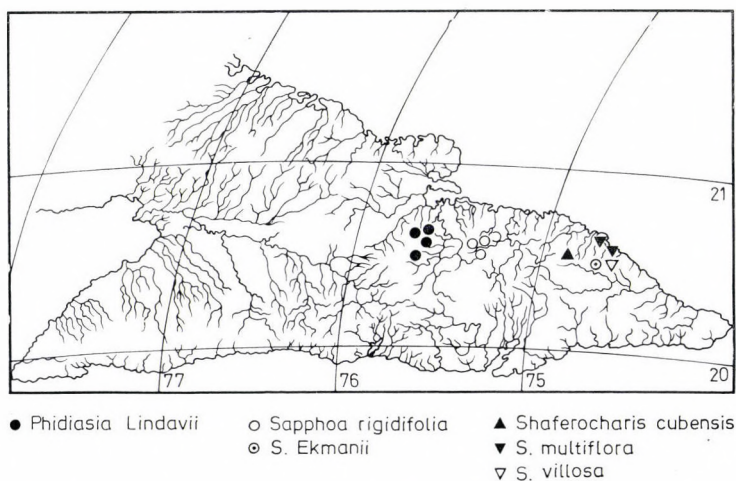


Fig. 44. Geographical distribution of the endemic genera *Phidiasia*, *Sapphoa* and *Shaferocharis* (after BORHIDI 1981, modified and original)

genera and the majority of the 725 endemic species. The number of vicarious species in the mountains is large. Also, many vicarious subspecies occur providing evidence for speciation in more recent times. The *Calycogonium rosmarinifolium* (Fig. 18), *Casasia nigrescens* (Fig. 17), *Moacrotan lanceolatus* (Fig. 12), *Anemia coriacea* (Fig. 11) and *Phyllanthus myrtilloides* aggregates are examples. All developmental stages of serpentine soils are found in this area and, as a result of the different ecological conditions of serpentine habitats, the floristic and vegetational variability ranges from the arid evergreen shrublands to the submontane rainforests.

District C.1.1.: Sierra de Nipe (Nipense)

a. Geography: A serpentine plateau at 600 m elevation, relieved by narrow and deep canyons and covered by old fossil ferrallitic and ferritic soils. The eroded forms of these soils are mixed with more recent serpentine rendzina on the ridges and covered by the humic drift of slopes in the valleys.

b. Climate: Seasonal with dry winter, 3–4 dry months in the south and 1–2 dry months in the interior. Two dry seasons of 3–4 months duration on the northern slopes. Montane rainforest climate at Loma Mensura. The annual precipitation is between 1200 and 2300 mm.

c. Flora: The relatively wide climatic conditions of this small area account partly for the uniqueness of the flora. Four monospecific endemic genera, *Dasytropis*, *Koehneola*, *Harnackia* (Fig. 10) and *Ciceronia*, and about 140 local endemic species, especially from the genera of *Tabebuia*, *Leucocroton*, *Chaptalia*, *Brunfelsia*, *Callicarpa*, *Eugenia*, *Calyptranthes*, *Phyllanthus* and *Rhynchospora* occur. Further 21 species are common to this district and the Cristal Mountains, examples are *Euphorbia podocarpifolia*, *Eugenia piedraensis*, *Schmidtottia cubensis*, *Suberanthus canellaefolius*, *Senecio subsquarrosus*, *Vernonia desiliens*, and *Gochnatia cubensis*, etc. Some species are exclusively found here and in Moa, being absent from the Cristal Mountains in between. These are *Pithecellobium nipense*, *Ravenia simplicifolia*, *Phyllanthus phlebocarpus*, *Ph. estrellensis*, *Buxus aneura*, *Phidiasia lindavii* (Fig. 44), *Matelea nipensis*, *Exostema stenophyllum*, and *Psychotria lopezii*. The richness of certain valleys (e.g., Rio Piloto) or peaks and ridges (Loma Mensura, Loma Bandera, Loma Winche) in local endemics is also of particular interest.

d. Vegetation: Semi-arid evergreen shrubwoods on the sharp ridges. Various natural and secondary *Pinus cubensis* forest communities on the slopes and the plateau. Semi-arid montane rainforests predominate along the watercourses. Semi-arid montane shrubwoods occur on the western and eastern slopes of Loma Mensura. The "montane serpentine savannas" of CARABIA (1945) have been resulted from the deforestation of relict pinewoods.

District C.1.2.: Sierras del Cristal and Micara (Cristalense)

a. Geography: Massif consisting of deeply inclined conical hills and sharp ridges. The lower sections are covered by ferrallitic soils. Over 700 m these are replaced by yellowish-red montane clays.

b. Climate: More uniform than the climate of the preceding district. The dry season is in the winter with 1–2 dry months at the margin of the mountains. Humid rainforest climate in the interior. Annual precipitation between 1600–2300 mm.

c. Flora: Strikingly poor and monotonous when compared to the flora of the neighbouring Nipe and Moa Mountains. This is indicated by breaks in the distribution of numerous species mentioned in the discussion of the preceding district. This situation may be partially accounted for by the deficiency of these mountains in extreme, dry rocky habitats. Another reason is that this area is not thoroughly explored. Thus, only one (!) endemic monospecific genus

(*Eosanthus cubensis*) and about 50 endemic species are known. Most of these species are markedly different from their relatives, for example, *Lagenocarpus cubensis*, *Freziera conocarpa*, *Moacrotan cristalis* (Fig. 12), *Buxus imbricata*, *B. olivacea*, *Croton pachyrrhachis*, *Ilex cristalis*, *I. eoa*, *I. paucinervis*, *I. subavenia*, *Chaetocarpus cordifolius*, *Leucocroton obovatus*, *Pachyanthus monocephalus*, *Jacquinia sessiliflora*, *J. oligantha*, *Senecio ekmanii*, *Sapphoa rigidifolia* (Fig. 44), *Acrosynanthus ovatus*, *Gesneria pachyclada*, *Dendropanax nervosus*, *Ossaea cristalis*, etc. Whereas the Cristal Mountains are poor only in comparison with the neighbouring districts, the coniferous forests of Sierra de Micara are monotonous by any standard with an only exception of the dry rocky ridge of Saca La Lengua: as few as 6–8 endemics, such as *Annona cristalis*, *Erythroxylum flavicans*, *Rondeletia bissei*, *Ossaea micarensis*, *O. pinetorum*, *Myrtus micarensis* and *M. del-riscoi* have been known.

d. Vegetation: The coniferous zone is much narrower than in Nipe, Seasonal evergreen forests run up to an altitude of 600 m with moist rainforest mosaics. Between 600 and 1100 m pine forests of *Pinus cubensis* are dominant. From 1100 to 1230 m semi-dry montane shrubwood, variant of cloud forest on serpentine, is found. On the southern serpentine cliffs of Pico del Cristal the existence of a peculiar vegetation, namely dry montane evergreen shrubwoods, may be assumed.

District C.1.3.: Sierras de Moa and Toa (Moaense)

The most extensive floristic district on serpentine. Its flora probably has the longest history in Cuba, as this area is considered to be the evolutionary centre of the vegetation in these mountains.

a. Geography: In general, wide and flat ridges and plateaux are typical (Cupeyal, El Toldo, Altos de Iberia) although the Cuchillas de Toa range between the Jaguani and Toa rivers consists of conical and pyramidal mounts. Very old, red ferritic soils predominate. In zones close to the coast (Cerro Miraflores, Yamanigüey) younger ferrallitic serpentine soils are found. The middle and upper section of the Toa valley is mainly covered by yellowish-red montane soils derived from serpentine.

b. Climate: The most humid area in Cuba. At the northern, western and southern boundary there are two dry seasons of 1–2 dry months duration. In the interior the climate is warm and moist throughout the year. At about 7–800 m altitude it is replaced by moist montane rainforest climate. Annual precipitation between 1400–3000 mm, occasionally near to 5000 mm in certain localities.

c. Flora: Very rich and diverse. Four endemic genera, *Kodalyodendron*, *Schaferocharis*, *Shafera* and *Feddea*, and nearly 200 local endemic species, e.g., *Hemithrinax rivularis* and var. *savannarum* (Fig. 13), *Moacrotan leonis*, *M. tetramerus*, *Phyllanthus chryseus*, *Callicarpa oblanceolata*, *Bonnetia cubensis*, *Laplacea moaensis*, *Talauma minor* ssp. *oblongifolia*, *Shafera platyphylla*, *Schaferocharis cubensis*, *S. multiflora*, *S. villosa*, *Cassia bucheri*, *Byrsonima bucheri*, *Acacia bucheri*, *Brya subinermis*, *Casearia ophiticola*, and 7 *Buxus*, 4 *Coccoloba*, 5 *Leucocroton*, 4 *Ilex*, 5 *Calyptranthes*, 4 *Myrcia*, 6 *Eugenia*, 6 *Miconia*, 5 *Calycogonium*, 6 *Ossaea*, 4 *Clusia*, 8 *Cordia*, 3 *Callicarpa*, 6 *Tabebuia*, 6 *Schmidtottia* and 6 *Senecio* species, etc. occur. Numerous endemics are in common with the Nipe Mountains (see above), with Sierra del Cristal (e.g., the endemic genus *Sapphoa*, *Neobraccia ekmanii*) (Fig. 9), the Baracoa-Jauco district discussed below (e.g., *Moacrotan ekmanii* (Fig. 12), *Cordia duartei*, *Platygyne obovata*, *Suberanthus stellatus*, *Casearia bissei*, *Feddea cubensis*, *Dracaena cubensis*, etc.) and even with the Monte Libano group (e.g., *Gesneria cubensis*, and *Columnea tinctoria*). Several minor developmental centres may be recognized within the mountains (Cerro Miraflores—Playa la Vaca, Yamanigüey, Alto de Iberia, El Toldo, Pico Galán, and the surroundings of old nickel mines: Mina Iberia, Mina Potosí, Mina Franklyn, Mina Cayo Guam, Mina Delta), although it has been shown (BORHIDI and

MUÑIZ 1972b) that many species had been thought to be local endemics turned to be in fact only regional endemics of wider distribution.

d. Vegetation: In the northern foothills, the Cupeyal Plateau and the upper Toa valley various forest communities of *Pinus cubensis* predominate. Along the coast these forests alternate with microphyllous evergreen shrubwoods very rich in species, including strongly isolated endemics such as *Kodalyodendron cubensis*, *Shaferocharis multiflora*, *Tabebuia linearis*, *Acrosynanthus minor*, *Miconia javorkaeana*, *Forchammeria emarginata*, *Coccoloba acuna*, *Phyllanthus comosus*, *Eupatorium minutifolium*. Over 400 m and up to 6–700 m semi-arid montane rainforests occur. At higher altitude semi-arid montane shrubwoods correspond to the climax vegetation type. On the dry tops of some serpentine plateaux (e.g. El Todo) a dwarf pine-woodland of *Pinus cubensis* is developed (Pócs, ex verb.). In the valleys of the Jaguani and Toa rivers are found the *Carapa guianensis* forests, representing the only submontane tropical rainforest zone in Cuba.

District C.1.4.: The serpentine areas of Baracoa and Jauco (Baracoëense)

a. Geography: This area, situated east of the Quibiján and Toa rivers, is younger, lower and, too, poorer in species than the preceding districts. Yellowish red montane soils and latosols occur in the west, latosolic red serpentine soils in the east.

b. Climate: Humid rainforest climate with no seasons. Annual precipitation between 1600 and 2900 mm.

c. Flora: Most species are in common with Moa. Approximately fifty local endemic species are found here, for example: *Melocactus radoczii* (Fig. 45), *Buxus baracoensis*, *Cordia baracoensis*, *Siphocampylus baracoensis*, *Schmidtottia multiflora*, *Ossaea elliptica*, *Henriettea cuabae*, *Exostema shaferi*, *Xylopia ekmanii*, *Spathelia leonis* (Fig. 6), *Leucocroton ekmanii*, *Rhamnidium pruinosum*, *Ternstroemia baracoensis*, etc.

d. Vegetation: Submontane rainforests in the west, pinewoods on ferritic soils, and mainly microphyllous evergreen shrubwoods in the Peladeros de Jauco zone in the east.

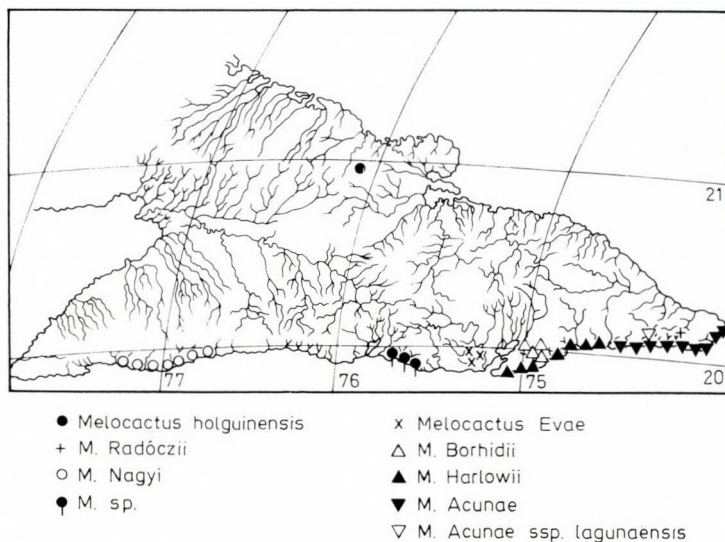


Fig. 45. Geographical distribution of the East-Cuban taxa of the genus *Melocactus* (after MÉSZÁROS 1977)

Sub-sector C.1.b.: The limestone karsts and other not serpentine ranges of the Nipe—Baracoa Massif (Yatericum)

This sub-sector includes the mogates of the southwestern Sierra de Nipe, the partially eroded limestone blocks folded at the margin of serpentine mountains, in the Monte Libano–Monte Cristo–Monte Verde group, the sandstone hills mingled with the limestone blocks, and the Sierra del Purial range with the Sierra de Imias which continues as a limestone plateau towards the end of the island. The endemics are not evenly distributed over the area. The deciduous forests occurring on sandstone have very few floristic specialities, whereas the limestone cliffs are very rich in endemics due to geographical isolation. In spite of this heterogeneity, the sub-sector played a significant role in the flora evolution of Cuba for two fundamental reasons: 1. Via this area migrated the montane flora from the north (Moa, Cristal) southward (Sierra Maestra). 2. The limestone cliffs are considered to be the cradle of the southern Oriente xerotherm flora which, in the Quaternary, moved both to the west and towards the terraced coastal area. The existence of these floristic relationship is best shown by the distribution of the vicarious species of *Gesneria*, *Eupatorium* and *Siphocampylus*.

District C.1.5.: Sierra del Purial, Yunque de Baracoa and the Gran Tierra Plateau (Purialense)

a. Geography: Diversified mountainous area. Sierra del Purial is a deeply inclined range up to 1100 m altitude, Gran Tierra is a "meseta" area. Quite different are the mogotes west of the Yumuri valley and the anvil-shaped Yunque de Baracoa monadnock consisting of limestone and dolomite. Tropical brown soils predominate in the Sierra del Purial and Yunque. In some elevated places yellowish-red montane soils occur. In the limestone area of Gran Tierra and Yumuri humic-carbonated soils are the most common.

b. Climate: Characterized by sudden changes along a gradient. There is hardly any transition between the bixeric climate of two dry seasons (3–4 dry months), the wet tropical and the montane rainforest climate. In the northeast a particular tropical seasonal climate occurs which is dry in the summer. Annual precipitation 1000–2200 mm.

c. Flora: The flora of Sierra del Purial and Sierra de Imias is little investigated so that only few endemics have been known (*Senecio sauetii*, *Croton tropidophyllus*, *Scolosanthus wrightianus*, *Phialanthus parvifolius*, *Ph. macrostemon*, *Ardisia baracoensis*, and *Platygyne leonis*) but the discovery of others is expected. A single endemic genus, *Bembicidium*, and several endemic species, e.g., *Callicarpa areolata*, *Gesneria gibberosa*, *G. yumuriensis*, *G. purpurascens*, *Victorinia regina*, *Siphocampylus yumuriensis*, *Spathelia yumuriensis* (Fig. 6), *Heptanthus yumuriensis* (Fig. 5), and *Ossaea yumuriensis*, etc. occur in the Gran Tierra and Yumuri area. The richest evolutionary centre is the Yunque de Baracoa monadnock from the Pliocene, which has one endemic genus (*Ekmania*) and about 25 endemic species, for instance, *Spaniopappus ekmanii*, *Vernonia yunquensis*, *Jacquinia yunquensis*, *Ossaea heterotricha*, *Calycogonium plicatum*, *Ilex wrightii*, *Croton yunquensis*, *Erythroxylum baracoense*, *Coccothrinax yunquensis* (Fig. 46), three *Gesneria* and 5 *Pilea* species, *Siphocampylus manettiaefolius*, *Arthrostyidium angustifolium*, etc.

d. Vegetation: This is the zone of seasonal evergreen forests, although over 7–800 m montane rainforests and, in the Sierra de Imias, even mossy forests may occur. The mogote zone is covered by karstic forests whose floristic composition is still unknown.

District C.1.6.: The mogotes of the Nipe—Yateras area (Yaterense)

a. Geography: Inclined conical karsts and, too, wide and terraced limestone plateaux with serpentine intrusions often reaching the surface. The limestone formations alternate with

monotonous sandstone ridges. The predominant soils are humic-carbonated soils on limestone, tropical brown soils on sandstone and ferritic soils on serpentine.

b. Climate: Seasonal with dry winter of 1–2 or 3–4 months duration. Annual precipitation 1000–1800 mm.

c. Flora: Two centres of flora development may be distinguished, both being rich in endemics. The first is the mogotes of Sierra de Nipe with about 15 endemic species, such as *Hemithrinax compacta* (Fig. 13), *Spathelia lobulata* (Fig. 6), *Plinia ramosissima*, *Calypttranthes paradoxa*, *Eugenia bayatensis*, *E. excisa*, *Hydrocotyle oligantha*, *Matelea bayatensis*, *Tabebuia picotensis*, *T. mogotensis*, *Gesneria lopezii*, and *Isidorea polyneura*. The other centre is the group of Monte Libano, Monte Verde and Monte Cristo which must have been the principal junction of migratory routes during the development of the Oriente flora. This area is still a rich meeting point of the limestone and serpentine floras, as well as of the semi-desert xerotherm elements. On the soils derived from serpentine the range of many species of Nipe and Cristal overlaps the distribution of Moa elements. Moreover, only at this point reach certain serpentophilous species (*Pinus cubensis*, *Agave shaferi*) the limestone zone. Also, some coastal species were able to spread up to 6–700 m on the southern slopes where the xerotherm elements and the montane rainforest species meet. The three mountains possess 40 endemics altogether, some of them exhibiting vicariance (e.g., *Siphocampylus*, *Gesneria*). Examples of characteristic plant species are *Hernandia cubensis*, *Auerodendron glaucescens*, *Salacia wrightii*, *Begonia libanensis*, *Scolosanthus granulatus*, *Spermocoe exasperata*, *Verbesina wrightii*, 3 *Dorstenia*, 6 *Pleurothallis*, 2 *Calypttranthes* and 2 *Ossaea* species.

d. Vegetation: Karstic woods in the mogotes, seasonal evergreen forests in the valleys as well as in the sandstone areas. Arid scrubs on limestone slopes and pinewoods on serpentine which may occasionally extend to the limestones. Rainforest patches may occur in some places in the deep valleys and montane rainforest fragments are found at higher altitudes.

Sector C.2.: Sierra Maestra (*Maestricum*) (Fig. 43)

The 250 km long and 15–20 km wide Sierra Maestra is almost 750 m higher than the ancient Sagua-Baracoa massif from which its flora originated. As a result of this altitude difference and of the presence of rocks more effectively enforcing the moist climate (limestone, sandstone, granite, grano-diorite and diorite), a wide montane rainforest and cloud forest belt developed, in which the ancient Sagua-Baracoa flora enriched in Jamaican and Hispaniolan elements, may have become a new evolutionary centre. This spontaneously formed secondary centre is characterized by two endemic genus (*Solonia* and *Cubacroton*) and 155 endemic species, for example, *Cneorum trimerum* (ancient relict!), *Pinus maestrensis*, *Laplacea urbani*, *Cleyera ekmani*, *Persea anomala*, *Pithecellobium maestrense*, *Platygyne dentata* (Fig. 14), *Pera microcarpa*, *Sapium maestrense*, *Cubacroton maestrensis*, *Maytenus saxicola*, *Clidemia pterosepala*, *Karwinskia bicolor*, *Cinnamodendron cubense*, *Talauma orbiculata*, *T. truncata*, *Scolosanthus maestrensis*, *Cordia longipedunculata*, *Solanum maestrense*, *Tabebuia oligolepis*, *T. hypoleuca*, *Justicia maestrensis*, *Peratanthe cubensis*, *Schradera cubensis*, 9 *Eugenia*, 6 *Miconia*, 6 *Ossaea*, 5 *Gesneria*, 5 *Eupatorium* and 6 *Rondeletia* species. The boundary of this sector runs at 300–400 m on the slopes in the south, and at the margin of the Cauto basin in the north.

District C.2.1.: The Western and Central Maestra (*Turquinense*)

a. Geography: This area extends from Pilón to the Santiago valley and includes two higher mountainous groups (Turquino and La Bayamesa), in between whose highest points are over 1500 m. These mountains comprise, deeply inclined sharp ridges and conical formations so

that the superficial drainage ratio is high (35–50 l/sec · km²) and the erosion is intensive. Tropical brown soils occur at medium elevation, up to 600 m and then yellowish-red montane soils are found up to 1300 m. Next, up to 1750 m, yellowish-brown montane soils become predominant, these are replaced by brown montane soils on the peaks. The northern slopes are covered by yellow montane soils over 1300 m.

b. Climate: Seasonal with dry winter. 3–4 dry months at the foothills, 1–2 dry months up to 800 m. Further up there is a moist montane rainforest climate which is replaced by a humid, high-altitude temperate rainforest climate at 1700 m. The annual precipitation ranges from 800 to 3000 mm.

c. Flora: Besides the characteristic endemics listed in section C.2., there are numerous regional endemic species of mossy forests in this district. For example, *Myrsine microphylla*, *Nectandra reticularis*, *Eupatorium paucibracteatum*, *E. praestans*, *Henriettea ekmanii*, *Hedyosmum cubense*, *Ossaea turquinensis*, *Rondeletia naguensis*, *Myrica cacuminis*, *Rubus turquinensis*, *Symplocos leonis*, *Sapium erythrococcum*, *Eugenia maestrensis*, and *E. laeteviridis*, etc. In addition, local endemics have been found in several mountain groups and valleys: Nagua has 4 endemics Pico Caracas is famous by the remarkable paleoendemism *Cneorum trimerum* and the *Podocarpus* woods; *Citharexylum ternatum*, *Tabebuia elongata*, *Eugenia naguana* and *Polygala rhynchosperma*, Rio Guamá, Hacienda Sevilla, Nima-nima, El Cuero, Rio Yara, Yao arriba, Pico Joaquín, and Loma Regino possess one-two endemics each, whereas in Pico Bayamesa 4 local endemics occur (e.g., *Vernonia maestralis*, *Purdiaea maestrensis*, *Lepanthes acunae* and *Psychotria ekmanii*). The most prominent evolutionary centre is the Turquino group having approximately 25 local endemics (e.g., *Coccothrinax acunana* — Fig. 46, *Agave pendentata*, *Satureja bucheri*, *Juniperus saxicola*, *Miconia turquinensis*, *Ilex turquinensis*, *I. nunezii*, *Lobelia cacuminis*, *Chaptalia turquinensis*, *Mitracarpus acunae*, *Lepanthes ekmanii*, *L. turquinoensis* and *L. pergracilis*, etc.).

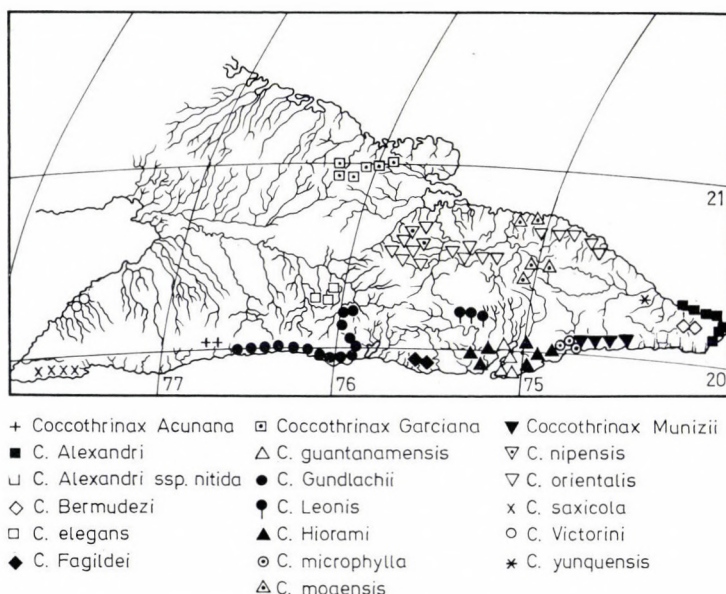


Fig. 46. Geographical distribution of the East-Cuban taxa of the genus *Coccothrinax* (after BORHIDI 1973, modified)

d. Vegetation: Arid evergreen shrubwoods on the southern slopes up to 300 m, semi-deciduous forests (Yayales p.p.) between 300–500 m, seasonal rainforests (Yayales p. maj. p.) between 500–800 m, moist montane rainforests (fangales) between 800–1600 m and mossy forests (monte fresco) between 1600–1900 m. Over 1900 m high altitude moist shrublands predominate. On the northern slopes the seasonal rainforest zone begins as low as 150–200 m. This is replaced by montane rainforests at 800–1000 m. At the boundary of these two rainforest types a 100–200 m wide belt of “extrazonal” pinewood stands (*Pinus maestrensis*) are found on sandstone which may extend even up to 1800 m on the northern slopes of Turquino. At 1500 m begins the mossy forest zone.

District C.2.2.: The eastern Sierra Maestra (Piedraënse)

a. Geography: This area includes Gran Piedra, a limestone range covered by granodiorite. Its highest point is 1219 m. North of it are found the limestone mountains of Sierra de Santa Maria Loreto. All mountains are deeply inclined, large bluffs occur in the north. Tropical brown soils predominate up to 800 m. Further up yellowish-red montane soils are found.

b. Climate: Similar to that of the preceding district.

c. Flora: As few as two local endemics (*Callicarpa floccosa* and *Rondeletia intermedia*) have been known. Here is the only population of *Pinus cubensis* in the Sierra Maestra, which is supposed to be a hybridogenous one between *P. cubensis* and *P. maestrensis*.

d. Vegetation: Similar zonation as in the preceding floristic district. The only difference is that the pine forest stands enclosed by the seasonal evergreen forest and montane rainforests are composed of *Pinus maestrensis* (or rather *P. cubensis* × *P. maestrensis*).

District C.2.3.: The mogotes of Baire, (northern Sierra Maestra) (Tablaënse)

a. Geography: These karsts are found within the Charco Redondo—Los Monos—Matias—Los Negros quadrangle. Conical hills of 400–600 m height with perpendicular rocky walls. Rendzina soils predominate, whereas in the valleys humic-carbonated soils occur.

b. Climate: Seasonal with dry winter of 3–4 months duration. Annual precipitation between 1200–1600 mm.

c. Flora: The flora of this area had been unexplored for a long time. Due to geographic isolation, the flora is very rich. A remote relationship to the mogotes of Nipe is indicated by the presence of the endemic genus *Synapsis* and of *Siphocampylus undulatus*, *Clerodendron denticulatum* and *Byttneria microphylla*. Also, there is a connection with the flora of arid limestone terraces in the Cabo Cruz area (*Catalpa brevipes*). More than ten local endemics are found here, e.g., *Coccothrinax elegans* (Fig. 46), *Neobraccia susannina* (Fig. 9), *Malpighia acunana*, *Rhytidophyllum mogoticola*, *Tabebuia candicans* and *Pilea uninervis*.

d. Vegetation: Semi-deciduous forests with *Coccothrinax* palms, cacti and agaves predominating in the mogotes. Seasonal evergreen forests occur in the valleys.

Sector C.3.: The southern and northeastern coasts of Oriente (Santiagicum) (Fig. 43)

This sector includes the most extensive and most extremely arid zone of Cuba: the area extending from Cabo Cruz over Maisi to Navas in the shade of the Sierra Maestra and the southern Baracoa Mountains which are mainly responsible for the dry climate. This region is continued as a narrow strip along the northern coast to Navas. The Sierra Canasta, the Guantanamo Basin, the southern slopes of Sierra Maestra up to about 200 m, and the terraces of

southern Baracoa up to 300–400 m are also included. In the Monte Libano group some coastal elements managed to reach 700 m altitude. This area is an old coastal land with an eventful geological past. During millions of years sections of this land rose and sunk, became separated and joined again in different points of time, resulting in several evolutionary centres of the flora. Therefore, the common species of this sector are mostly widely distributed xerophilous species, such as *Dendrocereus nudiflorus*, *Lemaireocereus hystrix*, *Cordia taylori*, *Pseudocarpidium avicennioides*, *Croton rosmarinoides*, *C. myricifolius* and *C. littoralis*. There are two monospecific endemic genera: *Cubacroton* and *Caribaea*, and about 110 endemic species, most of them being confined to a given locality or a floristic district. The number of endemics found throughout the sector is relatively small (e.g., *Guettarda cueroensis*, *G. coxiana*, *Galactia cuneata*, *Consolea macracantha*, *Myrtus oonophylla*, *Cordia leucosebestena*, *C. leptoclada*, *C. brittonii*, *Lantana parvifolia*, *Callicarpa grisebachii*, *C. bucheri*, *Pseudocarpidium multidentens*, *Spirotecoma spiralis*, *Eupatorium helianthemoides*, *Vernonia complicata*, *Gochnatia calcicola*, *Bonania elliptica*, *Croton micradenus*, *C. munizii*, etc.). The vicarious *Melocactus* species and *Coccothrinax* palms (Figs 45–46) are also typical.

District C.3.1.: The coast and terraced land between Belic and Pilón (Pilonense)

a. Geography: The Pliocene limestone cliffs, sometimes reaching 50 m height, the western end of Sierra Maestra having several terraced levels, and the plain at Pilón Bay with sedimentary origin from the Quaternary are included. Limestone rendzina and humic-carbonated soils predominate in the first two. The plain is covered by tropical alluvial soils.

b. Climate: Seasonal bixeric with two dry seasons of 7–8 or 5–6 months duration. Annual precipitation is 700–1200 mm. At higher altitudes 3–4 dry months, all in the winter, and 1000–1400 mm annual precipitation.

c. Flora: Fairly isolated from that of the other districts in the sector. It is characterized by the low number of regional endemics and by many local endemic species with several centres of flora development. For example, Media Luna (*Coccothrinax victorini* — Fig. 46), Niquero (*Copernicia humicola* — Fig. 42, *Cassia niqueroensis*, *Chamaesyce niqueroana*), Cabo Cruz (*Cordia corallicola*, *C. dumosa*, *Eugenia peninsularis*, *E. aceitillo*, *Amyris polymorpha*, *Croton corallicola*, *Rondeletia peninsularis*, *Coccothrinax saxicola* — Fig. 46 and *Portulaca tuberculata*) and Pilón (*Chaptalia comptonioides*, *Justicia agria*, *Belairia parvifolia*, *Pilea cowellii*, *P. carnososa*, *Begonia cowellii*, *Leptocereus sylvestris*). There is certain relationship to the flora of the mogotes of Baire as shown by the occurrence of *Catalpa brevipes*.

d. Vegetation: Arid evergreen shrublands in the coastal zone, dry evergreen forests in the lower terraces, and semi-deciduous forests higher up. The original vegetation of the plain was a tropical humid woodland.

District C.3.2.: The coastal area between Marea del Portillo and Nima-nima (Uveroense)

a. Geography: Narrow and mostly rocky coasts at the western wing of Sierra Maestra. Gravelly and sandy beaches at the estuaries, and the lower parts of slopes exposed to the south. Rendzina and humic-carbonated soils are usual, whereas tropical brown soils occur in the valleys.

b. Climate: Evenly warm bixeric climate with two dry seasons of a total of 5–6 months duration. Annual rainfall 800–1200 mm.

c. Flora: Very little studied. Probably several evolutionary centres could be detected here. *Rhytidophyllum minus* is an endemic in common with the preceding district, and some local endemic species, e.g. *Tabebuia acunana*, *Rondeletia sevilensis*, *Erigeron taylori*, *Pilea*

sevillensis, *Melocactus nagyii* (Fig. 45) characterize the area. There is also an endemic palm, common with the Sierra Maestra, is *Coccothrinax gundlachii* (Fig. 46).

d. Vegetation: Microphyllous evergreen shrublands, dry evergreen forests with deciduous elements, and locally, mangroves in the estuaries and the gravelly coastal depressions.

District C.3.3.: Coastal belt and terraces between Santiago de Cuba–Guantánamo–Maisi and Baracoa (Guantanamense)

a. Geography: High cliffs and low limestone terraces with small inlets and coastal plains. Rendzina and cinnamon-coloured humic carbonated soils predominate. Also the plain in the Guantánamo Basin covered partly by brown humic carbonated soils. The district includes the southern coasts at the foots of the Gran Piedra range, the Guantánamo Basin with Sierra de Canasta, the coasts and terraces from Guantánamo to Maisi up to an elevation of 400 m, and the northern Baracoa shores between Maisi and Navas.

b. Climate: Evenly warm seasonal bixeric climate with two dry seasons (5–8 dry months) and annual precipitation totalling 600–1100 mm. Also, semi-desert climate with 9–10 dry months and 300–600 mm annual rainfall develops in the rain shadow of the Sierra de Puriales and Sierra de Imias, south and east of Guantánamo ranging eastward to Jauco. Between Maisi and Baracoa seasonal climate with short summer dry period is characteristic.

c. Flora: Very rich and diverse xerothermophilous flora, with several small areas characterized by local endemics. A single monospecific endemic genus is *Caribaea* (Nyctaginaceae), a particular littoral cushion plant with very restricted area. A great number of regional endemic species occur also, as *Coccothrinax alexandri* s. l. *C. hiorami*, *C. munizii* (Fig. 46), *Rhytidophyllum acunae*, *Melocactus acunai* (Fig. 45), *Caesalpinia pinnata*, *Passiflora santiagana*, *Castela victorini*, *Consolea macracantha*, *Rondeletia apiculata*, *Tabebuia libanensis*, *Reynosia mucronata* ssp. *azulensis* (Fig. 16), *Maytenus buxifolia* ssp. *cochlearifolia* (Fig. 15). The area abounds in very important local evolutionary centres with 80 endemic taxa altogether. Local endemic species are at Santiago de Cuba: *Rondeletia norlindii*, *Acacia cowellii*, *Caesalpinia subglaucua*, *Eugenia amblyophylla*, *E. itephylla*, *Lasiocroton gracilis* and *Tephrosia clementis*; at Aguadores: *Nashia armata*, *Rochefortia oblongata*, at Siboney: *Neobrassa martiana* (Fig. 9) and *Barleriola saturejoides* ssp. *hirsuta* (Fig. 47); at Daiquiri: *Cassia scleroxyla*, *Chamaesyce microclada* and *Coccothrinax fagildei* (Fig. 46); at Baconao: *Justicia maestrensis*, *Jacquinia verticillaris* and *Machaonia urbaniana* (Fig. 37) occur. Fifteen local endemics live around Guantánamo,

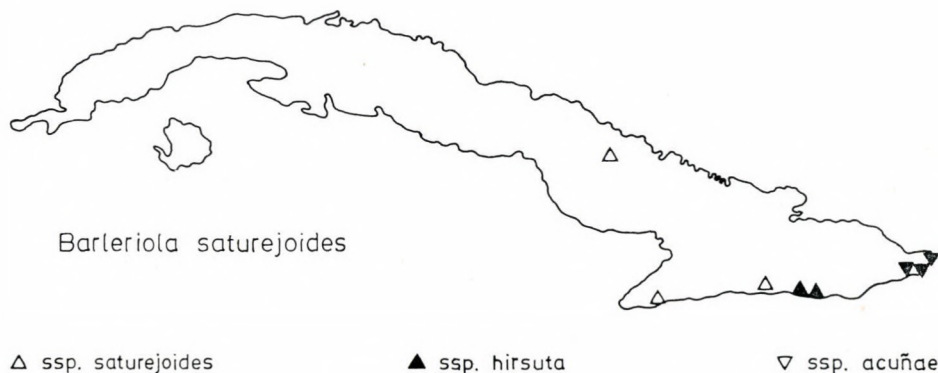


Fig. 47. Geographical distribution of *Barleriola saturejoides* (Acanthaceae) (after BORHIDI 1973)

e.g. *Coccothrinax guantanamoensis* (Fig. 46), *Andrachne brittonii*, *Croton excisus*, *Colubrina obtusata*, *Opuntia militaris*, *Melocactus erae* (Fig. 45), *Myrtus nummularioides* and *Geophila multiflora*. Between Guantánamo and Macambo *Agave albescens*, *Casearia comocladifolia*, *Thouinia leonis*, *Stigmaphyllon coccolobaefolium*, *Coccothrinax microphylla* (Fig. 46), *Scolosanthus strictus* occur; at Macambo *Caribaea littoralis*, *Drymaria glandulosa* and *Apassalus parvulus* are local endemics, whereas between Cajobabo and Jauco *Pheidonocarpa cubensis*, *Gyminda orbicularis*, *Isidorea rheedioides*, *Tabebuia jaucoensis*, *Micromeria suborbicularis*, *Barleriola saturejoides* ssp. *acunae* (Fig. 47), *Scolosanthus hirsutus* are found. Additional 15–20 endemics are known from the Maisi plain and the surrounding terraces, for example, *Isidorea leonis*, *Pseudocarpidium shaferi*, *Cnidoscolus matosii*, *Acacia seifriziana*, *Tabebuia leonis*, *Duranta arida*, *Harpalyce maisiana*, *Galactia maisiana*, *Jacquinia maisiana*, *Scolosanthus hispidus* and *S. nannophyllus*. On the young serpentine outcrops around the lagune of the Jojó valley some local neoendemics live as *Rondeletia ingrata* and *Melocactus acunai* ssp. *lagu-naënsis* (Fig. 45).

The role of xerotherm elements that are also found in Hispaniola is increased (e.g. *Coccothrinax fragrans*, *Pithecellobium oppositifolium*, *Bellonia spinosa*, *Jacquinia berterii*, *Caesalpinia glandulosa*, *Exostema spinosum*, etc.). Floristic relations with Hispaniola is especially manifested at the easternmost part of the southeast coast of Oriente around Maisi, where some common species of Cuba and Hispaniola with very restricted areas occur, as *Omphalea commutata*, *Petitia urbanii*, *Victorinia regina*, etc. (Fig. 21).

d. Vegetation: Microphyllous evergreen and deciduous shrubwoods and shrublands. Open shrublands with cacti in the understorey and semi-desert scrubs with columnar cacti occur in many areas. Eastward of Guantánamo the dominant vegetation type is the semi-desert scrub with tree-shaped and columnar cacti. On the terraces arid evergreen shrubwoods, open scrubs with agaves, dwarf and tall thin palms predominate. In the flat valleys of rivers secondary savannas composed of short grasses, with *Sabal parviflora* palms are found.

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REINTERPRETATION OF THE ECOLOGICAL NICHE

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As a consequence of concept pair, environment and tolerance, a distinction between n -dimensional niche and effector spaces is suggested. The axes of effector space correspond to ecological effective factors, whereas those of niche space are associated with the tolerances of a population.

Introduction

Recently, the elaboration of unambiguous ecological concepts and terms has started. The interpretation of ecological environment and tolerance is related to ecological factors and raised questions unexamined so far.

The populations live on geographically defineable sites. In the topographic space different factors are present. From the standpoint of ecology, factors influencing the survival of populations are important (effective factors; exterior complex). The populations are able to tolerate the effects or not, depending on their biological features (tolerance; interior complex). The interior complex is influenced by the exterior limiting complex. The limiting factors form the ecological environment. The population is able to endure such factors if they do not exceed its own tolerance limits. Theoretically and potentially there is an infinite number of external factors and internal features. However, in practice only an enumerable subset of factors form ecological environment—tolerance relationships.

The concepts ecological environment and tolerance are complementary, we can explain one by the other (JUHÁSZ-NAGY and VIDA 1978, JAKUCS et al. 1984, JUHÁSZ-NAGY 1984).

We point to an important consequence of an unambiguously explained concept pair (environment and tolerance) in the niche theory.

After HUTCHINSON (1958, 1967), the niche is interpreted as an n -dimensional space the axes of which are habitat factors. Later, the interpretation of niche shifted to the direction of resources: "Recently however, the ecological niche has become increasingly identified with resource utilization spectra..." (PIANKA 1976). However, we may assign to MacArthur's opinion this explanation (MACARTHUR 1968).

The term biotope space was used by HUTCHINSON (1958). Nowadays experts do not apply the biotope space in interpretation of their investigations.

WHITTAKER et al. (1973) combined the niche and habitat in the term ecotope and proposed the use of terms habitat hyperspace, niche hyperspace and ecotope hyperspace. SZABÓ distinguishes external and internal niche (SZABÓ 1984).

Niche space and effector space

Populations have genetically determined tolerance limits regarding different factors. Inside the tolerance limits live the individuals of a population, at some places with a reduced vigour. Tolerance limits concerning effective factors mark out the niche of the population, and form an n -dimensional space, the niche space. The axes of niche space are given by internal features

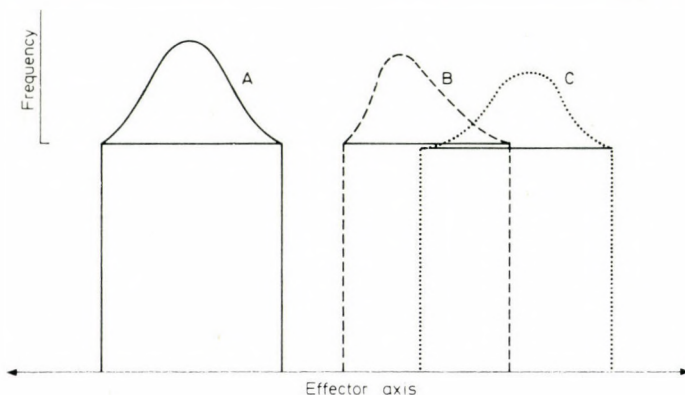


Fig. 1. The realized niche and place of populations (A, B and C) on effector space

of the population (tolerances). If biotic and abiotic limiting factors are absent we may speak of the fundamental niche of the population.

In nature, biotic and abiotic effective factors (e.g., other populations, resources, etc.) influence the niche of a population. From the factors we may construct another n -dimensional space, the effector space. The effective external factors constitute the axes of effector space.

Populations will fill up different parts of the effector space according to their niche. Since usually there is competition among populations, they change their niche among themselves, this is called the realized niche.

Thus, we may construct two n -dimensional spaces, effector and niche spaces, in accordance with the environment and tolerance concept pair.

In Fig. 1 we show the above-mentioned ideas. Since the fundamental niche is hardly determinable in practice (see e.g., KREBS 1978), we present a hypothetical example.

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THE ACOLUTHIC SPACE AND ITS IMPORTANCE IN THE ECOLOGICAL RESEARCH

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The introduction in ecology of the concept of acoluthic space is made reasonable by the fact that the successional stages follow each other in space and time and this process can be conceived as one taking place in abstract space. Since the biotic communities represent an organization level different from that of the populations, and their special characteristics are different from those of the populations, therefore the term niche space, a concept relating to populations cannot be used in the case of communities.

By acoluthic space an n -dimension space is understood in which the successional stages — acoluthoses — are arranged along certain axes. The acoluthoses occupy certain sections of space. The axes represent the factors important for the (temporary) survival and temporal changes of the acoluthoses, and the responses given by the acoluthoses to the de facto effective factors, respectively. On the axes the breadth of acoluthos and the overlap of acoluthoses can be estimated.

The new concept even makes it possible to characterize communities adjacent in actual (topographic) space from more than one point of view. Further, it may give information on the regulation and control of communities, and possibly on the approximation of homeostasis.

Subsequently two examples (afforestation of sand-hills and dolomite rock slopes) of the use of the new concept in the case of succession are shown.

Introductory remarks

The niche- and succession researches occupy a central place in the ecology of these days.

The supraindividual studies are made at various organization levels. The organization levels form a hierarchy. The levels following one after the other in the hierarchy have special characteristics interpretable only at the given level (KREBS 1972). For setting up the hierarchy of the organization levels an example is found in ODUM's (1959) book. Recently JAKUCS, DÉVAI and PRÉCSÉNYI (1984) have dealt with this subject. The so-called collective levels suggested by them correspond with a single exception to the levels given in ODUM. The authors mentioned separate the following collective levels: (individual) → population → biotic community → biome → biosphere (JAKUCS, DÉVAI and PRÉCSÉNYI 1984).

The niche studies are made at population the succession examinations at community level.

The populations are characterized among others by their position in the niche space, namely by the section of space they are situated, the breadth of niche on the niche axes, and by the size of the overlap.

In the communities a number of different population collectives are simultaneously present with their behaviour types more or less co-ordinated (JUHÁSZ-NAGY and VIDA 1978). The special characteristics of the populations do not agree with those of the communities.

The plant communities are specially characterized e.g. by the species (population) composition, the diversities (e.g. species-individual, -cover), the layering and the aspects; a further characteristic of them is that populations belonging to different life forms, growth- and areal-types, and to different complex indicator numbers coexist in a more or less orderly form.

The communities often can be regarded as stages of a given succession series. They follow each other at longer or shorter intervals. On the succession and its up-to-date interpretation a number of books and papers have been published, see e.g. HORN (1974), GOLLEY (1977), FEKETE (1985).

As pointed out in the foregoing the niche is a concept relating to populations. A concept relevant at a certain organization level (population) cannot be used with another one (community), as e.g. WUENSCHER (1974) attempted to do it: "That part of niche space occupied by a plant community consists of the total volume of the niches of all the species within the community". It follows from the character of the community that community niche cannot be spoken of. A community though organized from populations is not simply the sum or even the product of the populations which compose it.

Acoluthic space

The successional stages following each other in space and time can be imagined as situated in an abstract space. We suggest to designate this abstract space by the term acoluthic space.* By the term acoluthic space an n-dimension space is understood in which the successional stages (acoluthoses) are arranged along certain axes. The acoluthoses occupy certain sections of space. The axes represent the factors important for the temporary survival and temporal changes of the acoluthoses, and the responses given by the acoluthoses to the de facto effective factors. On the axes the breadth of each acoluthos and the overlap of adjacent acoluthoses can be sized up, and changes in them during the succession can be studied. It can be seen that the formulation of the acoluthic space is very similar to but not identical with the formulation of the niche space. The introduction of the new concept is made necessary by the difference between the organization levels.

We suggest to use the following terms: niche space, -breadth and -overlap for populations; acoluthic space, breadth of acoluthos and overlap of acoluthoses for biotic communities.

Succession of plant communities on sand hill and dolomite rock

Two examples of how to size up the breadth of acoluthos and overlap of acoluthoses are given below. The succession leading to afforestation is shown on sand hills in one of the examples, and on dolomite rock slopes in the other.

The data of the first succession series were obtained from the publication of ZSOLT (1943). In the series the following stages were included (with the original names published by

* Acoluthos is a word of Greek origin, it means: ruler succeeding on the throne.

the author): *Festucetum vaginatae* (sward on sand hill with low cover), *Festucetum sulcatae* (sward on sand hill with high cover) and *Convallario-Quercetum* (oak forest on sand hill with closed canopy). As for the stage(s) between *Festucetum sulcatae* and *Convallario-Quercetum* phytosociological relevés were not available (it is indicated by empty places in Figs 1 and 2).

The phytosociological data of the other succession series were placed at our disposal by ZÓLYOMI. The members of the series are: *Sesleleo leucospermo-Festucetum pallentis* (sward on dolomite rock with low cover), *Chrysopogono-Caricetum humilis* (sward on dolomite rock with high cover), *Cotino-Quercetum pubescentis* (shrub-forest with *Cotinus coggygria* and *Quercus pubescens* on dolomite rock) and *Orno-Quercetum pubescenti cerris* (calcicole oak forest).

For the two axes of the acoluthic space we chose the so-called W- and R-, soil dryness and soil reaction, axes. The indicator numbers of W and R are used on the basis of publications by ELLENBERG (1950), ZÓLYOMI (1964) and ZÓLYOMI et al. (1967); the meaning of indicator numbers: frequent species on extreme dry (W0), very dry (W1), dry (W2), moderate dry (W3), moderate fresh (W4), fresh (W5), moderate moist (W6) soil; R0 indifferent species,

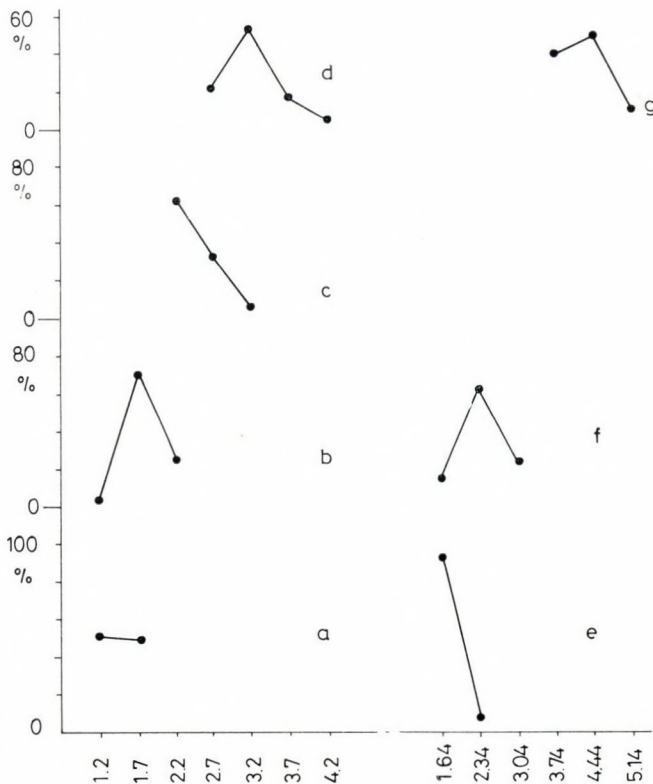


Fig. 1. Distribution of means of W indicator numbers calculated from the phytosociological relevés

X axis: class means - Y axis: % - n: number of relevés - a) *Sesleleo-Festucetum* (n = 35); b) *Chrysopogono-Caricetum* (n = 28); c) *Cotino-Quercetum* (n = 50); d) *Orno-Quercetum* (n = 50); e) *Festucetum vaginatae* (n = 15); f) *Festucetum sulcatae* (n = 13); g) *Convallario-Quercetum* (n = 10)

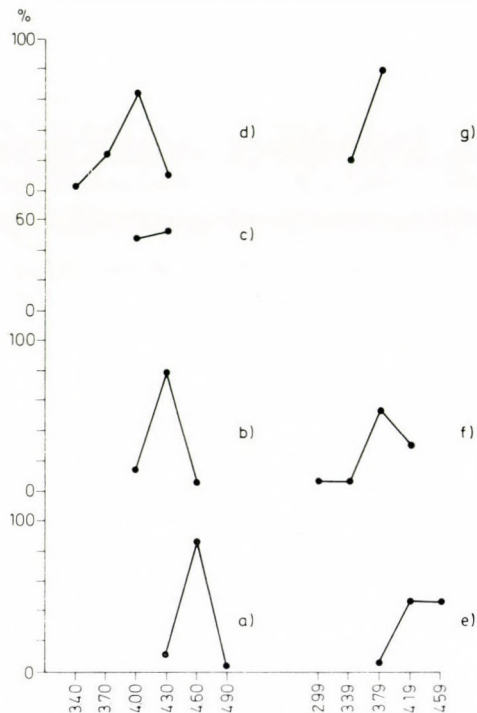


Fig. 2. Distribution of means of R indicator numbers calculated from the phytosociological relevés. For the designation see Fig. 1

R1 absolutely calcifuge species, R2 calcifuge species, R3 on weakly acid soil, R4 on neutral soil frequent species, R5 calcicole species. The above classification is only relevant in a given (geographic, climatic) region; in another region the same species may be given different W and R indication numbers according to its behaviour displayed there.

Of the plant communities belonging to the two succession series 10–50 phytosociological relevés per each were in hand (BRAUN-BLANQUET 1951, BECKING 1957). The means of W and R indicator numbers calculated for each releve placed in the same community were categorized* (Figs 1 and 2).

On the basis of means placed in classes we sized up the breadth of acoluthos and overlap of adjacent acoluthoses on each axis. The breadth (B) and overlap (α and β) were determined with formulae by LEVINS (1968):

$$B_i = 1/\sum p_{ij}^2, \quad \alpha = \alpha_{hi} = \frac{\sum p_{hj} \cdot p_{ij}}{\sum p_{hj}^2} \text{ and } \beta = \alpha_{ih} = \frac{\sum p_{hj} \cdot p_{ij}}{\sum p_{ij}^2}$$

where p_{ij} means the relative frequency, α relates to overlap of h -acoluthos by i -acoluthos, β to overlap of i -acoluthos by h -acoluthos, j is the number of classes on the axes (cf. FEKETE et al. 1976).

* Thanks are due to Prof. B. ZÓLYOMI for establishing the W and R indicator numbers for the species and compiling the tabellar material.

Results

On the W (soil dryness) axis the breadth of acoluthoses following each other increases towards the final (climax) stage in both succession series (Tables 1 and 3). The increase indicates that at the beginning populations of the few species that survive even on very dry soil are prevalent. With the progress of the succession, when the soil becomes more and more thicker, the

Table 1

*Breadths and overlaps of acoluthoses on the W axis
(sand-hill series)*

	<i>Festucetum vaginatae</i>	<i>Festucetum sulcatae</i>	<i>Convallario- Quercetum</i>
<i>Festucetum vaginatae</i>	1.1422	0.6285	
<i>Festucetum sulcatae</i>	0.3268	2.1965	0.0000
<i>Convallario-Quercetum</i>		0.0000	2.3809

In the main diagonal the B_i values, in the right upper matrix the α -, in the left lower matrix the β -values are found.

Table 2

*Breadths and overlaps of acoluthoses on the R axis
(sand-hill series)*

	<i>Festucetum vaginatae</i>	<i>Festucetum sulcatae</i>	<i>Convallario- Quercetum</i>
<i>Festucetum vaginatae</i>	2.2724	0.0248	
<i>Festucetum sulcatae</i>	0.0224	2.5221	0.0305
<i>Convallario-Quercetum</i>		0.0523	1.4706

For explanation see Table 1.

Table 3

*Breadths and overlaps of acoluthoses on the W axis
(dolomite-rock series)*

	<i>Seseleo- Festucetum</i>	<i>Chrysopogono- Caricetum</i>	<i>Cotino- Quercetum</i>	<i>Orno- Quercetum</i>
<i>Seseleo-Festucetum</i>	1.9984	0.7300		
<i>Chrysopogono- Caricetum</i>	0.6364	1.7422	0.2700	
<i>Cotino-Quercetum</i>		0.3761	2.0391	0.2096
<i>Orno-Quercetum</i>			0.2734	2.6596

For explanation see Table 1.

Table 4
Breadths and overlaps of acoluthoses on the R axis
 (dolomite-rock series)

	<i>Seseleo-Festucetum</i>	<i>Chrysopogono-Caricetum</i>	<i>Cotino-Quercetum</i>	<i>Orno-Quercetum</i>
<i>Seseleo-Festucetum</i>	1.3359	0.2017		
<i>Chrysopogono-Caricetum</i>	0.2349	1.5556	0.7422	
<i>Cotino-Quercetum</i>		0.9528	1.9968	0.7172
<i>Orno-Quercetum</i>			0.7521	2.0938

For explanation see Table 1.

shrubs and trees establish themselves, and the canopy makes its shade effect felt, species with different soil moisture demands are able to coexist.

The first two acoluthoses in the series have large overlaps on the W axis (Tables 1 and 3). This may indicate that swards with higher cover (*Festucetum sulcatae* and *Chrysopogono-Caricetum*) gain ground at the expense of those with low cover. We put forward the interpretation that the influence of swards with high cover on those with low cover is greater than that exerted by the latter on the former.

On the R (soil reaction) axis the last acoluthos in the series of succession taking place on sand hill has the smallest breadth (Table 2). This decrease in breadth is indicative of a concentration of dominance. In the succession series on dolomite rock the breadth of acoluthoses increases from the initial state onwards (Table 4). It can be seen that the breadths of sward communities at the beginning of the series are distinct from those of plant communities including shrubs and trees. The latter (*Cotino-Quercetum* and *Orno-Quercetum*) hardly differ in breadth. In this succession series the overlaps of *Chrysopogono-Caricetum* and *Cotino-Quercetum*, and of *Cotino-Quercetum* and *Orno-Quercetum* are large (Table 4). Studying these communities from a different point of view JAKUCS (1972) pointed out a close successional relationship between swards on dolomite rock and shrub forests (polycormon succession).

Concluding remarks

It seems to be advisable when working with categories (e.g. species, life form composition, areal types, constancy, etc.) to place the diversities calculated for each releve of the phytosociological table in classes and so determine the position of the acoluthos concerned in the acoluthic space.

The question of population-groups (-collections) between the levels of population and biotic community remains to be solved.

The interpretation of α and β in the case of acoluthoses requires consideration. Perhaps they could give some clue to the competition between acoluthoses.

Summary

We suggest to introduce the concept of acoluthic space in ecology. The new concept implies that during the succession the individual stages (acoluthoses) follow each other in space and time, and this process can be conceived as one taking place in abstract space. Since the community as an organization level differs from the population, and has special characteristics different from those of the population, the concept of niche which relates to populations cannot be used in the case of communities. The applicability of the concept of acoluthic space is shown by the example of two succession series.

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SPATIAL PROCESSES IN A GRASSLAND COMMUNITY, III.

SPECIES-AREA RELATION, DOMINANCE-DIVERSITY CURVES,
CHANGES IN THE FREQUENCY AND DENSITY OF THE SPECIES*

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As a sequel of the previous papers (MOLNÁR and NOSEK 1979, 1980), the author investigated the behaviour of the number of species, total number of individuals, the number, density, relative density, frequency, and relative frequency of each species, as well as the dominance-diversity curves by means of a spatial process involving plot size change.

The investigation were carried out in a sandy grassland, *Festucetum vaginatae danubiale*, near Vác-rátót, North Hungary. Eleven plot sizes ranging from 100 cm² to 25 600 cm² were applied. Sampling was made by a computer placing 180 quadrats of each size randomly on a map of a scale 1 : 10 drawn on the basis a photographed section of the community.

The species-area curve of the community could be separated into two sections with different functions fitted. This separation was due to the difference in the dominance of species.

The dominance relation of species and the reflected niche segregation proved invariant at different plot sizes on the basis of the dominance-diversity curves. The rankorder of species along the curves supports the conclusions about the generalist-specialist character of the species indicated in a previous study.

The frequency values were approximated by logistic curves. These curves reflected also the dominance structure of the community and made possible to calculate the minimum plot size necessary to reach a pre-determined-frequency value.

The number of individuals gave strong positive linear correlation with plot size. The "functional minimum area" detected in this community is about 3200 cm².

Introduction

The fact that vegetation (and also the fauna) is spatially heterogeneous has long been recognized by field biologists. The problem and explanation of spatial variation of various populations and/or communities are as interesting as temporal variation, as spatial variability has been investigated nearly since the recognition of the phenomenon itself.

Spatial variability may have influence on the estimation of population and community parameters, such as the number of species, density, diversity, characteristic areas, etc. On the other hand, the actual values of these parameters may change according to the spatial heterogeneities. From these facts it is obvious that sampling has a key role in the study of spatial variability. The literature of this question is fairly rich, however, investigations applying spatial processes are in minority. Under the term "spatial process" we mean the

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same as in the previous two papers, i.e., the behaviour of several characteristics in the function of sampling unit size. About the general theory and application of spatial processes there is an excellent overview (PODANI 1984).

In this paper we continue the study of different vegetation characteristics by means of a spatial process. Some of these were discussed to a certain degree in Parts I and II (MOLNÁR and NOSEK 1979, 1980). In this paper they are also discussed, because the sampling process is somewhat different from that described in I and II, further species are involved in the analysis and different methods of evaluation are used.

As this topic has an enormous literature it cannot be the task of this paper to give even a superficial review. Therefore, only those papers necessary for the discussion will be mentioned or cited.

Material and methods

1.1. The investigations were carried out in a sandy grassland (*Festucetum vaginatae danubiale*) near Vácrátót, North Hungary. A detailed description of this community is given in FEKETE et al. (1976).

1.2. The data were obtained using a map of a scale 1 : 10. The map was drawn on the basis of photographs of an area of 4.8×10 m, taken in July 1975. (This map is the same as used in NOSEK 1976.) The date of sampling corresponds to the summer aspect in Parts I and II.

Sampling was carried out on this map using quadrats of different sizes, each of 180 replications. The quadrats were randomly placed on the map using a HP 9820A calculator and plotter. The quadrats were drawn by the plotter using the same scale of 1 : 10. The counting of the individuals was made taking a survey of these quadrats of the map. 11 plot sizes were applied: 100, 200, 400, 800, 1600, 3200, 3600, 6400, 10 000, 12 800 and 25 600 cm². In the sequel plot sizes will be referred to by numbers 1, 2, ..., 11. From the sizes two series can be set up:

a) by powers of two, 100×2^n , $n = 0, \dots, 8$ (sizes 1, 2, 3, 4, 5, 6, 8, 10 and 11);

b) increasing the side of the quadrat by 20 cm from the 20×20 cm size (plot sizes 3, 5, 7, 8 and 9).

Series "b" was needed to compare the results with those established in the previous two parts. In this paper these two series of sizes will be used together.

In some cases the total photographed area of 480 000 cm² had to be added to the series. This "size" will be denoted by "T".

As a consequence of the limited size of the study area (4.8×10 m) and the relatively high number of replications, the quadrats were more or less overlapping.

1.3. Ten vascular plant species were found on the mapped area. These are: *Festuca vaginata*, *Thymus* sp., *Fumana procumbens*, *Medicago minima*, *Carex stenophylla*, *Festuca wagneri*, *Cynodon dactylon*, *Plantago indica*, *Centaurea arenaria* and *Onosma arenaria*. The last one was represented only by two specimens, so it was neglected from the evaluation.

As in the case of some species there was no possibility to separate the individuals within a patch, a patch was regarded as a single individual. For these patch-forming species a single individual was recorded as present even if only a small fraction of the patch fell within the sampling unit.

1.4. The following symbols will be used throughout:

$$\bar{X}_{ij}$$

is the arithmetic mean of characteristic X for the 180 replications; i denotes the species (in actual cases the i -s are replaced by abbreviations: *Fe*, *Th*, *Fu*, *Me*, *Ca*, *Fw*, *Cy*, *Pl*, *Ce*. This order is the same as that of the species list above); j denotes the plot size, $j = 1, \dots, 11$ and T (cf. 1.2).

The following characteristics were measured and/or calculated:

A_j — plot size (cm²)

$\bar{S}_j$ — the mean number of species at plot size j

$\bar{n}_{ij}$ — the mean number of individuals of species i at plot size j , $\sum_i \bar{n}_{ij} = \bar{N}_j$

$\bar{d}_{ij}$ — the absolute density of species i at plot size j (no. of individuals/m²)

$$\bar{d}_{ij} = \frac{\bar{n}_{ij}}{A_j} 10^4, \quad \sum_i \bar{d}_{ij} = \bar{D}_j$$

$\bar{f}_{ij}$ — the frequency of species i at plot size j = the number of plots of size j in which species i is present divided by the number of replications (here 180).

$$\sum_i \bar{f}_{ij} = \bar{F}_j$$

$\bar{d}_{ij}^r$ — relative density

$$\frac{\bar{d}_{ij}}{\bar{D}_j} 100$$

$\bar{f}_{ij}^r$ — relative frequency

$$\frac{\bar{f}_{ij}}{\bar{F}_j} 100$$

Curve fitting was made using the non-linear least squares method (DRAPER and SMITH 1966).

Results and discussion

2.4. Species-area relation

2.1.1. The relationship between the number of species and the sampled area has been studied for more than 60 years. These investigations can be regarded as "pioneer" applications of spatial processes.

The majority of the species-area curves were obtained for large areas (in geographical sense), and far less investigations were carried out within a community. CONNOR and MCCOY (1979) reviewed 100 species-area curves of which very few had been derived from smaller areas comparable to a single community.

The species-area curves originally were regarded as a useful tool to determine or predict several characteristics (cf. CONNOR and MCCOY 1979), such as optimum sample plot size and number, minimum area, rate of species accumulation, the expected number of species in a community, etc. For these purposes the above authors attempted to give some biological interpretations — with more or less success — to the parameters of the fitted curves.

Several functions were proposed to describe the behaviour the number of species in relation to the area (BALOGH 1953, CONNOR and MCCOY 1979, KOBAYASHI 1979, PODANI 1984).

Recently, KOBAYASHI provided a general theory and on this basis some models "which demonstrate the process (i.e., the general process underlying the curves) and give some community parameters of ecological significance" (KOBAYASHI 1979). His models are based on the probability for a species to be present in a sampling unit. He proposed equations for a community in an "open habitat" ($S = \lambda \ln(1 + x/E)$) and for a "delimited community" ($S = T [1 - (1 + x/E)^{-A}]$).

To the parameters in the equations he gave the following meaning. "E is, the elemental area, and may be regarded as a parameter characterising the factors control the spatial segregation of species in a smaller area". Its value depends on the size of the individuals and on the size of clumps or territories. "λ" is the measure of specific diversity, that is the expected number of species in the characteristics area, C [$C = (e - 1)E$, where e is the base of the natural logarithm]. The parameter A equals to $\ln [T/(T - \lambda)]$, where T is the maximum number of species in a delimited community. S approaches T as the plot size increases. The

detailed meaning and the ecological significance of them are detailed in his paper (KOBAYASHI 1979).

His two models — to a certain degree — can be considered equivalent to studies over geographical areas and/or within a community. Most of the previous functions (e.g., ARRHENIUS' curve, GLEASON'S curve, KILBURN'S "power function", etc.) are derived from or adapted to his models. However, the "ecological significance" of the parameters of his models does not seem interpretable in every case.

Detailed review of the species-area problem (historical aspects, purposes, applicability for the minimum area approach as well as statistics and related topics) can be found in the papers of KILBURN (1966), TÜXEN (1970, cit. in PODANI 1984), CONNOR and MCCOY (1979) and PODANI (1984).

2.1.2. In this study the change of $\bar{S}_j$ in relation to A_j was investigated over two area intervals;

a) from A_1 to A_{11} (100–25 600 cm²), denoted by I_1 ,

b) from A_1 to A_T (100–480 000 cm²), denoted by I_2 .

The observed $\bar{S}_j$ values are represented in Figures 1–7 by dots. The behaviour of ΔS ($\Delta S = \bar{S}_{+1} - \bar{S}_j$) was also investigated (Figs 1–2).

Several functions were attempted to fit to the $\bar{S}_j$ values in both cases. Values of the fitted curves as well as the common or original formulae are found in Table 1.

On the whole length of I_1 and I_2 the power function (Figs 1 and 3) and the GLEASON'S curve (Figs 2 and 4) could be fitted.

Having a closer look at the fitted GLEASON'S curves and the original $\bar{S}_j$ values, some tendency in the position of the points relative to the curves can be recognized. On the basis of this phenomenon, $\bar{S}_j$ values can be separated into two sets, and therefore the intervals I_1 and I_2 can also be divided into two parts. These subsets and subintervals are $\bar{S}_1 - \bar{S}_6$ ($A_1 - A_6$), $\bar{S}_7 - \bar{S}_{11}$ ($A_7 - A_{11}$) and $\bar{S}_7 - \bar{S}_T$ ($A_7 - A_T$), denoted by I_{11} , I_{12} and I_{22} respectively. (Note that $I_1 = I_{11} + I_{12}$ and $I_2 = I_{21}$.) These subsets of $\bar{S}_j$ will be treated separately.

Considering the curve of ΔS_j versus A_j (Figs 1 and 2) two local minima can be detected, between A_6 and A_7 , and between A_9 and A_{10} .

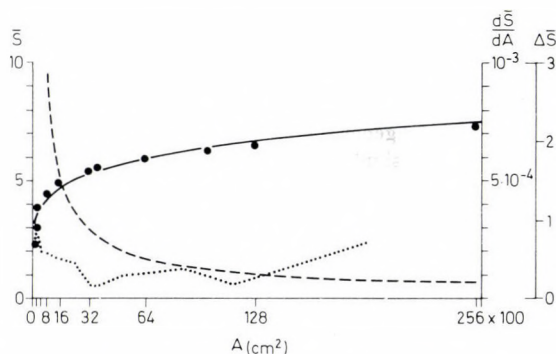


Fig. 1. Change of $\bar{S}_j$ over plot size in interval I_1 [dots represent the observed $\bar{S}_j$ values, solid line is the fitted power function ($\bar{S} = 1.394X^{0.166}$), dashed line is the first derivative of the power function, pointed line reflects the change of ΔS_j]

In I_{11} the logistic function (Figs 5 and 6) and KOBAYASHI's function for a delimited community (Fig. 7) gave the best (and almost the same) fit. The fit of the GLEASON's curve was looser (Table 1). The values of the parameters of the latter curve are very similar to the results of a previous study ($a = 2.295$, $b = 0.689$, $F = 482.3$ in NOSEK 1976).

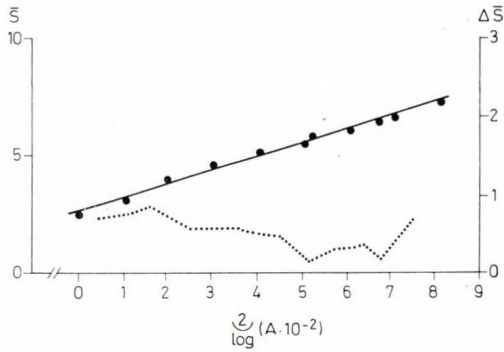


Fig. 2. The fitted GLEASON's curve in interval I_1 ($\bar{S} = 2.583 + 0.581X$, pointed line as in Fig. 1)

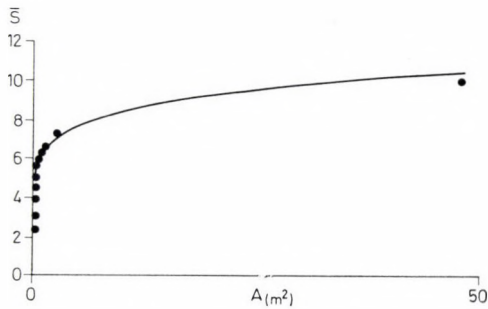


Fig. 3. The fitted power function in interval I_2 ($\bar{S} = 1.760X^{0.136}$)

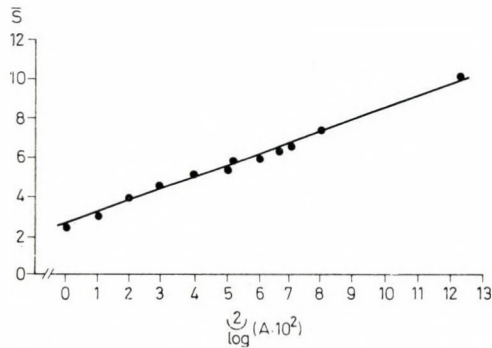


Fig. 4. The fitted GLEASON's curve in interval I_2 ($\bar{S} = 2.518 + 0.599X$)

In I_{12} three functions could be fitted. The best fit was resulted using the exponential curve (Fig. 5). The fit of KOBAYASHI's open "habitat" function was also significant at the level of 0.1%, but the F-value of the fitting is lower.

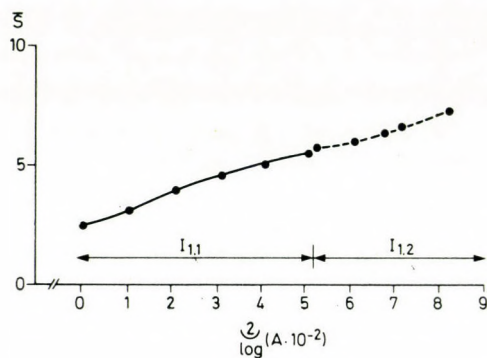


Fig. 5. The fitted logistic curve in I_{11} [$\bar{S} = 6.24/(1 + 1.644e^{-0.491X})$, solid line] and the fitted exponential curve in I_{12} ($\bar{S} = 3.498e^{0.09X}$, dashed line)

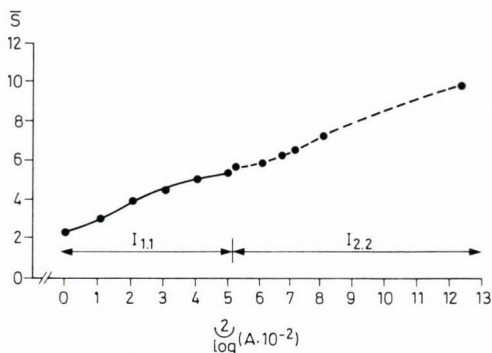


Fig. 6. The fitted logistic curve in I_{22} [$\bar{S} = 22.05/(1 + 5.634e^{-0.125X})$, the solid line is the same as in Fig. 5]

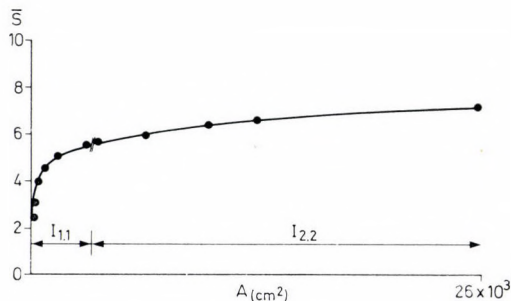


Fig. 7. The fitted KOBAYASHI's function in I_{11} [$\bar{S} = 7.104/[(1 - (1 + X/46.45)^{-0.348})]$] and in I_{12} ($\bar{S} = 0.826 \ln(1 + X/4.317)$)

Table 1

The various functions fitted to the $\bar{S}$ versus A relationship

Scale of the x-axis: (1) = arithmetic scale, $X = A$ in cm^2 , (2) = logarithmic scale, $X = \log_2 (A/100)$. Significance levels: *** = 0.1%, ** = 1.0%. α corresponds to A in the common form of logistic function, θ and θ correspond to T and A , respectively in KOBAYASHI's functions

A_j Interval	Common form	Fitted with function parameters	Value of F-test	Scale of x- axis
A_1-A_{11}	$Y = a + b \log X$	$\bar{S} = 2.583 + 0.581X$	1135.8***	(2)
	$Y = aX^b$	$\bar{S} = 1.394X^{0.166}$	234.6***	(1)
A_1-A_T	$Y = a + b \log X$	$\bar{S} = 2.518 + 0.599X$	1961.0***	(2)
	$Y = aX^b$	$\bar{S} = 1.760X^{0.136}$	251.3***	(1)
A_1-A_6	$Y = \alpha/[1 + (ae^{-cX})]$	$\bar{S} = 6.24/[1 + (1.644e^{-0.491X})]$	1378.0***	(2)
	$Y = \theta/[1 - (1 + X/E)^{-\theta}]$	$\bar{S} = 7.104/[1 - (1 + X/46.45)^{-0.348}]$	1362.5***	(1)
	$Y = a + b \log X$	$\bar{S} = 2.490 + 0.632X$	310.4	(2)
A_7-A_{11}	$Y = aX^b$	$\bar{S} = 2.113X^{0.587}$	107.3**	(2)
	$Y = ae^{cX}$	$\bar{S} = 3.498e^{0.09X}$	329.0***	(2)
	$Y = \lambda \ln(1 + X/E)$	$\bar{S} = 0.826 \ln(1 + X/4.317)$	167.5***	(1)
A_7-A_T	$Y = \alpha/[1 + (ae^{-cX})]$	$\bar{S} = 22.05/[1 + (5.634e^{-0.125X})]$	993.7***	(2)

In I_{22} , regarding the significance of fitting, only the logistic curve was acceptable (Fig. 6).

Which is the "best model"? Goodall states: "A decision between the two proposed forms of the species-area curve cannot be made on a priori grounds, but must rest on observational data" (cit. in CONNOR and MCCOY 1979). On the basis of the F-test we can choose the GLEASON's curve in both I_1 and I_2 . But we must not rely only on the significance of the fit and neglect the small "discrepancy" between the points and the fitted curve, because this can have an important meaning. Do not forget that in the total I_1 and I_2 neither KOBAYASHI's functions, nor the logistic curve could be fitted.

The ΔS values, after the initial increase, decrease from A_3 to A_6 . Then an increase begins again, with a local decrease after A_9 . These two ordinates on the x-axis correspond to the plot sizes between 1600 and 3200 cm^2 as well as between 10 000 and 12 800 cm^2 . The S values belonging to these areas are about 5 and 6.

The good fit of the logistic and KOBAYASHI's delimited curve in I_{11} shows a delimited community character, as if it were a "subcommunity" within the *Festucetum vaginatae danubiale*, with a maximum (saturation level) species number of 6 and 7, respectively. Regarding the I_{12} interval, the fitted curves suggest an open character. Involving A_T , too in the I_{22} interval the logistic curve had the best fit with a saturation level of 22 species. That is the tendency of the increase in species number with the plot size also refer to a delimited character. It is to be noted that the curves of the power function for I_1 and I_2 also show a flattening.

Pócs (1954) published the species-area curve drawn on the basis of his investigations carried out in another stand (at Rákoskeresztúr, at the fringe of Budapest) of this community. His curve — regarding the shape of it — must be of the type of power-function, and flattens at about 40 m^2 with a species number about 25. In a third occurrence (in Szent-

endre-Island) of *Festucetum vaginatae danubiale* the average species number was found on the basis of plots of 25 m², to be 24.67 (PRÉCSÉNYI 1981).

FEKETE and KOVÁCS present species-area curves for the open (*Sesaleo-Festucetum pallentis*) and for the closed (*Festuco pallenti-Brometum pannonicae*) dolomitic rocky grassland (FEKETE and KOVÁCS 1978). As the authors write: "... the sandy meadow" (i.e. *Festucetum vaginatae danubiale*) "is a vicarious pair in the Plain of the community examined by us (especially, of the open grassland)". Having fitted the power function and the GLEASON's curve on the published data, for the open rocky grassland the latter, for the closed rocky grassland the former gave better fit, regarding the values of the F-test, although the fit of the GLEASON's curve to the data of the closed grassland was also significant at the level of $p < 0.001$. The rate of the increase in species number of the open rocky grassland was closer to that of the sandy meadow than the rate in the closed rocky grassland ("b" values of the GLEASON's curve; 0.581; 0.782 and 1.837 for sandy meadow, open and closed rocky grassland, respectively).

The rates of increase in species number with the plot size (cf. "b" values of the GLEASON's curve in Table 1) are almost equal for I_1 and I_2 on the basis of the GLEASON's curves. The corresponding values of the logistic function ("c" in Table 1) are different for I_{11} and I_{22} and indicate a more rapid increase in I_{11} than in I_{22} .

These results suggest that the increase in species number with plot size takes place in two steps. First the increase is rapid and tends to an area slightly greater than the 40 × 40 cm plot. This is due to the predominant and dominant species (*Festuca vaginata*, *Thymus* sp., *Fumana procumbens*, *Medicago minima* and *Carex stenophylla*). In the second step (I_{22}) the first increase is due to *Festuca wagneri*, whereas the second to the remaining species (*Cynodon dactylon*, *Plantago indica* and *Centaurea arenaria*).

2.1.3. To determine the minimum area of a community several methods are applied, usually with little success. The majority of the methods are based on the flattening phase, or certain slope values of the fitted curves. KILBURN (1966) suggested the first derivative of his "power function" to choose an "appropriate slope value" for determining the minimum area, but this procedure is quite arbitrary.

In Fig. 1 the dashed line represents the first derivative of the fitted power function ($\bar{S} = 1.394 A^{0.166}$). The intercept of the original and first derivative curves is between the area of A_5 and A_6 . This result seems to be in good agreement with the position of the end of I_{11} , but the place of this intercept depends on the scale of $d\bar{S}/dA$. Thus, this approach is also sensitive to arbitrary decisions.

2.2. Dominance-diversity curves

Analyses of the dominance-diversity curves usually have in view to make conclusions on niche partitioning in a community (WHITTAKER 1965). Although most studies compare several communities or stages of a successional series, in this context it may be interesting whether on the basis of successively increased plots the same conclusion could be drawn for a single community.

The dominance-diversity curves for all plot sizes are shown in Fig. 8.

The shape of every curve approximates the logistic one. In the above mentioned study PRÉCSÉNYI (1981) found also the dominance-diversity curve approaching the sigmoid form. A single species is predominant (*Festuca vaginata*), four are subordinate (*Thymus* sp., *Fumana procumbens*, *Medicago minima* and *Carex stenophylla*) and other four are rare (*Festuca wagneri*, *Cynodon dactylon*, *Plantago indica* and *Centaurea arenaria*).

The upper part of the curves reflecting the predominant and subordinate species is very similar, and suggests that the niche partitioning of these species prove the same regard-

ing all the plot sizes. However, the rank order of these species is not the same for all A_j -s (Table 2). The first, or most successful species is the generalist *Festuca vaginata* in every case occupying a larger part of the niche space (cf. PRÉCSÉNYI 1981). The second most successful species is *Thymus* sp. Starting from A_3 almost every plot size *Medicago* is the third, *Carex* is the fourth and *Fumana* is the fifth. This is in good agreement with the conclusions of an earlier series of investigations on the niche structure of this community (FEKETE et al. 1976, PRÉCSÉNYI et al. 1977a, 1977b, 1980). In these investigations *Festuca vaginata*, *Thymus* sp.,

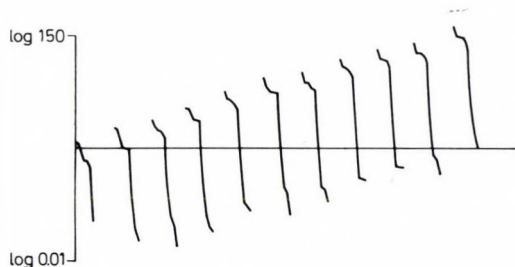


Fig. 8. Dominance-diversity curves of the separate A_j -s ($j = 1, \dots, 11$, from left to right). The uppermost end of each curve represent the first species of the rankorder (here *Festuca vaginata*)

Medicago minima and *Carex stenophylla* proved to be generalist (the generalist character decreased from *Festuca* to *Carex*) and *Fumana procumbens* was found to be a specialist.

The first six species are present in every seasonal aspect of the community. *Festuca wagneri* is in every case at the sixth place, indicating its transitional position between the dominant and rare species regarding the dominance and density relations. On the basis of this stable sixth place we may suppose that *Festuca wagneri* is having the most specialist character among the "all-season present" species. (The above mentioned studies did not include *F. wagneri*.) But we must not forget, the dominance-diversity curves — and the niche partition-

Table 2

The rank order of the species in the dominance-diversity curves

Rank number	Plot size										
	A_1	A_2	A_3	A_4	A_5	A_6	A_7	A_8	A_9	A_{10}	A_{11}
1	Fe	Fe	Fe	Fe	Fe	Fe	Fe	Fe	Fe	Fe	Fe
2	Th	Th	Th	Th	Th	Th	Th	Ca	Me	Th	Me
3	Fu	Fu	Me	Me	Me	Me	Me	Me	Th	Me	Th
4	Me	Me	Ca	Fu	Ca	Ca	Ca	Th	Ca	Ca	Ca
5	Ca	Ca	Fu	Ca	Fu	Fu	Fu	Fu	Fu	Fu	Fu
6	Fw	Fw	Fw	Fw	Fw	Fw	Fw	Fw	Fw	Fw	Fw
7	—	Cy	Ce	Ce	Ce	Ce	Cy	Cy	Pl	Cy	Cy
8	—	Ce	Pl	Pl	Pl	Cy	Ce	Pl	Ce	Ce	Pl
9	—	—	Cy	Cy	Cy	Pl	Pl	Ce	Cy	Pl	Ce

ing indicated by them — are based here on the abundance relations, so *Festuca wagneri* seems to be a specialist only on this basis and only in this community. In the next stage of the succession series — where *F. wagneri* is the dominant species — it will prove — without any doubt — to be a generalist.

Examining the terminal part of the curves, the rare species, there are differences in both shape and rank order. These three species occur in the autumn aspect, rather than in spring or summer so in the time of sampling the individuals were not totally developed, or not all present, so reliable conclusions cannot be drawn on the niche partitioning among them.

2.3. Frequency and relative frequency of species

2.3.1. Frequency of species will be used here in the traditional phytosociological sense (cf. 1.4.).

Several authors agree that frequency depends on plot size and the spatial pattern of species. It is also known that with increasing plot size the frequency of dominant species of great density increases more rapidly than that of the rare ones (e.g., WEAVER and CLEMENTS 1938, CURTIS and MCINTOSH 1950, GREIGH-SMITH 1964, etc.).

Table 3

The frequency of species at increasing plot sizes

Species	Plot size										
	A ₁	A ₂	A ₃	A ₄	A ₅	A ₆	A ₇	A ₈	A ₉	A ₁₀	A ₁₁
<i>Fe</i>	65.6	73.3	90.0	96.1	99.4	100.0	100.0	100.0	100.0	100.0	100.0
<i>Th</i>	53.9	68.3	73.9	90.0	94.4	98.3	98.3	99.4	100.0	100.0	100.0
<i>Fu</i>	43.9	57.8	69.4	85.6	93.3	97.8	97.8	97.8	98.9	100.0	100.0
<i>Me</i>	36.7	50.6	68.3	77.8	87.2	93.3	93.9	92.8	98.9	100.0	100.0
<i>Ca</i>	32.2	41.7	68.9	71.7	87.8	92.2	94.4	98.9	99.4	100.0	100.0
<i>Fw</i>	4.44	9.44	13.9	17.8	28.3	42.8	50.6	63.9	81.1	83.3	100.0
<i>Cy</i>	—	2.78	1.67	2.78	3.89	12.2	11.7	13.9	23.9	32.2	56.1
<i>Pl</i>	—	—	2.22	2.22	2.78	3.33	5.56	11.7	15.0	10.6	26.1
<i>Ce</i>	—	2.22	5.00	6.11	8.33	12.2	11.7	16.7	19.4	25.0	33.3

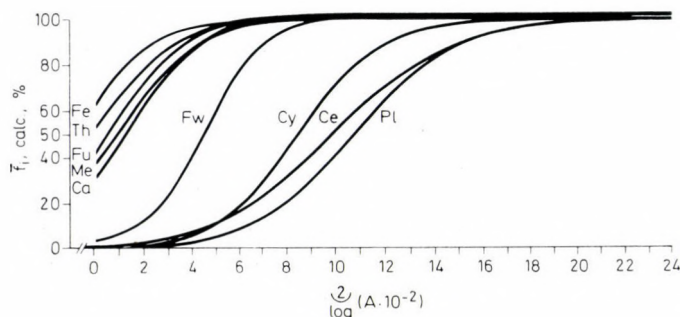


Fig. 9. The logistic curves fitted to the frequency data

Table 4

The parameters of logistic curves fitted to the frequency values of the different species

$$(f_i, \text{calc} = L/[1 + ae^{-cX}], X = \log_2 (A/100))$$

Species	Parameters			Value of F-test
	L	a	c	
<i>Fe</i>	101.2	0.598	-0.706	147.2***
<i>Th</i>	102.4	0.924	-0.565	266.5***
<i>Fu</i>	101.9	1.409	-0.632	574.4***
<i>Me</i>	101.0	1.742	-0.601	800.0***
<i>Ca</i>	101.9	2.303	-0.637	249.5***
<i>FW</i>	100.0	35.79	-0.784	64.8***
<i>Cy</i>	100.0	148.4	-0.586	76.9***
<i>Pl</i>	100.0	183.1	-0.481	50.9***
<i>Ce</i>	100.0	55.36	-0.405	446.9***

Significance level: *** = 0.1%

Table 5

Minimum plot sizes needed to reach a frequency of 50% and 90% on the basis of the fitted curves

(The upper values are the area in cm², the lower ones are the corresponding A_J-s, if they exist)

Species	Frequency	
	50%	90%
<i>Fe</i>	58.97 -A ₁	466.9 A ₃ -A ₄
<i>Th</i>	85.7 -A ₁	1 032.4 A ₄ -A ₅
<i>Fu</i>	139.8 A ₁ -A ₂	1 339.4 A ₄ -A ₅
<i>Me</i>	185.5 A ₁ -A ₂	2 142.7 A ₅ -A ₆
<i>Ca</i>	238.0 A ₂ -A ₃	2 239.5 A ₅ -A ₆
<i>FW</i>	2 363.7 A ₅ -A ₆	16 487.0 A ₁₀ -A ₁₁
<i>Cy</i>	3.7 × 10 ⁴	49.7 × 10 ⁴
<i>Pl</i>	18.2 × 10 ⁴	431.8 × 10 ⁴
<i>Ce</i>	9.6 × 10 ⁴	413.2 × 10 ⁴

2.3.2. As the maximum frequency for a given species cannot be more than 100%, it seemed to be worth trying to fit some theoretical curves having an upper limit to the observed frequency-area curves. On the basis of the actual data (Table 3) the logistic function proved the best for all species (Fig. 9).

Regarding the position of the curves the species can be divided into three groups reflecting the dominance structure of the community (cf. 2.2.).

The parameters of the fitted curves are given in Table 4. In the rate of the frequency increase ("c" in Table 4) there are no significant differences among the predominant, subordinate and rare species. The differences in densities are better reflected by values of "a".

The fitted curves enable us to determine the plot size belonging to a given frequency value. The calculated values for 50% and 90% are given in Table 5.

2.3.3. In Fig. 10 are depicted the changes of relative frequencies. The three groups, separated already in the previous results, can also be recognized here.

After CURTIS and McINTOSH (1950), the relative frequencies tend to approach the value of $100/S$ (S is the number of species) as plot size increases. In this community, on the basis of the fitted frequency curves, $100/S$ could be obtained at a plot size of about 1500 m^2 .

If we regard only the dominant five species, the case of equal relative frequencies is reached between A_8 and A_9 . Involving *Festuca wagneri*, too this situation is obtained between A_{10} and A_{11} . This fact suggests that regarding the first six species (the so-called "all-season present" species) the community is homogeneous (CURTIS and McINTOSH 1950).

2.4. Number of individuals, absolute and relative densities

2.4.1. There are strong positive linear correlations between $\bar{n}_{ij}$ and A_j as well as between N_j and A_j in both I_1 and I_2 . The corresponding values for I_1 are in Table 6. (The values for I_2 are not indicated because the correlations are even stronger and there is no F-value lower than 10^4 .)

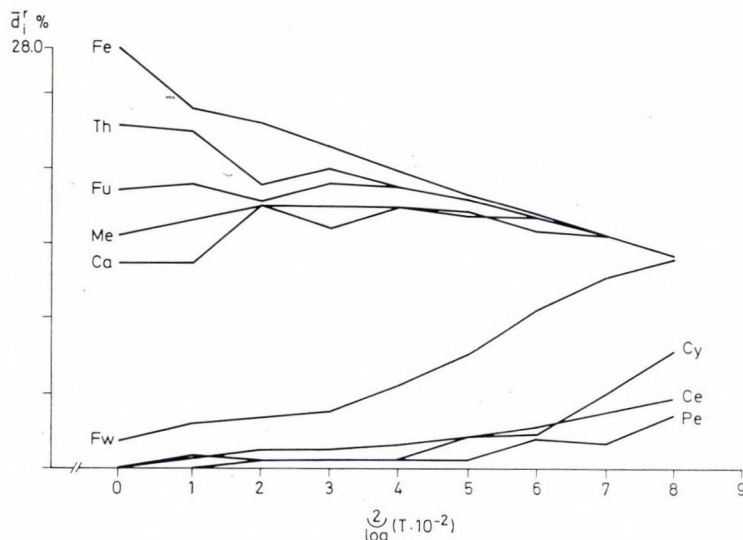


Fig. 10. Change of relative frequencies over plot size

The b_i values of the linear curves also reflect the dominance structure demonstrated by the dominance-diversity curves and frequency values.

The percentage differences between the observed and calculated n_i values based on A_g are:

<i>Festuca vaginata</i> :	— 2.5,
<i>Thymus</i> sp.:	— 3.5,
<i>Fumana procumbens</i> :	— 7.8,
<i>Medicago minima</i> :	— 4.2,
<i>Carex stenophylla</i> :	— 2.7,
<i>Festuca wagneri</i> :	—15.3,
<i>Cynodon dactylon</i> :	+67.3,
<i>Plantago indica</i> :	—12.9,
<i>Centaurea arenaria</i> :	—16.3 and
N_j :	— 3.3.

(Negative values indicate underestimates of the observed density.)

Table 6

*The correlation and linear regression coefficients
between the $\bar{n}_i$, $\bar{N}$ and A values*

Species	Coefficients			Value of F-test
	a	b	r	
<i>Fe</i>	1.646	50.14	0.9945	18 128.0***
<i>Th</i>	1.569	29.22	0.9991	4 957.0***
<i>Fu</i>	0.987	22.22	0.9996	11 209.0***
<i>Me</i>	0.529	31.81	0.9993	6 654.0***
<i>Ca</i>	0.260	28.71	0.9994	15 088.0***
<i>Fw</i>	0.094	2.161	0.9979	2 155.0***
<i>Cy</i>	—0.066	0.651	0.9806	199.8***
<i>Pl</i>	—0.0057	0.358	0.9765	143.6***
<i>Ce</i>	0.046	0.340	0.9955	879.2***
$\bar{N}$	4.808	166.0	0.9998	26 647.0***

Significance level: *** = 0.1%

2.4.2. The absolute density values show decrease with plot size (Fig. 11). In the figure there are also indicated the confidence limits (95 and 99%) calculated on the basis of the $\bar{d}_{ig}$ values (see also Table 7).

The density values of the rare species are almost within the confidence limits at every plot size, but the values of the confidence intervals, as percentage of the corresponding means are very high (*Cynodon*: $\pm 159.6\%$, *Plantago*: $\pm 204.0\%$ and *Centaurea*: $\pm 167.0\%$). These values for the other species are: *Fe*: $\pm 11.8\%$, *Th*: $\pm 28.6\%$, *Fu*: $\pm 25.3\%$, *Me*: $\pm 39.4\%$, *Ca*: $\pm 35.0\%$, and *Fw*: $\pm 57.3\%$.

The values of $\bar{d}_{iT}$ enable us to calculate a more narrow interval uniform for all species. Two intervals, $\pm 10\%$ and $\pm 5\%$ of $\bar{d}_{iT}$ (called "tolerance intervals"), were calculated.

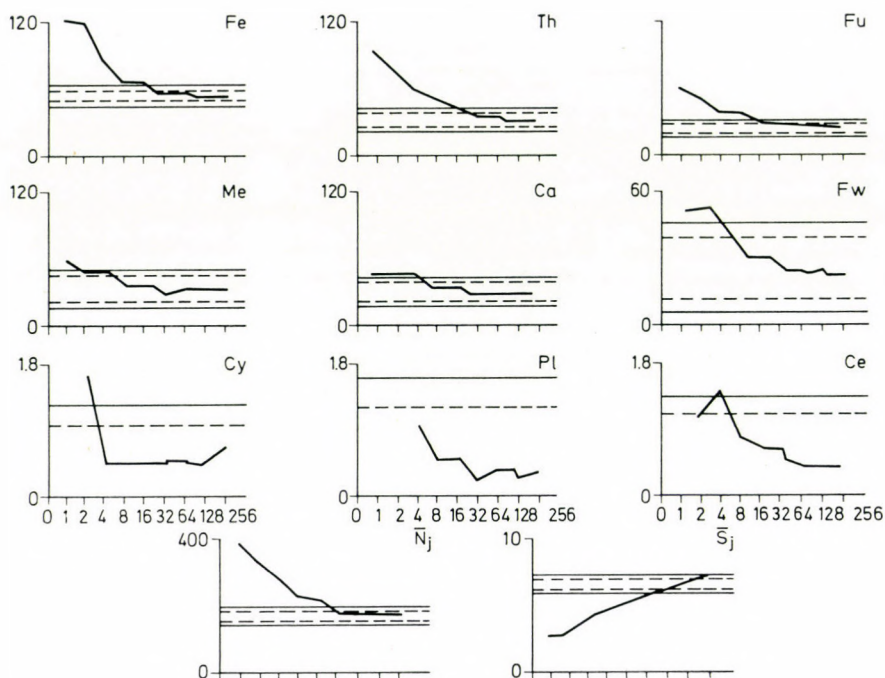


Fig. 11. Change of absolute density values over plot size. (The solid lines represent the 99%, the dashed the 95% confidence limits)

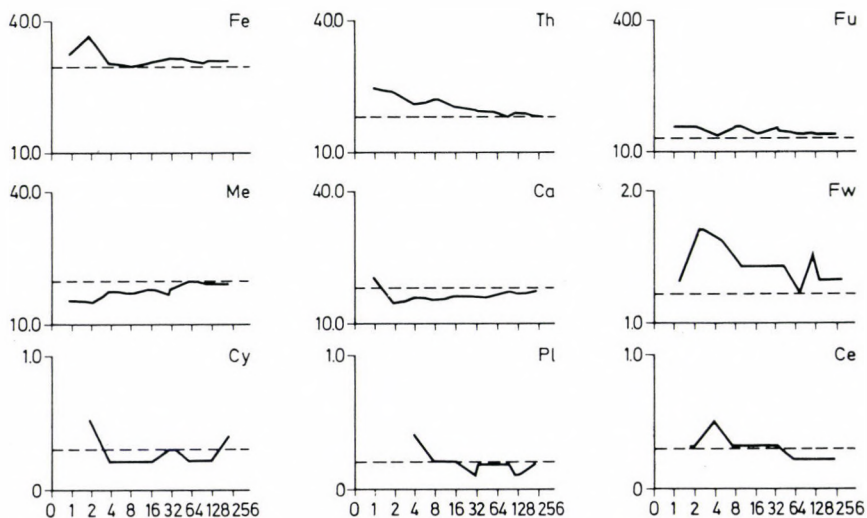


Fig. 12. Curves of the relative density values of the different species (dashed lines represent the $\bar{d}_{iT}^r$ value)

Table 7

The values of the various confidence and tolerance intervals
for the $\bar{d}_i$, $\bar{N}$ and $\bar{S}$ values

Species	Confidence intervals					
	99%			95%		
	$\pm \mu$	$\mu_{up.}$	$\mu_{lw.}$	$\pm \mu$	$\mu_{up.}$	$\mu_{lw.}$
<i>Fe</i>	8.62	60.02	42.78	6.1	57.5	45.3
<i>Th</i>	12.26	42.56	18.04	8.67	38.97	21.63
<i>Fu</i>	8.62	32.72	15.48	6.1	30.2	18.0
<i>Me</i>	18.48	51.68	14.73	13.07	46.27	20.13
<i>Ca</i>	14.6	44.10	14.90	10.33	39.83	19.17
<i>Fiw</i>	2.06	4.61	0.49	1.46	4.00	1.09
<i>Cy</i>	0.88	1.27	-0.49	0.62	1.01	-0.23
<i>Pl</i>	1.206	1.62	-0.79	0.84	1.25	-0.43
<i>Ce</i>	0.964	1.37	-0.56	0.68	1.08	-0.27
$\bar{N}$	30.7	202.5	140.9	21.76	193.5	149.9
$\bar{S}$	0.819	7.36	5.72	0.579	7.12	5.96

Species	Tolerance intervals					
	10%			5%		
	$\pm \eta$	$\eta_{up.}$	$\eta_{lw.}$	$\pm \eta$	$\eta_{up.}$	$\eta_{lw.}$
<i>Fe</i>	5.25	57.75	47.25	2.63	55.13	49.87
<i>Th</i>	3.14	34.54	28.26	1.57	32.97	29.83
<i>Fu</i>	2.26	24.86	20.24	1.13	23.73	21.47
<i>Me</i>	3.54	38.94	31.86	1.77	37.17	33.63
<i>Ca</i>	3.16	43.76	28.44	1.58	33.18	30.02
<i>Fiw</i>	0.21	2.31	1.89	0.105	2.21	2.00
<i>Cy</i>	0.048	0.527	0.431	0.024	0.503	0.455
<i>Pl</i>	0.035	0.389	0.319	0.018	0.372	0.336
<i>Ce</i>	0.050	0.550	0.450	0.025	0.525	0.475
$\bar{N}$	17.7	194.6	159.2	8.85	185.7	168.1
$\bar{S}$	1.0	11.0	9.0	0.5	10.5	9.5

The plot sizes for which density values lie within the different confidence and tolerance intervals are found in Table 8. The narrower the intervals the greater is the plot size needed to estimate the real density of a species with a given accuracy. If we are satisfied with an accuracy of 10% the minimum plot size needed to estimate the absolute density of the dominant species varies from 3200 to 6400 cm². For $\bar{N}$ this minimum plot size was given in every tolerance interval to 3200 cm².

There was no single plot size from which the number of species could be estimated with the given accuracy.

Table 8

Plot sizes falling between the upper and lower limit of the intervals in Table 7

Species	Confidence interval		Tolerance interval	
	99%	95%	10%	5%
<i>Fe</i>	A_6-A_T	A_6, A_8-A_T	A_6, A_8-A_T	A_6-A_{11}
<i>Th</i>	A_5-A_T	A_6-A_T	A_9-A_{10}	A_6-A_{11}
<i>Fu</i>	A_5-A_T	A_5-A_T	$A_{10}-A_{11}$	A_8-A_{11}
<i>Me</i>	A_2-A_T	A_4-A_T	A_4, A_7-A_8	A_4, A_5, A_7-A_{11}
<i>Ca</i>	A_3-A_T	A_4-A_T	A_4, A_4	A_4, A_5, A_7-A_{11}
<i>Fw</i>	A_3-A_T	A_4-A_T	$A_{10}-A_{11}$	A_8, A_{10}, A_{11}
<i>Cy</i>	A_3-A_T	A_3-A_T	A_6, A_{10}	A_5-A_7, A_{10}
<i>Pl</i>	A_3-A_T	A_3-A_T	—	A_{11}
<i>Ce</i>	A_2, A_4-A_T	A_4-A_T	—	A_7
$\bar{N}$	A_6-A_T	A_6-A_T	A_6-A_{10}	A_6-A_{11}
$\bar{S}$	A_9	A_9	—	—

2.4.3. The relative density of a species is the probability of the random encounter with one individual of that species. Figure 12 shows the change of relative densities in the function of plot size. In case of the dominant species a tendency could be detected in this change to approach the relative density at A_T . The values of the rare species proved to be fluctuating and independent of plot size.

Summary

The *Festucetum vaginatae danubiale* community is a semi-closed sandy grassland. Of the vascular plant species one is predominant and four are subordinate. Among the rare species *Festuca wagneri* was the "most dominant". This dominance structure of three groups was reflected well in the results.

For the dominant five species a plot size between 1600 and 3200 cm² proved large enough to estimate several parameters.

Including *Festuca wagneri* in this group the plot size necessary to the reliable estimate increases to about 1 m².

For the rare species reliable estimates could not be obtained even on the basis of the largest (~ 2.5 m²) plot.

The position of *Festuca wagneri* between the dominant and rare species is rather interesting. The next stage of the successional series on calciferous sandy soil between the Danube and Tisza rivers following *Festucetum vaginatae danubiale* is the association *Festucetum strictae* (*Festucetum stricta* = *F. wagneri*) (PÓCS 1954, PRÉCSÉNYI 1981, FEKETE pers. comm.). The result suggest that *Festuca wagneri* — the most successful species in its own association — appears as a pioneer invader in the previous stage of the successional series.

For certain characteristics of the whole community (e.g., dominance structure, niche partitioning, total number of individuals, living phytomass (cf. MOLNÁR and NOSEK 1979), etc. conclusions could be drawn from a plot size of about 3200 cm². The number of species is an obvious exception.

It is clear that the extent of the functional responses (e.g. production, flows of energy or matter, amount of accumulated elements, etc.) depend on the species forming considerable share of the community that is on the dominant species. The so-called rare species — especially if they are in minority regarding their mass — due to their subordinated role do not alter significant the functional responses. It is also clear that the minimal plot size necessary to estimate the functional characteristics of a community is different from that of characteristic areas reflecting some important property of the vegetation e.g. maximum resemblance of plots, the maximum of florula diversity, etc. (cf. JUHÁSZ-NAGY and PODANI 1983). In the former case we want to estimate certain characteristics with a predetermined accuracy.

Thinking over these fact we come to the conclusion that the plot size sufficient to estimate several functional characteristics of a community correspond to an area delimited by the dominant species constituted the larger part of the community. This area may be called to “functional minimum area”. Although the estimation of several functional characteristics with a predetermined accuracy and the determination of some characteristic areas can be carried out on the basis of spatial processes, they mean different approaches in the study of vegetation and result different areas. But it seems that there is a point where these two approaches (and areas) overlap. If we restrict the species list of a community only to the dominant species and investigate the characteristic functions (e.g. florula diversity) of this restricted set, the resulted characteristic area may correspond to the “functional minimum area”. If we reduce the number of species the area of maximum florula diversity will obviously shift to left on the plot-size axis. [This result was obtained also by VIRÁGH (pers. comm.).]

In terrestrial communities the functional minimum area is probably smaller than that of the area of maximum florula diversity, but in aquatic environment (e.g. in the case of phytoplankton) the reverse may be true, as rare phytoplankton species may be larger of several magnitude order in their biomass than the dominant ones.

The results (cf. the break in the species — are curves, the grouping of the frequency — plot size curves, the plot sizes necessary to reach a predetermined frequency valve or accuracy of estimation) suggest that the functional minimum area of the investigated *Festucetum vaginatae danubiale* is about 3200 cm².

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SPATIAL PROCESSES IN A GRASSLAND COMMUNITY, IV.

INVESTIGATION OF THE SPATIAL ARRANGEMENT PATTERN BY VARIOUS INDICES*

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The arrangement pattern of the separate species, total number of individuals and number of species were investigated in a semi-closed sandy meadow (*Festucetum vaginatae danubiale*) near Vácrátót, North Hungary. The following indices of arrangement pattern (IAP) were involved in the study: $s^2/\bar{x}$, "pattern intensity", mean crowding, patchiness, exponent k from the negative binomial series, MORISITA's index, IWAQ's p_i -index, the ratio of MORISITA's index, TAYLOR's power law and IWAQ's patchiness regression.

The different indices gave similar results to one another. Randomness was acceptable only in a very few cases at the smallest and at the greatest plot sizes. The IAP-s suggest for the overwhelming majority of species and plot sizes aggregation.

The two ecological generalist and at the same time the dominant species of the present and next stage of the succession series, *Festuca vaginata* and *Festuca wagneri*, respectively, showed random arrangement pattern at the two end of the plot size scale and the less departure from randomness over the intermediate plot sizes. *Thymus* sp. and *Fumana procumbens* showed moderate, *Carex stenophylla* and *Medicago minima* showed stronger aggregation. Strong aggregation was detected in the case of the rare species (*Cynodon dactylon*, *Plantago indica* and *Centaurea arenaria*), however these results may be dubious.

The total number of individuals has also aggregated arrangement pattern.

The size of the aggregates can be made to correspond partly to the size of the plants, partly to particular areas in this community.

The number of species showed a regular arrangement pattern over the whole scale of plot sizes. This may be an indication of competition between the species.

Introduction

One of the concurrent structures (cf. JUHÁSZ-NAGY 1972) of the vegetation is the phenetic structure referring to the arrangement of the individuals of a species to each other in the topographic space, that is the spatial arrangement pattern (SAP).

Investigations of SAP have been oriented from the recognition of the phenomenon in two directions: <1> the recognition and description of the three cases of SAP (that is, regular, random or aggregated) and <2> the explanation of this cases. Clearly these two aims are not independent from each other. The recognition of SAP is immediately followed by the question, "Why?".

The first step is anyways <1>. For the description of the arrangement pattern (AP) there are two possibilities: <a> the use of the different, so called "indices of dispersion" (fur-

* "Tece Studies" No. 39.

ther on I use the term "indices of arrangement pattern", IAP), $\langle b \rangle$ the use of several theoretical frequency distributions, or their parameters.

The overview of $\langle 2 \rangle$ is beyond our power, some examples or possibilities are given in the papers cited.

In the overwhelming majority of the studies of type $\langle 1 \rangle$ the main objective was to recognize the size of the aggregate (or aggregates), since the aggregated SAP seems to be the most widespread in the nature. As the value of the different IAP-s change plotted versus the sampling unit size (except for the random AP) (cf. e.g. PIELOU 1969, 1976, ELLIOT 1971, PODANI 1984), the use of sampling units of different sizes serves for the detection both of the type of AP and of the size of the aggregates. For this purpose the spatial processes (cf. FEKETE and SZŐCS 1974, PODANI 1984) are of the most advantage. GREIG-SMITH's block-size variance analysis method based on grid design and the use of belt transects are of this kind. These two sampling methods are the most widespread although they have some drawbacks, e.g. in the grid design the shape of the sampling unit changes at the successive levels of combination and/or in both design the successive sizes are not independent from each other. Moreover these designs — and the nested design also — overestimate the significance of the rare species, since if an individual of a rare species occur in the smallest, or in the first unit, it will counted in the successive levels, too.

"Theoretically, the use of independent random plots would represent the most satisfactory sampling design, since the result pertaining to each plot size could be compared by statistical tests. The second best strategy would be random sampling by nested plots (Fig. 2a-d), although the possibility of testing significance is lost. In practice, however the use of grids and transects of contiguous quadrats has become widespread in ecology, since the randomization and especially, repeated sampling with various plot sizes is exceedingly time consuming and the vegetation becomes more and more trampled as the sampling proceeds" (PODANI 1984). These two drawbacks, however may be overcome using a map based on photographs of the vegetation and performing the further elaboration on this map (SZŐCS 1977, 1979, MOLNÁR and NOSEK 1979). Of course the area photographed cannot be of any size (theoretically aerial photographs may be used).

The results of HAIRSTON et al. (1971) seem to contradict the random design. They used a grid design of 64 contiguous quadrats and from these different numbers were chosen randomly for test the efficiency of random design. They conclude: "Randomly placed samples gave very poor results in our study, and sampling that less than one fourth of the total area was so unreliable as to be considered worthless for revealing patterns of distribution". We must not forget however that their design was not really random and the "total area" was relative small (8×8 inch) even taken into account the size of the organisms studied.

To overcome the drawbacks of the quadrat sampling, with contiguous plots, the plotless or distance methods are used (cf. PIELOU 1976).

In the studies of AP the "classic" method — despite its drawbacks — is the GREIG-SMITH's "pattern analysis" (GREIG-SMITH 1964, 1979, KERSHAW 1964, PRÉCSÉNYI 1964, PRÉCSÉNYI et al. 1967, WESTMAN 1975). For random design (non-contiguous quadrats) the ratio of MORISITA's index ($I_{\delta,q} I_{\delta,2q}$) may be used to the GREIG-SMITH's method in analogous way (ELLIOT 1971, SOUTHWOOD 1978). In further papers MORISITA (1962, 1964, 1971), gave "some basic theories on the relations between the intra- and inter-group dispersion" using his I_{δ} , as well as its application for several sampling techniques. His I_{δ} was also applied in studies of the AP of widely different representants, e.g. for the SAP of the sex expression in silver maple (SAKAI and ODEN 1983), for the detection of stratification of zooplankton in a river (BUCHANAN and SCHLOSS 1983), or for the SAP of Lumbricida species in an oak forest (MOLDOVÁN et al. 1984).

LLOYD's patchiness (and the "Index of Mean Crowding") as well as the "m—m method, or patchiness regression" developed by Iwao on the basis of LLOYD's patchiness are also

used for the description of SAP (LLOYD 1967, PIELOU 1976, IWAO and KUNO 1971, IWAO 1977, etc.).

To detect the size of the aggregate (beside the GREIG-SMITH's method) IWAO's p_i -index and the ratio of I_0 of two successive plot size is used (cf. ELLIOT 1971).

Several other indices were also used, e.g. the variance/mean ratio and its derivatives (e.g. NUMATA's coefficient of homogeneity, ASHBY and STEVENS's test, DAVID and MOORE's Index of CLUMPING, Index of LEXIS, GREEN's Index, LEFKOVITCH's Index, CHARLIER's coefficient, etc.) as well as the exponent k (and $1/k$) of the negative binominal series, the coefficient b from TAYLOR's power law, etc.

Very good overviews of the different IAP-s are to be found in GREIG-SMITH (1964), ELLIOT (1971) and SOUTHWOOD (1978). Further detailed treatment of them are in PIELOU (1976) and in the papers of the authors (see reference list).

Investigations of SAP in the home literature are rare, only a few papers deal with this topic (PRÉCSÉNYI 1964, PRÉCSÉNYI et al. 1967, SZŐCS 1977, 1979, GALLÉ 1979, MOLDOVÁN et al. 1980, 1984).

Aim of the study

In this paper the change of several IAP-s are investigated by means of a spatial process involving plot size change in the sandy grassland *Festucetum vaginatae danubiale*. That is the study is essentially of type <1>.

Material and methods

3.1. Sampling area and sampling process was described in Part III (NOSEK 1986). For the sake of a better insight some informations must be however reiterated.

11 randomly placed plot sizes (each of 180 replications) were applied on a 1 : 10 map of the community. The sizes were: 100, 200, 400, 800, 1600, 3200, 6400, 10 000, 12 800 and 25 600 cm² (in the sequel they will be referred to A_j , $j = 1, 2, \dots, 11$) respectively).

The following ten vascular plant species were found on the mapped total sampling area of 4.8×10 m in July 1975: *Festuca vaginata*, *Thymus* sp., *Fumana procumbens*, *Medicago minima*, *Carex stenophylla*, *Festuca wagneri*, *Cynodon dactylon*, *Plantago indica*, *Centaurea arenaria*. The last one was represented only by two exemplars so it was neglected in the evaluation. The species will be denoted by the following abbreviations: *Fe*, *Th*, *Fu*, *Me*, *Ca*, *Fw*, *Cy*, *Pl* and *Ce*, respectively. Moreover the total number of individuals (that is of all species) and the number of species were examined (denoted by $\bar{N}$ and $\bar{S}$, respectively).

For each species and $\bar{N}$ and $\bar{S}$ at each plot size a frequency distribution were established. (The distributions themselves will be discussed in the next part of the series.) In the present paper were treated only the different IAP-s derived from the moments ($\bar{x}$ and s^2) of the empirical frequency distributions.

3.2. The following indices were calculated: "Index of Dispersion": $ID = \frac{s^2}{\bar{x}}$ (ELLIOT 1971), to test the agreement with the POISSON series (randomness) the variable

$$d = 2(n-1) \frac{s^2}{\bar{x}} - 2n - 3 \quad (\text{ELLIOT 1971})$$

"Index of Mean Crowding": $\dot{x} = \frac{\sum_{i=1}^n x_i(x_i - 1)}{\sum_{i=1}^n x_i}$ (LLOYD 1967)

"patchiness": $PA = \frac{\dot{x}}{\bar{x}}$ (LLOYD 1967)

Table 1
Values of *d* at

Species	Plot				
	A ₁	A ₂	A ₃	A ₄	A ₅
<i>Fe</i>	1.46	-0.61	4.42	5.03	2.75
<i>Th</i>	1.34	4.47	6.81	6.85	14.28
<i>Fu</i>	-0.66	1.44	3.12	3.96	5.47
<i>Me</i>	3.67	4.75	9.15	14.96	20.40
<i>Ca</i>	1.94	8.32	8.80	14.37	18.27
<i>Fw</i>	1.65	1.05	2.02	4.74	5.39
<i>Cy</i>	—	2.74	-0.08	2.74	12.71
<i>Pl</i>	—	—	8.63	8.63	17.02
<i>Ce</i>	—	-0.13	1.40	-0.51	2.18
$\bar{N}$	0.23	2.38	4.22	6.13	12.97
$\bar{S}$	-6.51	-8.13	-9.01	-10.66	-12.46

$$\text{"MORISITA's Index of Dispersion": } I_{\delta} = n \frac{\sum_{i=1}^n (x_i^2) - \sum_{i=1}^n x_i}{\left(\sum_{i=1}^n x_i \right)^2 - \sum_{i=1}^n x_i} \quad (\text{ELLIOT 1971})$$

significant departures from randomness were tested by the value of

$$g = I_{\delta} \left(\sum_{i=1}^n x_i - 1 \right) + n - \sum_{i=1}^n x_i \text{ using the } \chi^2 \text{ distribution at the corresponding degree of freedom and } p < 0.05 \text{ (cf. ELLIOT 1971).}$$

$$\text{"pattern intensity": } PI = \frac{s^2 - \bar{x}}{\bar{x}^2} \quad (\text{HILL 1973})$$

$$\text{"IWAOKI's } p_i\text{-index": } p_i = \frac{\dot{x}_j - \dot{x}_{j-1}}{\bar{x}_j - \bar{x}_{j-1}} \quad (\text{SOUTHWOOD 1978})$$

$$\text{the ratio of MORISITA's index: } Q = \frac{I_{\delta} \text{ for plot size } q}{I_{\delta} \text{ for plot size } 2q} \quad (\text{ELLIOT 1971})$$

the exponent "k" from the negative binomial series; two methods were applied for the estimation of k,

$$(1) \hat{k}_1 = \frac{\bar{x}^2}{s^2 - \bar{x}}$$

$$(2) n \ln \left(1 + \frac{\bar{x}}{\hat{k}_2} \right) = \sum \left(\frac{A_x}{k + x} \right) \quad (\text{WEBER 1957, SOUTHWOOD 1978})$$

where A_x is the sum of frequencies of samples containing more individuals than x (cf. ANSCOMBE 1950, cit. in SOUTHWOOD 1978, WEBER 1957). Depending on the value of $\hat{k}_1$ and $\bar{x}$ $\hat{k}_1$ was either accepted or used as initial value for the second estimate (that is $\hat{k}_2 = \hat{k}_1$ in the first step of the iteration),

increasing plot sizes

sizes					
A_6	A_7	A_8	A_9	A_{10}	A_{11}
6.04	2.96	4.84	5.34	8.42	9.09
14.69	16.88	19.02	26.07	28.43	29.94
7.61	10.42	15.07	16.55	24.02	30.23
25.55	28.85	44.86	45.81	49.15	56.40
23.80	22.12	27.99	35.34	28.84	31.41
4.96	7.04	5.19	7.18	6.03	0.33
2.69	7.46	11.49	7.82	13.84	20.12
13.63	12.19	12.57	13.94	15.64	17.73
6.64	7.26	5.25	9.67	10.81	13.48
13.65	13.54	25.16	28.48	28.55	29.10
-12.95	-11.88	-12.17	-12.37	-12.43	-13.04

the parameter "b" of TAYLOR's power law:

$$\log s^2 = \log a + b \log \bar{x} \text{ (TAYLOR 1961, cit. in ELLIOT 1971),}$$

the parameters α and β from IWA0's " $\dot{m}$ — m relation, or patchiness regression":

$$\dot{x} = \alpha + \beta \bar{x} \text{ (IWA0 and KUNO 1971, IWA0 1977)}$$

(where $\dot{m}$ and m are the values of mean crowding and mean density of the population whereas $\dot{x}$ and $\bar{x}$ are the corresponding values of the sample). It must be noted, that the symbols $\dot{m}$ and $\dot{x}$ are used according to the original papers, and they does not mean the first derivate of m and x .

TAYLOR's power law and IWA0's patchiness regression were calculated both on the basis of the data of the different plot sizes (original data) and on the basis of the data converted from each plot size to 1 m² (converted data). This conversion could be made owing to the strong and significant positive correlations between the number of the individuals and the plot size (cf. NOSEK 1986).

The i in the symbols refers to the number of replications (sample size) in each plot size ($i = 1, 2, \dots, 180$), j to the plot sizes ($j = 1, 2, \dots, 11$, cf. 3.1.).

Results

4.1. As the indices are based on $\bar{x}$ and s^2 there are some relations between them, that is some of them may be calculated from each other:

$$\left(1 + \frac{ID - 1}{\bar{x}}\right) = (1 + PI) = \left(1 + \frac{1}{k}\right) = PA, \text{ and } I_d = \frac{\dot{x}}{\bar{x} - (1/n)} \approx PA$$

(cf. LLOYD 1967, PIELOU 1969, 1976, ELLIOT 1971, PATIL and STITELER 1974, cit. in SOUTHWOOD 1978, SOUTHWOOD 1978).

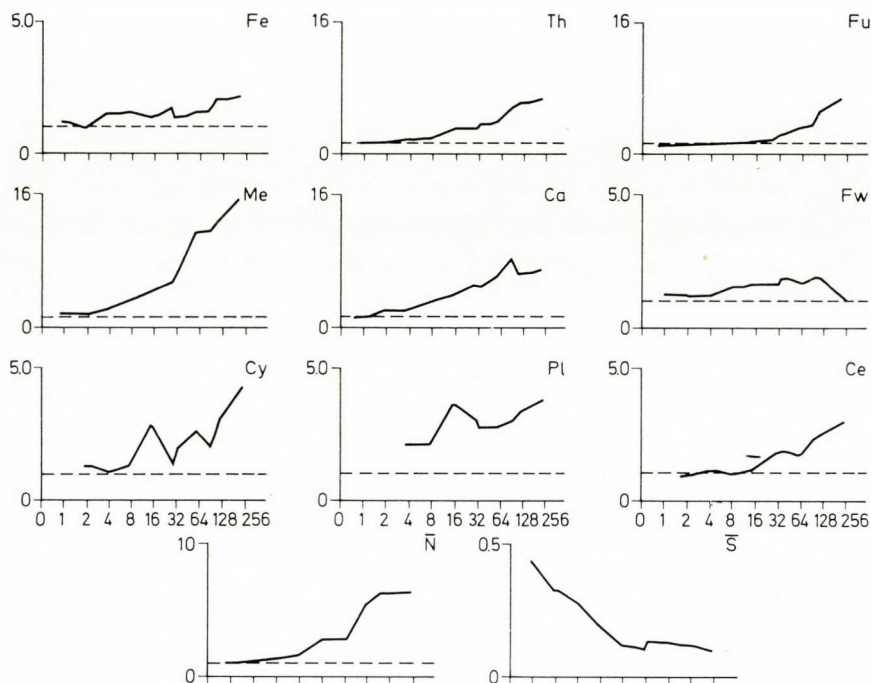


Fig. 1. Change of ID over plot sizes (values of the x axis are to be multiplied with 100 to get the area in cm². Dashed line indicates ID = 1.0)

4.2. Variance/mean ratio

The change of ID versus plot size is shown in Fig. 1. The values of d are in Table 1. d values falling between -1.96 and $+1.96$ refers to an agreement with the POISSON series (that is the random AP).

For the random AP the value of ID = 1.0, values greater or smaller than unity reflects aggregated or regular arrangement pattern of the representants, respectively.

The variance/mean ratio was criticized by several authors e.g. EVANS wrote "the $s^2/\bar{x}$ ratio may give a widely different estimate of non randomness from a χ^2 -test of goodness of fit" (EVANS 1952), or JAMES (1955-56) stated that $s^2/\bar{x}$ is unreliable when the mean density is very low or high, as well as it depends on quadrat size (SKELLAM 1952) (all cited in KER-SHAW 1964).

ID in itself is only an estimate of a population parameter (cf. PIELOU 1969) the test of randomness is made by the value of d .

4.3. Mean crowding and patchiness

Mean crowding can be interpreted as "the mean density which the population could have and be no more crowded on the average than it is now, if it had a random distribution" (LLOYD 1967). Therefore the ratio of $\bar{x}$ and $\bar{\bar{x}}$ (the patchiness) may be regarded as an estimator of the deviation from the randomness. For the value of PA the same is valid that for ID.

Values of mean crowding and mean density are in Table 2, the change of PA is shown in Fig. 2.

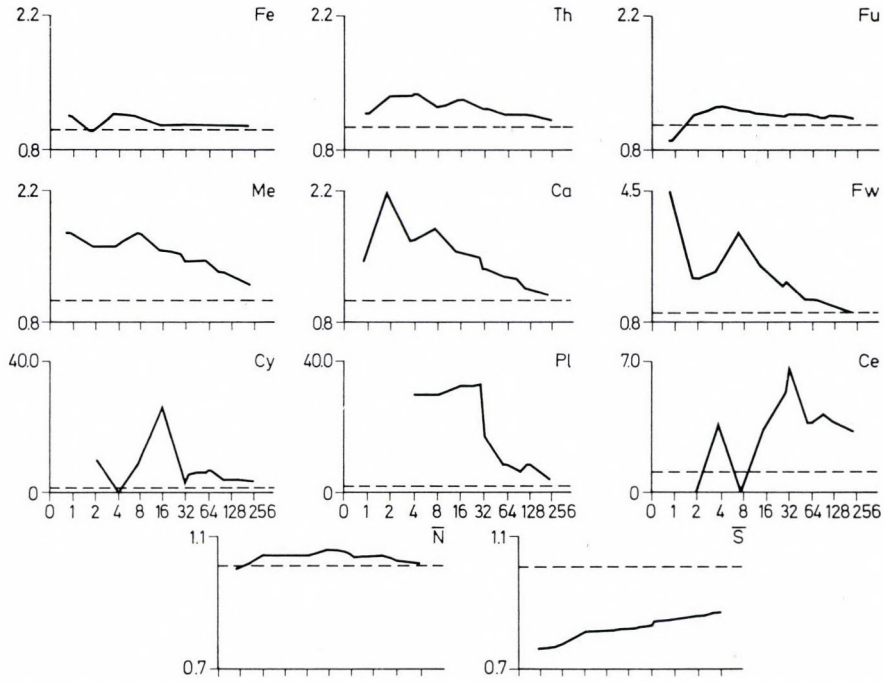


Fig. 2. Change of PA over plot sizes (x axis as in Fig. 1, dashed line indicates $PA = 1.0$)

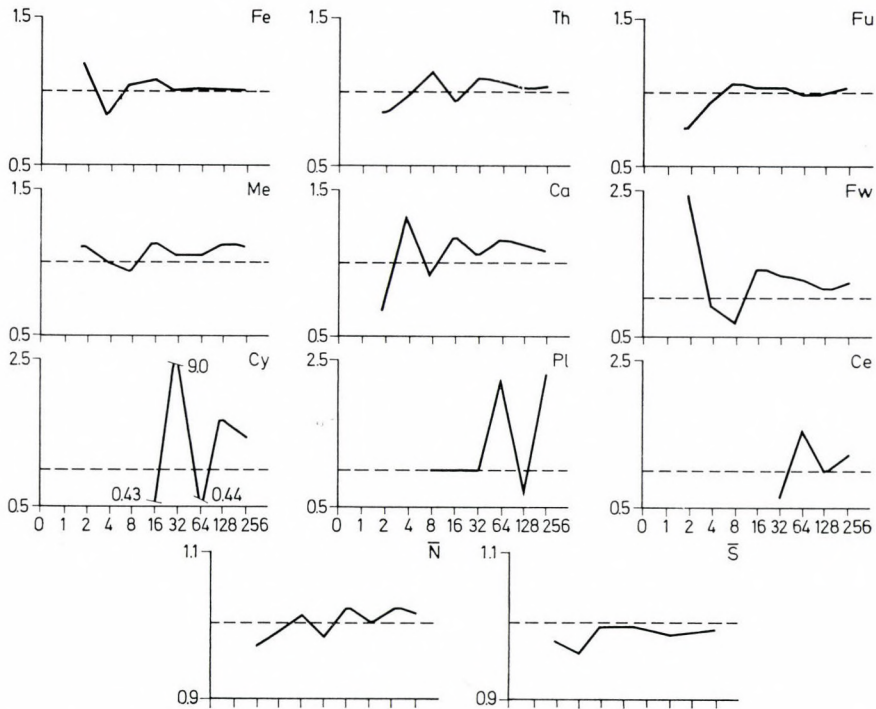


Fig. 3. Change of Q over plot sizes (x axis as in Fig. 1, dashed line indicates $Q = 1.0$)

Table 2
Changes of mean crowding $\bar{x}$ (upper value) and mean density $\bar{x}$ (lower value) with increasing plot size

Species	Plot size										
	A ₁	A ₂	A ₃	A ₄	A ₅	A ₆	A ₇	A ₈	A ₉	A ₁₀	A ₁₁
<i>Fe</i>	1.35*	2.22*	3.79	5.71	10.3	17.8	21.1	35.7	52.0	68.2	130.2
	1.20	2.30	3.28	5.13	10.0	17.1	20.8	35.1	51.4	67.1	129.1
<i>Th</i>	1.04*	1.98	3.08	4.74	8.67	12.7	15.1	24.5	34.9	46.3	80.8
	0.900	1.46	2.24	3.90	6.61	10.6	12.6	21.5	30.3	41.0	75.2
<i>Fu</i>	0.490*	1.21*	1.80	3.21	5.15	9.34	10.9	17.8	26.6	33.7	63.0
	0.567	0.967	1.46	2.76	4.51	8.39	9.47	15.6	24.1	29.5	57.3
<i>Me</i>	0.980	1.49	3.10	5.10	9.28	13.5	17.4	33.1	43.8	52.4	96.5
	0.567	0.939	1.92	2.92	5.99	8.99	12.1	22.8	33.2	40.5	81.7
<i>Ca</i>	0.650*	1.96	2.87	4.70	8.21	12.7	14.0	24.2	36.7	41.2	80.1
	0.444	0.906	1.74	2.63	5.37	8.64	10.3	19.1	29.5	35.9	74.1
<i>Fr</i>	0.222*	0.211*	0.387*	0.791	1.12	1.33	1.80	2.04	3.44	3.47	5.61*
	0.050	0.106	0.172	0.239	0.478	0.744	0.928	1.43	2.55	2.74	5.58
<i>Cy</i>	—	0.333	0.0	0.333	1.85	0.444	1.12	1.84	1.37	2.62	4.98
	—	0.033	0.017	0.033	0.072	0.150	0.189	0.272	0.389	0.644	1.75
<i>Pl</i>	—	—	1.14	1.14	2.67	2.00	1.79	2.00	2.41	2.62	3.69
	—	—	0.039	0.039	0.083	0.061	0.106	0.250	0.411	0.306	0.961
<i>Ce</i>	—	0.0	0.200*	0.0	0.333	1.00	1.07	0.864	1.67	1.98	2.80
	—	0.022	0.056	0.061	0.100	0.189	0.167	0.244	0.406	0.528	0.889
$\bar{N}$	3.74*	6.59	11.4	18.4	35.1	56.8	68.5	119.9	176.9	223.4	432.4
	3.73	6.33	10.9	17.6	33.2	54.8	66.5	115.5	171.7	218.2	427.1
$\bar{S}$	1.80	2.39	3.20	3.70	4.17	4.59	4.79	5.09	5.48	5.66	6.35
	2.37	3.07	3.93	4.51	5.05	5.49	5.65	5.96	6.36	6.54	7.26

* Indicate the acceptability of randomness, based on g (cf. 4.1 and 4.5).

4.4. The exponent k of the negative binomial series

Values of k are in Table 3. They were computed only for the cases when ID values suggested random or aggregated AP. Low values of k (especially $k < 1$) refers to high aggregation (cf. SHORROCKS et al. 1984), whereas high values indicate a tendency toward random AP. If $k \rightarrow \infty$ the negative binomial series approaches the POISSON series.

Table 3
Values of k at increasing plot sizes

Species	Plot sizes										
	A_1	A_2	A_3	A_4	A_5	A_6	A_7	A_8	A_9	A_{10}	A_{11}
<i>Fe</i>	6.95	—	6.03	7.19	29.4	23.2	62.0	60.2	79.7	61.9	108.6
<i>Th</i>	5.02	2.91	2.02	3.85	2.52	4.03	3.70	6.20	6.52	7.81	13.3
<i>Fu</i>	—	5.57	3.97	4.93	5.99	7.96	6.02	5.65	7.46	7.13	9.98
<i>Me</i>	1.17	1.47	1.40	1.28	1.34	1.60	1.75	1.46	2.30	3.40	—
<i>Ca</i>	1.78	0.61	1.51	1.07	1.52	1.75	2.03	2.85	3.69	6.69	12.2
<i>Fr</i>	0.25	0.87	0.60	0.48	0.54	1.11	1.21	2.05	2.56	3.07	172.6
<i>Cy</i>	—	0.09	—	0.09	0.04	0.48	0.16	0.14	0.40	0.38	0.53
<i>Pl</i>	—	—	0.02	0.02	0.02	0.03	0.05	0.10	0.10	0.07	0.17
<i>Ce</i>	—	—	0.33	—	0.34	0.19	0.21	0.33	0.20	0.27	0.31
$\bar{N}$	172.8	24.0	22.2	23.5	18.1	28.0	34.3	26.1	32.6	41.3	—

4.5. MORISITA's Index of Dispersion and the Q

As in the study n was equal to 180, the difference between I_0 and PA occurred only in the third decimals, so the presentation of I_0 was neglected (cf. 4.1.). However the cases when the random AP could be accepted on the basis of g are marked with an asterisk in Table 2.

Plotted Q against the plot size corresponding to the denominator, we get a curve in which the peaks reflect the plot sizes approximately equal with the size of the aggregates. The plots for the separate species, $\bar{N}$ and $\bar{S}$ are given in Fig. 3.

4.6. IWAOKI's p_i -index

Plotting the p_i values versus plot size, on the basis of the curves it is possible also to draw conclusions on the type of the arrangement pattern and on the size of aggregates. If there is a random AP, the p_i curve remains in the close neighbourhood of unity. In the case of aggregated AP the curve lies above the unity and shows decreases at plot sizes corresponding to the sizes of the aggregates. Values lesser than unity indicates regular AP. Fig. 4 represents the curves of the species, $\bar{N}$ and $\bar{S}$.

4.7. TAYLOR's Power Law

The value of the parameter a depends first of all on the sampling unit. Value of b can be regarded as an IAP, its value is ranging from 0 (for regular AP) to very high positive values (extremely aggregation). The case of $a = b = 1.0$ refers to random AP. Values greater than unity indicate aggregated AP.

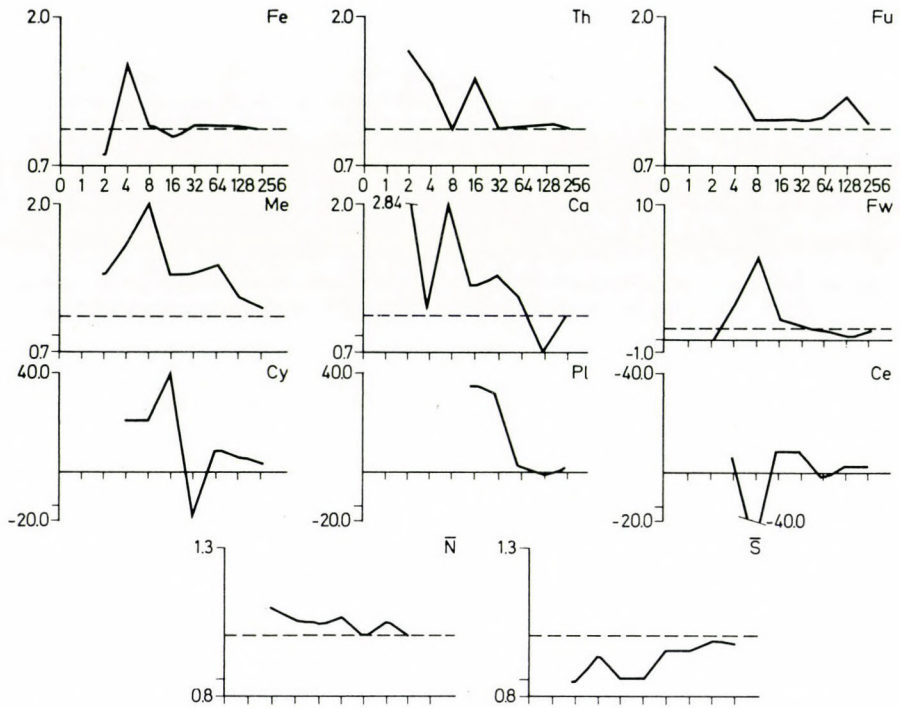


Fig. 4. Change of p_i over plot sizes (x axis as in Fig. 1, dashed line indicates $p_i = 1.0$)

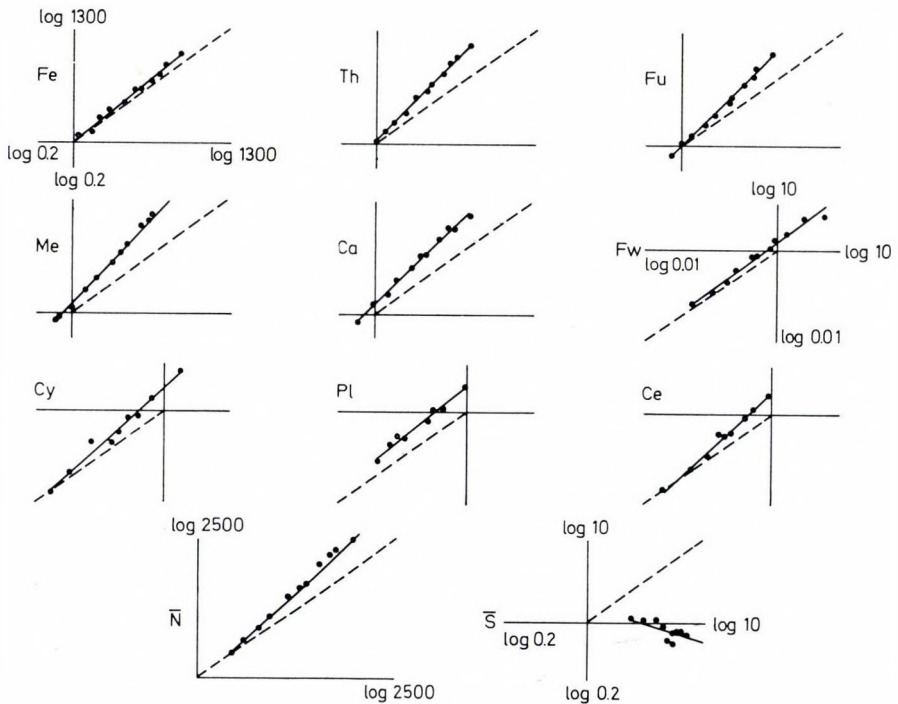


Fig. 5. Relationship between $\log \bar{x}$ and $\log s^2$ (TAYLOR's power law) on the basis of the original data. (Dashed line represent the case of randomness)

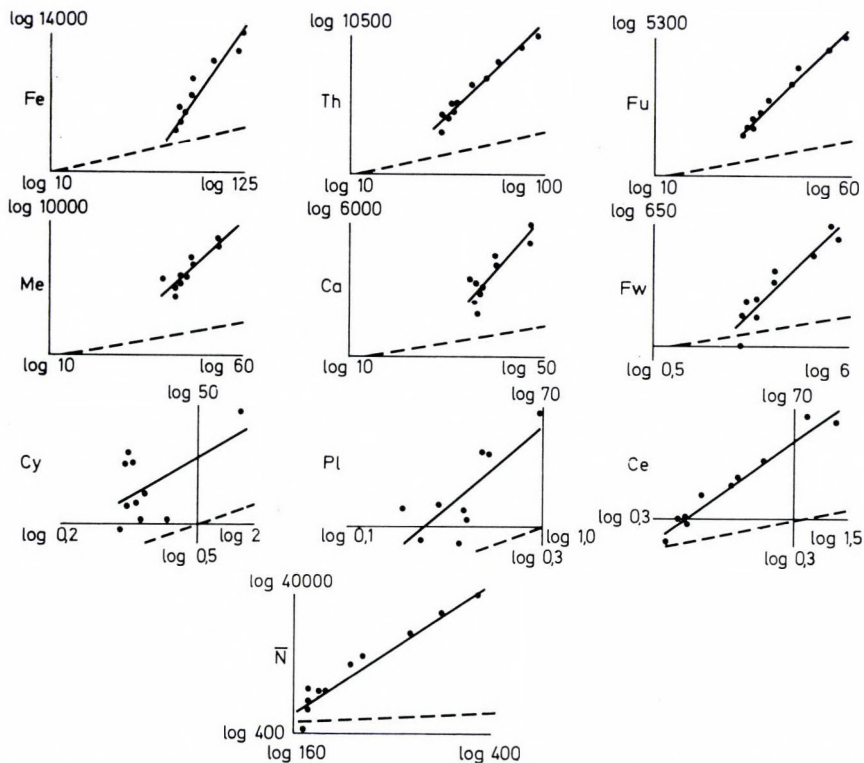


Fig. 6. Relationship between $\log \bar{x}$ and $\log s^2$ (TAYLOR's power law) on the basis of the converted data. (Dashed line represent the case of randomness)

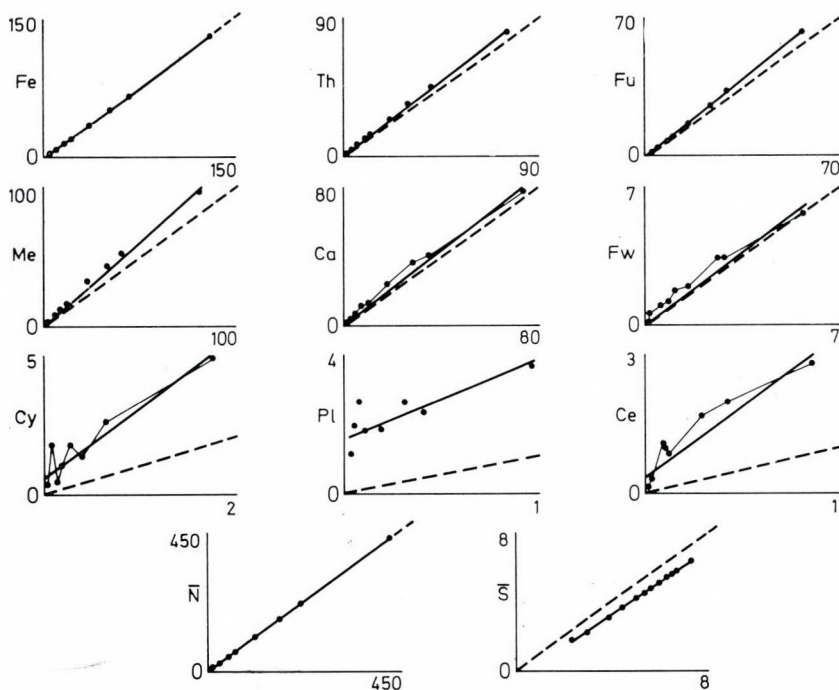


Fig. 7. IWA0's patchiness regression of the original data. (Dashed line represents the case of randomness)

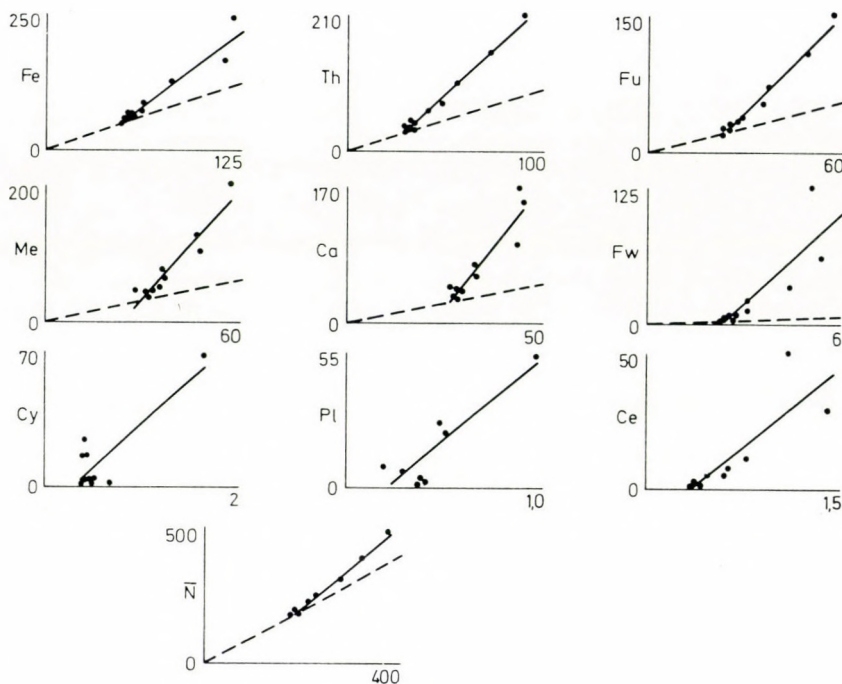


Fig. 8. Iwao's patchiness regression of the converted data. (Dashed line represents the case of randomness. At *Cy*, *Pl* and *Ce*, owing to the scales, the line of randomness cannot be visualized, it is practically on the x axis)

The power law was found to be valid over large scales of s^2 and $\bar{x}$, but values of a and b calculated on the basis of samples having arithmetic means below two and variance below four, are not reliable (TAYLOR and WOJWOD 1982).

The fitted linears are represented in Figs 5 and 6, the corresponding parameter values in Table 4.

4.8. The patchiness regression

According to the basic concept of Iwao, the values of α and β have different meanings (Iwao and Kuno 1971). α (called "index of basic contagion") refers to the association between the individuals, its value is greater or less than zero when positive or negative association occur. β (called "density-contagiousness coefficient") may be less than, equal to, or greater than unity according to the type of the arrangement pattern (regular, random or aggregated, respectively). Parameters of the fitted curves are to be found in Table 5, the graphs are presented in Figs 7 and 8.

Discussion

It must note that the values of b and β (as IAP) give an "overall" or "averaged" description of the cases of AP, since the several $\bar{x}$, s^2 and $\bar{x}$ values correspond to different plot sizes, therefore plot sizes where AP may change,

Table 4

The coefficients of Taylor's power law
(upper values are from the original,
lower values from the converted data)

Species	Coefficients			Value of F-test
	a	b	r	
<i>Fe</i>	1.071	1.132	0.996	1163.0
	-7.59	5.648	0.943	71.8
<i>Th</i>	1.247	1.411	0.999	4080.0
	-3.862	4.091	0.982	240.2
<i>Fu</i>	1.051	1.411	0.998	1772.0
	-4.566	4.780	0.990	434.9
<i>Me</i>	1.736	1.543	0.999	5535.0
	-4.875	4.992	0.929	56.7
<i>Ca</i>	1.979	1.360	0.997	1820.0
	-6.863	6.359	0.905	40.5
<i>Fw</i>	1.508	1.056	0.992	544.6
	-1.344	5.648	0.938	65.6
<i>Cy</i>	3.259	1.269	0.991	425.4
	0.980	1.637	0.567 ^o	3.8 ^{ns}
<i>Pl</i>	3.605	1.106	0.993	408.3
	1.522	2.533	0.783 ^{**}	11.1 [*]
<i>Ce</i>	2.960	1.329	0.997	1228.0
	1.347	3.454	0.977	168.2
$\bar{N}$	0.551	1.439	0.998	2481.0
	-7.875	4.875	0.972	155.8
$\bar{S}$	1.538	-0.426	-0.673	7.4

Values of r and F-test without marks are significant at $p < 0.001$, other levels of significance: * = $p < 0.1$, ** = $p < 0.01$, ns = non significant.

remain "hidden". The conversion of the original values to 1 m² was meant to make disappear the differences due to the increase in plot size. (This seems to contradict the use of spatial process, but the use of these regressions cannot be restricted only to spatial process, since we may get different densities from the same plot size from different places.)

Using the original values random AP is suggested by b for *Festuca wagneri*, by β for *Festuca vaginata*, *Festuca wagneri* and $\bar{N}$. For the other species (except for $\bar{S}$) these values refer to aggregation. Curves resulted by the converted values reflects (except also for $\bar{S}$) all aggregation which is stronger as in the original case, although the fitting to the original data is better.

The acceptability of patchiness regression of the rare species — despite the F values — however is dubious (see the points around the regression lines at *Fw*, *Cy*, *Pl* and *Ce*).

Table 5

The coefficients of Iwao's patchiness regression
(the upper values are from the original,
the lower values from the converted data)

Species	Coefficients			Value of F-test
	α	β	r	
<i>Fe</i>	0.383	1.007	0.999	1.7×10^6
	— 65.22	2.241	0.970	142.0
<i>Th</i>	1.061	1.077	0.999	8.3×10^3
	— 54.03	2.791	0.997	1.3×10^3
<i>Fu</i>	0.214	1.104	0.999	2.5×10^4
	— 59.18	3.510	0.993	547.2
<i>Me</i>	2.275	1.188	0.998	1.9×10^3
	— 129.9	5.382	0.957	98.4
<i>Ca</i>	2.210	1.076	0.998	2.4×10^3
	— 143.2	6.267	0.941	69.8
<i>FW</i>	0.506	0.988	0.984	265.5
	— 60.55	27.13	0.865	26.8
<i>Cy</i>	0.557	2.624	0.933	54.02
	— 12.72	44.79	0.859	22.4**
<i>Pl</i>	1.602	2.231	0.830	15.47
	— 14.99	66.72	0.902	30.37
<i>Ce</i>	0.113	3.298	0.966	112.9
	— 13.91	38.72	0.859	22.55**
$\bar{N}$	1.054	1.014	0.999	1.7×10^6
	— 72.29	1.437	0.999	3.2×10^3
$\bar{S}$	0.475	0.933	0.999	9.9×10^3
	—	—	—	—

Values of r and F-test without marks are significant at $p < 0.001$, other levels of significance: ** = $p < 0.01$.

Calculating the patchiness regression by the original values, the α -s were all greater than zero, indicating positive association between the individuals of the separate species. This may refer that there are aggregates of the individuals. Calculating however on the basis of the converted values, all the α -s change their sign, indicating a negative association. It is to be mentioned, that in the case of the original data only $\bar{S}$ has a negative α .

The other indices of the SAP shows similar results to one another.

Randomness was acceptable only in very few cases at the smallest plot sizes. The IAP-s suggest for the overwhelming majority of the species and plot sizes aggregated AP.

The two *Festuca* species showed random pattern in the beginning and at the end of the plot size scale. In the intermediate sizes they also showed a tendency of aggregation, but it was the weakest of all species. In this community the two *Festuca* species proved to be ecological generalist. The *Festuca*

vaginata is the dominant species of this stage of the successional series, the *Festuca wagneri* is that of the next stage (cf. PRÉCSÉNYI et al. 1980, NOSEK 1986).

Moderate aggregation is shown by *Tymus* sp. and *Fumana procumbens*. Stronger aggregation is indicated by *Carex stenophylla* and *Medicago minima*. *Carex* is a stoloniferous species, the crop of *Medicago* is of thorny character so their spread is made difficult and they remain in the neighbourhood of the parent plant.

The rare species showed a strong aggregation on larger plot sizes.

Except for the two *Festuca* species and for a few cases at A_1 and A_2 (*Fu*, *Th*, *Ca*) significant change in the type of SAP could not be demonstrated.

The dominant species — except for *Fu* — *Fe*, *Th*, *Me*, *Ca* and *Fw* form aggregates of size between the plot sizes 40×40 and 56×56 cm. On the basis of previous results (cf. MOLNÁR and NOSEK 1979, 1980, NOSEK 1986) the plot size between 1600 and 3200 cm² have a particular significance in this community.

The peaks of *Th* and *Fu* (800 cm²) as well as of *Ca* (400 cm²) are probably in connection with the individual sizes. *Th* and *Fu* are chamaephyton and nanophanerophyton species with a relative great size, and the 400 cm² of *Ca* may refer also to the average size of the stolon system. Similarly the "half-peaks" of the two *Festuca* species may indicate the average size of the individual patches. (The lack of the left side of the peak is due to the calculation technique of Q and p_i .)

Cy, *Pl* and *Ce* show two peaks at larger plot sizes. But, as it was pointed out, the interpretation of the rare species (owing to their rare character and to the fact, that they are members rather of the autumn aspect) is dubious.

The total number of individuals ($\bar{N}$) can be regarded as if the individuals of the separate species were belonging to one "hypothetic" species. The indices show partly random AP (patchiness, Iwao's β and the k), partly moderate aggregation. If we accept the aggregated AP, there are two peaks, at 3200 and at 12 800 cm². The significance of 3200 cm² was already mentioned. If we include to the dominant species the *Festuca wagneri*, too, the plot size necessary to reliable estimates of the different population parameters (cf. NOSEK 1985a) is about 1 m².

Very interesting is the case of $\bar{S}$. It may be regarded — analogously to $\bar{N}$ — so, if there were only one "hypothetic" species with $\bar{S}$ number of "individuals". In this context, both $\bar{N}$ and $\bar{S}$ refer to the whole community.

All the indices at every plot size refer to a regular AP. It is commonly accepted that a regular arrangement reflects negative interactions and/or competition between the individuals (cf. MACARTHUR and CONNELL 1966, PRÉCSÉNYI et al. 1967). In the Tece meadow there is a limitation in water supply in the summer period. This results suggest that between the species (and probably between the individuals of the species, cf. the negative α values of the patchiness regression from the converted data) there is a competition.

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SPATIAL PROCESSES IN A GRASSLAND COMMUNITY, V. FREQUENCY DISTRIBUTIONS OF THE SPECIES*

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Directly connecting with Part IV, this paper is concerning with the arrangement pattern (AP) of the separate species, number of individuals and number of species on the basis of the frequency distributions in the same community. Twelve theoretical frequency distributions (TFD) were involved, their parameters were calculated from the moments of the empirical frequency distributions (EFD) by maximum likelihood methods. The parameter estimates of four TFD-s were unreliable, so finally the positive binomial, the Poisson, the negative binomial series, two cases of the generalized Neyman distributions, the normal, the lognormal and the uniform distributions were investigated. The goodness of fit was made by χ^2 -test.

The fitting indicated random and aggregated AP at the same cases as the several indices of dispersion (cf. Part IV), however the indication of the regular AP was not supported by the fitting in every cases indicated by the indices.

Random AP could be accepted — similarly to the indices — only in few cases. This randomness however, seems to be of all probability an apparent one, since it occurred at low densities and at the same time the TFD-s referring to a contagious AP had also the same, good, or even better fit.

All of the species and $\bar{N}$ showed aggregated AP, fitted by different TFD-s. The regular AP of $\bar{S}$ could be accepted only below the plot size of 40×40 cm.

The detected type of AP depends on the plot size and on the relative abundance of the species. Appropriate plot sizes in this community for the dominant species are between 800 and 3200, for the rare species between 3600 and 10 000 cm².

Introduction

For the description of the types of the arrangement pattern (AP) besides the so called "indices of dispersion" (cf. NOSEK 1986b) the different theoretical probability or frequency distributions (TFD-s) are used. The use of the latter ones however is much laborous than that of the several indices, but e.g. "the $s^2/\bar{x}$ ratio may give a widely different estimate of non-randomness from a χ^2 -test of goodness of fit" (EVANS 1952, cit. in KERSHAW 1964). Moreover the computer facilities made the evaluation more easy, so nowadays the fit of same theoretical distributions to the observed data is not much more difficult than the computation of the several indices of dispersion.

The types of AP are distinguished on the basis of the relationship between the "things" (e.g. individuals of a species) of which AP is investigated. This relationship can be formulated on probabilistic basis, too. If the probability of occurrence of one individual is not affected by the presence of another one, the AP is random. In the second case the probability of occurrence of the single individuals is not independent from one another. If this probability is

* "Tece Studies" No. 40.

enlarged by the presence of others, this leads to an aggregated (or contagious) AP. On the contrary, if the probability of occurrence is decreased, a regular AP is resulted.

Several theoretical distributions are used for the description of AP. The most frequent used ones are: for regular AP the positive binomial series and the hypergeometric series; for random AP the POISSON series; for the contagious AP the negative binomial series, the POLYA-AEPLI distribution, the THOMAS distribution, the NEYMAN distributions (A, B, and C) or the generalized NEYMAN distribution (cf. BEALL and RESCIA 1953, ELLIOT 1971, PIELOU 1969, 1976, MOLDOVÁN et al. 1980, etc.).

Several hypothesis are constructed regarding the causes of the arrangement pattern and the applicability of the theoretical frequency distributions. It is commonly accepted that the fit of the POISSON series means the lack of any limitation (cf. JUHÁSZ-NAGY and VIDA 1978). Most of the theories have concerned with the aggregated or contagious (sensu NEYMAN, cit. in BEALL and RESCIA 1953) AP. Several ways of reproduction or the course of colonization together with the way of reproduction have been regarded to be responsible for the resulted aggregated AP. The vegetative reproducing plant species form aggregated AP, and also similarly the colonial animals. The THOMAS, NEYMAN and POLYA-AEPLI distributions have several biological conditions, and if these conditions are met, the resulted aggregated AP can be described and/or the empirical frequency distributions (EFD) can be fitted by these TFD-s. More details and further examples are to be found in several books, e.g. ELLIOT 1971, SOUTHWOOD 1978 (first of all for insects); or in KING and WOODDELL 1984, ORD et al. 1979, MOLDOVÁN et al. 1980.

We must be however in aware of the fact, that the sampling process may led to "detection" any of the AP-s, that is we may fit some TFD-s to the EFD-s although that AP does not exist.

The use of small sampling plot sizes may be misleading (c.f. e.g. PRÉCSÉNYI 1964, ELLIOT 1971, PIELOU 1976, SOUTHWOOD 1978). But even using larger plot sizes, we may got "apparent contagion" (sensu FELLER 1943, cit. in CALOW 1974) due to several causes, as the patchiness of the habitat or the sampling techniques (c.f. SOUTHWOOD 1978).

The choice of the entity (of which AP is to be investigated) may also cause troubles e.g. in the case of colony forming species the colonies and the individuals within a single colony may have different AP-s.

These difficulties may overcome by precise determination of the entities and/or — the coincidence of the AP (cf. patchiness of the habitat) and sampling scale — by the use of spatial processes.

The number of the observable EFD-s is probably infinite. In contrary the known TFD-s — especially the more or less simple ones, preferred for fitting — are of finite number. It often occurs that no or even several TFD-s can be fitted at a certain predetermined level of probability to the observed data (BEALL and RESCIA 1953, MOLDOVÁN et al. 1980).

There are a relative great number of TFD-s which are not directly related to one or another type of AP (e.g. the normal-, lognormal-, gamma-, χ^2 -, t-distributions, the MAC-ARTHUR's "broken stick model", several compound distributions). In other words, the biological or ecological conditions, lead to the detection such TFD-s, are unknown.

For the investigation of the frequency distributions there are two possibilities. Once we may start from the known TFD, generating theoretical scatter diagrams and investigate the AP of these simulated maps. This approach is especially useful to work out and to test sampling procedures, processes or several indices of AP (cf. IWAQ 1977, SZŐCS 1977, 1979, MOLDOVÁN et al. 1980, 1984).

The other way is to start from the observed situations, from the given AP, and try to find the TFD of the best fit. In this approach several sampling problems may arise. (They were touched in Part IV, NOSEK 1986b.)

Aim of the study

The aim of this study was to detect the EFD-s of the several species, total number of individuals and species of a semi-closed sandy grassland (*Festucetum vaginatae danubiale*) at different plot sizes, as well as to find from some simple TFD-s one of the best fit and to compare these results with that of the indices (Part IV. NOSEK 1986b) from point of view of the arrangement pattern.

Material and methods

1.1. Sampling area and sampling process were described detailed in Part III and IV (NOSEK 1986a, b).

11 plot sizes were applied, placed out randomly on a 1 : 10 map of the community. The sizes were 100, 200, 400, 800, 1600, 3200, 3600, 6400, 10 000, 12 800 and 25 600 cm² (referred to A_j ; $j = 1, 2, \dots, 11$, respectively). Nine vascular plant species were analysed (*Festuca vaginata*, *Thymus* sp., *Fumana procumbens*, *Medicago minima*, *Carex stenophylla*, *Festuca wagneri*, *Cynodon dactylon*, *Plantago indica* and *Centaurea arenaria*, referred as i ($i = Fe, Th, Fu, Me, Ca, Fw, Cy, Pl$ and Ce , respectively), as well as the total number of individuals (of all species) $\bar{N}$, and the number of species, $\bar{S}$. Sample size was 180 quadrats for each plot size ($l = 1, 2, \dots, 180$). So

$$x_{ijl}$$

is the number of individuals of the i -th species in the l -th replication of plot size j .

For each species, $\bar{N}$ and $\bar{S}$ and for each plot size the EFD was established.

1.2. Twelve TFD-s were involved in the investigation. The choice of the TFD-s was based either on the relation to the different types of AP, or on the shape of the EFD diagrams. Parameters of the separate TFD-s were calculated from the first ($\bar{x}$) and second (s^2) moments of the corresponding EFD-s, using the maximum likelihood estimates (cf. BEALL and RESCIA 1953, WEBER 1957, PRÉKOPA 1972).

In four cases (geometric, hypergeometric and exponential series as well as the gamma distribution of the first order) the parameter estimates were unreliable, so these distributions were neglected in the further elaboration.

Finally eight TFD-s were fitted to the empirical data. In the formulae below r denotes the number of events in one quadrat (that is the value of r is equal to $x_{i,j,l}$), P_r is the probability of occurrence of the quadrat containing r events, n is the sample size (180), $\bar{x}$ and s^2 are the moments of the EFD-s, α , λ , m , σ , k , m_1 , m_2 , p , q and h are the parameters of the separate TFD-s. The TFD-s to be fit were:

1. Positive binomial (or PASCAL) series

$$P_r = \binom{\alpha}{r} p^r q^{\alpha-r}$$

2. POISSON series

$$P_r = \frac{\lambda^r}{r!} e^{-\lambda}$$

3. Negative binomial series:

$$P_r = \binom{k+r-1}{k-1} \left(1 + \frac{\bar{x}}{k}\right)^{-k} \left(\frac{\bar{x}}{\bar{x}+k}\right)^r$$

In this case two estimates of k were applied

a) the estimate based on the moments (ME):

$$\hat{k}_{ME} = \frac{\bar{x}^2}{s^2 - \bar{x}}$$

b) the maximum likelihood estimate (ML):

$$n \ln \left(1 + \frac{\bar{x}}{\hat{k}_{ML}} \right) = \sum' \left(\frac{A_x}{\hat{k}_{ML} + x} \right)$$

where A_x is the sum of frequencies of samples containing more events than x (cf. ANSCOMBE 1950, cit. in BLISS 1953, WEBER 1957, ELLIOT 1971, SOUTHWOOD 1978). The choice between the two estimates depends on the sample size, the value of x and k (cf. SOUTHWOOD 1978). WILSON et al. investigated the bias of the two estimates. They concluded that the ME "does not seem to be influenced as much as the MLE (= ML) — when some samples are discarded, and in none of the cases considered was the MLE overwhelmingly better than the MME" (= ME) —. They suggest a multistage procedure using the ME versus the fixed sample-size estimate. As in the case of this study the sample size was fixed, instead of the suggested procedure both estimates were applied, and the choice between them was made after ANSCOMBE (1950, cit. in SOUTHWOOD 1978). Depending on the value of $\hat{k}_{ME}$ and $\bar{x}$, $\hat{k}_{ME}$ was either accepted or used as initial value for the ML estimate. Fitting was made in many cases using both estimates of k , but only that one, resulted the better fit, was accepted.

The cases of the generalized NEYMAN's distributions were also applied. The generalized form is the following, according to BEALL and RESCIA (1953), using their original symbols:

$$P_r = \frac{1}{r!} \frac{d(r)}{dz} \left\{ \exp(-m_1) \exp \left[m_1 n! \sum_{s=0}^{\infty} \frac{m_2^s (z-1)^s}{(s+n)!} \right] \right\}$$

Setting $n = 0, 1$ or 2 , we get the original NEYMAN functions A, B and C, respectively. In the generalized form n may have, of course, other values, too, till ∞ . The two cases applied are (using the symbols of this paper):

4. $n = 0$

$$P_{(r+1)} = \frac{m_1}{(r+1)} \sum_{t=0}^r F_t P_{(r-t)} \quad t = 0, 1, \dots, r$$

where

$$P_0 = \exp(-m_1) \exp(m_1 \exp(-m_2))$$

$$F_0 = m_2 \exp(-m_2)$$

$$F_r = \frac{\exp(-m_2) m_2^{(r+1)}}{r!}$$

5. $n = \infty$

$$P_{(r+1)} = \frac{m_1}{(r+1)} \sum_{t=0}^r F_t P_{(r-t)} \quad t = 1, 2, \dots,$$

where

$$P_0 = \exp \left\{ -\frac{2\bar{x}}{(2+c)} \right\} \quad c = \frac{(s^2 - \bar{x})}{\bar{x}}$$

$$F_0 = \frac{1}{m_1} \left\{ \frac{4\bar{x}}{(2+c)^2} \right\}$$

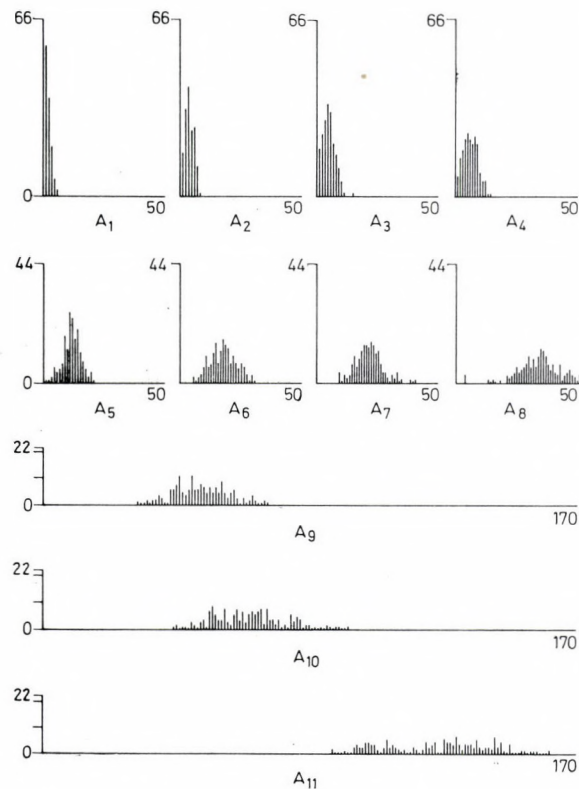


Fig. 1. The EFD diagrams of *Festuca vaginata* at different plot sizes (x axis: values of r , y axis: values of $f(r)$)

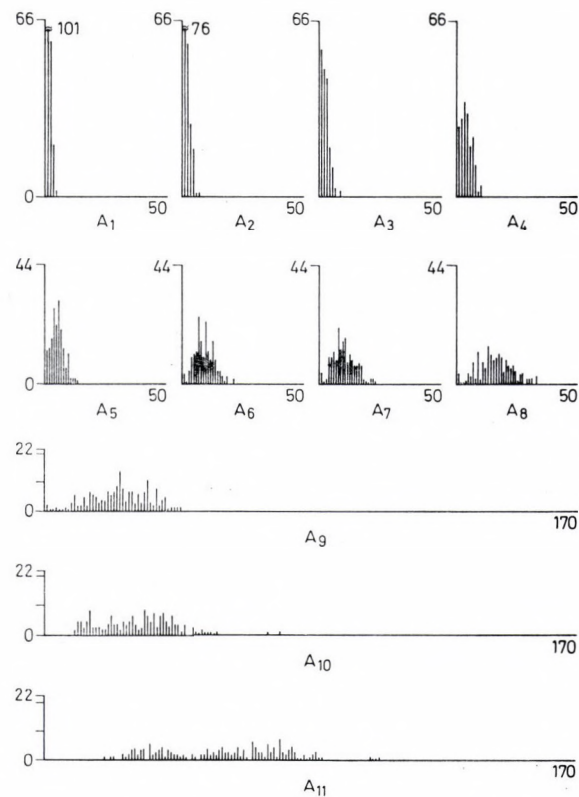


Fig. 2. The EFD diagrams of *Fumana procumbens* (axes as in Fig. 1)

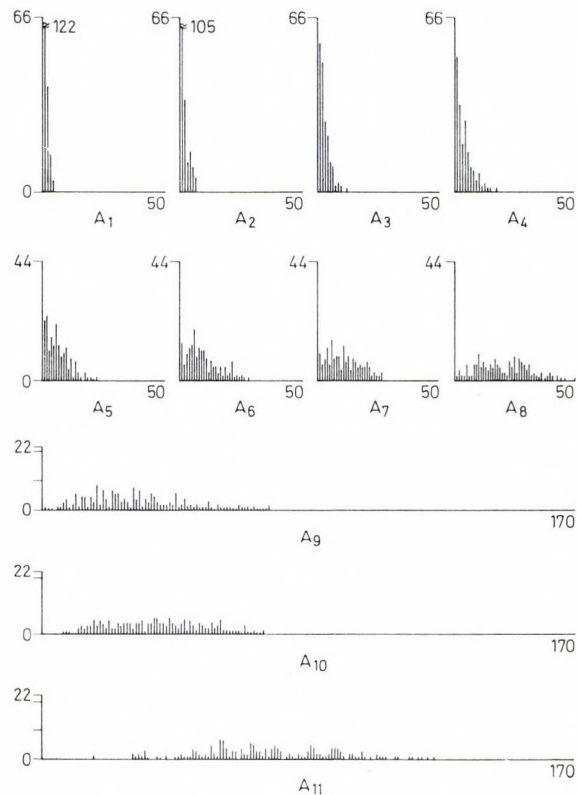


Fig. 3. The EFD diagrams of *Carex stenophylla* (axes as in Fig. 1)

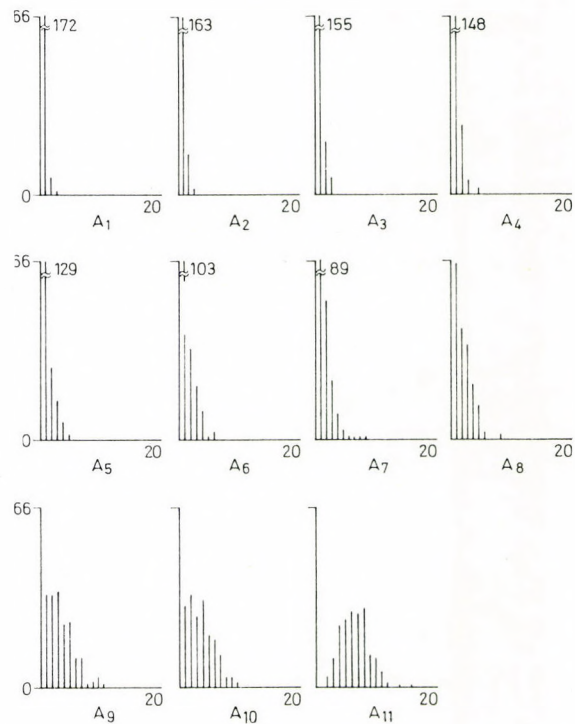


Fig. 4. The EFD diagrams of *Festuca wagneri* (r and $f(r)$ values of the axes are the same for all plot sizes)

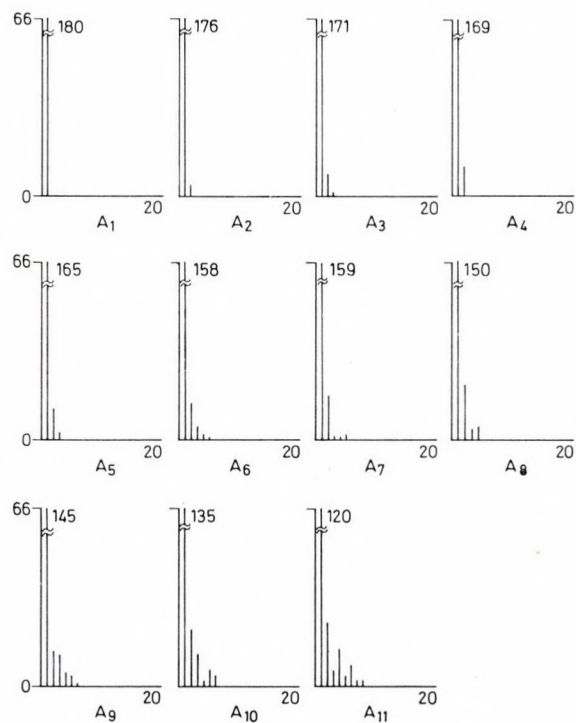


Fig. 5. The EFD diagrams of *Centaurea arenaria* (r and $f(\bar{r})$ values of the axes are the same for all plot sizes)

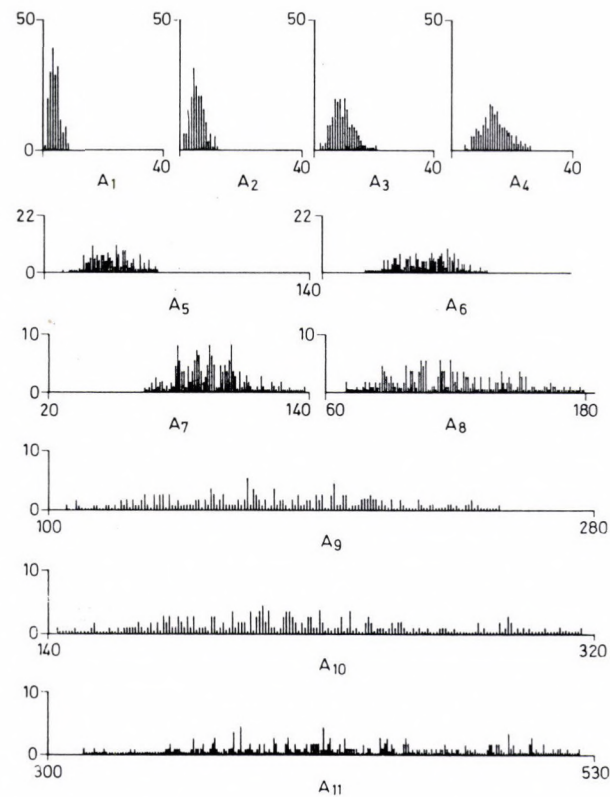


Fig. 6. The EFD diagrams of $\bar{N}$ (axes as in Fig. 1)

Table 1
The probability values of the goodness of fit

Species	TFD	Plot sizes										
		A ₁	A ₂	A ₃	A ₄	A ₅	A ₆	A ₇	A ₈	A ₉	A ₁₀	A ₁₁
<i>Fe</i>	POI	30	0.1	0.1	0.1	5	0.1	50	1	0.1	0.1	0.1
	NBI	90	0.1	70	50	5	70	70	90	70	5	0.1
	GNZ	90	0.1	70	50	5	0.1	0.1	0.1	—	—	—
	GNI	90	0.1	70	50	5	0.1	0.1	0.1	—	—	—
	NOG	—	—	—	70	30	50	70	70	50	10	—
	LGN	—	—	1	0.1	5	5	50	70	70	10	—
	UNI	—	—	—	—	—	—	—	—	0.1	0.1	0.1
<i>Th</i>	POI	5	5	0.1	0.1	0.1	—	—	—	—	—	—
	NBI	30	90	10	50	10	10	5	10	1	50	1
	GNZ	10	95	50	70	10	10	10	30	1	0.1	1
	GNI	10	90	10	50	10	10	5	10	1	0.1	1
	NOR	—	—	—	—	—	10	50	10	5	50	10
	LGN	—	—	—	—	—	—	—	—	0.1	0.1	0.1
	UNI	—	—	—	—	—	—	—	—	0.1	0.1	0.1
<i>Fu</i>	POI	90	10	5	0.1	0.1	0.1	0.1	—	—	—	—
	NBI	0.1	50	50	10	5	10	50	30	0.1	1	0.1
	GNZ	70	50	70	10	5	30	50	30	1	0.1	—
	GNI	70	50	50	10	5	10	50	30	0.1	0.1	—
	NOR	—	—	—	—	—	—	—	10	0.1	0.1	0.1
	LGN	—	—	—	0.1	0.1	0.1	0.1	10	0.1	0.1	0.1
	UNI	—	—	—	—	—	—	—	0.1	0.1	0.1	0.1
<i>Me</i>	POI	0.1	0.1	0.1	0.1	0.1	—	—	—	—	—	—
	NBI	70	70	50	70	10	70	0.1	10	0.1	5	—
	GNZ	50	95	70	1	1	0.1	0.1	10	0.1	1	—
	GNI	50	70	70	50	30	70	0.1	10	0.1	5	—
	NOR	—	—	—	—	—	—	—	—	0.1	0.1	—
	LGN	—	—	—	—	—	—	—	—	0.1	0.1	—
	UNI	—	—	—	—	—	—	—	0.1	0.1	0.1	5
<i>Ca</i>	POI	5	0.1	0.1	0.1	0.1	—	—	—	—	—	—
	NBI	50	5	90	30	10	30	5	10	95	10	—
	GNZ	50	5	30	5	0.1	30	10	30	70	0.1	—
	GNI	50	5	70	50	10	50	10	30	50	0.1	—
	NOR	—	—	—	—	—	—	—	30	5	30	—
	LGN	—	—	—	—	—	—	0.1	0.1	0.1	0.1	—
	UNI	—	—	—	—	—	—	—	0.1	0.1	0.1	0.1
<i>Fw</i>	POI	70	70	30	10	0.1	0.1	0.1	0.1	0.1	0.1	90
	NBI	95	95	70	90	30	70	95	30	50	50	90
	GNZ	99	95	90	30	50	95	10	50	70	50	90
	GNI	99	95	90	50	30	90	50	50	70	50	90
<i>Cy</i>	POI	—	—	95	—	—	—	—	—	—	—	—
	POI	—	70	—	70	5	10	0.1	0.1	0.1	0.1	0.1
	NBI	—	90	—	90	90	90	70	30	99	5	0.1
	GNZ	—	95	—	95	70	90	70	5	30	0.1	0.1
	GNI	—	95	—	95	70	90	70	70	70	0.1	0.1
<i>Pl</i>	POI	—	—	10	10	1	10	5	0.1	0.1	0.1	0.1
	NBI	—	—	70	70	70	90	90	50	1	5	0.1
	GNZ	—	—	90	90	95	70	70	50	10	50	0.1
	GNI	—	—	70	70	70	70	95	50	5	10	0.1

Table 1 (continued)

Species	TFD	Plot sizes										
		A ₁	A ₂	A ₃	A ₄	A ₅	A ₆	A ₇	A ₈	A ₉	A ₁₀	A ₁₁
Ce	PBI	—	95	—	90	—	—	—	—	—	—	—
	POI	—	—	70	—	70	0.1	10	1	0.1	0.1	0.1
	NBI	—	—	95	—	90	70	50	90	10	50	5
	GNZ	—	—	95	—	95	95	5	90	70	70	1
	GNI	—	—	95	—	95	90	10	95	10	90	1
$\bar{N}$	POI	10	30	5	0.1	0.1	0.1	0.1	0.1	0.1	0.1	—
	NBI	10	95	90	90	10	5	70	10	50	—	—
	GNZ	—	0.1	0.1	0.1	0.1	0.1	0.1	—	—	—	—
	GNI	10	0.1	0.1	0.1	0.1	0.1	0.1	—	—	—	—
	NOR	—	30	50	70	10	5	50	5	50	1	0.1
	LGN	0.1	1	10	30	5	1	50	5	30	10	0.1
	UNI	—	—	—	—	—	—	—	0.1	1	0.1	1
$\bar{S}$	PBI	10	50	50	10	0.1	5	0.1	0.1	0.1	0.1	1
	POI	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1

$$F_t = \frac{1}{m_1} \left(\frac{t+1}{t} \right) \left(\frac{c}{2+c} \right) F_{(t-1)} \quad t = 1, 2, \dots, r$$

6. uniform distribution:

$$P_r = \frac{1}{h} \quad (h = r_{\max} - r_{\min} + 1)$$

(where $r_{\min}$ and $r_{\max}$ are the corresponding values of the EFD-s).

7. normal distribution (for $x = r$):

$$f(x) = \frac{1}{2\pi\sigma} \exp \left\{ -\frac{(x-m)^2}{2\sigma^2} \right\}$$

8. lognormal distribution (for $x = r$):

$$f(x) = \frac{1}{2\pi\sigma x} \exp \left\{ -\frac{(\ln x - m)^2}{2\sigma^2} \right\}$$

The TFD-s were denoted further on by PBI, POI, NBI, GNZ, GNI, UNI, NOR and LGN. The goodness of fit was tested by χ^2 -test.

Results

Although the EFD-s were established for all the species as well as for $\bar{N}$ and $\bar{S}$, in lack of space they will not be presented. As it was illustrated earlier (cf. Part III, NOSEK 1986a) the species could be divided into three groups, according to their dominance relations. Therefore only the EFD diagrams of *Festuca vaginata* (Fig. 1), *Fumana procumbens* (Fig. 2), *Carex stenophylla* (Fig. 3), *Festuca wagneri* (Fig. 4) and *Centaurea arenaria* (Fig. 5) are presented. Fig. 6 contains the EFD diagrams of $\bar{N}$, Table 1 contains the results of the fitting. For the sake of saving in space, only the probability values are presented for the separate TFD-s. Values printed in italics mean probabilities lesser than the given value, the other mean probabilities greater than the given value.

Discussion

Random arrangement pattern could be accepted only in a few cases, although the χ^2 test indicates more random AP as the IAP-s (cf. Table 2 and Part IV, NOSEK 1986b), but similarly at the smallest plot size (except for *FW* in A_{11}).

The smaller the relative density of the separate species the larger is that plot size interval over which the randomness is acceptable, however the prob-

Table 2

Cases of significant randomness ($p > 5\%$) indicated by the variance/mean ratio and Morisita's index

Species	Plot sizes										
	A_1	A_2	A_3	A_4	A_5	A_6	A_7	A_8	A_9	A_{10}	A_{11}
<i>Fe</i>	X	X	—	—	—	—	—	—	—	—	—
<i>Th</i>	X	—	—	—	—	—	—	—	—	—	—
<i>Fu</i>	X	X	—	—	—	—	—	—	—	—	—
<i>Ca</i>	X	—	—	—	—	—	—	—	—	—	—
<i>Fw</i>	X	X	X	—	—	—	—	—	—	—	X
<i>Ce</i>	—	—	X	—	—	—	—	—	—	—	—
$\bar{N}$	X	—	—	—	—	—	—	—	—	—	—

ability values decrease toward the larger plot sizes. Above A_5 and A_6 (40×40 and 56×56 cm) the hypothesis of randomness must be rejected.

Although it is commonly accepted that ecological generalist species would have random AP (as the random AP indicates the lack of limitation, cf. JUHÁSZ-NAGY and VIDA 1978), the results of the fitting do not support this, since there were no plot sizes when only the fit of POI had been accepted. These results suggest, that the randomness detected is all probability an apparent one — due to the sampling and the density relations — since it occurs at low relative densities and at the same time the TFD-s referring to contagious AP are also of the same good — or better — fit.

In the majority of the cases, the fitting support the contagious AP. On the basis of the probabilities of fitting at the simultaneous occurrence none of the TFD-s of NBI, GNZ and GNI can be preferred. In *Fe* and *Me* the generalized Neyman distributions can be hold only till A_6 and A_7 . In the case of *Ca* and the rare species (*Fw*, *Cy*, *Pl*, and *Ce*) GNZ and GNI are — beside NBI — acceptable almost till the largest plot size.

This fact suggest — comparing with the results derived from the ratio of MORISITA's Index (double peaks at larger plot size (cf. Part IV), that these species may form aggregates of random AP, with random AP of the individuals within each aggregatum.

In the case of *Fe* and *Th* — the first two member of the relative dominance rank — the normal distribution can be accepted from A_4 and/or A_6 with the simultaneous rejection of GNZ and GNI.

To the EFD-s of the dominant species in the larger plot size (A_9 – A_{11}), that of the rare species at A_{11} none of the investigated TFG-s could be fitted.

Regarding the community as if it were the population of one hypothetical species $\bar{N}$ refers to a contagious AP whereas $\bar{S}$ indicates a regular one till A_4 .

The several IAP-s and the χ^2 of goodness of fit gave the same results in the case of the separate species and $\bar{N}$. Remarkable difference was although in the case of $\bar{S}$, where the regular AP is verified by the χ^2 -test only at the small plots, below the 40×40 cm size.

These results suggest that the IAP-s are good indicators of the AP in the case of the random and aggregated ones, but the indication of the regular one can be accepted only under reserve.

The detected type of the AP is depending on the plot size and on the relative abundance of the species. Too small and/or too large plots are inappropriate for the investigation of the real AP. In the community investigated for the dominant species the plot sizes between A_4 and A_6 (28×28 and 56×56 cm), for the rare species the plot sizes between A_7 and A_9 (60×60 and 100×100 cm) proved to be appropriate.

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EL PROYECTO ZAPATA

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Principal and partial objectives, ecological and social fundamentals of the project is briefly presented, the general scheme of the planned researches is outlined and the executing and participating institutes are listed. The project belongs to the Man and Biosphere Programme of the UNESCO, more precisely to the project No. 9. "Contamination of the natural ecological systems by agricultural activity, fertilizer and pesticide consumption." Execution of the researches is carrying on by fourteen research institutes and other institutions of Cuba with the participation of the experts of three Hungarian institutes — at the actual period of the investigations. The first results of the jointed hydrobiological studies are published in this volume.

El tema y sus objetivos

El título completo del tema de investigación es: Influencia del impacto humano resultante de la actividad socio-económica sobre la Ciénaga de Zapata y el Golfo de Batabanó (Proyecto Zapata).

Su objetivo general es: Determinar las condiciones actuales y el impacto ambiental sobre la Ciénaga de Zapata y el Golfo de Batabanó, con el fin de elaborar variantes de modelos ecológicos que viabilicen la toma de decisiones sobre los incrementos planificados de producción en las áreas vinculadas a dichas zonas y que permitan, al mismo tiempo, hacer un uso racional de los recursos naturales contenidos en ella y su protección.

Los objetivos parciales son los siguientes:

1. Conocer la proporción de materia orgánica y otras sustancias contaminantes provenientes de la agricultura y de la industria que llegan a la Ciénaga de Zapata y de ella, al Golfo de Batabanó.

2. Determinar las características y estado actual de los principales ecosistemas terrestres y acuáticos existentes en el área y el papel que juegan los mismos en la relación Ciénaga-Golfo de Batabanó.

3. Valorar de forma integral, el impacto ambiental de la actividad socio-económica en la región.

4. Elaborar variantes de modelos ecológicos.

5. Elaborar recomendaciones para la utilización más racional de los recursos naturales, que incluyan consideraciones económicas y sociales.

Fundamentación

El Golfo de Batabanó situado en la región sur-occidental de Cuba, posee un área de 20 850 km² y una profundidad media de 6 m. Su topografía se distingue por los numerosos grupos y cordones de cayos que hasta cierto punto, lo dividen en subzonas, dificultando el intercambio de aguas en el interior del mismo. Por otra parte, el conjunto de cayos y bajos fondos que lo rodean en el borde exterior, crea una especie de barreras, que obstruye considerablemente el intercambio con las aguas de mar abierto adyacente. Este cordón exterior coincide casi con el borde de la plataforma, cuyo limite está perfectamente definido por el abrupto declive del talud de la plataforma.

Por otra parte, la Ciénaga de Zapata, situada en la costa sur de la región central del país, con una extensión de 1500 km², en su porción occidental se encuentra en contacto directo con el Golfo de Batabanó, constituyendo un área que por sus características propias, desempeña un papel determinante en cuanto a la interrelación entre los ecosistemas terrestres y acuáticos. En cuanto a la porción oriental, también ejerce su acción sobre la plataforma, mediante las corrientes superficiales, ya que constituye una de las áreas de mayor intercambio entre el Golfo de Batabanó y las áreas oceánicas adyacentes.

El borde exterior de la Ciénaga, en contacto con el mar, está constituido en mayor parte por manglares, uno de los ecosistemas costeros más abundantes en nuestro país y de gran importancia, tanto para la fauna terrestre como marina.

Tanto el Golfo de Batabanó, como la Ciénaga de Zapata, por su importancia socio-económica, han sido objeto a través de los años de múltiples investigaciones, pero de carácter aislado, con objetivos muy concretos, que aunque constituyan una valiosa información básica, no permiten hacer la valoración integral que se persigue con este trabajo.

En cuanto a su importancia socio-económica, el área objeto de estudio, constituye una zona de primera importancia para el país, ya que el Golfo de Batabanó, es una de las áreas



Fig. 1. El mapa de la área de investigación



Fig. 2. Area de recreación: Cabañas de la Laguna del Tesoro en Guamá. (Foto: A. BORHIDI)

de pesca más ricas de nuestro país, capturándose en ella, más del 80% de la langosta que se pesca en el país, la que constituye a su vez un importante rubro de exportación, además del peso que tiene esta área en la pesquería total y nacional.

La Ciénaga de Zapata tiene una gran importancia económica, social y científica. Desde el punto de vista hidrológica garantiza la cantidad y calidad del manto freático de la vertiente sur de la provincia de Matanzas, en la cual se desarrolla uno de los mayores planes citrícolas del país además de importantes áreas de producción cañera y arroceras. Desde el punto de vista ecológico, influye sobre las características mesoclimáticas de una gran parte del área; constituye un refugio natural de muchas especies de la flora y la fauna, es un punto de escala de numerosas especies de aves migratorias, por lo que está propuesta como un área protegida.

La Ciénaga es también una zona valiosa de explotación forestal. A esto debe agregarse los significativos valores históricos, culturales y turísticos contenidos en ella.

El desarrollo agrícola e industrial de la zona conlleva el uso generalizado de crecientes volúmenes de pesticidas y fertilizantes, en las áreas citrícolas, cañeras y arroceras, un aumento de desechos industriales procedentes principalmente de la industria azucarera y un incremento en la utilización del agua tanto superficial como subterránea. Todo lo anterior requiere de estudios ecológicos integrales que permitan fundamentar medidas adecuadas para asegurar la estabilidad de los ecosistemas terrestres, costeros y marinos, ricos en especies animales y vegetales y la explotación eficiente y racional de los mismos, tanto a corto como a largo plazo.

El proyecto es, en primer lugar, parte integral del Problema "Caracterización de los principales ecosistemas en la plataforma sur de Cuba", del Plan de Problemas Principales Estatales de Investigación de la República de Cuba, lo que garantiza la prioridad nacional requerida para su ejecución. Por otra parte cuenta con el apoyo de los respectivos Comités Ejecutivos del Poder Popular de la Provincia de Matanzas y del Municipio Ciénaga de Zapata, lo cual viabiliza la realización de las actividades en la región, incluyendo la obtención de

información, así como la incorporación de los criterios e intereses locales en la formulación de recomendaciones.

En segundo lugar, este proyecto se basa en la colaboración bilateral suscrita entre las respectivas Academias de Ciencias de Cuba y Hungría, en cuanto a la realización de investigaciones ecológicas conjuntas en la zona de referencia.

Finalmente, esta propuesta se inscribe dentro del Proyecto No. 9 del Programa MAB de la UNESCO: "Evaluación ecológica de la influencia del uso de pesticidas y fertilizantes ejercidos sobre los ecosistemas acuáticos y terrestres" por lo que se podría contar con el apoyo de este Organismo Internacional, el que recibiría la contribución y colaboración de la Academia de Ciencias de Hungría a los fines de esta proyecto.

El área de estudio ha sido delimitado por la zona litoral desde Batabanó hasta el límite sur-oriental de la provincia de Matanzas y por el norte comprende toda la vertiente sur del área, hasta el partaguas central.

Actividades a desarrollar

La actividad de investigación se ha agrupado en cinco bloques principales de investigación.

I. Aspectos generales

Objetivo: Recopilar y procesar la información existente sobre el área de estudio, fundamentalmente desde el punto de vista de las características físico-geográficas del área, demografía y actividad económica.

II. Ecosistemas terrestres del área agropecuaria de la llanura Sur de Habana—Matanzas

Objetivo: Determinar las características de los distintos ecosistemas naturales y artificiales presentes y los factores ambientales y antrópicos que regulan ellos.

El logro de este objetivo comprende las siguientes tareas:

1. Estudio de las características climáticas (incluyendo meso- y bioclimáticas) del área

Ejecutores: Instituto de Meteorología, ACC (IM); Instituto de Geografía, ACC (IG)

2. Caracterización físico-geográfica de la cuenca

— Estudio (incluida cuantificación) de la intensidad de los procesos denudativos, transportativos, y acumulativos

— Mapificación de las condiciones físico-geográficas de la migración geoquímica de los elementos sobre la base de los complejos territoriales naturales

Ejecutor: Instituto de Geografía, ACC (IG)

3. Caracterización física, química y biológica de los suelos

— Elaboración del mapa de uso actual de los suelos

Ejecutores: Instituto de Geografía, ACC (IG); Instituto de Suelos, ACC (IS)

4. Caracterización hidrológica e hidrogeológica de la Cuenca

a) Hidrología superficial del área

— Caracterización de los parámetros hidrometeorológicos de la región

— Balance hídrico y su análisis multiobjetivo

— Aporte superficial hídrico a la plataforma

Ejecutor: Instituto de Hidroeconomía (IHE) con la participación del Instituto de Geografía, ACC

b) Hidrología subterránea de la cuenca

— Variación de niveles y composición química

— Escurrimiento subterráneo

— Cálculo de reservas

— Equilibrio de agua dulce — agua salada

Ejecutor: Instituto de Hidroeconomía

5. *Caracterización de los geosistemas (incluida ecosistemas) presentes y su mapificación*

— Caracterización y mapificación de los geosistemas

— Caracterización y mapificación de los ecosistemas naturales y artificiales, mayormente agrícolas

Ejecutores: Instituto de Geografía, ACC; Instituto de Botánica, ACC IB

6. *Determinar la dinámica de los contaminantes (metales pesados, plaguicidas y herbicidas) en las aguas, suelos, plantas y animales de los ecosistemas*

— Inventario de las fuentes de contaminación

Ejecutores: DIMARNA-ACC; Delegación de ACC en Matanzas; Centro de Investigaciones Pesqueras (CIP)

— Investigación de la migración y acumulación de los contaminantes

Ejecutores: Instituto de Investigaciones de Sanidad Vegetal (IISV); Centro de Investigaciones Pesqueras (CIP)

7. *Actividad económica del área*

— Actividad agropecuaria

— La actividad industrial, en especial: la industria azucarera

— Sistema de transporte

— Infraestructura de los servicios

Ejecutor: Instituto de Geografía ACC (IG)

III. Ecosistemas de la Ciénaga de Zapata

Objetivo: Caracterizar los distintos ecosistemas presentes en la Ciénaga, incluyendo la zona litoral, y determinar sus factores ambientales y la influencia socio-económica de la región sobre ellos.

El logro de este objetivo comprende las siguientes tareas:

1. *Estudio de las características climáticas (incluidas meso- y bioclimáticas) de la Ciénaga*

Ejecutores: Instituto de Meteorología, ACC (IM); Instituto de Geografía, ACC (IG)

2. *Caracterización físico-geográfica de la Ciénaga*

— Estudio y cuantificación de la intensidad de los procesos denudativos, transportativos y acumulativos

— Mapificación de las condiciones físico-geográficas de la migración geoquímica de los elementos sobre la base de los complejos territoriales naturales

Ejecutor: Instituto de Geografía, ACC (IG)

3. *Caracterización física, química y biológica de los suelos de la Ciénaga*

— Génesis, clasificación y uso de los suelos pantanosos de la Ciénaga de Zapata

— Elaboración del mapa del uso actual de los suelos

— Mapificación de los suelos orgánicos (tomando en cuenta el índice del grado de humificación de las turbas)

— Aplicar métodos térmicos de análisis para caracterizar las turbas de la Ciénaga correlacionándolas con sus características

— Caracterización microbiológica de los suelos

Ejecutor: Instituto de Suelos ACC (IS)

4. *Caracterización hidrológica de la Ciénaga de Zapata*

— Caracterización de los parámetros hidrometeorológicos de la Ciénaga de Zapata

— Balance hídrico y su análisis multiobjetivo

— Aporte superficial hídrico a la plataforma

Ejecutor: Instituto de Hidroeconomía (IHE) con la colaboración del Instituto de Geografía, ACC



Fig. 3. Vegetación acuática en la costa sur de la Laguna del Tesoro. Comunidades de *Nymphaea ampla*, *Thalia geniculata*, *Typha domingensis*, y bosque de ciénaga en el fondo con *Bucida palustris* y *Sabal parviflora*. (Foto: A. BORHIDI)

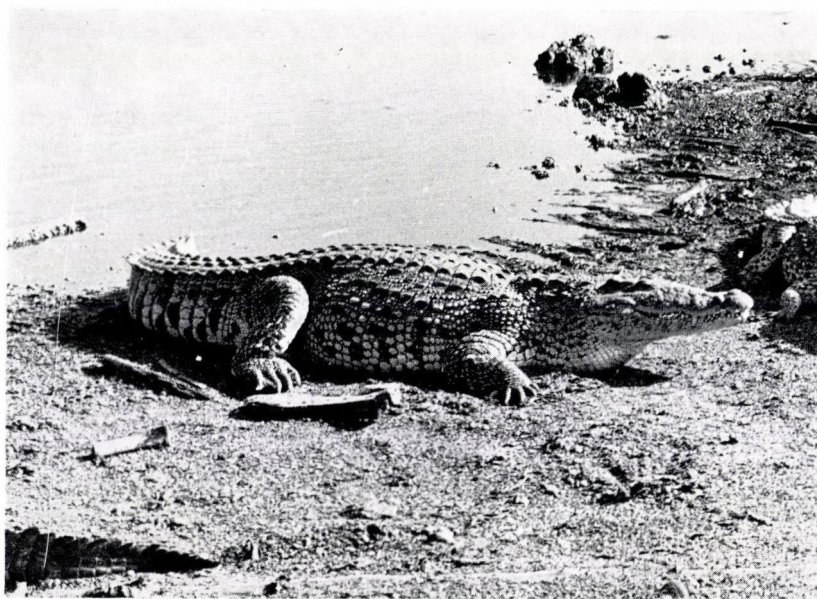


Fig. 4. Area de protección natural: El cocodrilo endémico de Cuba (*Crocodilus rhombifer*). (Foto: A. BORHIDI)

5. *Caracterización y mapificación de los ecosistemas presentes en la Ciénaga de Zapata (incluyendo los de la zona litoral)*
 - Estudio ecológico y fitocenológico de los ecosistemas herbazales, vegetación acuática y litoral
 - Estudio, clasificación y mapificación de los diferentes tipos de bosques existentes

Ejecutores: Dirección de Silvicultura MINAGRI; DIMARNA-ACC; Centro de Investigaciones Forestales (MINAGRI); Instituto de Botánica, ACC (IB)

 - Estudio para el mejoramiento de bosques degradados

Ejecutor: Centro de Investigaciones Forestales (CIF)
6. *Estudios zooecológicos sobre las poblaciones de algunas más interesantes de la Ciénaga*
 - Estudios de las poblaciones de dos especies de aves endémicas de habitats restringidos (*Ferminia cerverai*, *Torreonis inexpectata*)

Ejecutor: Instituto de Zoología, ACC (IZ)

 - Estudio ecológico de las poblaciones de cotorra (*Amazona leucocephala*) y catey (*Aratinga euops*)

Ejecutor: Instituto de Zoología, ACC (IZ)

 - Estudio sobre las poblaciones naturales del cocodrilo cubano (*Crocodilus rhombifer*)

Ejecutor: Instituto de Zoología, ACC (IZ)
7. *Determinar la dinámica de los contaminantes en las aguas, suelos, plantas y animales de los ecosistemas*
 - Investigación de la migración y acumulación de los contaminantes
 - La vegetación como biofiltro de los contaminantes, en especial: manglares y bosque de pantano
 - Definir el impacto de las pesticidas en la ecología de la colmena
 - Elaborar métodos de teledetección y mapificación de la distribución de los contaminantes

Ejecutores: Instituto de Investigaciones de Sanidad Vegetal (IISV-MINAGRI); Centro de Investigaciones Pesqueras (CIP); DIMARNA-ACC; Estación de Investigaciones Apícolas (EIA)
8. *Bioindicación de la distribución de la contaminación*
 - Bioindicación de la contaminación por plantas superiores (acumulación, resistencia, actividad fotosintética)
 - Bioindicación de la contaminación por algas
 - Bioindicación de los contaminantes mediante animales, en especial abejas melíferas y melíponos

Ejecutores: DIMARNA-ACC; Estación de Investigaciones Apícolas (EIA)
9. *Actividades económicas en la Ciénaga de Zapata*
 - El sitio cienaguero y su función
 - La explotación forestal y producción de carbón
 - La cría de especies y la caza
 - Papel de la pesca en la economía de la zona
 - La actividad industrial; en especial: la extracción y elaboración de materiales de construcción
 - Sistema de transporte
 - Infraestructura de los servicios
 - La actividad turística en la región

Ejecutor: Instituto de Geografía, ACC (IG)
10. *Caracterización social de la Ciénaga de Zapata*
 - Las estructuras demográficas y su comportamiento



Fig. 5. Bosque semideciduo de la Península de Zapata, cerca de Soplillar, con ejemplar grande de la ceiba (*Ceiba pentandra*) cubierta por masas colgantes de la barba española (*Tillandsia usneoides*). (Foto: A. BORHIDI)

- La estructura ocupacional
 - Efecto de las migraciones en las estructuras
 - Características de poblamiento y su evolución
- Ejecutor: Instituto de Geografía, ACC (IG)

IV. Ecosistemas marinos

Objetivo: Determinar la influencia de la Ciénaga de Zapata y de la actividad socio-económica de la región sobre los distintos ecosistemas marinos de la plataforma en función de su potencial productivo.

El logro de este objetivo requiere:

1. *Determinar las características físicas y químicas de los principales biótupos (estuarios, seibadales, arrecifes coralinos etc) de la plataforma*

- Características hidrológicas e hidroquímicas
- Circulación de las aguas
- Distribución y caracterización de los sedimentos

Ejecutores: Instituto de Oceanología, ACC (IOC); Centro de Investigaciones Pesqueras (CIP)

- Procesos de Eutroficación
- Características climáticas del área
- 2. *Caracterización biológica de los biótopos y ecosistemas marinos de la plataforma — estudio de la estructura de las comunidades en ecosistemas marinos*
 - Distribución, composición cualitativa y cuantitativa de la producción bacteriana heterótrofa
 - Variaciones temporales de la población bacteriana en relación con algunos factores abióticos
 - Ejecutor: Instituto de Oceanología, ACC (IOC)
 - Comunidades bentónicas de macro-, meso- y fitobentos
 - en la macrolaguna del Golfo de Batabanó
 - en arrecifes, seibadales y manglares aledaños
 - Ejecutor: Instituto de Oceanología, ACC (IOC)
 - en la ensenada de la Broa
 - Ejecutor: Centro de Investigaciones Pesquera (CIP)
 - en la zona Sur de la Península de Zapata, en arrecifes y lagunas prearrecifales
 - Ejecutor: Centro de Investigaciones Marinas (CIM)
 - Plancton en los biótopos representativos de la langosta
 - Ejecutor: Instituto de Oceanología (IOC)
- 3. *Determinar las características y distribución de los contaminantes en los ecosistemas y en las especies mas importantes marinas*
 - Caracterización de los distintos contaminantes presentes en el agua y sedimentos, sobre todo el nivel de los organoclorados
 - Determinar el nivel de organoclorados en la langosta
 - Ejecutor: Instituto de Oceanología, ACC (IOC)

Nota: Las investigaciones hidrobiológicas se ejecutan paralelamente en los Institutos mencionados en una división geográfica:

El Instituto de Oceanología trabaja en el Golfo de Batabanó



Fig. 6. Uso de los bosques de la ciénaga: campo de carboneros cerca de Meneadero Chiquito. (Foto: A. BORHIDI)

El Centro de las Investigaciones Pesqueras en la Ensenada de la Broa, y el Centro de Investigaciones Marinas en la zona Sur de la Península de Zapata (Golfo de Cazones)

4. *Mapificación de la vegetación de la cayería adyacente a la Península de Zapata y su dinámica*

Ejecutor: Instituto de Botánica, ACC (IB)

V. **Análisis integral de los resultados**

Objetivo: Elaborar las recomendaciones para la utilización racional y la protección de la zona objeto de estudio.

El logro de este objetivo comprende las siguientes tareas:

1. *Analizar los resultados obtenidos en cada uno de los aspectos considerados, incluyendo el tratamiento estadístico adecuado*
2. *Elaborar variables de modelos ecológicos*
3. *Elaborar recomendaciones para la utilización racional, así como la protección de la zona objeto de estudio, incluyendo consideraciones económicas y sociales*

Colaboración Internacional

La colaboración bilateral entre la Academia de Ciencias de Cuba y la Academia de Ciencias de Hungría comenzó hace veinte años y se ha desarrollado de manera creciente y efectiva durante este periodo.

La colaboración entre ambas Academias dentro del programa MAB, se basa en la investigación conjunta, así como la asesoría y entrenamiento del personal cubano en los siguientes aspectos:

1. Física, química y microbiología de los suelos.
2. Química de pesticidas.
3. Investigación y metodología para el estudio de los procesos de eutroficación.
4. Investigación sobre los ecosistemas terrestres y litorales, incluyendo bioindicación.
5. Elaboración de modelos matemáticos de circulación.
6. Utilización de la computadora en sentido general.
7. Análisis económico de las recomendaciones propuestas. Elaboración de variantes de manejo

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HYDROBOTANICAL STUDIES IN THE FRAMEWORK OF CUBAN ZAPATA PROJECT

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Introduction

In 1981 on the initiative of the Academy of Sciences of Cuba Cuban and Hungarian ecologists elaborated an international programme for environment protection to which they were given assistance by the UNESCO and UNEP. The research work falls within the project No. 9 of the MAB programme of UNESCO titled "Contamination of natural ecological systems by agricultural activity, fertilizer and pesticide consumption".

The site of research is an about 15 000 km² area in the southern part of Central Cuba with the native moor- and forest covered Zapata peninsula in the centre, of which the project was named Zapata Project. In the work 12 Cuban and 3 Hungarian research institutes have joined so far. The research work covers three closely connected regional units. The first of them is a highly important agricultural area on the southern fertile lowlands of the provinces Havana and Matanzas, with deep latosolic, red tropical soils on which intensive sugar cane, citrus and other fruit production is carried on and extensive rice fields and pig- and poultry farms are found.

All these cause contamination to the surface and subsurface waters of the area due, on the one hand, to the considerable volume of fertilizer and pesticide used, on the other hand with the liquid manure production. The waters flowing southwards carry the contamination to the second regional unit, the Zapata peninsula. This area is a vast native moor similar to the famous Floridan Everglades, with national parks, bird- and crocodile reservations and tropical forests.

The holiday and tourist centres of the area (Guamá, Laguna del Tesoro, Playa Larga) as well as the places of historical fame in the neighbourhood of the Pig Bay (Playa Girón) are of special value.

The contamination acculumating in the stagnant water of the marshy basin endanger the flora and fauna of the reservations and the hygiene of the recreation area. Finally, through the water system of the Rio Negro the waters of the former two areas reach the third regional unit, the Batabano Bay with its 6 m average depth of water. This bay is the most important basis of crayfish and sponges fishing in Cuba, supplying 80 per cent of the crayfish exports from the country. This highly important economic resource is also threatened by contaminations whose accumulation is but slightly counterbalanced by the sea currents.

In addition to solving numerous problems of environment protection the research programme has the ultimate purpose of elaborating an ecologic-economic model which finds the right ratio between agricultural development, efficient fishing and the interests of tourism and environment protection.

To approach the aim we set ourselves we had to follow the changes in the biological quality of surface waters from the agricultural areas to the bay. Since the waters of the agricultural areas are regularly analysed at the laboratory of the Cuban Water Management Institute in Matanzas Province, and the water quality of the Batabano Bay is controlled by the research centre of fishing (CIP) it seemed necessary to examine the waters of the Zapata Peninsula, the region occupying a key position between the two systems. In April–May 1983 Hungarian experts and specialists of the Commission of Rational Use of Natural Resources, Protection of Nature and Environment (COMARNA), Cuba, organized two expeditions to the Laguna del Tesoro and the river system of Rio Negro and Rio Hatiguanico, as well as to the water conduct system of the Zapata moorland in order to determine the major trophic characteristics of these waters.

Material and method

In the course of the expeditions, for two weeks in April–May 1983, we carried on a field-survey of the pH, water temperature and dissolved oxygen content of still waters and rivers in the Zapata Peninsula, to the full depth of the body of water, at 28 measuring stations (Figs 1 and 3) with an Aquacheck-3 type (RADELKIS made) portable instrument.

At each station we studied the composition and stratification of the vegetation, and collected samples for the determination of the dissolved organic carbon (DOC) concentration of water, and for the purposes of phytoplankton examinations. The determination of DOC was carried out with a Beckman TOC analyser by István HOFFMAN, worker at the VITUKI (Research Institute for Water Management).

In the Laguna del Tesoro, at the measuring stations 1 and 2 (Fig. 3) we measured the changes of oxygen saturation and temperature in the water column every 3 hours in a 24-hour cycle, in order to estimate the primary production. From the 24-hour curves of oxygen we calculated the daily primary production with ODUM's (1958) method improved by OLÁN et al. (1977). The ODUM's method generally used for the evaluation of the daily oxygen curves is based on the assumption that the respiration calculated for the night remains constant throughout the day. The method we use eliminates this deficiency of the ODUM's method by supposing a positive correlation between the oxygen concentration and the respiration.

The water samples taken for the purpose of phytoplankton examination were preserved with Lugol solution, and the quantitative analyses were carried out with reversed plankton microscope.

The data obtained were compared to the results of examinations made by the Zoological Institute of the Academy of Sciences of Cuba on the Laguna del Tesoro 5 years earlier, and from the comparison conclusions were drawn on the tendencies of changes.

Results and discussion

A) LAGUNA DEL TESORO

The moor lake with its 9 km² surface of brown water is the largest fresh-water lake of Cuba. The lake is surrounded by the peaty mudd of the Zapata moor interspersed with groups of *Cladium* and fan-palm; it has a maximum depth of 11 and an average depth of 3–4 metres. In the south-western and eastern part of the lake there are several smallish islands with touristic establishments built on them.

A considerable proportion of the lake is covered by aquatic vegetation, the dominant components of which are: *Chara domingensis*, a stonewort species which covers the bottom some 1.5 m high, and the similarly submerged *Najas guadelupensis* which reaches a height of 2–2.5 m. The plant found in the largest quantities and almost everywhere in the lake is

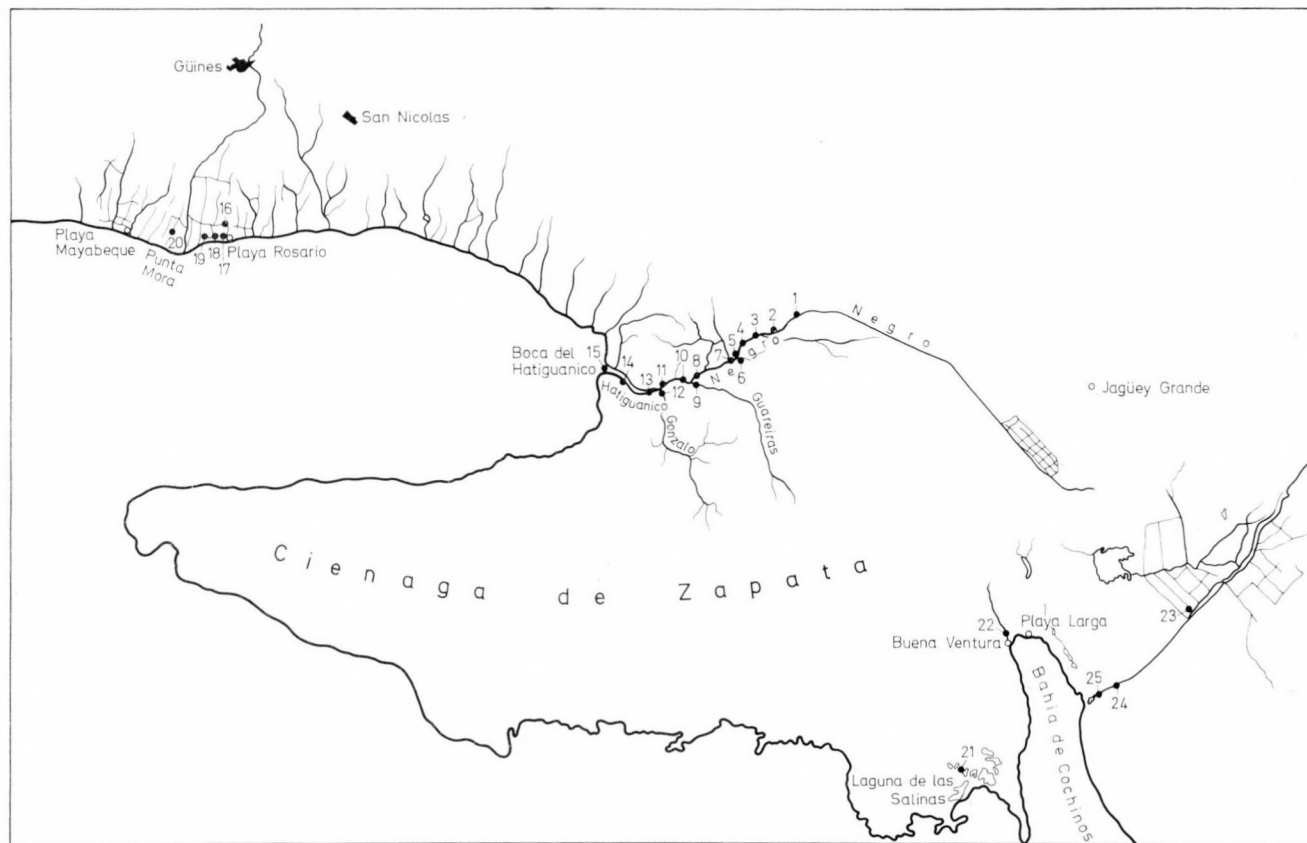


Fig. 1. Sampling stations (1-25) in the Zapata Peninsula

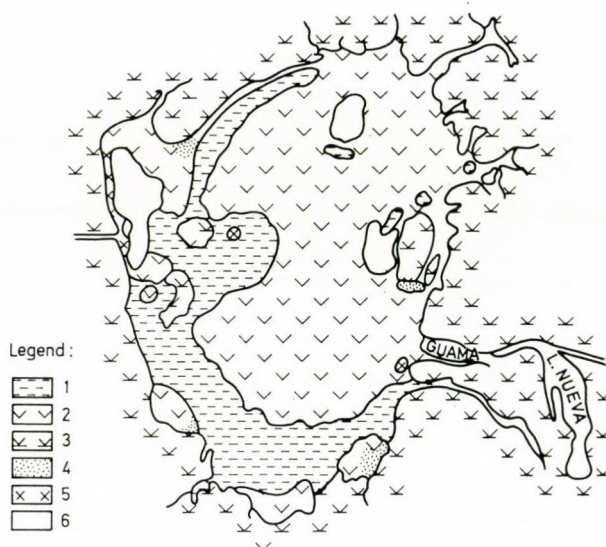


Fig. 2. Distribution of macrophyte stands in the Laguna del Tesoro in 1979. (Made by the Institute of Zoology of the Academy of Sciences of Cuba.) — 1. *Potamogeton illinoensis*; 2. *Vallisneria neotropicalis*; 3. *Cladium jamaicense*; 4. *Schoenoplectus americanus*; 5. *Chara domingensis*; 6. Water table without vegetation

the 3–4 m high *Vallisneria neotropicalis*. The largest size aquatic plant of the lake is the *Potamogeton illinoensis*; its stems and leaves rise to the surface and may reach a height of 4–5 m. The aquatic vegetation includes floating weeds: *Utricularia foliosa* and *U. juncea*.

The appearance of *Potamogeton illinoensis* of all the weed species listed can have unpleasant consequences insofar as its mass reproduction may hinder the navigation and the touristic use of the water — including fishing.

According to the survey made by the Zoological Institute of the Academy of Sciences of Cuba in 1979 *Vallisneria neotropicalis* stands were found everywhere in the lake, while pondweed only covered one-third of the water surface (Fig. 2). This picture is similar to the one that BORHIDI observed in 1970 and repeatedly controlled in 1974 and 1975, with the difference that the *Potamogeton* stands appeared then only on 10 per cent of the water surface.

Our survey in 1983 showed that in the previous five years the weed growth of the lake further increased, and today the *Potamogeton* stands cover some 60 per cent of the water surface (Fig. 3).

In the course of studying the structure of the aquatic vegetation we found that the mentioned change in it did not come about through the replacement of certain weed species by others, but during the succession the weed species living at different depths of the water formed a multilevel community of very large biomass. The first stage in the succession of this multilevel aquatic vegetation is represented by stonewort (*Chara domingensis*) mats covering the bottom. It is in this mat that individuals of the spinose pondweed (*Najas guadelupensis*) population settle forming a higher story of vegetation. The next phase of succession is the appearance of *Vallisneria neotropicalis*, first one by one, then in masses, with a parallel thinning of the populations of lower stories. This *Vallisneria* mat reaches to the surface of the water. Between the levels of *Vallisneria* and *Najas* the aquatic animals find a rich supply of

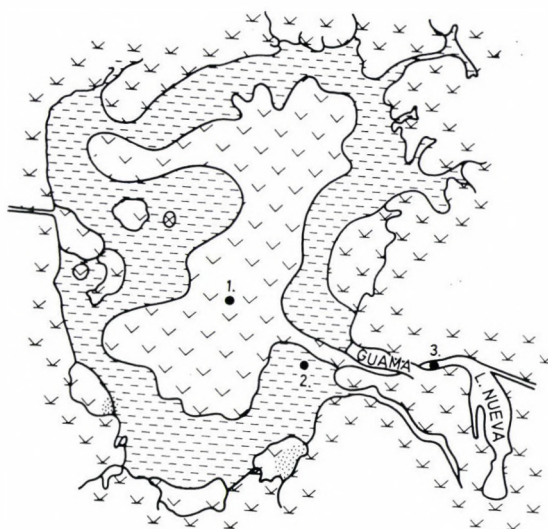


Fig. 3. Distribution of macrophyte stands in the Laguna del Tesoro in 1983, and sampling stations 1-3 on the lake. Made by A. BORHIDI and L. VÖRÖS (for signs see Fig. 2)

oxygen and optimum bedding which is favourable for the appearance of insect-catching floating water-weed species. Finally, as the last successional stage of the aquatic vegetation the large-sized water spike forms stands.

The structure of the water weed communities is reflected in their photosynthetic activity, and in the vertical stratification of the dissolved oxygen as well. In the middle of the lake (Fig. 3, station 1) *Vallisneria* is the dominant plant, here the community has three stories. In the early afternoon hours on 4 May the oxygen saturation of the 28.0 °C water was as high as 180 per cent, which slightly decreased with the depth and was 80-90 per cent even at a depth of 5.5 m, near the bottom. In the night hours the temperature of the water was 27.5 °C, the oxygen saturation 130 per cent on the surface and 10 per cent near the bottom (Fig. 4a). Judging by the 24-hour curve of oxygen the gross primary production per unit area was 29.42 g O₂/m²/day.

In the four-storied community of a shallower part of the lake (Fig. 3, station 2) *Potamogeton* is the dominant species. In this weed community which was denser than the former one the maximum value of the oxygen concentration reached 200 per cent in the early afternoon hours of 4 May, when the water temperature was 28 °C. Here the decrease in the oxygen concentration was steeper than in stands characterized by the dominance of *Vallisneria*, owing to the self-shading of the thick stand. Near the bottom, at a depth of 2.5-2.7 m anaerobic conditions occurred throughout the day. Here the fluctuation of the oxygen content in the course of the day was also higher than in the former plant stand; on the surface the minimum oxygen saturation was 110 per cent in the night hours in the 27 °C water (Fig. 4b). In spite of the higher oxygen saturation near the surface the daily gross primary production was lower — 2.52 g O₂/m² — here than in the middle of the lake. The lower production per unit surface area was due to the fact that owing to the shallowness of the water and the intensive self-shading effect of the thick plant stand the photosynthetically active zone was narrower here. In this case the method certainly underestimates the primary production, because it leaves the oxygen production by the above-water parts of the *Potamogeton* out of consideration.

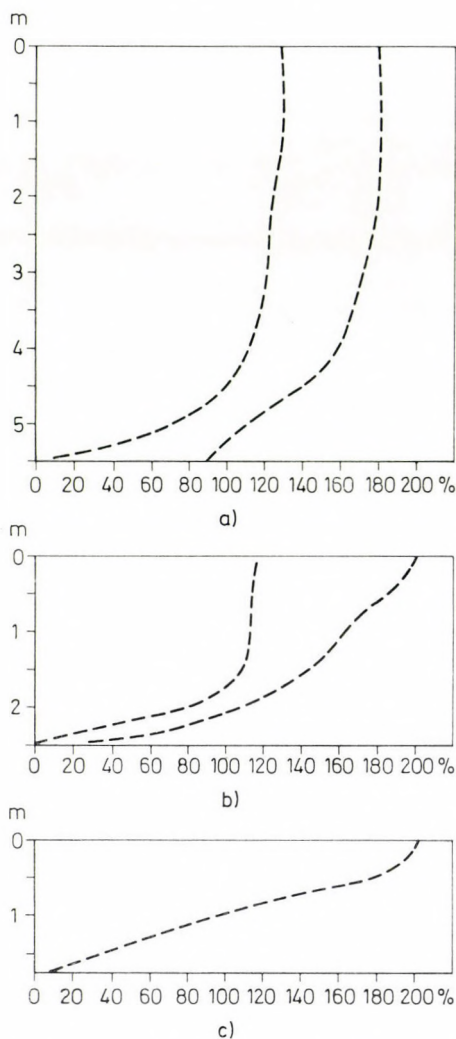


Fig. 4. Vertical changes in oxygen saturation and water temperature ($^{\circ}\text{C}$) in the Laguna del Tesoro (a = station 1, b = station 2, c = station 3)

Photosynthesis was earlier measured in the Laguna del Tesoro by STRASKRABA et al. (1969) who determined the primary production of the phytoplankton by dark-light bottle method, with oxygen indication. According to the results the primary production of the phytoplankton was $120 \text{ mg O}_2/\text{m}^2/\text{hour}$ which approximately corresponds to a daily value of $1.44 \text{ g O}_2/\text{m}^2$ i.e. a 20-times lower production than the one we obtained in the middle of the lake. This difference does not, however, mean a 20-fold increase in the productivity of the lake. In the Laguna del Tesoro the planktonic primary production cannot be higher today than when STRASKRABA et al. measured it; the water of the lake is even now transparent to the bottom and poor in phytoplankton. In 1969 the biomass of the phytoplankton was 0.29 mg/l (STRASKRABA et al. 1969), in 1983 we measured 0.23 mg/l alga-biomass in the same place.

The difference is explained by the fact that a decisive proportion of the primary production comes from macrophytes whose production is not measured by the dark-light bottle method. In waters with extensive macrophyte stands the primary production can only be measured with methods based on changes in the oxygen content of the water. We can say that in the Laguna del Tesoro the benthic primary production exceeds by orders of magnitude the primary production of the phytoplankton; the $29.42 \text{ g O}_2/\text{m}^2/\text{day}$ ($= 9.2 \text{ g C}/\text{m}^2/\text{day}$ /gross production ranks it with the high productivity lakes of the world.

At the mouth of the canal connecting the lake with the Laguna Nueva (Fig. 3, station 3) in the 1.6 m deep water the species *Ceratophyllum echinatum* and *Nymphaea ampla* occur in masses. In this very thick vegetation the oxygen stratification is even more intensive than in the former two stands. At 3 p.m. on 5 May we measured 202 per cent oxygen saturation on the surface of the 33°C water; at a depth of 1 m the oxygen saturation was only 94 per cent and decreased to 17 per cent near the bottom. The temperature did not change with the depth (Fig. 4c).

Owing to the thick water-weed stands this canal is not navigable by motor boats, these water areas do not serve the purpose of either recreation or tourism; at the same time the filling up succession accelerates, on the oxygen deficient deposit surface the mineralization slows down whereby the bed is filled up at a higher rate. The overgrowth of weed plants greatly reduces the use-value of the Laguna del Tesoro, and at the same time forecasts its turning swampy within a relatively short time; consequently, with the view of saving the lake the weed stands must be eradicated and the causes of water-weeds overgrowing the lake eliminated. The causes lie in the fact that the lake is overloaded with plant nutrients which, in turn, is related with the extensive rice fields found in the catchment area. The role of the latter in loading the lake with plant nutrients is put to examination in 1984.

B) WATER SYSTEM OF RIO NEGRO AND RIO HATIGUANICO

It is the largest continuous water system of the Zapata Peninsula which besides the Rio Negro and Rio Hatiguanico and their minor affluents includes canals dewatering the area (Fig. 1). In studying the water system we started from a canal (Fig. 1, station 1), and completed our investigations where the Rio Hatiguanico flows into the Batabano Bay (Fig. 1, station 15). Oxygen measuring in the water system was performed on 6 May 1983, between 2 and 5 p.m., in the probable period of daily maxima.

In the canal flowing into the Rio Negro, at a spot farther back from the mouth (Fig. 1, station 1) *Vallisneria neotropicalis* forms a thick stand with a cover of 80–90 per cent. The upper third of the leaf-blade floats on the water surface spread in a thick layer, often covered by filamentous algae. The thickness of the stand is increased by the *Utricularia foliosa* floating submerged in the upper half-metre layer of water. The *Vallisneria* stand is interspersed with single plants of *Potamogeton illinoensis*. In the thick *Vallisneria* stand the dissolved oxygen showed intensive vertical stratification; the oxygen saturation was 140 per cent on the surface, its value decreased rapidly with the depth to fall to mere 80 per cent above the bottom (Fig. 5a). The water temperature was 27°C , the pH value 8.1.

Before joining the river the canal is moderately overgrown by vegetation (Fig. 1, station 2). As a visible sign of the decreased trophic condition the cover of the *Vallisneria* stand is only 30–40 per cent, and there are neither rooting nor floating water-weeds in it. Due to the thinned vegetation the oxygen saturation does not change with the depth, it is uniformly 120 per cent in the transparent 27°C water. The water is rich in dissolved organic matter, the DOC concentration is 22.6 mg/l , the pH value 7.5. The lower value of pH and lower oxygen saturation are also indicative of a reduced trophic state.

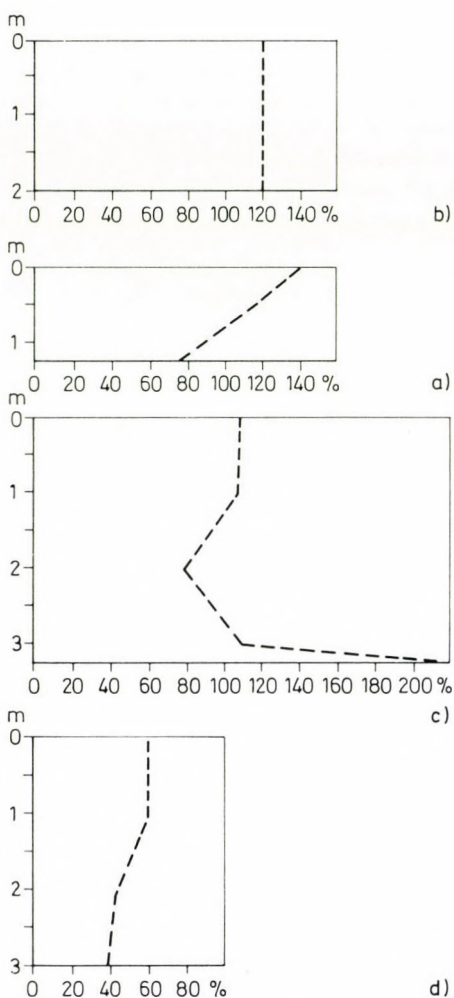


Fig. 5. Vertical changes in oxygen saturation and water temperature ($^{\circ}\text{C}$) in the water system of Rio Negro (a = station 1, b = station 2, c = station 5, d = station 6)

In the Rio Negro, after the place where the canal joins it (Fig. 1, station 3) macrophyte vegetation no longer appears on the surface as a further sign of the reduced trophic state, and the water is transparent down to the bottom. At the same time, it must also be taken into consideration that the hard rocky bed is not favourable for large size plants to settle. At the bottom of the river, at a depth of 3–3.5 m a 20–30 cm thick *Chara* mat develops. The oxygen saturation is only 80 per cent on the surface, and this value is characteristic of the whole body of water except above the bottom in the *Chara* mat where it rises steeply to 140 per cent. The temperature of water is 27°C over the full column of water, and the value of pH is 7.3.

The further 2–3 km long stretch of the Rio Negro is overgrown by *Vallisneria*, because below the inflow of the El Roble sediment accumulates at both sides of the river bed. The

loose stands of *Vallisneria* in the vicinity of minor affluents flowing into the river are covered by mucous algal coating. At the sampling station 4 (Fig. 1), owing to the photosynthesis of the relatively rich vegetation the oxygen saturation is considerably higher (140–150 per cent), vertical stratification does not develop, the water temperature is 27 °C, the pH rises here to 7.6.

At station 5 (Fig. 1) the *Vallisneria* stand disappears from the river, and in the 3.5 m deep rocky river bed the 20–30 cm thick *Chara* mat reappears. The temperature of water is 26 °C, its oxygen saturation to a depth of 3 m about 100 per cent, rising above 200 per cent in the *Chara* mat at the bottom (Fig. 5c).

Towards the mouth of the Rio Negro the first major water flowing into it from the south is the Rio Azul, or by another name Los Cristales; its brown water at the mouth is transparent to the bottom (3–3.5 m) (Fig. 1, station 6). The river is composed of two narrow branches completely shaded by mangrove vegetation. Owing to the rocky bottom and intensive shading macrophytes are almost totally absent from their beds. The rocky bottom is covered by the fallen leaves of the mangrove trees. The oxygen conditions also indicate the lack of photosynthesis by aquatic plants, and the prevalence of decomposing processes; the oxygen saturation is about 60 per cent on the surface and 40 per cent near the bottom, the water temperature is 25 °C, the pH value is low, 7.1 (Fig. 5d).

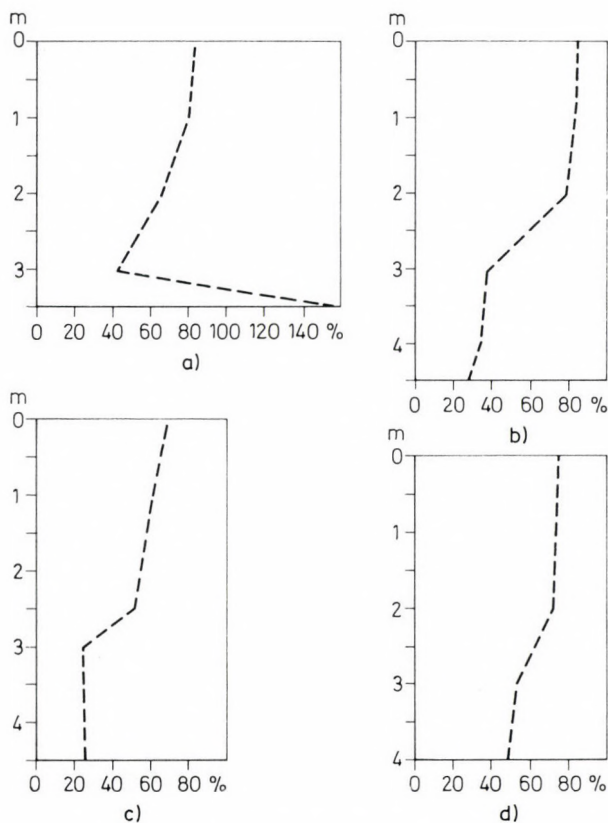


Fig. 6. Vertical changes in oxygen saturation and water temperature (°C) in the water system of Rio Negro (a = station 7, b = station 8, c = station 9, d = station 10).

After the inflow of the Rio Azul (Fig. 1, station 7) the conditions in the Rio Negro are similar to those above the mouth, but under the influence of the water from the Rio Azul the oxygen saturation is somewhat decreased, its value on the surface is about 80 per cent lessening slightly with the depth to 3.0 m, then in the *Chara* mat over the bottom suddenly rises to 150 per cent (Fig. 6a). The water temperature is 26 °C, the pH value 7.2, the DOC concentration 5.5 mg/l. Above the mouth of the Rio Guareiras (Fig. 1, station 8) the river is deeper than in the preceeding reach. In the 4–5 m deep water macrophyte vegetation does not develop either on the surface or on the bottom. The oxygen saturation is constant at about 80 per cent to a depth of 2 m, then gradually decreases to 30 per cent at the bottom; the water temperature is 26 °C (Fig. 6b).

The Rio Guareiras at the place it flows into the Rio Negro is 4.5 m deep (Fig. 1, station 9). The conditions are similar to those at the former station as regards both the absence of considerable amounts of macrophytes and the values of oxygen saturation (Fig. 6c). Farther towards the mouth of the Rio Negro, at stations 10 and 11 no remarkable change compared

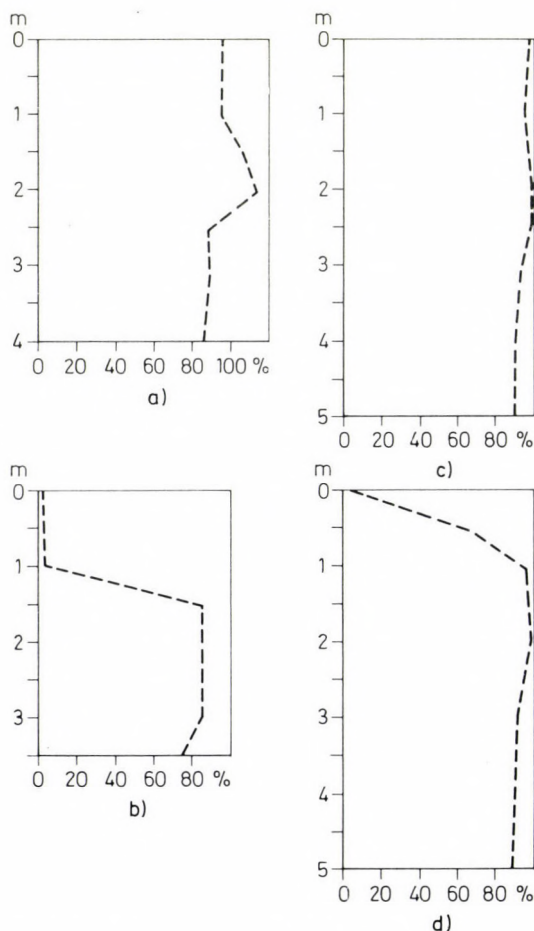


Fig. 7. Vertical changes in oxygen saturation and water temperature (°C) in the water system of Rio Negro (a = station 11, b = station 12, c and d = station 13)

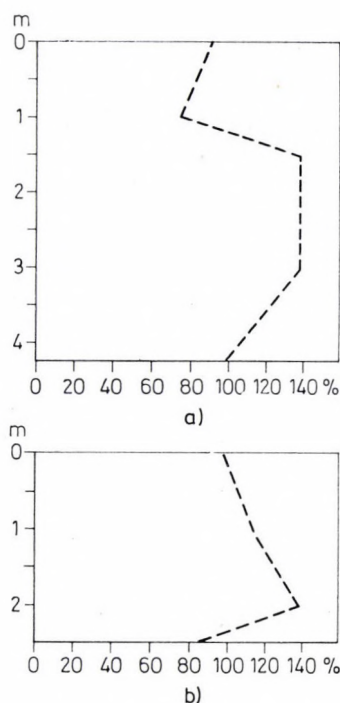


Fig. 8. Vertical changes in oxygen saturation and water temperature ($^{\circ}\text{C}$) in the water system of Rio Negro (a = station 14, b = station 15)

with the former two stations can be observed either in the plant stands or in the oxygen conditions (Fig. 6d, Fig. 7a).

The Rio Gonzalo — otherwise known as Rio Hatiguanico — is a wide river of greenish colour flowing into the Rio Negro from the south (Fig. 1, station 12) without a surface macrophyte vegetation. It is bordered by mangrove vegetation on both sides; at the bottom there is an about 1–1.5 m high more or less continuous *Najas guadelupensis* mat. In the river we found a peculiar inverse oxygen stratification; to a depth of 1 m there was no oxygen in the 27°C water, from 1.5 m to the bottom (3.5 m) we measured values around 80 per cent in the *Najas* mat (Fig. 7b). The water of the river was rich in dissolved organic matter, the DOC concentration was 20.5 mg/l, the pH value 7.1.

In the river, after its confluence with the Rio Gonzalo (Fig. 1, station 13) there is no macrophyte vegetation, in the overwhelming proportion of the water the oxygen saturation does not show any considerable vertical change; it is about 100 per cent (Fig. 7c). In a broad midstream zone, where the water of the Rio Gonzalo is not yet intermingled with the main branch, we found the surface layer of water to be almost free of oxygen, though at a depth of 1 m the oxygen saturation was already about 100 per cent in the 27°C water (Fig. 7d).

Nearing the mouth the river grows wider, 4–5 km before the mouth the river bed becomes muddy, owing to the rise and fall of the sea the water is of brackish water character. At station 14 turtle-grass (*Thalassia testudinum*), a plant characteristic of seacoasts appears in the bed-silt (Fig. 1). The photosynthetic activity of this thinnish *Thalassia* sward is reflected in the oxygen conditions. In the upper 1 m layer of water the oxygen saturation is about

80–90 per cent rising to 140 per cent in the *Thalassia* sward (Fig. 8a). Here the DOC concentration was 11.5 mg/l and the temperature of water 27 °C.

At the mouth of the river (Fig. 1, station 15) the water is shallower; under the influence of a more intensive light reaching the bed-silt closed *Thalassia* swards develop in which the oxygen saturation is considerably higher (Fig. 8b); the temperature of water is 29 °C.

C) SOUTHERN PLAIN OF THE HAVANNA PROVINCE

(Water system of the coastal sector between Playa Mayabeque and Playa Rosario)

The canal receiving the waste-waters of the Oswaldo Sanchez sugar factory was examined at the Juan Borrel road-junction (Fig. 1, station 16). The 50–70 cm deep canal is overgrown by various *Cyperus* species. On 23 April 1983 the oxygen saturation already reached 110 per cent in the morning hours, due to the large number of macrophytes and the rich epiphytic alga coating; the water temperature was 28 °C, the pH value 7.7.

The next measuring was performed in the lateral branch of the same canal running parallel with the coastline, between Playa Rosario and Playa Mayabeque, some 1 km west of Playa Rosario (Fig. 1, station 17). The main function of the canal was to drain the water of the coastal mangrove vegetation thus making the seacoast suitable for bathing. The mangrove vegetation cast a deep shadow on the canal, the water was yellowish brown and turbid, the full body of the 1 m deep water was without aquatic vegetation and had a mere 25 per cent oxygen saturation; the water temperature was 27 °C, the value of pH 7.2. At station 18 in the same canal (Fig. 1), west of station 16, the mangrove vegetation along the canal was destroyed, the water was no longer shaded therefore its oxygen saturation rose to 70 per cent, the value of pH to 7.4 and the water temperature to 28 °C. Five kilometres farther in the canal (Fig. 1, station 19) the water became transparent, its brownish colour disappeared, its temperature was 28 °C; the bottom was covered by a continuous alga mat and as a consequence the oxygen saturation rose to 125 per cent and the pH value to 7.6.

The next sampling station was a canal of north-south direction perpendicular to the former canal, west of Punta Mora (Fig. 1, station 20). A considerable proportion of its catchment area is planted to pineapple and sugar-cane. The full length of the canal was overgrown by floating (*Pistia stratiotes*) and rooting (*Elodea canadensis*) water-weeds. The water was crystal-clear, transparent to the bottom, not brown, 1.5 m deep; its temperature was 28 °C, its oxygen saturation only 40 per cent because of the shadow cast on it by the vegetation. The water was poor in dissolved organic matter, the DOC concentration was 6.6 mg/l, the pH value 7.4. There are no large size plants on the banks of the canal therefore the surface of the water is not shaded; this circumstance and the plant nutrients washed in from the catchment area promote the multiplication of water-weeds. These plants have a favourable effect on the quality of water, but when accumulating around the bridges at the time of floods they reduce the water-delivery of the canal and jeopardize therefore the basic function of the drainage system.

D) LAS SALINAS

The Laguna la Churrosa (Fig. 1, station 21) is surrounded by the community of black mangrove (*Batidi-Avicennietum nitidae*) while in its salty water populations of *Ruppia maritima* form community. The water is 50–60 cm deep, yellowish brown and transparent to the bottom; the oxygen saturation was about 80 per cent, the water temperature 28 °C, the pH value 8.0 on 21 April 1983, and the value of DOC 25.5 mg/l.

On 21 April we carried out measuring at the inflow of a moorland canal, in the inner part of the Bahía de Cochinos between Buena Ventura and Caletón (Fig. 1, station 22). The water of the canal flowing out from the thick forest of red mangrove (*Rhizophora mangle*) was red-brown, very poor in oxygen, of 17 per cent saturation. The water temperature was as low as 25 °C, the pH value 6.9. The water was rich in organic matter, the DOC concentration was 21.5 mg/l.

The waters of the moorland flowing into the bay, in addition to carrying plant nutrients colour the coastal zone brown lessening thereby its attraction for the visitors at the holiday resorts, although the high humic matter content has no harmful effect on health.

E) CANAL DE SOPLILLAR

It is a canal system draining off the water of the rice fields adjacent to the Laguna del Tesoro, delivering a part of it to the lake and another part to the Pig Bay. Measuring was carried out on this area on 20 April 1983, between 4 and 7 p.m.

Station 23 (Fig. 1) is found at a sector of the canal past the rice fields, after which the canal branches off. One of the branches leads to the Laguna del Tesoro, the other towards the sea. In this sector of the wide, open canal system there is no considerable macrophyte vegetation, the transparency of the water is low — 30–40 cm —, because the lift-pumps carry muddy water from the rice fields. The water is rich in dissolved organic matter too, we obtained 21.5 mg/l for the value of DOC. The surface of water is not shaded, but because of the high turbidity there is no considerable oxygen production and decomposing processes prevail in the water. The temperature of the water was 26 °C, its oxygen saturation 84 per cent on the surface and 39 per cent near the bottom, at a depth of 3 m. The pH value was relatively high: 7.8.

At its middle sector the canal grows wider (Fig. 1, station 24); its maximum depth is 1.25 m. Streaming water is only found in a narrow strip in the middle of the canal, in other parts the water is stagnant. In the vicinity of the streamline completely closed *Potamogeton illinoensis* stands are seen which towards the banks are replaced by *Nymphaea ampla* and *Nuphar luteum* ssp. *grandiflorum* stands. The canal is bordered by bulrush. Round the bridge-columns local stonewort vegetation develops formed by populations of *Chara domingensis* and *Nitella hyalina*. In the streaming 27 °C water we measured 80 per cent oxygen saturation for the full column of water, and 7.8 for the value of pH. In the closed macrophyte stands by the side of the streaming water and in areas overgrown by stonewort self-shading was of such an extent that at a depth of 20–30 cm already anaerobic conditions prevailed.

The canal arrives at the bay as a subsurface water, before the coast it disappears in a cavern. Before disappearing (Fig. 1, station 25) the water seeps through large *Typha domingensis* stands; swift current of water is only found in a 5–10 m wide strip. Of the water-weeds *Chara domingensis*, *Potamogeton illinoensis*, *Hydrocotyle umbellata* and *Utricularia juncea* form minor stands. The streaming water is 1 m deep and transparent to the bottom. The water temperature was 27 °C, the oxygen saturation 80 per cent, the pH value 7.8 and the concentration of DOC 18.8 mg/l.

Summary

In the most important flowing- and still-waters of the Zapata Peninsula eutrophization manifests itself in the extreme multiplication of aquatic macrophytes. In comparison to the mass and production of water-weeds the biomass and production of the phytoplankton is negligible.

In an overwhelming proportion of the waters on the area in question thick plant stands are formed whose spreading is determined first of all by the light conditions. There are not aquatic macrophytes in these brown moorland waters where the light does not reach the bottom but is absorbed in the body of water, and where the rivers are shaded from above by a thick mangrove vegetation. The species composition and mass of the aquatic macrophyte vegetation are influenced by the physical characteristics of the bed too.

The water weeds occurring in the largest numbers in the Laguna del Tesoro are: *Vallisneria neotropicalis* and *Potamogeton illinoensis*; stands of the latter cover 60 per cent of the surface of the lake (Fig. 3), prevent to use the water for sport fishing and touristic purposes, and hinder the water transport. On 4–5 May 1983 the joint primary production of phytoplankton and macrophytes was 29.42 g O₂/m²/day in the open water. There was an oversaturation of oxygen on the surface, while near the bottom anaerobic conditions prevailed (Fig. 4a, b, c). The water-weed stands must by all means be reduced, this would check the siltation of the lake too.

In the water system of the Rio Negro and Rio Hatiguanico *Vallisneria neotropicalis* and *Potamogeton illinoensis* are the characteristic plants of the rivers and canals flowing through the moorland; their thick stands hinder the water transport and reduce the delivery capacity of the bed. On the surface oversaturation, while near the bottom saturation deficiency of oxygen is shown (Fig. 5a).

In the water system of the Canal de Soplillar the hydrobiological conditions are similar.

In the main branch of the Rio Negro few plant stands are found, the rocky bottom is not favourable for macrophytes to settle; the bottom is covered by a 20–30 cm thick *Chara* mat where oversaturation of oxygen develops while in other parts of the body of water saturation deficiency is shown (Fig. 5c, Fig. 6a).

In the lateral branches flowing through a thick mangrove vegetation there are not plants in the river bed, the oxygen saturation is everywhere below 100 per cent and in some cases anaerobic conditions occur (Fig. 5d, Fig. 7b).

The canals on the southern plain of Havanna Province rise on agricultural areas above the mangrove moorland bordering the coast and reach the sea by flowing through the mangrove moorland. The oxygen conditions in their water are highly varied. In the waters flowing in the mangrove thicket there is no considerable aquatic vegetation, here the water is poor in oxygen. On less shaded areas floating and rooting water-weeds form thick stands reducing the delivery capacity of the canals. In rooting weed stands the oxygen conditions are similar to those in the lake, while on areas overgrown by floating weeds shading makes the water poor in oxygen.

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UNTERSUCHUNGEN AN DIE WIRKUNG DER CHLORID-IONEN AUF GEHÖLZE IN BUDAPEST

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Einleitung

Auf die Verkehrssicherheit der Straßen im Winter verwendet man in Budapest große Menge von salzhaltigem Streumittel (im Winter 1977/78: 7-12 000 t NaCl, 4-5000 t Magnesiumlauge/MgCl₂) (TÖRÖK und KLINCSEK 1978; KOVÁCS et al. 1979, 1980).

In mehreren europäischen Städten wird eine der wichtigsten Ursachen der Baum Schäden und Baumverfall auf den Last, der aus dem winterlichen Streusalz stammende Cl⁻-Ionenakkumulation angeschrieben (STEULING und KIRSCHBAUM 1976, GLATZEL und KRAPPENBAUER 1975).

Wir wollten mit unseren Untersuchungen klarmachen, ob sich in den geschädigten (verfallenen) Bäumen von Budapest auch der aus Winterstreusalz stammende Cl⁻-Ionengehalt sich anhäuft?

Dabei haben wir auch sog. resistente Arten gesucht, die an der Belastung von Cl⁻-Ionen unempfindlich sind, die sich gut zur Stadtbäumung eignen. Wir haben den Cl⁻-Gehalt der aus den Stadtinnern sowie aus der Kontrollfläche (Vácrátót) gesammelten Blattmuster (zweite Hälfte des Sommers), nach einem Heißwasser-Aufschuß (HECKMANN 1965) mit einem ungarischen Chlorid-meßgerät (Radelkis OP 2/L) gemessen.

Ergebnisse

Die untersuchte Arten sind: *Acer platanoides*, *Aesculus hippocastanum*, *Ailanthus altissima*, *Celtis occidentalis*, *Platanus acerifolia*, *Robinia pseudoacacia*, *Tilia tomentosa*.

1. Für die Darstellung an Cl⁻-Belastung der Bäume sind die Blätter am besten verwendbar. — In den Blättern der widerstandsfähigen Baumarten, die keine sichtbare Schäden aufzeigen, findet man wenig Cl⁻-Ionengehalt, was einerseits mit den tiefen Wurzeln (*Robinia*), anderseits mit der selektiven Ionenaufnahme (*Celtis*) zu erklären ist.

Mäßig widerstandsfähige Arten: an der Belastung des Cl⁻-Ions, schon in der Vegetationszeit (Ende Sommer, Herbst) werden die Blätter vergilben, — meist am Rande vertrocknen. Ihr Cl⁻-Ionengehalt wird auf die Belastung ziemlich erhöht (Tab. 1) solche Art ist z. B.: *Platanus acerifolia*.

Tabelle 1

Cl⁻-Ionengehalt der Blätter (auf Trockensubstanz %) von Stadtbäume in Budapest und im Kontrollgebiet (n = 5)

Taxon	Budapest				Vácrátót		
	1979	1980	1981	1982	1979	1980	1981
<i>Acer platanoides</i>	—	0,93*	—	1,07*	0,52	0,20	—
<i>Aesculus hippocastanum</i>	1,9*	0,87*	1,93*	—	0,37	0,13	0,17
<i>Ailanthus altissima</i>	—	0,38	—	—	—	0,15	—
<i>Celtis occidentalis</i>	0,24	0,06	0,10	—	0,12	0,03	0,04
<i>Platanus acerifolia</i>	1,41	—	—	—	0,33	—	—
<i>Robinia pseudoacacia</i>	—	0,20	—	0,40	0,21	0,07	—
<i>Tilia tomentosa</i>	2,85*	1,04*	1,73*	0,83*	0,11–0,14	0,05	0,11

* = sichtbare Nekrosen

Tabelle 2

Cl⁻-Ionengehalt der Baumblättern in verschiedenen Kronenschichten (in %, TS)

	<i>Celtis occidentalis</i>	<i>Platanus* acerifolia</i>	<i>Tilia tomentosa</i>
Gipfel	0,57	4,98	4,57
Mitte der Baumkrone	0,75	5,01	—
Untere Schicht der Baumkrone	0,88	5,78	4,43

* Zwischen den einzelnen Schichten sind minimum 2 m. Entfernung.

In den Blättern der stark salzempfindlichen Arten wird der Cl⁻-Ionengehalt ziemlich angehäuft, und schon am ersten drittel der Vegetationszeit wird die Blattnekrose sichtbar; manchmal fallen die Blätter ab und der Baum treibt wider aus. Im Folge des Not austriebes werden die Bäume schwach und früher oder später sterben sie ab. Empfindliche Arten sind: *Acer platanoides*, *Aesculus hippocastanum*, *Tilia tomentosa*.

Diese Arten werden schon bei 0,6–1% Cl⁻-Gehalt (in der Blätter gemessen) stark geschädigt.

2. Im Stadttinnern gesammelte Blätter, wo der Verkehr am größten ist (bei allen Arten) kann eine ziemlich große Menge an Cl⁻-Ionengehalt gemessen werden, viel größer, als in den Blättern der Kontrollbäume (Tab. 1) — obwohl die Angaben bei verschiedenen Jahren, je der Maße der Salzbelastung voneinander abweichen.
3. Auch in den Blättern der Straßenbäume — aus dem verkehrsreicheren Stadttinnern werden größere Cl⁻-Gehalte gemessen, als in den Blättern der Straßenbäume wo weniger Verkehr herrscht (Außenstadt) — (Tab. 1, Abb. 1).

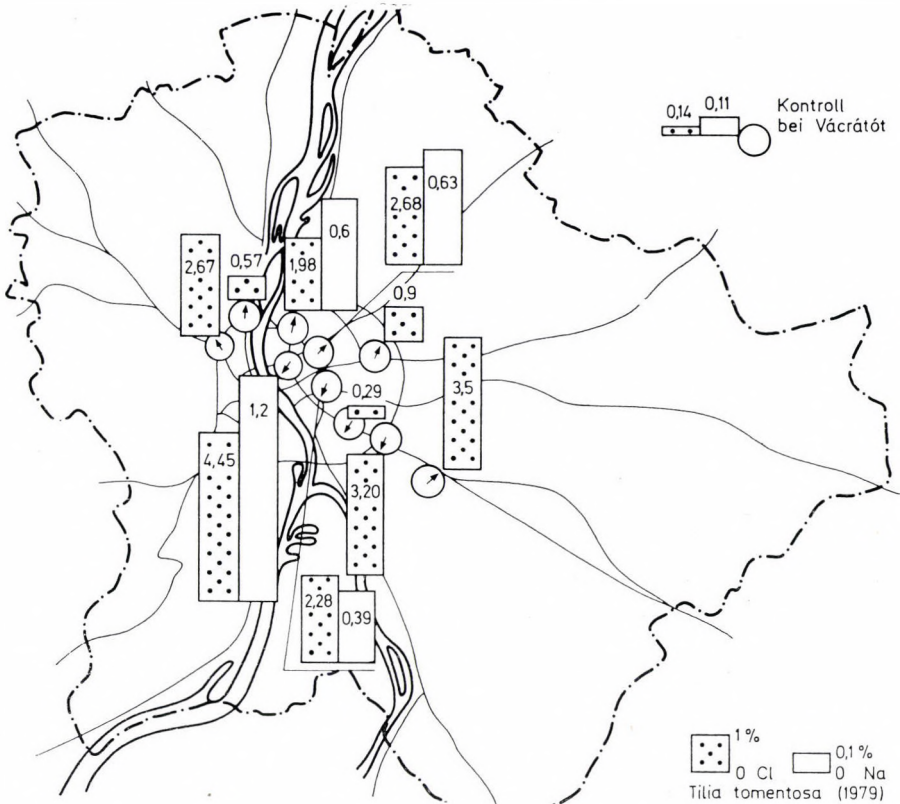


Abb. 1. Salzbelastungskarte in Budapest aufgrund des Chlorid-Ionengehaltes der Blätter von *Tilia tomentosa* 1979

4. Auf Grund der Untersuchung der Blattprobenahme von verschiedenen Kronenschichten wird festgestellt, daß zwischen den Cl^- -Gehalt der Probeentnahme aus dem Gipfel, mittlere Schicht der Baumkrone, wie aus der unteren Schicht der Baumkrone, kann keine signifikante Differenz festgestellt werden (Tab. 2), d. h. darinnen sind bald die gleichen Cl^- -Ionengehalt nachweisbar.
5. Auch die verschiedenen Organe der Bäume enthalten verschiedene Mengen von Cl^- -Gehalt. Der größte Cl^- -Gehalt ist in den Blättern (0,07–5,26%), weniger werden in den Trieben und Ruten (0,26–0,99%) gemessen. Am wenigsten Cl^- -Ionengehalt — abhängig vom Jahrgang und Baumart — ist im Stamm und in der Rinde (0,01–0,37%). Auch die Wurzeln enthalten wenig Cl^- -Ionen, doch etwas mehr, als der im Stamm (0,036%) (Abb. 2 und Tab. 3).
6. Der Cl^- -Gehalt der Blätter bei den untersuchten Arten aus streusalzfreien Gebieten vom Herbst bis zum Laubfall wird stufenweise wachsen (Abb. 3). An streusalz-belasteten Gebieten sind die Blätter der empfindlichen Arten

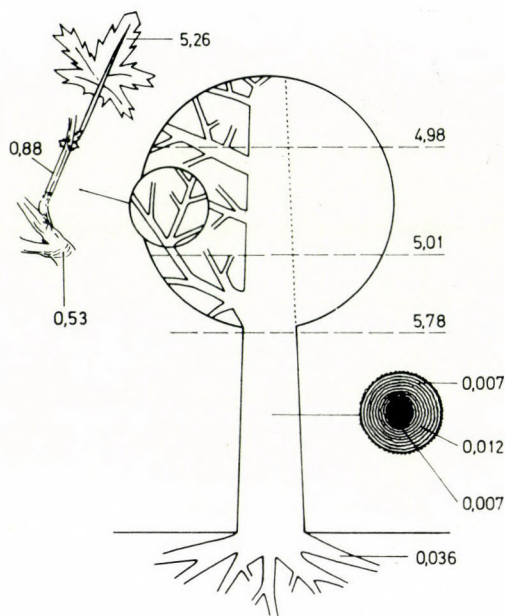


Abb. 2. Gehalt an Chlorid-Ionen (TS) in den verschiedenen Organen und in den Blättern von verschiedenen Kronenschichten des Baumes: *Platanus acerifolia* 1977

(*Tilia*, *Aesculus*) beim Austrieb (Frühling) hoch an Cl^- -Gehalt; das erhöht während des Sommers weiter, und am Ende der Vegetation absinkt (aber es bleibt noch immer an relativ höherem Niveau) (Abb. 4).

In den Blättern der unempfindlicher Gattung *Celtis*, ist die Veränderung an Cl^- -Ionengehalt ähnlich sowohl in salzbelasteten, als auch in

Tabelle 3

Cl^- -Ionengehalt der verschiedenen Baumorganen (auf Trockensubstanz %, $n = 5$)

Organum	Jahr	<i>Acer platanoides</i>	<i>Celtis occidentalis</i>	<i>Platanus acerifolia</i>	<i>Populus sp.</i>	<i>Robinia pseudoacacia</i>	<i>Tilia tomentosa</i>
Blätter	1977	—	0,079	5,26	—	—	4,49
Blätter	1979	—	—	1,01	—	—	—
Blätter	1980	0,93	—	—	—	0,20	1,04
Triebe	1977	—	0,26	0,86	—	—	0,99
Ruten und Äste	1977	—	0,21	0,53	—	—	0,79
Stamm Rinde	1979	0,03	—	—	—	0,012–0,018	0,024
Holz	1979	0,02	—	0,007	0,22	0,011–0,016	0,013
Holz	1974/75	0,02	—	0,012	0,24	0,011–0,015	0,011
Holz	1970	—	—	0,007	0,37	0,10 –0,016	—
Wurzel	1979	—	—	0,036	—	—	—

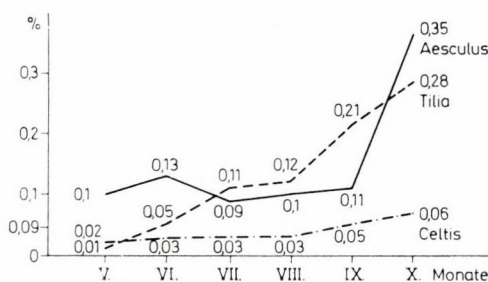


Abb. 3. Die Veränderung des Chlorid-Ionengehaltes in den Blättern (in %, TS) im Laufe der Vegetationszeit auf salzfreiem (kontroll-)Gebiet (Vácrátót) 1980

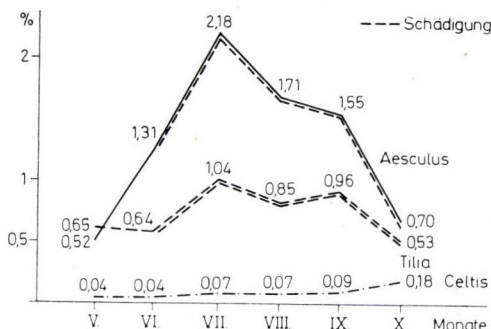


Abb. 4. Die Veränderung des Chlorid-Ionengehaltes in den Blättern von Straßenbäume aus dem Stadtkern Budapest, im Laufe der Vegetationszeit 1980

Kontrollgebieten; d. h. der Cl^- -Gehalt der Blätter erhöht sich am Ende der Vegetationsperiode gleichmäßig.

Für die Anwendung, als Straßenbäume wo winterlicher Streusalz regelmäßig verwendet wird, sind die folgende Arten zu empfehlen: *Ailanthus altissima*, *Celtis occidentalis*, *Robinia pseudoacacia*.

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GENETIC DISTANCES, I.

GENETIC DISTANCE IN THEORY AND PRACTICE

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In this paper the present state of the genetic distance theory is reviewed. Several genetic distance measures are presented in a graceful layout using vector spaces.

Two different models of measuring genetic distances are treated. (i) In the first model $x(a) \in R_+^n$ where $x^i(a)$ represents a measurement of some metric trait. Here the genetic statistics is due to the usual gene-phene dispersion. (ii) In the second model $p(a) \in \Delta$, the allele simplex. No statistics are involved here (except possibly in estimating $p(a)$ of the population from a sample).

In the paper we discuss vector space and the inner product structure on R^n . Then we introduce both models (i) and (ii). Finally, genetic distance measures are presented in a unique manner based on vector spaces, and the connection between them is also discussed.

Introductory notes

The problem of measuring genetic distances between populations has been crucial to an understanding of evolutionary processes for many years. It has occupied several theoretical and experimental investigators.

In the (mathematical) models of evolution we have studied what conditions would lead to changes in the genetic structures of populations. So far very little attention has been paid to the study of data from natural populations. If we study the process of evolution as a result of various combinations of selection, mutation, recombination, random drift, migration, and nonrandom mating, we must agree some convenient way to measure the amount of evolution. One of suitable approaches is the study of genetic distances between populations. This tells us what changes have taken place in the genetic composition of the examined population.

The problem of finding an efficient measure of genetic distance and several others of theoretical importance were discussed by CAVALLI-SFORZA and EDWARDS 1967, JACQUARD 1974, NEI 1976, ROGERS 1972. (See also: CROW and DENNISTON 1974, EDWARDS 1971, HEDRICK 1975, NEI 1975.)

The measure of genetic distance between populations is based on the number of codon differences per structural genic locus for proteins. In this case we consider how nucleotide frequencies can be used to define a genetic distance between populations (see EWENS 1979, NEI 1976, SPIESS 1977).

The most elementary distance measure, when there is no genetic variation within populations, is the number N of sites at which the prevailing nucleotides in the two populations differ; FITCH and MARGOLASH 1967, EWENS 1979.

It is the simplest measure of genetic distance. There are more complicated models. Some mathematical preliminaries are given before discussing these models.

Vector spaces

Let R denote the field of real numbers. A vector space V over R is a set V together with two operations

$$V \times V \rightarrow V, (v, w) \mapsto v + w$$

$$R \times V \rightarrow V, (a, v) \mapsto av$$

satisfying the following axioms:

1. $v + w = w + v$
2. $(v + w) + x = v + (w + x)$
3. there is a vector $0 \in V$ such that $0 + v = v$
4. for each $v \in V$, there is a vector $-v \in V$ such that $v + (-v) = 0$
5. $a(v + w) = av + aw$
6. $(a + b)v = av + bv$
7. $(ab)v = a(bv)$
8. $1v = v$

for all $v, w, x \in V$, $a, b \in R$.

The linear combination of the vectors $v^1, \dots, v^n \in V$ is

$$a^1 v^1 + \dots + a^n v^n = 0$$

implies $a^1 = \dots = a^n = 0$. The vectors $v^1, \dots, v^n$ form a basis of V if they are linearly independent and spans V . It is easy to see that any other basis of V has the same number n of elements called the dimension of V .

If $a^1, \dots, a^n$ is a basis for V then the $(a^1, \dots, a^n)$ scalars are called the coordinates of $v = \sum a^i v^i$ with respect to this basis. A different basis will in general give different lists of coordinates for the vector v .

The vector space is called Euclidean if there is a function (inner product)

$$(\cdot, \cdot): V \times V \rightarrow R$$

defined by the following axioms

9. $(x, x) > 0$ and $(x, x) = 0$ if and only if $x = 0$
10. $(x, y) = (y, x)$
11. $(ax + by, z) = a(x, z) + b(y, z)$

for all $x, y \in V$ and $a, b \in R$.

The norm or length of a vector defined by

$$\|v\| = (v, v)^{1/2}. \quad (1)$$

By analogy with the real numbers, the distance between v and w is defined to be the lengths of the difference, $\|v - w\| = \|w - v\|$. For any inner product on a vector space V

$$(v, w) = \|v\| \|w\| \cos \vartheta \quad (2)$$

where ϑ is the angle between the two vectors; so

$$\cos \vartheta = (v, w) / (\|v\| \|w\|). \quad (3)$$

The most important example is R^n , the set of ordered n -tuples of real numbers with coordinate-wise addition and multiplication

$$(v^1, \dots, v^n) + (w^1, \dots, w^n) = (v^1 + w^1, \dots, v^n + w^n)$$

$$t(v^1, \dots, v^n) = (tv^1, \dots, tv^n)$$

On the vector space R there is a so-called usual inner product

$$(v, w) = \sum v^i w^i. \quad (4)$$

Basic models

Model I

In general, let us consider a set of populations $P = \{P_a; a \in A\}$, each of which characterised by n non-negative numbers. For example, we can characterise a population by the number of individuals it contains, by gene frequencies at certain loci, or by the frequencies of certain phenotypes among the population members. Each observed quantitative characteristic will furnish a measure. This set of numbers can be considered as a vector $v(a)$ characterising an object

$$v(a) = (v^1(a), \dots, v^n(a))^T$$

where $A = \{a, b, c, \dots\}$ is an arbitrary index set. The set of all $v(a)$ vectors ($a \in A$) form a vector space.

Model II

The typical case for measuring genetic distance in the "classical" theory, when the objects in question are populations characterised by allele frequencies at a locus. In this case, each population is characterised by the $p^i(a)$ frequencies or probabilities. The set of vectors $p^i(a)$ constitutes a space bounded by the conditions

$$\left. \begin{array}{l} p^i(a) \geq 0 \text{ for all } i \\ \sum_i p^i(a) = 1 \end{array} \right\} \text{ for all } a \in A. \quad (5)$$

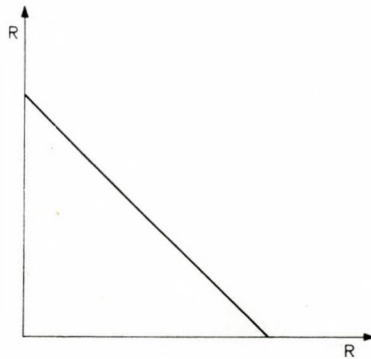


Fig. 1. A simplex when $n = 2$ is a segment of a straight line

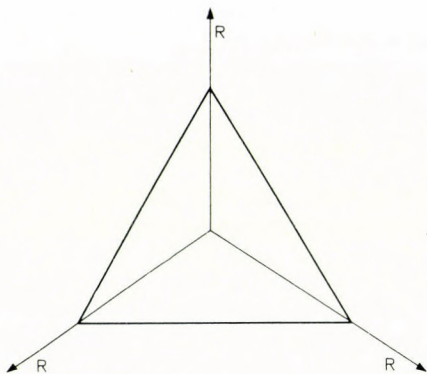


Fig. 2. A simplex when $n = 3$ is a triangle

From geometrical point of view the space bounded by the conditions (5) is a simplex. So, the distribution of the examined genetic trait is a p vector in the simplex

$$\Delta = \{p : R^n; p^i \geq 0 \text{ and } \sum p^i = 1\}. \quad (6)$$

Here, and hereafter we denote by p a general element of Δ notwithstanding $p(a)$, $a \in A$.

In the case when $n = 2$, the simplex is a segment of a straight line situated in the first quadrant (Fig. 1); when $n = 3$, the simplex is a triangle (Fig. 2); when $n = 4$, the simplex is a tetrahedron, etc.

GENETIC DISTANCES

The Mahalanobis' distance

Let us consider a Euclidean space with orthogonal coordinate axes having no difference in scale. The distance, D , between two points, $x(a)$ and $x(b)$, can be determined using the PYTHAGORAS' theorem

$$D = \|x(a) - x(b)\| \quad (7)$$

or

$$D^2 = (x(a) - x(b))^T (x(a) - x(b)) \quad (8)$$

The above geometrical conditions can be translated into statistical language: They are of equal-scale when the diagonal elements of the variance-covariance matrix are units, and they are orthogonal when variables are uncorrelated, i.e. the variance-covariance matrix is a diagonal matrix.

After the transformation of the above conditions to statistical language, they are satisfied when the variance-covariance matrix is a unit matrix

$$E[(x^i(a) - \bar{x}(a))(x^j(a) - \bar{x}(a))^T] = I. \quad (9)$$

It can be shown that, if $\text{Var}(\mathbf{x}(a) - \overline{\mathbf{x}(a)}) = \mathbf{S} (\neq \mathbf{I})$, there is such a matrix, $\mathbf{A}$, that

$$\mathbf{A}\mathbf{S}\mathbf{A}^T = \mathbf{I}.$$

From this follows that

$$D^2 = ((\mathbf{x}(a) - \mathbf{x}(b))^T \mathbf{S}^{-1} (\mathbf{x}(a) - \mathbf{x}(b))). \quad (10)$$

It is widely known as the MAHALANOBIS distance (MAHALANOBIS 1936, JACQUARD 1974). Originally it was conceived for the purpose of data discrimination (MAHALANOBIS 1936).

In that special case when the variables are uncorrelated the variance-covariance matrix $\mathbf{S}$ is a diagonal matrix of the form

$$\mathbf{S} = \begin{bmatrix} V_1 & \dots & \dots & 0 \\ \vdots & \ddots & & \vdots \\ \vdots & & V_i & \vdots \\ \vdots & & \vdots & \ddots \\ 0 & \dots & \dots & V_n \end{bmatrix}$$

In this case

$$D^2 = \sum_i \frac{(x^i(a) - x^i(b))^2}{V_i}$$

In this special case the D^2 distance is equivalent to the PEARSON's Coefficient of Racial Likeness (PEARSON 1926). When the variance-covariance matrix $\mathbf{S}$ is a unit matrix the distance D^2 coincides with the Euclidean distance.

The χ^2 distance

The χ^2 distance between populations is based on the following principles (JACQUARD 1974):

1. Let us give a greater weight to a difference

$$(p^i(a) - p^i(b))$$

between the frequencies of the i -th character if it is rare.

2. If two characters are in the same proportion to one another in all the populations let us replace the two characters by a single character.

The χ^2 distance

$$\chi_{ij}^2 = \frac{(p^i(a) - p^i(b))^2}{M_i} \quad (11)$$

satisfies these conditions, where M_i is the mean frequency.

Similarity indices proposed by Nei

NEI (1972) proposed a measure of genetic similarity (I_N) defined by

$$I_N = \frac{\sum p^i(a) \cdot p^i(b)}{\sqrt{\sum (p^i(a))^2 \cdot \sum (p^i(b))^2}}, \quad (12)$$

where $p^i(a)$ and $p^i(b)$ denote the frequencies of the allele A at a locus in the two populations P_a and P_b . This measure was developed to estimate the divergence time between closely related species in the supposition of neutrality to selection.

The genetic distance (D) is, simply, the complement of the similarity

$$D_N = 1 - I_N.$$

This index of similarity proposed by NEI is the angle between the vectors $p(a)$ and $p(b)$. Or, in statistical terms, it is the correlation coefficient of measurements $p(a)$ and $p(b)$. So

$$D_N = 1 - \cos(p(a), p(b)). \quad (13)$$

NEI's measure of standard genetic distance is

$$D = -\log_e I_N.$$

The genetic distance proposed by Powell, Levene and Dobzhansky

POWELL, LEVENE, and DOBZHANSKY (1972) proposed a genetic distance measure defined for the case of chromosomal polymorphism in populations of *Drosophila pseudoobscura*:

$$D_E = \frac{\|p(a) - p(b)\|}{2} \quad (14)$$

where $\|\cdot\|$ is the Euclidean norm, $p(a)$ is the frequency of the i -th allele in P_a and $p(b)$ is the frequency of the i -th allele in P_b .

D_E is a simple Euclidean distance.

Hedrick's measure

An index of genetic similarity proposed by HEDRICK (1971, 1975) is based on genotype frequencies rather than allelic frequencies

$$I_H = \frac{\sum p^i(a) \cdot p^i(b)}{\frac{1}{2} [\sum (p^i(a))^2 + \sum (p^i(b))^2]}, \quad (15)$$

where $p^i(a)$ = genotype frequency in P_a population, and $p^i(b)$ = genotype frequency in P_b population.

Sneath's index of genetic similarity

An index of genetic similarity was proposed by SNEATH (SOKAL and SNEATH 1963):

$$I_S = \frac{1}{L} \sum_{i=1}^k \sum_{j=1}^L p^{ij}(a) p^{ij}(b) \quad (16)$$

where L is the total number of loci; $p^{ij}(a)$ and $p^{ij}(b)$ are corresponding frequencies of the j -th allele in P_a and P_b locus. The genetic distance is defined evidently by

$$D_S = 1 - I_S.$$

The arc measure of Cavalli-Sforza and Edwards

In the vector space R^n a possible measure of difference ("distance") between vectors $p(a)$ and $p(b)$ is the angle between them. (It is evident that the other possible distance originates from the scalar product of the vector space.) This measure has the disadvantage that it changes nonlinearly.

Let us consider the

$$\pi: R_+^n \rightarrow R_+^n, p^i \mapsto 2\sqrt{p^i} = \pi^i$$

transformation (see Fig. 3).

The map

$$p: R^n \rightarrow R_+^n \cup \{0\}, \pi^i \mapsto (\pi^i)^2/4 = p^i$$

admits a smooth inverse on R_+^n defined by

$$\pi: R_+^n \rightarrow R_+^n, p^i \mapsto 2\sqrt{p^i} = \pi^i.$$

After the transformation the angle between the two vectors $\pi(a)$ and $\pi(b)$ is

$$\cos \alpha = \sum_i \pi^i(a) \pi^i(b). \quad (17)$$

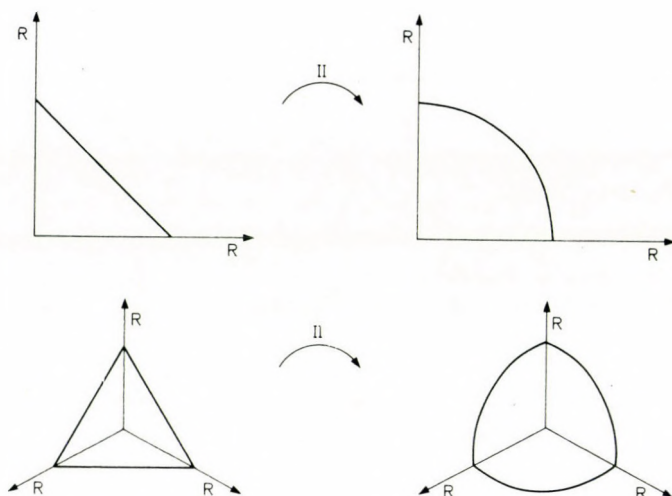


Fig. 3. The $\pi: R_+^n \rightarrow R_+^n$, $p \mapsto 2/\sqrt{p^i}$ transformation when $n = 2$ and $n = 3$, respectively

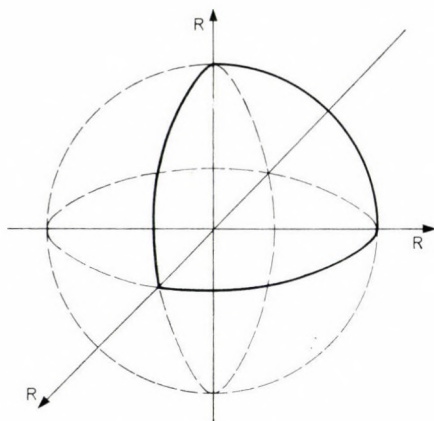


Fig. 4. The transformation π transforms every simplex into the $(1/2)^n$ portion of sphere of radius two in n -dimensional space

That is

$$\alpha = \cos^{-1}(\sum \pi^i(a) \pi^i(b)) = \arccos(\sum \pi^i(a) \pi^i(b)). \quad (18)$$

This is the CAVALLI-SFORZA and EDWARDS measure of distance. The angle varies between 0 and $\pi/2$, and the problem of nonlinear scale has been overcome (CAVALLI-SFORZA and EDWARDS 1967, JACQUARD 1974, KEMPTHORNE 1969).

The above transformation, π , transforms every Δ simplex into the $(1/2)^n$ portion of sphere of radius two in n -dimensional space (into the zone in which the coordinates are positive); see Fig. 4.

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GENETIC DISTANCES, II.

NEW TREATMENT OF AN OLD PARADIGM

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This paper provides an exact stochastic Riemannian geometric treatment of genetic distance theory.

Consider a set of populations where each population is characterised by a density function $f(x, a)$, where x is a metric character which we think of as a real valued function of the zygotic genotype. A method for measuring distances between distributions of a parametric family is proposed.

Evolutionary and environmental conservation interpretation of results in actual situations is given. Some ideas about genetic diversity, insular populations and the speed of evolutionary change are also treated.

Introduction and the outline of paradigm

Population genetics and evolutionary theory occupy a central position in a variety of biological disciplines. Modern population genetics embraces empirical observational and experimental and theoretical components (cf. CROW and KIMURA 1970, EWENS 1979, and LI 1955).

In population genetics theory, the concept of genetic distance has an important place because of theoretical and practical significance. In macroevolutionary theory one of the most useful applications of genetic distance is the construction of phylogenetic trees (EWENS 1979, FELSENSTEIN 1982, FITCH and MARGOLISH 1967, JACQUARD 1974). In microevolutionary studies the genetic distance is used to study the speed of evolutionary changes. It is important to emphasize that increase in genetic distance between populations indicates more ancient evolutionary divergence. The study of the genetic distances between different populations of the same species (or between the characteristics of the same population measured at different times) should tell us what evolutionary changes have taken place in the genetic composition of the species.

In this paper consider how distributions of a metric trait (which is genetically uniquely determined) can be used to define a genetic distance between populations. It is assumed that the genetic distance is calculated from a sample of individuals of different populations and is based on the distributions of a genetic trait. Our main purpose is that this distance should provide a measure of the tendency and intensity for evolutionary change.

This paper is about genetic distance theory. We give an exact stochastic Riemannian geometric foundation and treatment of genetic distance.

There is a large literature on genetic distance theory (see CAVALLI-SFORZA and EDWARDS 1967, NEI 1972, NEI 1975, CROW and DENNISTON 1974).

The biomathematical model

1.1. OUTLINE OF THE MODEL

There is an extensive literature on the measures of distance between populations. The distance measures used can be grouped broadly into two categories:

- (i) Measures based on ideas from information theory.
- (ii) Measures related to the geometrical concept of distance.

A wide variety of measures of the distance type have been used e.g. in multivariate analysis (see, e.g., ANDERBERG 1973, GOWER 1967, MARDIA et al. 1979, ORLÓCI 1978, SOKAL and SNEATH 1973). In this paper we consider a method for measuring distances between distributions of a parametric family. The measure is based on a metric of a Riemannian geometry. The formalized model is the following.

Consider a set of populations $P = \{P_a; a \in A\}$, where the individuals of each population are characterised by a metric character x which we think of, from genetic point of view, as a real valued function of the zygotic genotype. Let, further, $S = \{f(x, a); a \in A\}$ be a family of probability density functions.

So the usual statistical functions are defined as follows:

$$\bar{x} = \int x f(x, a) dx,$$

$$\text{Var}(x) = \int (x - \bar{x})^2 f(x, a) dx$$

cf. KULLBACK 1959 and SCHMETTERER 1966).

1.2. STOCHASTIC RIEMANNIAN GEOMETRY I.

The methods of differential geometry have been applied to mathematical statistics for a considerable time (see FISHER 1921, MAHALANOBIS 1936, RAO 1949, KULLBACK and LEIBLER 1950, CHENTSOV 1964). These are based on FISHER's information matrix (interpretable as a Riemannian metric tensor), on KULLBACK's asymmetric information distance, and on CHENTSOV's probabilistic affine connection.

From mathematical point of view let us consider a family $S = \{f(x, a); a \in A\}$ of probability densities $f(x, a)$ on a measurable space $(X, \mathcal{A})$, parametrized smoothly by a vector parameter $a \in A$, with respect to some carrier σ -finite measure on a σ -algebra of the subsets of the sample space X . $(X, \mathcal{A}, P = \{P_a; a \in A\})$ is said to be a statistical space. A distribution is specified by a set of n real parameters $a = (a^1, \dots, a^n)$. Then we can construct an n -dimensional space S of distributions with a coordinate systems $a = (a^1, \dots, a^n)$. We assume that $f(x, a)$ is defined for a belonging to an open subset A of n -dimensional Euclidean space $\mathbb{R}^n$.

Let $T_a S$ be the tangent space of S at a . Let e_i ($i = 1, \dots, n$) be the natural basis of $T_a S$ associated with the coordinate systems. Then

$$da = \sum_{i=1}^n da^i e_i$$

in the tangent space $T_a S$.

Let $\mathcal{L}(x, a) = \log f(x, a)$. Since each point of S carries a function $\mathcal{L}(x, a)$ of x , it is natural to regard $e_i(a)$ at a as representing the function

$$e_i(a) = \partial_i \mathcal{L}(x, a),$$

where ∂_i is the abbreviation for the partial derivative with regard to a_i , $\partial_i = \partial/\partial a^i$.

Then a metric is defined in S by the tensor

$$g_{ij}(a) = E\{\partial_i \mathcal{L}(x, a) \partial_j \mathcal{L}(x, a)\}, \quad (1)$$

where E denotes the expectation with respect to $f(x, a)$ (see AMARI 1982a and b). The tensor $g_{ij}(a)$ is a covariant tensor of second order and is called the Riemannian metric tensor. As it is well known, (1) is nothing other than the FISHER's information matrix (at a); KULLBACK 1959.

In order that $g_{ij}(a)$ is well defined and that g_{ij} is positive definite (or e_i 's are linearly independent), we need some regularity conditions. Namely, that S is a smooth submanifold in a full, regular, minimally represented exponential family (BARNDORFF-NIELSEN 1980 and AMARI 1982a).

In this manner we endow the space S with the quadratic differential metric

$$(ds)^2 = \sum_{i,j=1}^n g_{ij}(a) da^i da^j. \quad (2)$$

We hereafter use the EINSTEIN's summation convention so that the summation is automatically taken for those indices that appear twice in one term once as subscript and once as superscript (unless the contrary is stated). Thus, $\alpha_i x^i$ means $\sum_{i=1}^n \alpha_i x^i$, where $n = \dim S$.

The expression (2) is a measure of infinitesimal distance between two probability distributions close to each other and the distance defined by it may be useful in (micro)evolutionary studies where gradual change takes place in the distribution of a genetic trait for a population in moving from state a to b .

Let us consider a full, minimally represented exponential family written in the form

$$f(x, a) = \exp \{a^i x_i - \psi(a)\}. \quad (3)$$

The metric tensor is easily calculated as the expected value of $\psi(a)$:

$$E(x_i) = \partial_i \psi(a),$$

and

$$g_{ij}(a) = \partial_i \partial_j \psi(a)$$

is the metric tensor of the space of probability distributions [type (3)] (AMARI 1982a and b).

Let us consider an example, where the distribution of the examined trait is normal distribution $N(m, s^2)$. The family of one-dimensional normal distributions $N(m, s^2)$ is specified by two parameters, the mean m , and the variance s^2 . The density function is

$$f(x; m, s^2) = \frac{1}{s\sqrt{2\pi}} \exp \left\{ -\frac{(x - m)^2}{2s^2} \right\},$$

Let us introduce the natural parameters

$$a^1 = \frac{m}{s^2}, \quad a^2 = -\frac{1}{2s^2}$$

and a vector defined by

$$x_1 = x, \quad x_2 = x^2.$$

Then we have

$$f(x, a) = \exp \{a^i x_i - \psi(a)\},$$

where

$$\psi(a) = -\frac{(a^1)^2}{4a^2} - \frac{1}{2} \log(-a^2) + \frac{1}{2} \log \pi.$$

So the metric tensor

$$g_{ij}(a) = \partial_i \partial_j \psi = \begin{pmatrix} s^2 & 2ms^2 \\ 2ms^2 & 4m^2s^2 + 2s^2 \end{pmatrix}$$

and the

$$ds = (g_{ij}(a) da^i da^j)^{1/2}$$

(infinitesimal) distance represent a measure of distance between distributions $f(x, a)$ and $f(x, a + da)$.

1.3. STOCHASTIC RIEMANNIAN GEOMETRY II.

Let $a(t)$ be a smooth curve in S where t is a parameter. In Riemannian geometry the length of the smooth curve is $v(t): A \rightarrow \mathbb{R}$ from $v(t_1) = b$ to $v(t_2) = c$ is defined to be

$$s(b, c) = \int_{t_1}^{t_2} \left(g_{ij}(a) \frac{da^i}{dt} \frac{da^j}{dt} \right)^{1/2} dt$$

where $b, c \in A$ (SPIVAK 1965). The minimization of $s(b, c)$ over all smooth curves between two points b and c of S defines a metric. Hence the space of probability densities S , whose all members satisfy certain regularity conditions, is a metric space. Let us denote

$$d(b, c) = \min_a s(b, c) \quad (4)$$

The function

$$d: S \times S \rightarrow \mathbb{R}, (b, c) \mapsto d(b, c)$$

is called distance function and $d(b, c)$ is the distance between the two points b and c . The space (S, d) is called a metric space (see, e.g. KELLEY 1955).

(4) is the distance which Rao proposed as a measure of distance between distribution with parameters b and c ; RAO 1982.

A curve which achieves the shortest distance between two points is called a geodesic.

For example the straight line is geodesic in a Euclidean space. On the sphere geodesics are arcs of great circles (i.e. the intersection of the sphere with planes through zero).

Geodesics can be defined in the usual way either as extremals of the variational problem $\min \int ds$ or as curves with zero geodesic curvature. A geodesic is given (from variational point of view) as the solution of the EULER-LAGRANGE equations

$$\frac{d^2 a^i(t)}{dt^2} + \Gamma_{ij}^k \frac{da^i}{dt} \frac{da^j}{dt} = 0$$

where Γ_{ij}^k is the CHRISTOFFEL symbol of the second kind and is defined by

$$\Gamma_{ij}^k = \frac{1}{2} g^{km} (\partial_i g_{jm} + \partial_j g_{mi} - \partial_m g_{ij}).$$

The family of geodesics coincides with the family of integral curves of this system (SPIVAK 1965, STOKER 1969).

The geodesic is a natural extension of the notion of straight line in a Euclidean space. If $\Gamma_{ij}^k(a)$ vanishes identically, the EULER-LAGRANGE equation is linear by t : $a^i(t) = \alpha^i t + \beta^i$.

Biological examinations

2.1. A SIMPLE EXAMPLE

Consider a genetic trait of the P_a population at points of time t_1 and t_2 . Assume that the distribution of the examined genetic trait is normal. The distribution at t_1 and t_2 differ only in the means (see Fig. 1). The distance between distributions $N(m_1, s^2)$ and $N(m_2, s^2)$ is given by

$$d(m_1, m_2; s^2) = |m_1 - m_2|/s = \frac{|m_1 - m_2|}{s}$$

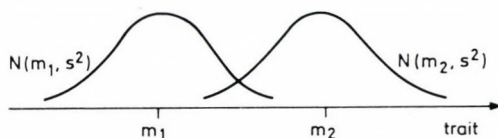


Fig. 1. The examined genetic trait is normally distributed and the distributions differ only in means

The EULER-LAGRANGE equations are in this case the following

$$\frac{dm_i}{dt} = 0, \quad i = 1, 2. \quad (5)$$

The solution of geodesic equation (5) is: $m_i(t) = \alpha^i t + \beta^i$. It is nothing other than the equation of the straight line in a Euclidean space.

The situation is less clear (from biological point of view) when the distributions do not differ in means but only in variances. The problem is most confused when the distributions differ in both means and variances.

The first case (when variance changes) is biologically very important because of the next interpretation.

2.2. A FEW IDEAS ABOUT GENETIC DIVERSITY

Genetic diversity is one of the central problems of population genetics and evolutionary theory and, also of environmental conservation (cf. MURRAY 1972 and VIDA 1978). There are numerous measures of diversity (see, e.g. RAO 1982). One of the best known function is the

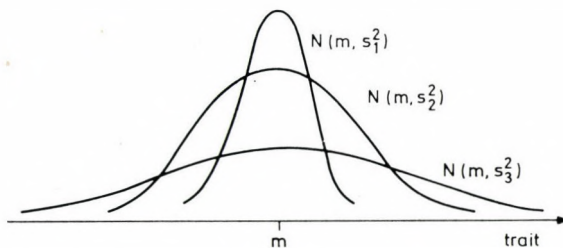


Fig. 2. How does genetic distance change when the mean is constant and only the genetic variability changes?

SHANNON-WEAVER's measure. However, there is a class of measures of information other than SHANNON's measure (cf. SCHÜTZENBERGER 1955). One member of this class is FISHER's information.

From this point of view the genetic diversity of one population with normally distributed genetic trait is $1/I$, where

$$I = \int_{-\infty}^{+\infty} \left(\frac{\partial \ln f(x, a)}{\partial a} \right)^2 f(x, a) dx$$

is the FISHER's information. Whereas (in this case)

$$f(x; m, s^2) = (V2\pi s)^{-1} \exp \left\{ -\frac{(x-m)^2}{V2\pi s} \right\} dx$$

So

$$I = \int_{-\infty}^{+\infty} \left(\frac{x-m}{s^2} \right)^2 (V2\pi s)^{-1} \exp \left[-\left(\frac{x-m}{2s} \right)^2 \right] dx = \frac{1}{s^2}$$

Thus, the genetic diversity of this population is s^2 .

The above question is: How does genetic distance change, when the mean is constant and only the genetic diversity changes? (It is assumed that the examined genetic trait is normally distributed.)

In this case the distance between the distributions $N(m, s_1^2)$ and $N(m, s_2^2)$ is given by

$$d(m; s_1^2, s_2^2) = \sqrt{2} |\ln(s_1/s_2)|$$

Reduction of this metric to one of a Euclidean space is impossible (cf. ATKINSON and MITCHELL 1982)! The geometry for the change of genetic variance is not Euclidean.

See the following examples.

(1) Let $s_1 = 0.11$ and the reduction of genetic diversity (variability) is 0.1 ($\Delta s = 0.1$). So $s_2 = 0.01$ and

$$d = 3.39$$

(2) Let $s_2 = 0.2$ and $s_1 = 0.1$. In this case

$$d = 0.98$$

(3) Let $s_1 = 1.1$ and $s_2 = 1.0$, so Δs is also 0.1.

$$d = 0.135$$

(4) Let $s_1 = 10.1$ and $s_2 = 10.0$

$$d = 0.014$$

(5) Let $s_1 = 100.1$ and $s_2 = 100.0$

$$d = 0.0014$$

The rates of changes for distances

$$d_1/d_2 = 3.5, \quad d_1/d_3 = 25, \quad d_1/d_4 = 242, \quad d_1/d_5 = 2421.$$

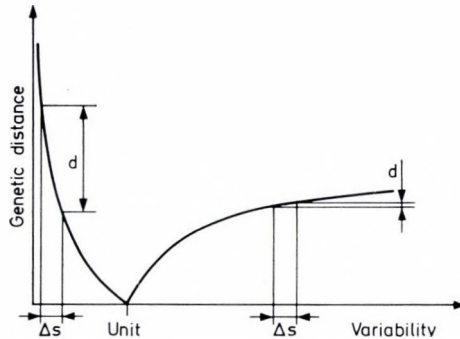


Fig. 3. "d" is the result of change, Δs , in genetic variability

The change of variability in each case is 0.1, but the genetic distance between $N(m, (s + 0.1)^2)$ and $N(m, s^2)$ is 2421 times larger in the first case (low variability) than in the case when the genetic variability of population is high (e.g. fifth case).

The result of change, Δs , in genetic variability is: when the genetic variability decreases in linear manner the genetic distance between $N(m, (s + \Delta s)^2)$ and $N(m, s^2)$ increases in $y = \sqrt{2} |\ln x|$ manner simultaneously (see Fig. 3). This fact has considerable consequences from two points of view.

(a) Interpretation from the point of view of environmental conservation. Probability of "degeneration" and extinction of population increases in $y = \sqrt{2} |\ln x|$ manner as a population variability decreases in linear manner. It means that environmental conservation (e.g. systems of gene banks) is fruitful if (and only if) the conserved countries have a large area.

(b) Evolutionary implications: In an island fauna or in an isolated population where the number of individuals and the genetic diversity of the population is low the evolution (of the population) is quicker than in a highly diverse population (and the population is more "vulnerable" too).

It is a well-known fact that the genetic variation diversity is underlying to evolutionary change. It implies the question: How is the level of variability (diversity) regulated in a population?

Genetic variation provides populations with evolutionary flexibility. However, individual variability can reduce the mean fitness when the individual carries the less fit variants in the gene pool of the population.

The question, how much genetic variation occurs in natural populations, is not easy to answer because variability cannot be measured readily. But we know that the detectable level of enzyme polymorphism (it is lower than the real) is high.

2.3. THE GENERAL CASE

The case when distributions of the family differing in both mean and variance is difficult. In this case the relevant distance is the following:

$$d(m_1, m_2, s_1^2, s_2^2) = \sqrt{2} \left| \int_{\varphi_2}^{\varphi_1} \frac{d\psi}{\sin \psi} \right| = \sqrt{2} \left| \log \frac{\tan(\psi_1/2)}{\tan(\psi_2/2)} \right|,$$

where

$$\psi_i = \sin^{-1}(s_i/\varrho) \quad i = 1, 2,$$

and

$$\varrho^2 = s_1 + [(m_1 - m_2)^2 - 2(s_1^2 - s_2^2)]^2 / [8(m_1 - m_2)^2],$$

where each ψ_i being taken to be the interval $\left(0, \frac{\pi}{2}\right)$ if $m_i \leq m_0$ and in $\left(\frac{\pi}{2}, \pi\right)$ if $m_i \geq m_0$ where

$$m_0 = \frac{1}{2} (m_1 + m_2) + (s_1^2 + s_2^2) / (m_1 - m_2)$$

(see ATKINSON and MITCHELL 1982).

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THE ULTRASTRUCTURE OF *AZOTOBACTER-CHLAMYDOMONAS* SYMBIOSIS

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Cells of cell-wall mutant and wild-type of *Chlamydomonas reinhardtii* were forced into association with nitrogen-fixing *Azotobacters* and were cultured on nitrogen and carbon free medium. The associated alga and *Azotobacter* cultures maintained for over two years showed that alga cells can support sufficient growth of *Azotobacters* and the alga cells retained their green colour and visible growth. The bacteria have been shown in the intercellular spaces and on the surface of the alga cells. The bacterium and alga cells can divide in symbioses as they do in pure cultures.

Introduction

Biological nitrogen fixation is one of the special and interesting phenomena in nature, because only certain prokaryotic micro-organisms have been shown to possess this ability, such as bacteria and blue green algae. These prokaryotes occur in so-called free-living forms e.g. aerobic *Azotobacters* or anaerobic *Clostridia*, or in associations with higher plants e.g. *Rhizobium* with legumes or *Azospirillum* spp. in rhizosphere of grasses. In the recent years many attempts have been made to find new sources of nitrogen fixation and to extend this ability to various non-leguminous species by establishing symbioses with nitrogen fixing organisms. Previous reports clearly demonstrated that nitrogenase activity could be induced in vitro in associations between *Rhizobium* and legume as well as non-legume tissue cultures (HOLSTEIN et al. 1971; CHILD 1975; SCOWECROFT and GIBSON 1975; RANGA RAO 1976) or between *Azospirillum brasilense* and sugarcane tissue cultures (VASIL et al. 1979; BERG et al. 1979; BERG et al. 1980). CARLSON and CHALEFF (1974a; 1974b) reported that callus cultures of carrot inoculated with *Azotobacter vinelandii* could grow on media lacking combined nitrogen, while uninoculated callus failed to grow in the same medium.

Azotobacter species have been shown to fix nitrogen in the free-living forms and were mixed with *Chlamydomonas reinhardtii* cells (GYURJÁN et al. 1984). In order to study the interaction of *Azotobacter* and higher plants, we have investigated the long-term relationship in forced associations between *Azotobacters* and alga cells. The ultrastructural aspects of this association are described in this paper.

Materials and methods

Azotobacter species: Species of *Azotobacters* such as *A. chroococcum*, *A. beijerinckii*, *A. agilis*, *A. vinelandii* were used in these experiments as we have written in a previous paper (GYURJÁN et al. 1984).



Fig. 1. Cells of wild-type and cell-wall mutant (cw15) of *Chlamydomonas reinhardtii*

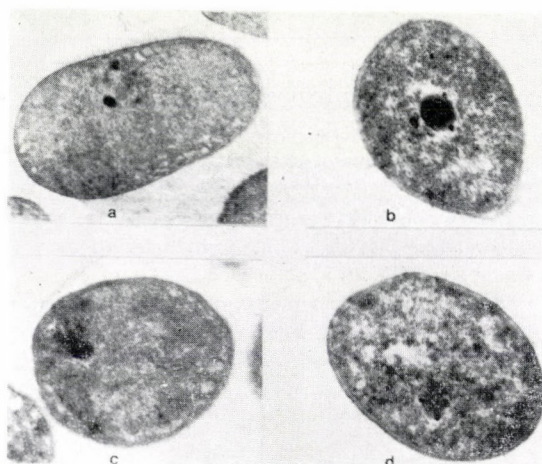


Fig. 2. Cells of *Azotobacters* — *A. chroococcum* (a) — *A. beijerinckii* (b) — *A. agilis* (c) — *A. vinelandii* (d)

Chlamydomonas reinhardtii: Wild-type and cell-wall mutants (cw15) of unicellular green alga, *Chlamydomonas reinhardtii* obtained from R. F. MATAGNE, Laboratory of Molecular Genetics, University of Liege, Belgium, were used.

Establishment of the associations: Cells of wild-type and cell-wall mutant of *Chlamydomonas reinhardtii* were forced into association with cells of strictly aerobic nitrogen fixing *Azotobacter* species and the alga-bacteria associated cultures have been maintained on a combined nitrogen and carbohydrate free medium since 1983.

Electron microscopy: Cells have been harvested and fixed in 1% glutaraldehyde (2 mM K—Na phosphate buffer, pH 7.2 for 2 h and post-fixed with 1% OsO_4 using the same puffer for 2 h. The samples were dehydrated in ethanol series and propylene oxid, then embedded in Durcupan ACM (Fluka). Thin sections were cut with a Porter-Blum MT-1 ultramicrotome, stained with uranyl acetate and lead citrate and then examined with a Tesla BS-500 electron microscope.

Results and discussion

The fine structure of original alga (wild-type and cell-wall mutant) and *Azotobacter* cells is shown in Fig. 1 and Fig. 2. Morphological forms of contact between bacteria and algae in symbiosis can be seen in Figs 3, 4 and 5. Figure 3 shows a total picture of symbiosis with many bacteria around the cell-wall mutant alga cell. Figure 4 shows one *Azotobacter* cell in contact with the membrane of alga cell and Fig. 5 shows bacterium cell between two alga cells.

Figure 6 shows the dividing bacteria beside the alga cells and in the intercellular space, suggesting that alga cells can support sufficient growth of *Azotobacters* in these associations.

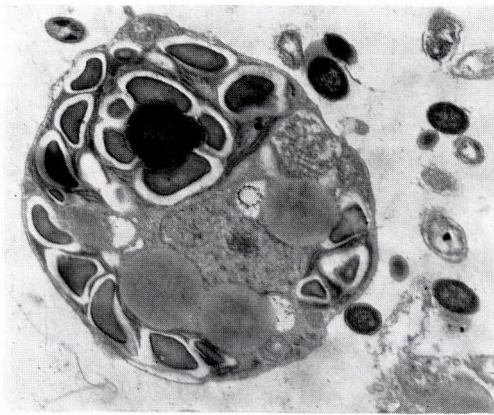


Fig. 3. cw15 alga cell with surrounding *Azotobacter* cells in forced association

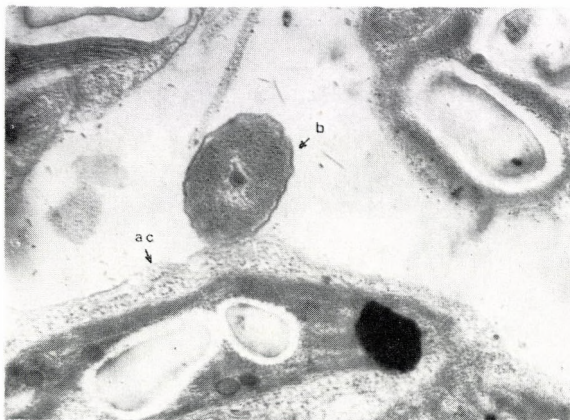


Fig. 4. Bacterium (b) on the surface of alga cell (ac)

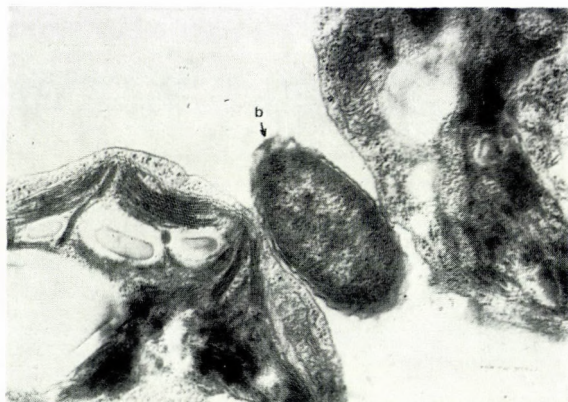


Fig. 5. Bacterium (b) between two alga cells

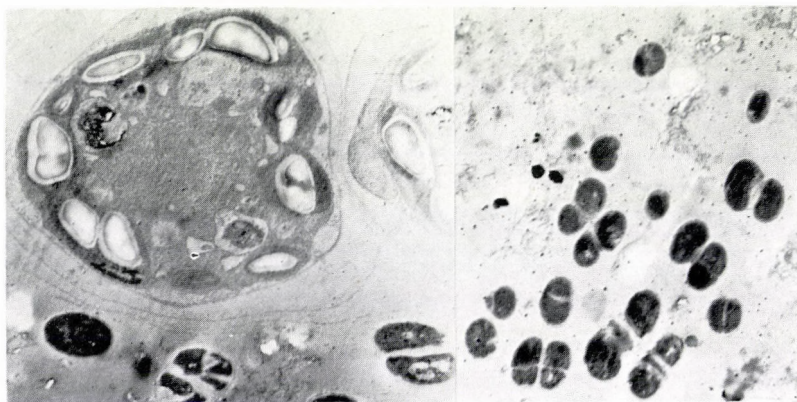


Fig. 6. Dividing *Azotobacter* cells beside the alga cells and in the intercellular space

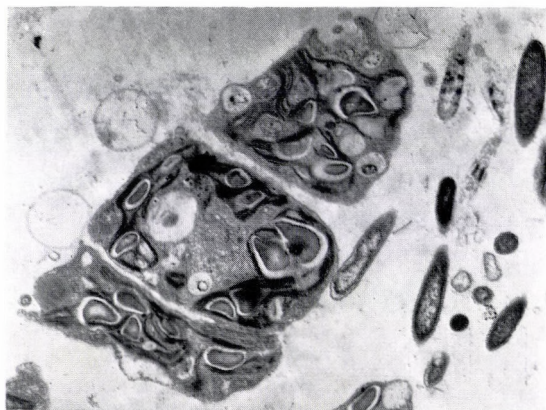


Fig. 7. Small alga cells after cell division

Figure 7 shows small alga cells after division into four daughter cells (tetrad), indicating that alga cell could get nitrogen from bacteria for their growth and development.

For three months we had always transferred *Azotobacter* cells associated with algae onto their own medium to check the presence and growth of bacteria and we always found abundant growth of them. In some associations when *Azotobacters* grew too quickly, they decreased effectively the growth of alga cells, but in most cases we found stable associations with sufficient growth and division of bacteria and algae. The best associations were maintained over two years and they retained their green colour and visible growth all the time. This fact allows us to suggest that algal cells in the association are photosynthetically active and *Azotobacters* can take up certain carbon compounds excreted by *Chlamydomonas* from the medium.

Algal glutamine synthetase activity was found to be high in symbiotic cultures (NGHIA et al. 1986), thus ammonia can readily built into *Chlamydomonas* cells. This assumption is supported by the results of several workers (NEWTON et al. 1953, KLEINER 1974, KARUBE et al. 1981) who demonstrated that nitrogen fixing *Azotobacters* are able to excrete ammonia and other nitrogenous compounds into the medium.

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CYTOLOGICAL INVESTIGATION OF *SCILLA BIFOLIA* POPULATIONS IN HUNGARY, II

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The authors give account of comparative cytological studies on 21 polyploid populations of the Hungarian *Scilla bifolia* species group, and of the first results of a cytogenetic evaluation. Of the populations 20 proved of tetraploid and 1 of hexaploid level. As to their karyotypes they show a greater variation than the diploids. It can be established that the species group forms in Hungary a polyploid complex with the following structure: $2n = 18-36-54$. However, certain phenomena like the conspicuously low DNA content of the hexaploid suggest a different line of evolution. In any case, natural hybridization is supposed to have played an important role in shaping up the present form of the complex. The karyotypes examined are highly diversified which confirms the results obtained with other methods (KERESZTY and PODANI 1985).

In the course of our cytological studies on the Hungarian populations of the *Scilla bifolia* species group we now give account of the karyotype analysis of polyploid populations and expound our view of the cytogenetic evaluation of the group. Previously we spoke of di-, tetra- and hexaploid populations of this species group as living on the area of Hungary (KERESZTY and SZILÁGYI 1984). We found the diploid populations in the Danube basin to be highly similar to each other both karyologically and morphologically, with a pair of SAT-chromosome as common feature. It became clear that this group was identical with the taxon described by Speta as *S. vindobonensis*. In populations living in the Transdanubian Middle Range we found karyograms basically corresponding to this group though as regards the arrangement of heterochromatin and size of chromosome still differing from it. Minor differences are shown again by the groups in Southern Hungary, in the mountains of Mecsek and Villányi. Diploid karyogram without demonstrable SAT-chromosome characterizes the populations to be found along the eastern frontier of the country; they even differ in outer morphological features from the former populations and on comparison proved identical with the *S. kladnii* Schur.

Higher diversity can be observed among the polyploid groups which even with biostatistical methods can be much better separated (KERESZTY and PODANI 1984). Present study serves for basic orientation concerning the variation of polyploid populations in Hungary.

Material and method

The preparation of the analyses, the condition and raising circumstances of the plants used, the composition of the living population sample collection, and the method of the cytological analysis were described in the first part (KERESZTY and SZILÁGYI 1984). Here we present the data of the polyploid populations used as grouped by chromosome number (Table 1). New data of Hungarian habitats are: Mátra-Gödörvölgy; Tarkő-alja; Berzence; Kisbajom.

We were first to identify a hexaploid stand in the Velence range of hills, near the village Nadap.

Table 1
Collecting data and chromosome numbers of the studied populations

Sample number	Village	Chromosome numbers	County	Geographical locality	Plant community	Altitude (m)
1.	Soponya	18	Fejér	Mezőföld, Fácános-forest	<i>Fraxino-Ulmetum</i>	130
2.	Nagyhideghegy	36	Pest	Börzsöny Mts.	<i>Aconito-Fagetum</i>	850
3.	Mátraháza	36	Heves	Kékes, Gödör valley	<i>Aconito-Fagetum</i>	700
4.	Somoskőújfalu	36	Nógrád	Karancs Mt.	<i>Melitti-Fagetum</i>	600
5.	Felsőtárkány	36	Borsod	Várhegy Eastern slope	<i>Tilio-Fraxinetum</i>	650
6.	Cserépfalu	36	Borsod	Hór-river valley	<i>Melitti-Fagetum</i>	250
7.	Répáshuta	36	Borsod	Kerekhegy, Kajlabérc	<i>Tilio-Fraxinetum</i>	650
8.	Répáshuta	36	Borsod	Répáskúti völgybejárat	<i>Melitti-Fagetum</i>	430
9.	Répáshuta	36	Borsod	Tarkő alja	<i>Melitti-Fagetum</i>	540
10.	Lillafüred	36	Borsod	Szent István lápa	<i>Melitti-Fagetum</i>	550
11.	Répáshuta	36	Borsod	Nagy rét	<i>Aconito-Fagetum</i>	760
12.	Szilvásvár	36	Borsod	Istállóskő peak	<i>Aconito-Fagetum</i>	958
13.	Újszentmargita	36	Hajdú	Hortobágy, Margittai-forest	<i>Galatello-Quercetum</i>	100
14.	Ikervár	36	Vas	Kemeneshát, Ikervári-forest	<i>Quercu-Ulmetum</i>	150
15.	Nagymákfa	36	Vas	Kemeneshát, Hollósi-forest	<i>Quercu-Ulmetum</i>	150
16.	Alsóújlak	36	Vas	Kincs-lyuk	<i>Quercu-Ulmetum</i>	160
17.	Kám	36	Vas	Kemeneshát, Jeli arboretum	<i>Quercu-Ulmetum</i>	230
18.	Kisbajom	36	Somogy	Belső-Somogy, Móriczi-forest	<i>Helleboro dumetorum-Carpinetum</i>	200
19.	Berzence	36	Somogy	Perdőczmajor, Parkforest	<i>Fraxino-pannonicae-Carpinetum</i>	130
20.	Pálfa	36	Tolna	Tolnai hegyhát, Simon-tornyai-forest	<i>Helleboeo dumetorum-Carpinetum</i>	200
21.	Kurd	36	Tolna	Somogyi-dombság, Hajagos-forest	<i>Quercu robori-Carpinetum</i>	130
22.	Nadap	54	Fejér	Velencei Mts., Templomhegy	<i>Aceri tatarico-Quercetum ornetosum</i>	250

Results

By classical karyotype analysis 20 of 21 populations proved tetraploid and 1 hexaploid. The tetraploids occur almost exclusively on the mountainous and hilly areas of the country, usually in very restricted habitats (Fig. 1). At first sight their karyogramê are similar; as a common feature, they have not clearly visible SAT-chromosomes. Still, in a number of populations we observed remarkable differences. Of the karyotypes we show the 4 most characteristic ones (Figs 2a, b, c, d), and a detailed karyogram analysis was made with samples 4 and 22 (Figs 3 and 4). The chromosome-pairs are grouped by symmetry and

Table 2
Data of chromosomes
of population sample 4
(*Scilla buekkensis* Speta)

Group	Lengths of arm, μm	Total, μm	AR
A			
1.	7 + 7	14.0	1.0
2.	6.5 + 6	12.5	1.0
3.	5 + 5	10.0	1.0
4.	6 + 5	11.0	1.2
B			
5.	9 + 6	15.0	1.5
6.	10 + 6	16.0	1.6
7.	9 + 6	15.0	1.5
8.	9.5 + 6	15.5	1.5
9.	8 + 5	13.0	1.6
10.	9 + 5	14.0	1.7
11.	9.5 + 5.5	15.0	1.7
12.	8 + 5.5	13.5	1.5
13.	9 + 4.5	13.5	2.0
14.	8.5 + 5	13.5	1.7
15.	9 + 4	13.0	2.2
16.	7 + 4	11.0	1.7
17.	8 + 4	12.0	2.0
18.	8.5 + 3.5	12.0	2.5
19.	9 + 4	13.0	2.2
20.	8.5 + 4	12.5	2.1
21.	9 + 4.5	13.5	2.0
22.	9 + 4	13.0	2.2
23.	6 + 4	10.0	1.5
24.	5.5 + 3	8.5	1.8
25.	6 + 3	9.0	2.0
26.	6 + 3	9.0	2.0
27.	5 + 2	7.0	2.5
28.	6 + 3	9.0	2.0
29.	5 + 2	7.0	2.5
30.	5 + 1.5	6.5	3.3
31.	5 + 2.5	7.5	2.0
32.	4 + 1.5	5.5	2.6
33.	5 + 2.5	7.5	2.0
34.	4.5 + 1.5	6.0	3.0
35.	5 + 1.5	6.5	3.3
36.	5 + 1.5	6.5	3.3

Table 3

*Data of chromosomes of population sample 22
(Scilla spetana Kereszty)*

Group	Length of arm in mM	Total in mM	%AR
A			
1.	6 + 6	12.0	1.0
2.	6.5 + 6	12.5	1.0
3.	5 + 5	10.0	1.0
4.	5.5 + 4.5	10.0	1.2
5.	6 + 5	11.0	1.2
6.	5 + 5	10.0	1.0
7.	6 + 5	11.0	1.2
8.	5.5 + 5	10.5	1.1
9.	6 + 4	10.0	1.5
10.	4 + 3.5	7.5	1.1
B			
11.	8.5 + 5	13.5	1.7
12.	8 + 6	14.0	1.3
13.	6.5 + 5	11.5	1.3
14.	8 + 5	13.0	1.6
15.	7.5 + 4	11.5	1.8
16.	8 + 4	12.0	2.0
17.	7 + 4.5	11.5	1.5
18.	6.5 + 5.5	12.0	1.1
19.	8 + 5	13.0	1.6
20.	7.5 + 3.5	11.0	2.1
21.	8 + 4	12.0	2.0
22.	7 + 3.5	10.5	2.0
23.	7 + 4	11.0	1.6
24.	8 + 3	11.0	2.6
25.	6 + 5	11.0	1.2
26.	7 + 4	11.0	1.6
27.	6 + 4	10.0	1.5
28.	7 + 4	11.0	1.6
29.	6 + 3	9.0	2.0
30.	7.5 + 3	10.5	2.5
31.	4 + 4	8.0	2.0
32.	6.5 + 3	9.5	2.1
33.	5 + 3.5	8.5	1.4
34.	4 + 3.5	7.5	1.1
35.	4 + 3	7.0	1.3
36.	5 + 3	8.0	1.6
37.	4 + 3	7.0	1.3
38.	5 + 3	8.0	1.6
39.	4.5 + 4	8.5	1.1
40.	5 + 4	9.0	1.2
41.	4.5 + 6	7.5	1.5
42.	3.5 + 3	6.5	1.1
43.	3.5 + 2.5	6.0	1.4
44.	5 + 3	8.0	1.6
45.	4 + 2.5	7.5	1.6
46.	4 + 3	7.0	1.3
47.	4 + 3	7.0	1.3
48.	3 + 3	6.0	1.0
49.	4 + 2.5	6.5	2.5
50.	4 + 2.5	6.5	2.5
51.	4 + 3.5	7.5	1.1
52.	3.5 + 3.5	7.0	1.0
53.	3.5 + 3	6.5	1.1
54.	3 + 2.5	5.5	1.2

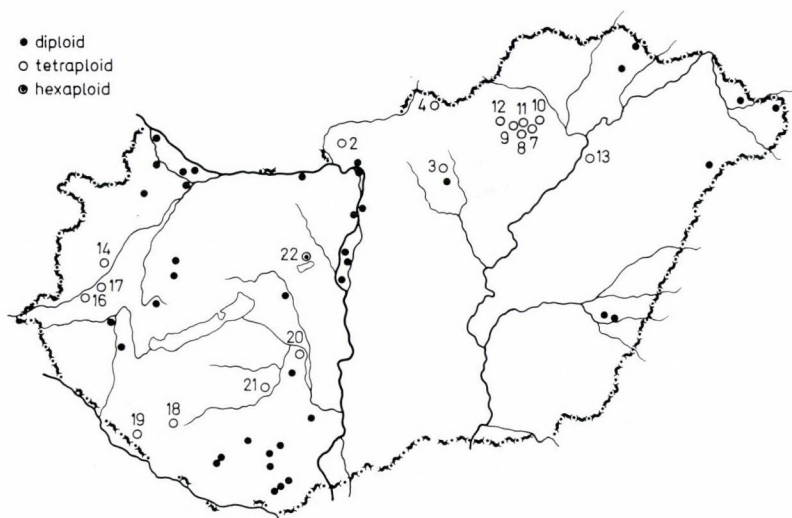


Fig. 1. Localities of the examined populations

size, and the most important data on them are given in Tables 2 and 3. The number of metacentric chromosomes increases in proportion to the ploidy level; the size of the submetacentric chromosomes gradually decreases; telocentric chromosome could not be observed.

The chromosome complements of samples 9 and 11 are particularly interesting because the habitats of the two populations are quite close to each other within the same regional unit. The chromatin content of chromosomes in sample 9 is of varied staining intensity, the protruding dark regions are easily observed (Fig. 2c). The 3 outstandingly large chromosomes of sample 11 show alternately staining stripiness, a phenomenon rare with the carmine acetic acid technique (Fig. 3d). This variation of staining generally reflect differences in the gene mechanism which — like in our case — do not necessarily manifest themselves in visible morphological differences.

A comparison of tetra- and hexaploid types immediately reveals that the metacentric chromosomes belong in both cases to the medium sized chromosomes. The difference between the two ploidy levels is also visible in the relative lengths of chromosomes. The five longest chromosomes in the tetraploids are 15 μm long, while in the hexaploids there are only three similarly long — 13–14 μm — chromosomes. The most striking difference appears in the value of the arm ratios: the maximum ranges from 3 to 3.4 in the tetraploids, while in the hexaploid it is 2.6. The gradual decrease in the lengths of submetacentric chromosomes is a common feature of both sample karyograms (Figs 3 and 4).

Discussion

The Hungarian populations of the *Scilla bifolia* species group are of di-, tetra- and hexaploid level. With the results of preliminary biostatistical and morphological examinations also taken into consideration we can say that the populations of the species group form a polyploid complex the levels of which,

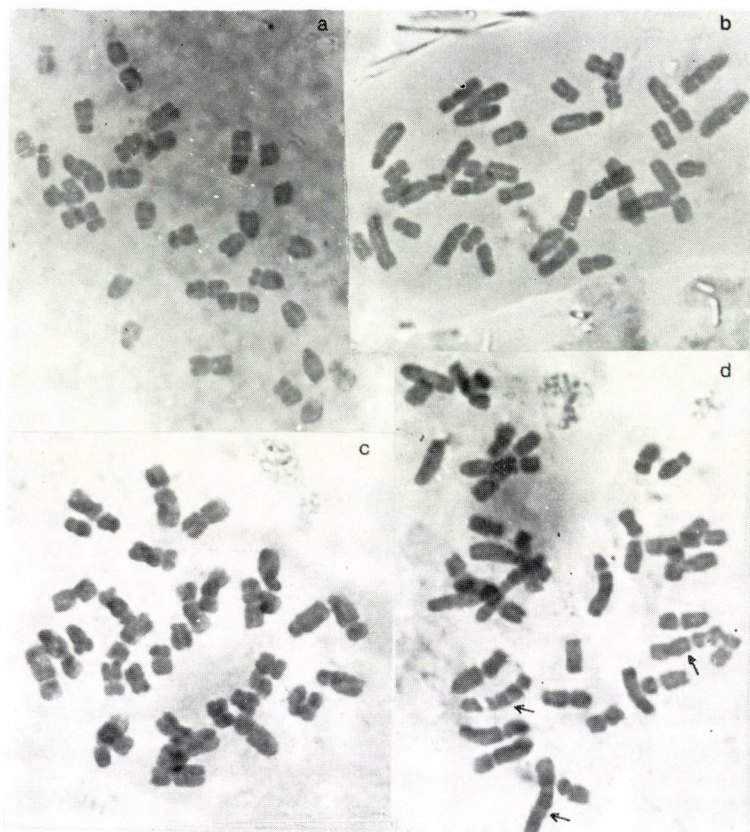


Fig. 2. Tetraploid metaphase cells of *Scilla bifolia* populations (a, b, c, d). Banded structures of chromosomes are marked by arrows

especially as regards their distribution, conceal very interesting evolution-genetic relations — similar to those in the populations of *Scilla autumnalis* (cf. YUAN 1982) —, as suggested by earlier investigations carried out by means of C-banding technique (GREILHUBER et al. 1981). *S. vindobonensis*, a taxon living in the Danube basin (SPETA 1974) possesses an extremely stable karyotype on an about 500 km long area of distribution, and is separated even morphologically by a great phylogenetic distance from *S. bifolia* s. str. while the polyploids show a certain degree of karyological unstableness (GREILHUBER and SPETA 1977). This fact is supported by the results of our investigations made on Hungarian populations too. Particularly striking results were obtained by GREILHUBER with quantitative DNA determinations of geographically distant populations. The DNA quantities of chromosomes — owing to their relative constancy — can be very well used to characterize populations in case an inner standard is used simultaneously (root-tips of *Allium cepa*).

Namely, in the absence of the latter the results are not suitable for comparative evaluation (BENNETT and SMITH 1976). Recent cytophotometric methods have made it possible to detect subspecies or even in population genom variations (DHILTON 1981, GREENLEE 1984, PRICE et al. 1983). It is highly probable that the variation of the genom quantity among and within the populations is a wide-spread phenomenon, and the only reason why it has not been accepted so far is that the DNA content as a function of the geographical distribution of populations has hardly been studied. It has also been established that changes in the DNA content are accompanied by lesser or greater taxonomic differences in a very large proportion of the cases (GREILHUBER and STRAHL 1984), though often it is of micromorphological level. On the basis of our investigations it seems that beside a similar phenotypic appearance the polyploid groups of the complex are composed of several different biological units, and the extent of variation is a specific feature.

In the polyploid complexes of flowering plants the gene flow from diploid to polyploid generally is unidirectional. The evolution of polyploids may even continue through secondary modifications: with new mutations and

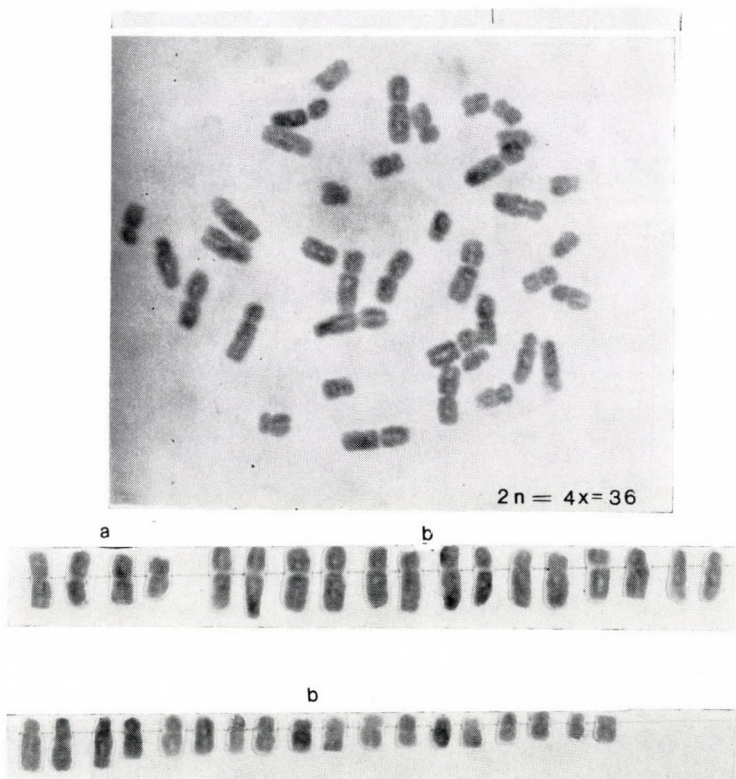


Fig. 3. Karyotype and karyogram of tetraploid *S. bifolia* population

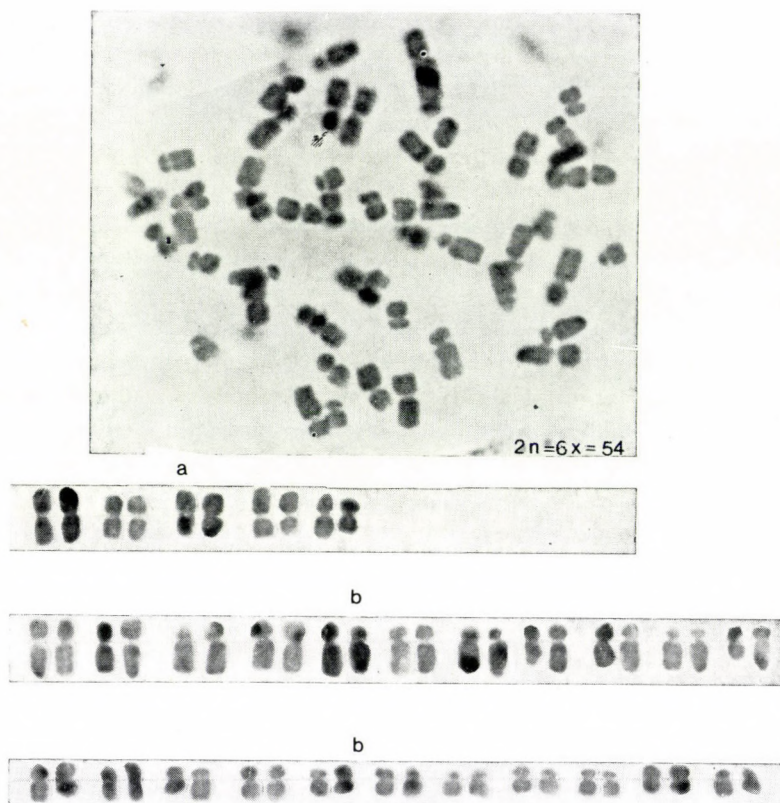


Fig. 4. Karyotype and karyogram of hexaploid *S. bifolia* population

recombinations the variability increases, the homology of the genoms decreases. Such a change of longer segments may even cause chromosome-level segregation, which leads to autopolyploidy or segmental allopolyploidy (STEBBINS 1971). In the simplest case the main line of development of the complex studied by us would be:

$$x = 9-18-36-54$$

$$x \quad 2x \quad 4x \quad 6x$$

On the basis of literary data and our own investigations it can be equally stated that the diploid level of the complex is $2n = 18$. In each of the populations along the Danube the largest pair of chromosome had satellites, which on higher ploidy levels is nowhere found. That is why we suppose the "amphiplasty" phenomenon of hybridization in which SAT-chromosomes do not develop among the somatic chromosomes of the hybrid progeny (NAVASHIN 1928).

To all appearances the higher ploidy levels came into existence by hybridization in our case too. However, to settle this question back-crossing of the polyploid species with the supposed progenitor and meiotic analysis of the hybrids obtained become necessary. From the coupling conditions of chromosomes we can conclude on the allopolyploid origin of the parent species; the cytogenetic processing of the polyploid complex of *Cystopteris fragilis* is a

Table 4

Cytological data averages of the polyploid taxa

		Total	AR	CI	L ^r
<i>S. buekkensis</i>	2n = 36	11.2 mM	1.99	0.65	0.27
<i>S. drunensis</i>	2n = 36	7.3 mM	2.10	0.64	0.27
<i>S. spetana</i>	2n = 54	9.1 mM	1.43	0.58	0.18

fine example of it. In Europe the diploid species of the complex are totally absent, and the existence of the octoploid level also suggests that the complex is rather old. In the course of meiotic analyses of natural species and synthetic hybrids the evolutionary relations on the diploid, triploid, tetraploid and hexaploid levels were cleared up (VIDA 1974). Similarly detailed cytological examination was carried out in the family Liliaceae.

In a thorough examination of the frequently occurring polyploidy in the genus *Allium* the symmetry of the karyotypes turned out to suggest the existence of autopolyploidy. Correlation was found between the increase in the ploidy level and the development of bulbils in the inflorescence (PASTOR 1981). The genetic centra of the area of the *Allium ampeloprasum* species complex was spotted on the basis of the chromosome variations and of the geographical diversity of the B- and the marker chromosomes. Owing to the difficulty of sterility and differences in ecological demand the introgressive hybridization seems to be of little likeliness, as also supported by the fact that transitional forms have not been found so far. It is much more probable that the diversity of the chromosome structure was preserved in the progeny in the course of descent from a common ancestor (BOTHAMER 1982).

The *Scilla bifolia* polyploids in Hungary are remarkable not only for their disjunct habitats and different ecological demands but also for their geographical distribution. Into the more or less uniform diploid area those of two tetraploid groups stretch from north and west (Fig. 1). Particularly interesting is the habitat of the hexaploid population on the crystalline rocks of the Velence-hills, situated far from the two polyploid areas almost as a connecting link between them. In the area of the tetraploids, on the other hand, diploids are scattered, which confirms the probability of hybridization.

It seems that the hexaploid developed from the diploids, since even the nearest tetraploid population is very far from here.

The endemic character of the species group (SPETA 1976) makes it necessary to take further aspects into consideration, which may explain the distribution of the different ploidy levels in time and space.

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CYTOLOGICAL STUDIES OF THE DATE PALM *PHOENIX DACTYLIFERA* L.

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Behavior of meiotic chromosomes of date palm *Phoenix dactylifera* L. has been described for the first time. The inconstancy in the chromosome number and the meiotic irregularities of four cultivars of date palm, namely Ghannami-Ahmar, Ghannami-Akhdhar, Ghaybani and Abualaib have been discussed.

Introduction

The date palm *Phoenix dactylifera* L. is one of the common cash crops in Iraq and in many other countries of the world. The genus belongs to the tribe Phoeniceae of the family Arecaceae. Under the genus *Phoenix* there are about twelve species distributed in the tropical and subtropical regions (BLATTER 1926), the most important species being *P. dactylifera*. The date palm is grown extensively along the banks of the river Shatt-al-Arab, especially in Basrah region. There are about 90 million date palm trees in the world of which about 22 million occur in Iraq, comprising 455 cultivars (ABDUL-HUSSIAN 1974). Its cytology has not yet been studied in detail. The karyotype analysis of the date palm has been studied by SOLIMAN and AL-MAYAH 1978. But detailed meiotic studies of the date palm has not been undertaken.

The present paper is the first in a series of papers that are to be published by the author on various aspects of the detailed cytological studies on the date palm (*P. dactylifera*).

Material and methods

Flower buds of four different male cultivars of *Phoenix dactylifera* L., namely, Ghannami Ahmar, Ghannami Akhdhar, Ghaybani and Abualaib, were collected from FAO in Basrah in Jan. 1978 and fixed in a mixture of one part of glacial acetic acid and 3 parts of absolute ethyl alcohol for 24 hours at room temperature and then transferred to 70% ethyl alcohol.

The anthers were squashed in acetocarmine after treating the buds with boiling HCl for a few seconds and then washing them in water for 15-30 minutes (AL-MAYAH and AL-SHEHBAZ 1977). Temporary slides were prepared and camera lucida drawings were made at a magnification of $\times 1200$.

Results

Cultivar Ghannami-Ahmar: At diplotene 18 bivalents were clearly observed (Fig. 1 no. 1). At late diplotene stage the bivalents showed condensation and terminalization. At metaphase the 18 bivalents regularly oriented themselves at the equator. At anaphase I, generally there

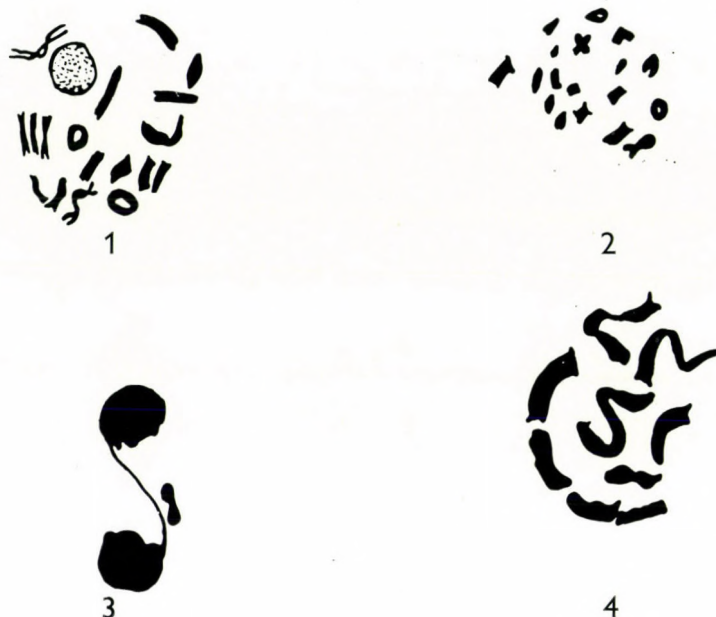


Fig. 1. Meiosis in P.M.C.'s of *Phoenix dactylifera* (1-4), (1-3) Cultivar Ghannami Ahmar. (1) Diplotene stage showing 18 bivalents. (2) Metaphase I, showing 18 bivalents. (3) Anaphase I, showing a bridge and a fragment. (4) Cultivar Ghannami Akhdhar, Metaphase I, showing 9 quadrivalents

was normal separation of the chromosomes. In a few cases chromatin bridges were seen. The number of such bridges was either one or two (Fig. 1 no. 3). The chromatin bridges were unaccompanied by any fragments. Normal separation of chromosomes was generally found at anaphase II but in a few cases stretched out chromatin bridges were found.

Cultivar Ghannami-Akhdhar: Eighteen bivalents were clearly observed at diplotene stage in most cases but in certain cases seventeen bivalents with two univalents and sixteen bivalents, with four univalents were observed at metaphase I, also nine quadrivalents were seen in a few cells (Fig. 1 no. 4).

Cultivar Ghaybani: Meiotic irregularities were more common and complex in this cultivar than in the preceding ones. Most of the flowers displayed abnormal pairing and separation. We observed no disjunction laggards, bridges chains (Fig. 2 nos 1-3). Besides these anomalies, spindle abnormalities and an inconstancy in the chromosome numbers were also observed. A part of P.M.C.'s were seen with 18 bivalents but many cells had 16, 20 and 21 bivalents as a gametic number (Fig. 2 nos 4-6).

This variation was observed in the P.M.C.'s of the same anther as well as different anthers of the same bud besides different buds of the same inflorescence.

Cultivar Abualalb: In this cultivar large number of meiotic irregularities were observed. These included multivalent and univalent formation, precocious separation of bivalents and chromatin bridges (Fig. 3 nos 1-5). Fourteen rod shaped and four ring shaped bivalents were seen at diakinesis, which on approach of metaphase I oriented themselves at the equator. A chain-shaped multivalent was observed at M_1 (Fig. 3 no. 1). In another case sixteen bivalents,



Fig. 2. Meiotic stages of date palm, Cultivar Ghaybani (1-6). (1) Metaphase I, with 16 bivalents and a chain shaped quadrivalent. (2) Anaphase I, showing laggards. (3) Anaphase I, with 2 chromatin bridges. (4) Metaphase I, showing 16 bivalents. (5) Metaphase I, showing 20 bivalents. (6) Anaphase I, showing $n = 21$

a Y-shaped trivalent and an univalent which remained unpaired were seen (Fig. 3 no. 2). In addition, many figures with 14, 17 and 20 bivalents could also be found (Fig. 3 nos 3 and 4). In the four cultivars studied 3 nucleoli could be seen in each daughter nucleus at first telophase (Fig. 3 no. 6). The tetrad formation is of simultaneous type. As many as 3 nucleoli have been observed in the tetrad nucleus.

Discussion

The constancy of the karyotype from one cell to another and from one generation to the next, lies in its capacity to duplicate itself exactly at each cell division (SWANSON 1957). This duplication results in the preservation of the number of genes and their linear relationship to one another, in the newly formed daughter cells. The above classical assumption has frequently been shown to be erroneous and an inconstancy in the chromosome number has been reported by workers. SHARMA and SHARMA (1956) suggested that "the idea of the constancy of the chromosome number in the cell is not strictly applicable to all plants". In a large number of the species investigated by them, they found a variation of chromosome numbers in the somatic cells, even of the same roottips in addition to the normal numbers. The variation in number may arise through accidents in chromosome segregation and cell division or as a result of the consequence of the regular development process of naturation (SWANSON 1957).

Besides a variation in the somatic complement a variation in the gametic cells has also been reported. BASK (1958) found a variation from 6 to 8 bivalents in the PMC's of *Corchorus sidoides* F. Muell. in which 7 is the normal haploid number.

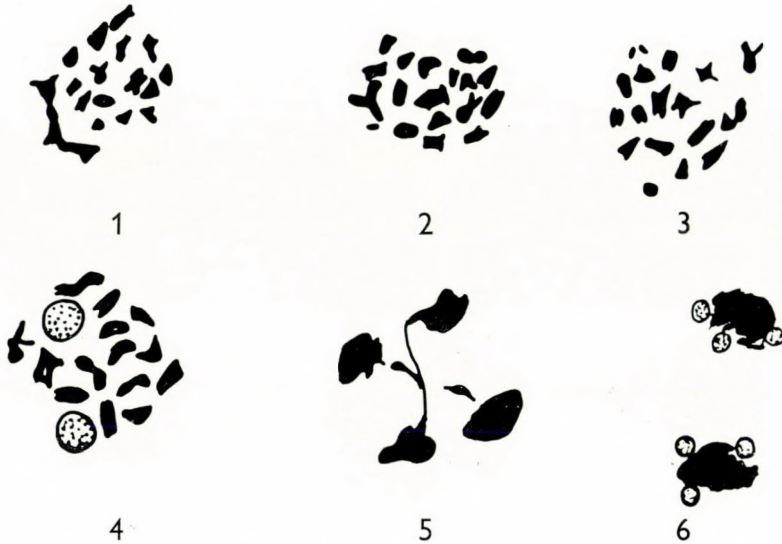


Fig. 3. Meiotic stages of date palm Cultivar Abualaib (1-6). (1) Metaphase I with 15 bivalents and a chain of 6 chromosomes. (2) Metaphase I with 16 bivalents, Y-shaped trivalents and a univalent. (3) Metaphase I, showing 16 bivalents with 2 univalents. (4) Prometaphase I, showing 14 bivalents. (5) Late Anaphase II showing a bridge and laggards. (6) Telophase I, showing 3 nucleoli in each daughter nucleus

LEWIS (1962) found in *Claytonia virginica* L. that "the P.M.C.'s in the same bud often differed from one another in chromosome number as well as the pollen and premeiotic cells from the same plants". He observed a variation of gametic number ranging from 7, 8, 9, 11, 12, 16 and 18 in the first pollen division of the same raceme, besides variation in the somatic number.

YANG (1964, 1965) found considerable numerical instability of chromosomes within the individuals of interspecific hybrids of *Nicotiana*. He observed a variation from 33 to 39 chromosomes in the microspore and 56 to 64 chromosomes in the somatic cells. BAGUAR (1967) found an intraindividual chromosome variation from 9 to 11 bivalents in *Fagonia cretica*. The same author (1968) also found a variation from 6 to 8 chromosomes as a gametic number in *Sesbania sesban*. AL-MAYAH and AL-SHEHBAZ (1977) found that in *Scorpiurus muricatus* the haploid chromosome number is 7 or 8. NEMEC (1910), DANGEARD (1937), and DOULAT (1944) as cited by FEDOROV (1974), found that in the date palm $2n = 28$, while BEAL (1937), MURIN and CHAUDHRI as cited in LÖVE (1970) and SOLIMAN and AL-MAYAH (1978) reported that $2n = 36$ in the same plant. This inconstancy of gametic number as reported above in *P. dactylifera* is very interesting. The study of meiosis shows the regular behavior of chromosomes and suggests that *P. dactylifera* is a diploid species. Continued cultivation and selection are responsible for the presence of a number of cultivars which differ mainly in shape of fruits. The abnormal meiotic behavior that appear in the cultivars Ghaybani and Abualaib indicate that polyploidy might have played some role in the evolution of new cultivars and in the speciation within the genus.

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HERBICIDE INDUCED EAR MORPHOSES IN BARLEY IN RELATION TO CHROMOSOME ABERRATIONS

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Experiments were carried out with two types of herbicides, to seek for their cytological and morphogenetic effects on three barley varieties. The two herbicides studied (Aniten D, Gabonil) showed different effectiveness in both aspects. A positive dose dependence was also found. The frequencies of chromosome aberrations and of ear morphoses also varied with the kind of variety, however the varieties differ in degree of cytological and morphological reaction. In each treatment seed number per ear decreased in morphotic ears. The possible importance of morphoses in natural selection has been emphasized.

Introduction

It is well known that certain classes of pesticides cause point mutations and chromosome aberrations (EPSTEIN and LEGATOR 1974) and consequently the treated population changes in genetic composition (MC CURDY and MOLBERG 1974; VIRÁGH 1982).

There are several publications dealing with organismic anomalies of plants caused by some herbicide treatment. These anomalies occur both in vegetative and generative organs (HOHLOVA 1977; SHARMAN 1978). It is also known from the literature, that after 2,4-D herbicide treatment of cereals ear modifications can be observed (DERSHEID 1972; SHARMAN 1978). HOLLY described in 1954 several morphological alterations generated by 2,4-D and MCPA. Besides, there are evidencies for causes of teratological changes: irregular mitoses during organogenesis and differentiation (SHKOLNIK 1981). It seems obvious from a number of works (KULIKOV et al. 1970; ELSAKOVA 1964) that 2,4-D is an inhibitor of nucleic acid and protein syntheses and causes disturbances in early phases of purine biosynthesis. Summing up, the outcomes of the changes in genetically determined course of cell divisions in meristematic tissues are modifications in morphogenetic processes and genesis of teratological forms.

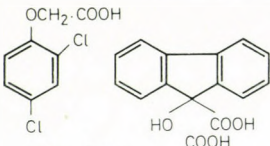
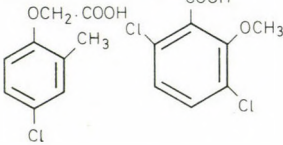
In this paper we report on the cytological and morphogenetic effects of two herbicides in three barley varieties.

Material and methods

Mutagenic effect of two herbicides, Aniten D and Gabonil (Table 1) currently used in Hungarian agriculture was investigated. Both of them were provided by the Research Institute for Plant Protection of Hungarian Academy of Sciences. The barley varieties were obtained from the Agricultural Research Institute of Hungarian Academy of Sciences and labelled by them as MFB 104, Mv 43 and Mv 48.

Table 1

Trade names, active ingredients and composition of the compounds tested

Trade name	Active ingredients	Chemical name	Structural formula
Aniten D	2,4-D + fluorenenol	2,4-dichlorophenoxyacetic acid 9-hydroxyfluorene-9-carboxylic acid	
Gabonil	MCPA + dicamba	4-chloro-2-methylphenoxyacetic acid 2-methoxy-3,6-dichlorobenzoic acid	

Cytological investigations were made as before (PUSZTAI and VÉGH 1978). As for generation of morphoses, we made outdoor experiments in Budapest. The area of each plot was 2 m² with plant density of 10×4 cm.

Sowings were sprayed with 2 l/ha Aniten D or 3 l/ha Gabonil (each in 500 l water) in accordance with the agricultural prescriptions for the use of these chemicals, just as their double concentrated solution: 4 l/ha and 6 l/ha, respectively. Sprayings were carried out when the plantlets had been growing thick. We worked with 250–300 specimens per treatment. The effectiveness of the herbicide treatments was determined at each harvest. We ascertained the percentage of plants with and without ear morphoses and the grain number per ears.

Results and discussion

Cytological results are illustrated on Fig. 1. The two herbicides showed various effectiveness for frequencies of chromosome aberrations. Treatments with Aniten D proved to be more effective reaching as high as $7.6 \pm 0.9\%$. The mutagenic effect of Gabonil was smaller, the chromosome aberrations found were only $3.1 \pm 0.5\%$. In general the proportion of

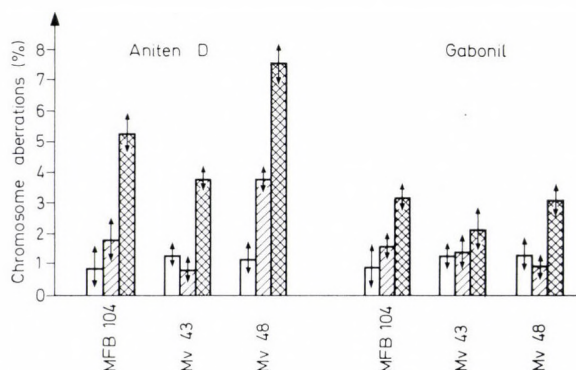


Fig. 1. Percentage of chromosome aberrations induced by herbicides in barley root tips. — white = control; ▨ 500 ppm; ▩ 1000 ppm

chromosome aberrations strongly enhanced in line with increase of herbicide concentration, e.g. 1000 ppm of Aniten D turned to be five times effective than its 500 ppm dose. It can be seen from the experimental data, that the used barley varieties differ in their herbicide susceptibility: Mv 48 and MFB 104 proved to be the most sensitive ones.

The ear morphoses were studied in M_0 generation. Several types of ear morphoses could be found in all of three barley varieties. Figure 2 shows the main types of morphoses.

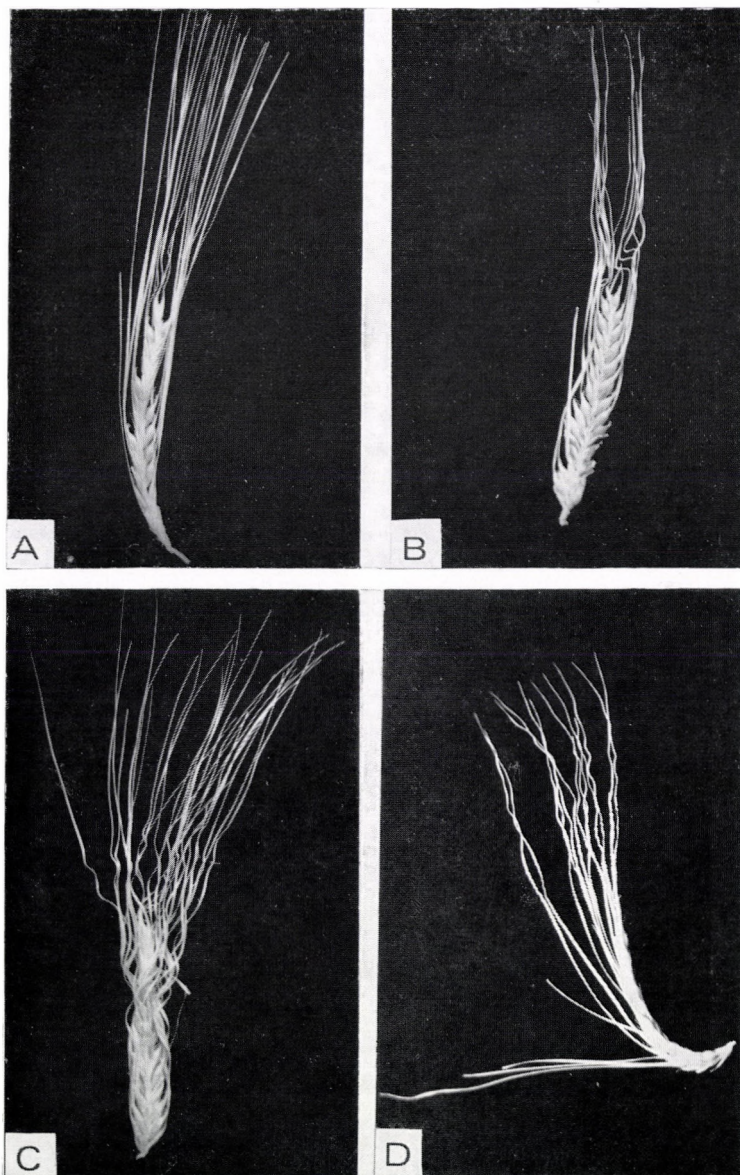


Fig. 2. Morphose types observed in barley plants. — A) Loss of earlets; B) Increased earlet number; C) Kinky spikelet; D) Spikelet asymmetry

Among them are loss of earlets, increase of earlet number, deformations of spikelet (kinking), unilateral formation of earlets and spikelets and so on. The barley varieties used turned to be different in types of morphoses, too. In Mv 43 curly spikelets appeared (Fig. 2C) and in Mv 48 unilateral formation of earlets and spikelets could be observed in 70% (Fig. 2D). As for MFB 104, the increase of earlet number (Fig. 2B) is more frequent. These alterations resulted in decrease of seed number per ear.

The data of ear morphoses are summarized in Table 2. The effects of the herbicides after Aniten D treatments, occasionally reaching 61%. Gabonil was less effective, although in some it caused 19% morphoses. It was a drastic increase in consequences of the agriculturally recommended and double dose of Aniten D. In the case of Gabonil use, the rate of ear morphoses was not proportional to the doses.

As it turns out of Table 2, the studied barley varieties responded differently to herbicide treatments. Mv 43 and Mv 48 varieties showed outstandingly high increase of morphoses. It should be mentioned that the proportion of plants possessing morphoses varied in consecutive years, which can be attributed to environmental differences during vegetation periods (i.e. temperature, moisture, humidity). That is why we compare the data year by year.

Comparative evaluation of seed number per ears of normal and morphotic ears was done. As it appears from Fig. 3, all the experiments resulted in reduced seed numbers. It seems to occur almost independently from the sort of herbicide used. As for Mv 43 and Mv 48 varieties, morphotic ear formations were always proportional to some decrease in seed number. The tendency of changes is the same in the case of MFB 104, but these features are not strictly proportional because of earlet number increasing morphosis types.

Table 2

Percentage of the plants with ear morphoses in barley plantiness after herbicide treatment

Strain	Years of investigation	Control	Dose Aniten D, l/ha		Dose Gabonil, l/ha	
			2	4	3	6
MFB 104	1979	0	3.8 ± 1.20	13.0 ± 2.13	5.8 ± 1.48	2.3 ± 0.95
	1980	6.2 ± 1.39	18.2 ± 2.22	31.9 ± 2.69	6.8 ± 1.45	8.2 ± 1.58
	1981	0.6 ± 0.47	10.8 ± 1.85	13.8 ± 2.06	3.8 ± 1.14	4.6 ± 1.25
	1982	10.8 ± 1.79	18.2 ± 2.22	43.5 ± 2.86	2.4 ± 0.88	19.0 ± 2.26
	1983	0	5.1 ± 1.27	8.3 ± 1.59	2.9 ± 0.97	0
Mv 43	1979	2.3 ± 0.86	6.1 ± 1.38	15.1 ± 2.07	3.1 ± 1.00	0
	1980	14.2 ± 2.12	34.0 ± 2.88	51.8 ± 3.04	16.1 ± 2.24	12.8 ± 2.03
	1981	1.8 ± 0.79	11.2 ± 1.88	19.7 ± 2.38	0	5.4 ± 1.35
	1982	11.1 ± 1.81	20.1 ± 2.31	61.0 ± 2.81	8.9 ± 1.64	9.8 ± 1.71
	1983	4.3 ± 1.17	3.8 ± 1.10	11.0 ± 1.81	0	3.1 ± 1.00
Mv 48	1979	3.9 ± 1.11	14.2 ± 2.01	29.2 ± 2.62	6.8 ± 1.45	0.8 ± 0.51
	1980	13.8 ± 1.99	48.1 ± 2.88	69.3 ± 2.66	17.2 ± 2.18	15.8 ± 2.10
	1981	0	9.3 ± 1.68	24.1 ± 2.47	3.1 ± 1.00	2.3 ± 0.86
	1982	7.1 ± 1.48	32.3 ± 2.70	58.1 ± 2.85	16.8 ± 2.15	2.3 ± 0.86
	1983	0	5.8 ± 1.34	3.1 ± 1.00	3.1 ± 1.00	9.8 ± 1.72

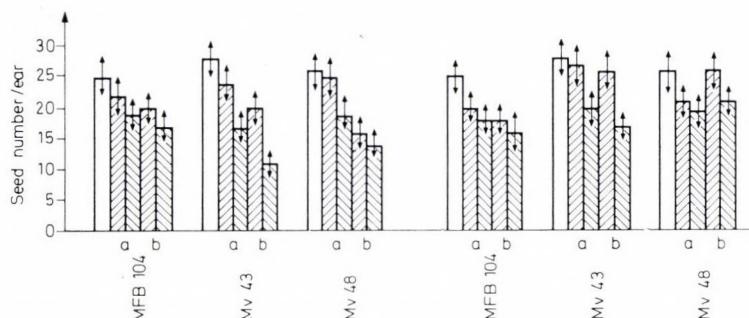


Fig. 3. Seed number in normal and ear morphose bearing barley specimens. — a) Dose used in agriculture; b) doubled agricultural dose — white = control; normal plants; morphotic plants

Comparing the data of morphoses with the cytological results, we can see that Aniten D was the more effective agent and a dose dependence is also obvious. Regarding the barley varieties in question, the best response was given by Mv 48.

Herbicide induced morphoses are similar to other agents, like temperature, other chemicals and so on. GRANT (1972) states that herbicides may modify evolutionary rate of species. The agents which can change the fertility also modify the strength of natural selection. Proneness to produce morphoses indicates genotypical susceptibility to environmental factors. It can be postulated that morphotic plants have altered genotype while plants that gave no responses are genotypically more stable. Herbicide treatment therefore may be one of the factors promoting genotypic differentiations within a variety and shed also some light on intraspecific variability.

In our studies the occurrence of ear morphoses appears to be dependent of the chemical composition of the given herbicide. Consequently, the genotypic responsiveness of the variety (genotype mixture) can be characterized, among others, by the proneness to make ear morphosis.

ACKNOWLEDGEMENT

The author is grateful to Miss K. Kováts for her help during preparation of the manuscript.

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HIFOMICETES DE TOPES DE COLLANTES, CUBA I.

ESPECIES HOLOBLÁSTICAS

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(Recibido: 15 Septiembre 1984)

Forty-seven species or varieties of saprophytic and holoblastic hyphomycetes belonging to twenty-seven genera from Topes de Collantes, Sancti Spiritus province are recorded. Seven genera and nineteen species are new records from Cuba. Four new species, two new varieties and some interesting or rare hyphomycetes are described in this paper.

Introducción

Topes de Collantes (784 metros de altura sobre el nivel del mar) está situada en la región central de Cuba; comarca muy montañosa que en general recibe el nombre de Grupo de Guamuhaya, Alturas de Trinidad-Sancti Spiritus o como mas se conoce en la actualidad, Sierra del Escambray. Dentro de este macizo Topes forma parte de las Alturas de Trinidad, las cuales según NUÑEZ JIMÉNEZ (1965) están constituídas por un conjunto de montañas de esquistos calcáreos y cristalinos que al parecer se originaron en el Jurásico Inferior y Medio.

Esta subregión presenta restos de una topografía cársica muy primitiva y muchas de sus elevaciones muestran la forma de conos como los mogotes de Sierra de los Organos, con grutas horadadas en sus laderas casi verticales.

La existencia de amplios valles, suelos arcillosos y montañas altas y húmedas hace que estén presentes en la vegetación natural un buen número de especies endémicas.

Durante los años 1982 y 1983 se realizaron varias expediciones micológicas a diferentes localidades de Topes de Collantes y como resultado de éstas, se colectaron 140 muestras, fundamentalmente ramas y fragmentos de troncos caídos de diferentes plantas.

En este trabajo se relacionan 47 especies o variedades de hifomicetes con conidiogénesis holoblástica distribuidos en 27 géneros, de los cuales 7 géneros y 19 especies son nuevos reportes para Cuba, y de éstos, 4 especies y 2 variedades pertenecientes a los géneros *Acrodictys* M. E. Ellis, *Gyrothrix* (Corda) Corda, *Mycoenterolobium* Goos, *Periconiella* Saccardo y *Pithomyces* Berkeley et Broome son propuestos como nuevos taxa para la ciencia. Los ejemplares y tipos se encuentran depositados en el Herbario del Instituto de Botánica de la Academia de ciencias de Cuba (HAC).

Reseña de especies

1. *Acrodictys bambusicola* M. B. Ellis, Mycol. Pap., 79: 6 (1961)

Sobre ramas muertas de *Bambusa* sp. Mogote de la Solapa. 13. VII. 1982. A. MERCADO 6779 (HAC).

Colonias dispersas, pardo oscuras a negras. Conidióforos pardos, hasta 257 μ m de longitud, 5-7,6 μ m de grueso. Conidios pardos, 18-23 $\times$ 10,5-13 μ m.

2. *Acrodictys globulosa* (Tóth) M. B. Ellis, Mycol. Pap, 103: 34 (1965)

Sobre ramas muertas no identificadas; sobre ramas muertas de *Licaria jamaicensis* (Nees) Kosterman; *Fischeria havanensis* Decne; *Ampelocera cubensis* Gris., *Zanthoxylum* sp., *Coffea* sp., y sobre hojarasca. Los Llanos de Padilla. 2. II. 1983. A. MERCADO 7004, 7006, 7007, 7036, 7040, 7044, 7046, 7047, 7051, 7053 (HAC).

Colonias dispersas, pardas. Conidióforos pardos $40-162 \times 4-5 \mu\text{m}$; hasta 8 proliferaciones percurrentes. Conidios pardo pálidos, $(16,5-19,5-25 \times 15,2-17,5 \mu\text{m})$.

El grosor de los conidios en el material de esta especie que se colectó en Topes de Collantes es menor que el reportado por ELLIS (1971), lo que trae como consecuencia que los conidios en vez de ser estrictamente globosos, tiendan, en nuestro caso, a ir desde ampliamente elipsoidales a subglobosos. Sin embargo, las medidas de los conidios de nuestro material se aproximan mucho a las reportadas por MATSUCHIMA (1975).

3. *Acrodictys stilboidea* Mena et Mercado spec. nova

Coloniae effusae, atro-brunneae, pilosae. Mycelium partim superficiale partim in substrato immersum. Synemata claviformia, atro-brunnea, $575 \mu\text{m}$ longa, $20,3 \mu\text{m}$ crassa ad medium, $25,5-50,8 \mu\text{m}$ ad basem, $30-38,1 \mu\text{m}$ ad apicem. Conidiophora magnifilamentosa cum filamentis junctis, $2-3 \mu\text{m}$ crassa ad apicem. Cellulae conidiogenuae monoblasticae, integrae, terminales, percurrentes, cylindricae. Conidia ellipsoidea, laevia, muriformia, olivaceo-brunnea, $(18-22-31 \times (11,5-13-16,5 \mu\text{m}))$. Cellula basalis, obconica, subhyalina, $5-7 \mu\text{m}$ crassa, $2-3 \mu\text{m}$ ad basim truncata.

Holotypus: in ramis mortuis *Zanthoxyli* sp. Los Llanos de Padilla, Topes de Collantes, Sancti Spiritus, Cuba, 2. II. 1983, A. MERCADO 7040 (HAC).

Colonias dispersas, pardo negruzcas, pelosas. Micelio parte superficial y parte inmerso en el sustrato. Sinemas fácilmente visibles bajo el microscopio estereoscópico, claviformes, pardo oscuros, hasta de $575 \mu\text{m}$ de largo por aproximadamente $20,3 \mu\text{m}$ de grosor en la parte media, $25,5-50,8 \mu\text{m}$ en la base y $30-38,1 \mu\text{m}$ justamente debajo del ápice. Conidioforos macronematosos, sinematosos, sin ramificar, rectos, con filamentos estrechos muy unidos hasta cerca de la zona apical, lisos, pardos en la base, subhialinos a oliváceos y de $2-3 \mu\text{m}$ de grosor en la parte superior. Células conidiógenas monoblásticas, integradas, terminales, percurrentes, mayormente cilíndricas, subhialinas a oliváceas. Conidios elipsoidales o piriformes, solitarios, lisos, muriformes, pardo oliváceos; $(18-22-31 \times (11,5-13-16,5 \mu\text{m}))$. Célula basal del conidio protuberante, obcónica, subhialina, $5-7 \mu\text{m}$ de grosor en su parte más ancha, $2-3 \mu\text{m}$ en la base truncada.

Holotipo: Sobre ramas muertas de *Zanthoxylum* sp. Los Llanos de Padilla, Topes de Collantes, Sancti Spiritus, Cuba, 2. II. 1983, A. MERCADO 7040 (HAC).

Acrodictys stilboidea difiere fundamentalmente de las restantes especies incluidas dentro del género, porque los conidióforos no se presentan aislados, sino que se agrupan formando típicos sinemas. A pesar de lo inusual de este hecho dentro del género, lo claro de la conidiogénesis y la existencia de géneros donde existen especies que forman estructuras sinemáticas y otras que no lo hacen, nos permite incluir este taxon dentro de *Acrodictys*. Los conidios de *A. stilboidea* presentan una célula basal protuberante que unido a su forma en conjunto y sus dimensiones se asemejan a los de la especie *A. bambusicola* M. B. ELLIS.

* Especie nueva para Cuba.

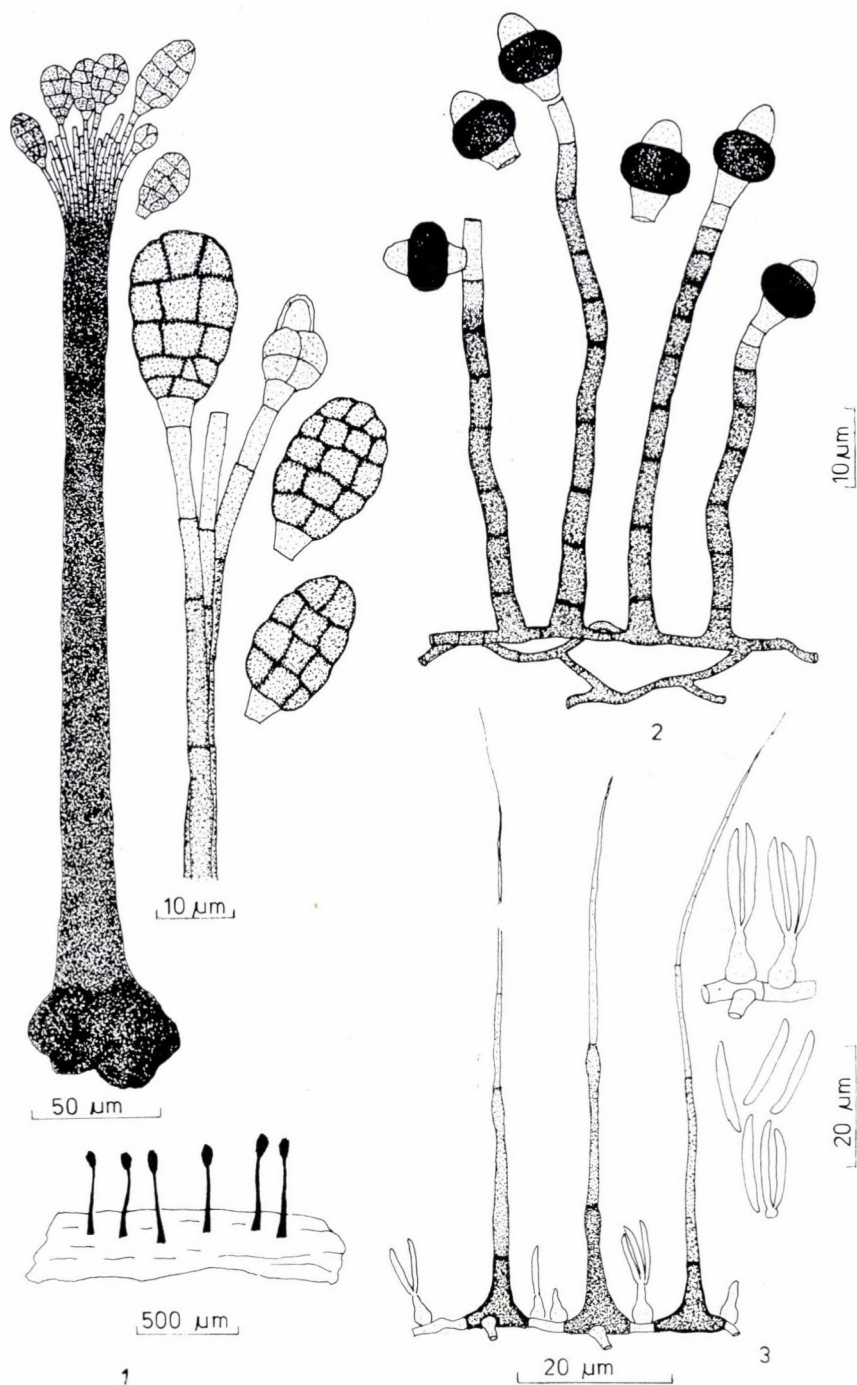


Lámina I

- Fig. 1. *Acrodictys stilboidea* Mena et Mercado spec. nova. sinemas, conidióforos, células conidiógenas y conidios. Se observa un aspecto de los sinemas en su hábitat
- Fig. 2. *Acrophragmis coronata* Kiffer et Reisinger. Conidióforos, células conidiógenas y conidios
- Fig. 3. *Circinotrichum papakurae* Hughes et Pirozynski. Setas subuladas, conidióforos, células conidiógenas y conidios

4. *Acrophragmis coronata*** Kiffer et Reisinger, Revue Ecol. & Biol., 7: 12-16 (1970)

Sobre rama muerta de *Coffea* sp. Los Llanos de Padilla. 2. II. 1983. A. MERCADO 7050 (HAC).

Colonias dispersas, pardo oscuras. Micelio superficial y parte inmerso en el sustrato. Conidióforos rectos o ligeramente flexuosos, pardos, lisos, septados, anillados, $50-110 \times 3,5-4,5 \mu\text{m}$. Conidios solitarios, acrógenos o en ocasiones acropleurógenos, lisos, con 2 septos, con una célula central parda muy oscura y las otras dos pardo pálidas; $11,5-16 \times 7,5-8 \mu\text{m}$; $3,5-4,5 \mu\text{m}$ de grueso en la base.

Esta especie, según ELLIS (1976), sólo se ha encontrado sobre ramas muertas caídas en el Congo, por lo que además de constituir un nuevo reporte para Cuba, también lo es para el Hemisferio Occidental. En el material cubano los conidios son ligeramente más largos que los del material tipo.

5. *Berkleasium caribense* Hol-Jech. et Mercado, Česka Mykol., 38 (2): 99-100 (1984)

Sobre raquis de la hoja de *Calyptronoma dulcis* (Wr. et Griseb.) Bailey. Monte de los Gallos. 13. VII. 1982. A. MERCADO 6748 (HAC).

Conidios pardos con un septo longitudinal y 3-4 septos transversales; $23-28 \times 13-20,3 \mu\text{m}$.

Los conidios son algo más pequeños que los descritos por HOLUBOVÁ-JECHOVÁ y MERCADO (1984) a partir de material que se encontró en Isla de la Juventud, Cuba.

6. *Brachysporiella arengae* (Matsuchima) Holubová-Jechová, Česka Mykol., 37 (1): 14 (1983)

Sobre pecíolo de la hoja muerta de *Roystonea regia* (H. B. K.) O. F. Cook. Los Llanos de Padilla. 2. II. 1983. A. MERCADO 7018 (HAC).

Colonias dispersas, negras. Conidióforos pardo oscuros, $170-260 \times 6-8 \mu\text{m}$, $7,6-9,5 \mu\text{m}$ de grueso en la base. Conidios pardos a pardo oscuros, con 3 septos; $20,3-29 \times 10-13 \mu\text{m}$.

Los conidios de esta especie que se colectó en Topes de Collantes presentan menores dimensiones que los que reportan MATSUCHIMA (1975), HUGHES (1978) y más recientemente para la Sierra de los Organos, Cuba HOLUBOVÁ-JECHOVÁ (1983).

7. *Circinotrichum papakurae** Hughes et Pirozynski, N. Z. Jl. Bot., 9: 39-45 (1971)

Sobre hojas muertas de *Roystonea regia* (H. B. K.) O. F. Cook y sobre hojarasca. Los Llanos de Padilla. 2. II. 1983. A. MERCADO 7043, 7044 (HAC).

Colonias hipófilas o anfigenas, dispersas, pardas cuando estériles, pardo grisáceas cuando están abundantemente esporuladas. Micelio superficial y parte inmerso en el sustrato. Setas rectas, pardo oscuras cerca de la base, pardo pálidas hacia el ápice, hasta de $235 \mu\text{m}$ de longitud, $2,5-4 \mu\text{m}$ de grosor en la base, disminuyendo gradualmente hacia la parte superior, hasta menos de $1 \mu\text{m}$ de grueso. Células conidiógenas obclaviformes a lageniformes, subhialinas; $5-7,6 \mu\text{m}$ de largo, $3-4 \mu\text{m}$ de grueso. Conidios fusiformes, rectos o ligeramente curvos, sin septos, hialinos; $12-16 \times 1,5-1,8 \mu\text{m}$.

** Género y especie nuevos para Cuba.

Este taxon se describe y se ilustra en este trabajo, por ser una especie poco colectada a nivel mundial y constituir un nuevo hallazgo para Cuba. Las setas en el especimen cubano pueden medir hasta $235\ \mu\text{m}$ de longitud, mucho más largas que las del especimen de Nueva Zelandia que sólo alcanzan $150\ \mu\text{m}$ (HUGHES y PIROZYNSKI 1971).

8. *Dictyosporium elegans* Corda, Weitenweber's Beiträge . . . : 87 (1836)

Sobre ramas muertas de *Smilax* sp. Los Llanos de Padilla. 2. II. 1983. A. MERCADO 7014 (HAC).

Colonias dispersas, pardo negruzcas. Conidios pardo dorados; $35\text{--}50 \times 18\text{--}26\ \mu\text{m}$, aplanados en un plano, compuestos de 5–7 hileras de células, de aproximadamente la misma longitud.

Los conidios de esta especie son más pequeños que los de la descripción de ELLIS (1971), pero coinciden con las dimensiones reportadas por MATSUCHIMA (1975).

9. *Dictyosporium heptasporum* (Garov.) Damon, Lloydia., 15: 118 (1952)

Sobre ramas muertas de árbol no identificado. Monte de los Gallos. 13. VII. 1982, A. MERCADO 6759 (HAC).

Conidios pardos, $48,5\text{--}68,5 \times 20,5\text{--}25,4\ \mu\text{m}$.

10. *Gangliostilbe* sp.**

Sobre tronco muerto. Monte de los Gallos. 13. VII. 1982, A. MERCADO 6759 (HAC).

Colonias dispersas, negras, pelosas. Micelio inmerso en el sustrato. Sinemas fácilmente visibles bajo el microscopio estereoscópico, cilíndricos, pardo negruzcos, hasta de $600\ \mu\text{m}$ de longitud por $22,8\text{--}35\ \mu\text{m}$ y $23\text{--}56\ \mu\text{m}$ en la base. Conidióforos macronematosos, sinematosos, rectos, con filamentos muy unidos hasta el ápice, lisos, pardos, $3\text{--}4\ \mu\text{m}$ de grosor en la parte superior. Células conidiógenas monoblásticas, integradas, determinadas, cilíndricas, pardas. Conidios obovoides o elipsoidales, solitarios, lisos, con dos septos transversales, pardo dorados a pardo algo oscuros; $30,5\text{--}36 \times 13,5\text{--}16\ \mu\text{m}$.

El género *Gangliostilbe* Subramanian et Vittal, sólo incluye la especie tipo *G. indica* que se colectó sobre hojarasca de *Bambusa* sp., según CARMICHAEL et al. (1980). Nosotros incluimos este hongo dentro del género, pero no podemos definir si se trata de la especie tipo, con la cual presenta gran semejanza, o de otra especie, debido a que no se ha podido consultar la descripción original. El género *Gangliostilbe* constituye un nuevo reporte para Cuba y para el Hemisferio Occidental.

11. *Gyrothrix cubensis* Mena et Mercado spec. nova

Coloniae effusae, cinereae, brunneae vel atro-brunneae, velutinae. Mycelium partim superficiale, partim in substratum immersum. Setae erectae, crassae, tunicatae, verrucosae, brunneae, 2–4 subdichotomae, dichotomae vel verticillatae, ramosae, $80\ \mu\text{m}$ longae, 4–5.2 basi μm crassae. Cellulae conidiogenae ex lateribus hypharum superficialium surgentes, obclavatae vel lageniformes; $5,5\text{--}9 \times 2,8\text{--}4,2\ \mu\text{m}$. Conidia fusiformia, recta, hyalina vel subhyalina; $6\text{--}8,5 \times 0,5\text{--}1\ \mu\text{m}$.

Holotypus: in cortice trunci mortui. Los Llanos de Padilla, Topes de Collantes, Cuba. 2. II. 1983, A. MERCADO 7027 (HAC).

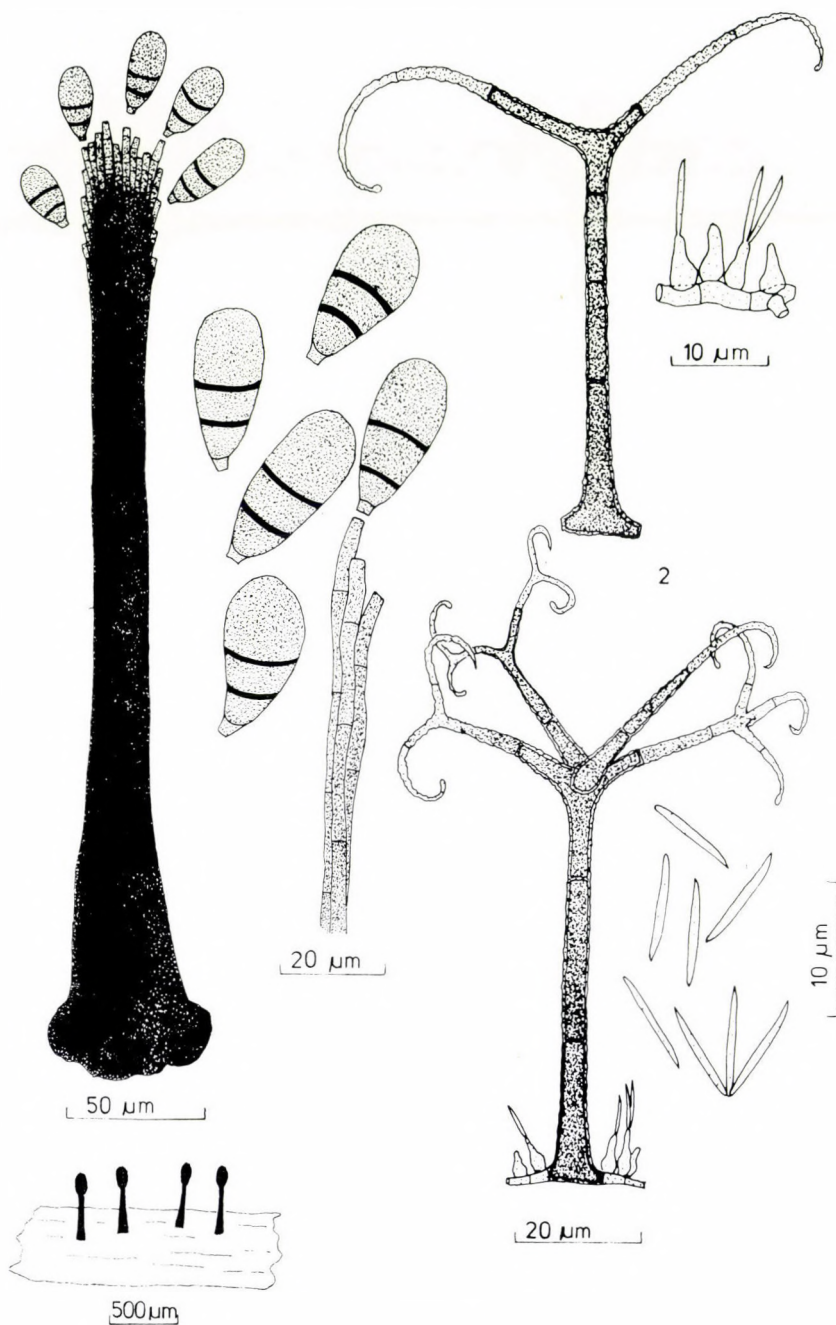


Lámina II

Fig. 1. Gangliostilbe sp. Sinema, conidióforos, células conidiógenas y conidios. Se observan varios sinemas en su hábitat

Fig. 2. Gyrothrix cubensis Mena et Mercado spec. nova. Setas ramificadas, conidióforos, células conidiógenas y conidios

Colonias dispersas, pardo gris a pardo oscuras, aterciopeladas. Micelio parte superficial y parte inmerso en el sustrato. Setas numerosas, erectas, septadas; paredes gruesas, rugosas, ramificadas 2-4 veces, subdicotómicamente, dicotómicamente o formando un verticilo en el extremo del tronco de las setas; hasta de 80 μm de longitud por 4-5,2 μm de grueso en la base. El tronco principal grueso es recto o ligeramente flexuoso, finamente verrugoso a verrugoso, pardo; ramas rimarias rectas e espiraladas, verrugosas, pardo oliváceas; ramas secundarias espiraladas, oliváceas o subhialinas, en ocasiones con el extremo algo engrosado. Células conidiógenas que surgen lateralmente de las hifas superficiales, obclaviformes o lageniformes; 5,5-9 $\times$ 2,8-4,2 μm . Conidios fusiformes, rectos, hialinos o subhialinos, 6-8,5 $\times$ 0,5-1 μm .

Holotipo: Sobre corteza de tronco muerto. Los Llanos de Padilla, Topes de Collantes, Sancti Spiritus, Cuba. 2. II. 1983, A. MERCADO 7027 (HAC).

Las setas de *Gyrophthrix cubensis* presentan diferente grado de ramificación que puede ir de una forma bastante sencilla, con dos o tres ramas principales, ramificadas fundamentalmente, en forma subdicotómica, similar a lo que ocurre en las setas de *G. thevetiae* y *G. circinata*, o puede formar una ramificación más compleja que consiste en que las ramas de las setas de esta especie se disponen formando verticilo en el extremo del tronco principal, algo parecido a lo que ocurre en *G. flagella*, pero en esta especie las ramas son muy largas y flageladas, además de que no se encuentran situadas en el extremo de las setas como ocurre en *G. cubensis*. La principal característica que diferencia las setas de *G. cubensis* de las setas de estas especies y de las otras incluidas dentro del género, es el pequeño tamaño que tienen, pues no sobrepasan nunca los 80 μm de longitud. Los conidios de este nuevo taxon son muy pequeños y delgados; 6-8,5 $\times$ 0,5-1 μm , y sólo *G. microsperma* y *G. thevetiae* tienen conidios que se aproximan en longitud, 6-8 μm y 7-10 μm respectivamente, no así en grosor, que en estas especies es mayor. Además los conidios de *G. thevetiae* son falciformes y los de *G. microsperma* son cilíndricos o elipsoidales, mientras que los de *G. cubensis* son fusiformes.

12. *Gyrophthrix grisea* Pirozynski, Mycol. Pap., 84: 17 (1962)

Sobre hojas muertas de *Roystonea regia* (H. B. K.) O. F. Cook. Los Llanos de Padilla. 2. II. 1983, A. MERCADO 7043 (HAC).

Colonias dispersas, pardo gris o pardo rojizas. Setas pardo oliváceas, más oscuras en la base y más pálidas hacia el ápice, hasta de 190 μm de largo, 3-5 μm de grueso en la base, alrededor de 0,5 μm en los extremos de las ramas. Células conidiógenas lageniformes, subhialinas; 5-9,5 $\times$ 3-4 μm . Conidios hialinos; (9,5-) 11,5-18 $\times$ 1-1,5 μm .

13. *Gyrophthrix podosperma* (Corda) Rabenhorst var. *falcatispora* Mercado et Mena var. *nova*

A var. *podosperma* conidiis falcatis longioribus, 13,5-20,5 μm longis differt.

Holotypus: in foliis mortuis caducis. Los Llanos de Padilla, Topes de Collantes, Sancti Spiritus, Cuba. 2. II. 1985, A. MERCADO 7044 (HAC).

Colonias dispersas, pardo oscuras, aterciopeladas. Micelio superficial compuesto por hifas septadas, lisas, subhialinas a oliváceo oscuras, ramificadas, anastomosadas, que portan células conidiógenas y setas, con paredes gruesas, y de color pardo algo oscuro en el punto de origen de las setas. Setas numerosas, erectas, septadas, de paredes gruesas, pardas, ramificadas subdicotómicamente 4-6 veces, hasta de 200 μm de longitud y 5-6,5 μm de grueso en la base.

El tronco principal recto, pardo algo oscuro, liso o finamente verrugoso; ramas primarias rectas o espiraladas, lisas o finamente verrugosas; ramas secundarias oliváceas, subhialinas hacia los extremos, mayormente verrugosas, espiraladas o circinadas, aproximadamente de $1\ \mu\text{m}$ de grosor en el final de las ramas. Células conidiógenas que surgen lateralmente de las hifas superficiales, obclaviformes a lageniformes, subhialinas; $6\text{--}10,1\ \mu\text{m}$ de largo por $3\text{--}5\ \mu\text{m}$ de grueso en la base. Conidios falciformes o ligeramente curvos, hialinos, sin septos, lisos; $13,5\text{--}20,5 \times 1,5\text{--}2\ \mu\text{m}$.

Holotipo: Sobre hojarasca. Los Llanos de Padilla, Topes de Collantes, Sancti Spiritus, Cuba. 2. II. 1983, A. MERCADO 7044 (HAC).

La variedad *falcatispora* difiere fundamentalmente de la variedad *podosperma* en que los conidios son mayormente falciformes y miden de $13,5\text{--}20,5\ \mu\text{m}$ de longitud, mientras que en *G. podosperma* var. *podosperma* son rectos o ligeramente curvos y miden $8\text{--}16\ \mu\text{m}$ de largo.

14. *Helicoma ambiens* Morgan, Cincinnati Soc. Nat. Hist. J., 15–45 (1892)

Sobre el pecíolo de la hoja muerta de *Roystonea regia* (H. B. K.) O. F. Cook. Los Llanos de Padilla. 2. II. 1983, A. MERCADO 7018 (HAC).

Conidióforos pardos, $150\ \mu\text{m}$ de longitud por $(4,5\text{--})\ 5\text{--}6\ \mu\text{m}$ de grueso. Conidios subhialinos con el filamento enrollado, con $(6\text{--})\ 7\text{--}9$ septos no constreñidos y un grosor de $5\text{--}6\ \mu\text{m}$. Diámetro total del conidio enrollado, $12,7\text{--}15,2\text{--}(16)\ \mu\text{m}$.

El diámetro de los conidios del espécimen de Topes de Collantes es menor que el reportado en descripciones anteriores de esta especie. En el material de Sierra del Rosario, Cuba, el diámetro total del conidio es de $14\text{--}18,5\ \mu\text{m}$ (MERCADO 1982).

15. *Helicoma muelleri* Corda, Icon. Fung., 1: 15 (1837)

Sobre ramas muertas de *Smilax* sp. Los Llanos de Padilla. 2. II. 1983, A. MERCADO 7014, 7035 (HAC).

Colonias dispersas, pardo negruzcas. Conidióforos pardos, oscuros hacia la base, más pálidos hacia el extremo apical, hasta de $425\ \mu\text{m}$ de longitud, $4,5\text{--}6\ \mu\text{m}$ de grosor, $6,5\text{--}9\ \mu\text{m}$ de grueso en la base. Conidios hialinos o subhialinos, filamentos enrollados, con $6\text{--}8$ septos, $5\text{--}6\ \mu\text{m}$ de grueso. Diámetro total del conidio $(14\text{--})\ 16,5\text{--}20,3\ \mu\text{m}$.

16. *Helicomyces roseus*** Linder, Ann. Missouri Bot. Gard., 16: 271–272 (1929)

Sobre hojas muertas de *Roystonea regia* (H. B. K.) O. F. Cook. Los Llanos de Padilla. 2. II. 1983. A. MERCADO 7043 (HAC).

Colonias dispersas, blancas. Micelio mayormente inmerso. Conidióforos muy cortos, hialinos a subhialinos; $25\text{--}35,6 \times 4,5\text{--}5,2\ \mu\text{m}$. Conidios hialinos; filamentos enrollados, multi-septados, $3\text{--}4,5\ \mu\text{m}$ de grueso, con el extremo libre subulado, el extremo basal redondeado y truncado lateralmente. Diámetro total del conidio $35\text{--}47\ \mu\text{m}$.

17. *Helicorhoidion botryoides* (Cooke) Hughes, Can. J. Bot., 36: 773 (1958)

Sobre ramas muertas de *Securidaca virgata* L. Mogote de la Solapa. 13. VII. 1982, A. MERCADO 6752 (HAC).

Colonias dispersas, pardo oliváceas a negras. Conidios pardo algo oscuros a pardo oscuros; $25\text{--}33 \times 15\text{--}18\ \mu\text{m}$.

18. *Helicosporium guianensis* Linder, Ann. Mo. Bot. Gard., 16: 280–281 (1929)

Sobre inflorescencia marchita. Mogote de la Solapa. 13. VII. 1982, A. MERCADO 6763 (HAC).

Colonias dispersas, parduscas. Conidióforos pardos, hasta de 185 μm de longitud, 3–4 μm de grueso. Conidios hialinos; filamentos enrollados higroscópicos, 1,5–1,8 μm de grosor. Diámetro total del conidio 20–23 μm .

19. *Idriella fertilis* (Pirozynski et Hodges) Matsuchima. Icones microfungorum a Matsuchima lectorum, Kobe, Japón, p 87 (1975)**

Sobre hojarasca. Los Llanos de Padilla. 2. II. 1983, A. MERCADO 7044 (HAC).

Colonias dispersas, pardas. Micelio inmerso en el sustrato. Estípites setiformes, subulados, pardos, septados, que en ocasiones presentan un engrosamiento cerca del ápice, muy raramente ramificados, hasta de 330 μm de longitud. Células conidiógenas agrupadas en uno o dos puntos sobre las setas, ampuliformes, subhialinas; 4,5–7,5 $\times$ 3–4,5 μm . Conidios subhialinos, falciformes, sin septos; (11–) 12,5–15,2 (–17) $\times$ 1,5–2 μm .

MATSUCHIMA (1975) transfiere *Circinotrichum fertile* al género *Idriella* como *I. fertilis*. En Topes de Collantes se encontró sobre hojarasca este taxon, que por constituir un nuevo reporte para Cuba, y estar poco colectada a nivel mundial, es ilustrada en este trabajo.

20. *Monodictys nigra** Matsuchima, Icones microfungorum a Matsuchima lectorum, Kobe, Japón, p 98 (1975)

Sobre ramas muertas de *Licaria jamaicensis* (Nees) Kosterman y sobre ramas muertas no identificadas. Los Llanos de Padilla. 2. II. 1983, A. MERCADO 7006, 7023 (HAC).

Colonias dispersas, negras. Conidios pardo algo oscuros o pardo negruzcos; (18–) 24–41 $\times$ (13–) 15–24 μm .

El espécimen cubano de *Monodictys nigra* solo difiere de la descripción original, en que los conidios son, en ocasiones, ligeramente menos oscuros.

21. *Monodictys* sp.

Sobre ramas muertas no identificadas y sobre ramas muertas de *Coffea* sp. Los Llanos de Padilla. 2. II. 1983, A. MERCADO 7023, 7051 (HAC).

Colonias dispersas, pardo negruzcas. Conidios pardos; 28–56 $\times$ (20–) 25–36 (–45) μm .

22. *Mycoenterolobium platysporum** Goos var. *magnum* Mercado et Mena var. *nova*

A var. *platysporo* conidiis majoribus, 85–153 $\times$ 95–246 μm in diametro differt.

Holotypus: in ramis mortuis *Securidacae virgatae* L., Mogote de la Solapa, Topes de Collantes, Sancti Spiritus, Cuba. 13. VII. 1982, A. MERCADO 6752 (HAC).

Colonias dispersas, negras, brillantes. Micelio parcialmente inmerso en el sustrato. Conidióforos micronematosos, lisos, hialinos o subhialinos, 2–3 μm de grosor. Conidios solitarios, aplanados en un plano, muy variables en forma, lobulados, muriformes, pardo muy oscuros a negros, lisos, brillantes; 85–153 $\times$ 95–246 μm .

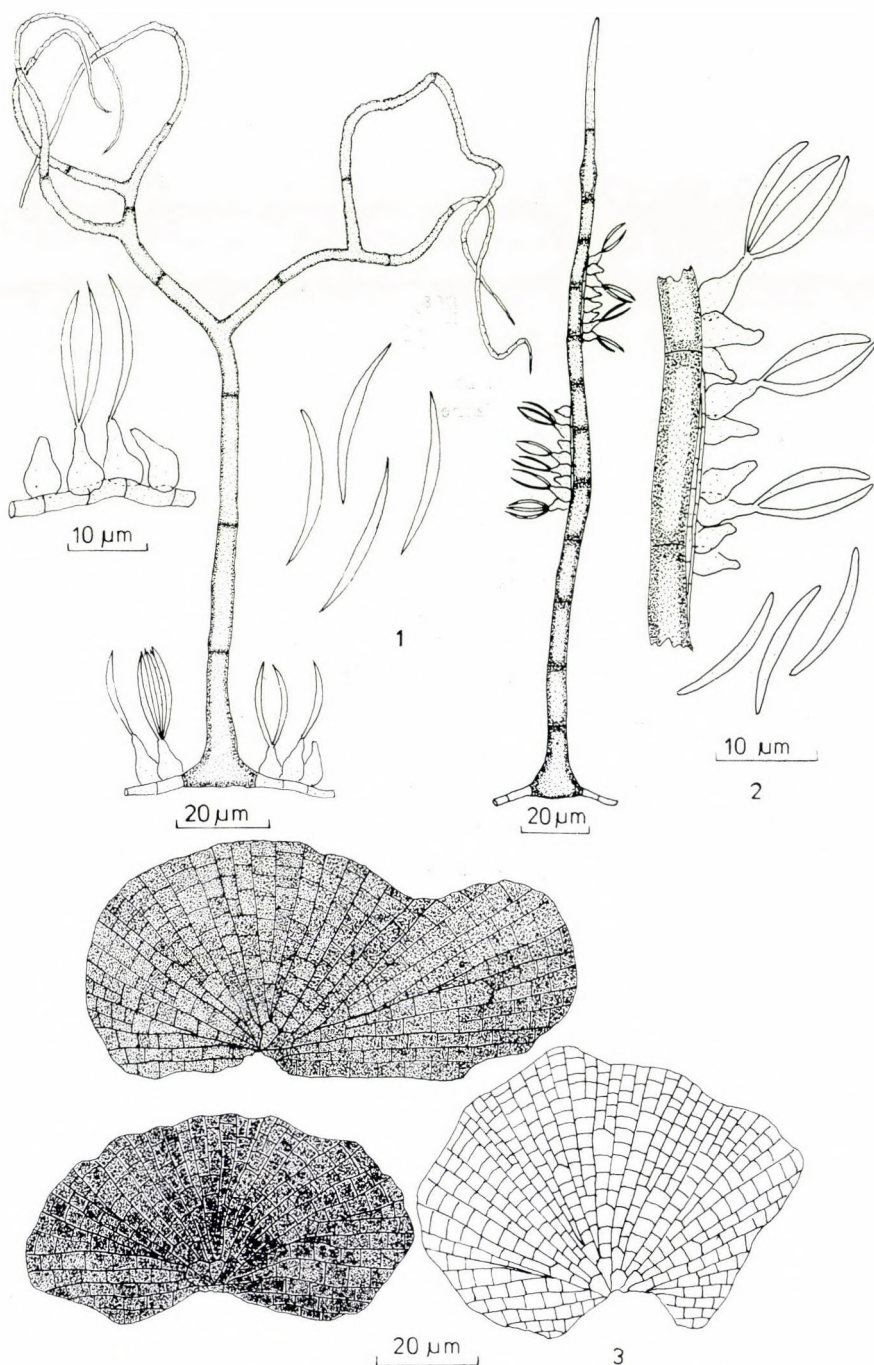


Lámina III

Fig. 1. *Gyrothrix podosperma* var. *falcatispora* Mercado et Mena var. nova. Setas, conidióforos, células conidiógenas y conidios falciformes

Fig. 2. *Idriella fertilis* (Pirozynski et Hodges) Matsuchima. Setas, células conidiógenas y conidios

Fig. 3. *Mycoenterotobium platysporum* Goos var. *magnum* Mercado et Mena var. nova. Conidios de forma irregular. Se observan las hileras de células que parten radialmente del punto de unión del conidio con el conidióforo

Holotipo: Sobre ramas muertas de *Securidaca virgata* L., Mogote de la Solapa, Sancti Spiritus, Cuba. 13. VII. 1982, A. MERCADO 6752 (HAC).

El género *Mycoenterolobium* lo estableció Goos (1970) con la especie tipo *M. platysporum*, a partir de material que colectó en Hawai. Los conidios de esta especie, según la descripción original son fuertemente aplanados, negros, de forma variable y están compuestos por hileras de células que parten radialmente del punto de unión del conidio con el conidióforo. *M. platysporum* se halló recientemente en Isla de la Juventud, Cuba (HOLUBOVÁ-JECHOVÁ y MERCADO 1984), y en este espécimen los conidios coinciden exactamente con la descripción original de la especie. La variedad *magnum* difiere de la variedad *platysporum* en que los conidios alcanzan dimensiones mucho mayores, casi el doble y presentan mayor variabilidad en su morfología.

23. *Periconia byssoides* Pers. ex Mérat., Nouv. Fl. Environs Paris, Ed. 2, 1: 18-19 (1821)

Sobre ramas muertas no identificadas. Mogote de la Solapa. 15. VII. 1983. A. MERCADO 6753 (HAC); sobre ramas muertas de *Serjania diversifolia* (Jacq.) Radlk. y sobre hojas muertas de *Cecropia peltata* L. Los Llanos de Padilla. 2. II. 1983, A. MERCADO 7003, 7041 (HAC).

Colonias dispersas, pardo oscuras. Conidióforos pardos, hasta de 1063 μm de longitud, 18-25 (-28) μm de grueso en la base, 12-15,2 μm debajo de la cabeza. Conidios pardos, 12-16 μm de diámetro.

24. *Periconia digitata* (Cooke) Sacc., Syll. Fung., 4: 274 (1886)

Sobre hojas muertas de graminea. Monte de Jesús Delgado. 14. VII. 1982, A. MERCADO 6787 (HAC).

Colonias dispersas, pardo oscuras. Conidióforos pardos, hasta de 600 μm de longitud, (10,1-) 12,7-15,2 μm de grosor en la base, (6,5-) 7,6-10,1 μm debajo de la cabeza. Conidios pardos; 7,6-8 μm de diámetro.

25. *Periconia minutissima* Corda, Icon. Fung., 1: 19 (1837)

Sobre hojas muertas de graminea. Monte de Jesús Delgado. 14. VII. 1982, A. MERCADO 6814 (HAC); sobre hojas muertas de *Roystonea regia* (H. B. K.) O. F. Cook. Los Llanos de Padilla. 2. II. 1983, A. MERCADO 7043 (HAC).

Colonias dispersas, negras. Conidióforos hasta de 600 μm de longitud, 9,5-16 μm en la base, 5,5-7,6 μm debajo de la cabeza. Conidios de 4-6 (-7,5) μm de diámetro.

26. *Periconiella trichostigmae Mena et Mercado spec. nova**

Coloniae effusae, cinereae vel olivaceo-brunneae. Mycelium superficiale e hyphis ramosis, septatis, brunneis, verrucosis, 4,5-6,5 μm crassis compositum. Conidiophora magnifilamentosa, unifilamentosa, brunnea, recta vel leviter flexuosa. Stipites 230 μm longi, 5,2-6 μm lati. Cellulae conidiogenae polyblasticae, apicales, cylindricae. Conidia precipue singula, ellipsoidea vel cylindrica, laevia, aseptata, hyalina vel subhyalina; 7,6-10,1 $\times$ 2-3 μm .

Holotypus: in ramis mortuis *Trichostigmae octandri* (L.) H. Walt. Los Llanos de Padilla, Topes de Collantes, Sancti Spiritus, Cuba. 2. II. 1983, A. MERCADO 7016 (HAC).

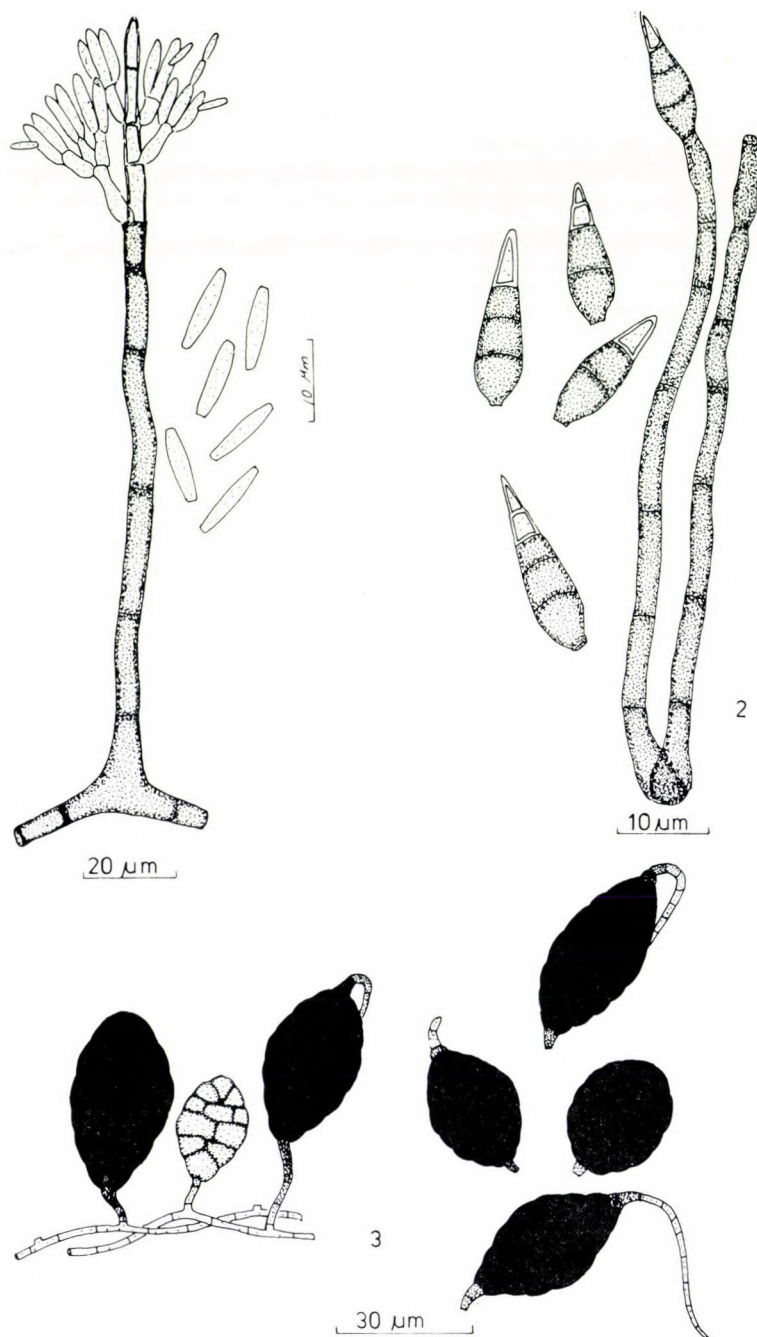


Lámina IV

Fig. 1. *Periconiella trichostigmae* Mena et Mercado spec. nova. Conidióforos, células conidiógenas y conidios

Fig. 2. *Sporidesmium coffeicola* M. B. Ellis. Conidióforos, células conidiógenas y conidios

Fig. 3. *Pithomyces niger* Mercado et Mena spec. nova. Micelio vegetativo, conidióforos, células conidiógenas y conidios apendiculados

Colonias dispersas, grises a pardo oliváceas. Micelio superficial compuesto de hifas ramificadas, septadas, mayormente rugosas, pardas, más oscuras en el punto donde surgen los conidióforos; 4,5–6,5 μm de grueso. Conidióforos macronematosos, mononematosos, compuestos de un estípito erecto, recto o ligeramente flexuoso, liso, pardo; 230 μm de longitud, 5,2–6 μm de grueso, y de una cabeza formada por ramas primarias oliváceas a pardo oliváceas y ramas. Células conidiógenas poliblasticas, terminales, cilíndricas, cicatrizadas. Conidios solitarios o muy raramente en cortas cadenas, elipsoidales o cilíndricos, lisos, sin septos, hialinos o subhialinos; 7,6–10,1 $\times$ 2–3 μm .

Esta especie está relacionada principalmente con *P. velutina* y *P. anisophylleae*. Las ramas de los conidióforos en *P. trichostigmae* no se disponen de forma tan esparcida como en *P. velutina*, ni tan apretadamente como en *P. anisophyllae*. Los conidios de *P. velutina* en ocasiones presentan un septo, pueden ser lisos o rugosos y miden 7–12 (9) $\times$ 2,5–4 (3,4) μm ; los de *P. anisophylleae* son ligeramente rugosos, sin septos y miden 5–8 (6,5) $\times$ 2,4–4 (3,2) μm (ELLIS 1967), mientras que en el nuevo taxon propuesto, los conidios son siempre lisos y sin septos y sus dimensiones van de 7,6–10,1 $\times$ 2–3 μm .

27. *Phaeoisaria clematidis* (Fuckel) Hughes, Can. J. Bot., 36: 795 (1958)

Sobre ramas muertas de *Smilax* sp., *Ampelocera cubensis* Gris. y *Zanthoxylum* sp. Los Llanos de Padilla. 2. II. 1983, A. MERCADO 7035, 7036, 7040 (HAC).

Colonias dispersas, negras. Sinemas hasta de 500 μm de largo por 20–40 (–51) μm de grueso en la base; 8,5–15,2 (–20) μm en el ápice. Conidios hialinos o subhialinos, 4–7 $\times$ 1,4–2 μm .

28. *Pithomyces cinnamomeus* Hol-Jech, Česka Mykol., 38 (2): 112 (1984)

Sobre tronco muerto de *Bambusa* sp. y sobre rama muerta de *Coffea* sp. Los Llanos de Padilla. 2. II. 1983, A. MERCADO 7019, 7050 (HAC).

Colonias puntiformes, pardo oscuras. Conidios pardo oliváceos, 20–43 $\times$ (12,7–) 15–22 μm .

29. *Pithomyces niger* Mercado et Mena spec. nova*

Coloniae punctiformes, nigrae. Mycelium superficiale e hyphis ramosis, septatis, laevibus, subhyalinis vel olivaceo-brunneis, 2–2,5 μm crassis compositum. Conidiophora singula, recta vel flexuosa, brunnea, circa 10,5 μm longa, 2,5–3 μm lata. Conidia singula, acrogena, limoniformia, ellipsoidea vel subglobosa, laevia, nigra, appendiculata, constricto-muriformia; 30,5–41 $\times$ 23–28 μm .

Holotypus: in truncis mortuis *Bambusae* sp. Los Llanos de Padilla, Topes de Collantes, Sancti Spiritus, Cuba. 2. II. 1983, A. MERCADO 7019 (HAC).

Colonias puntiformes, negras. Micelio superficial compuesto de hifas ramificadas, septadas, anastomosadas, lisas, subhialinas a pardo oliváceas, 2–2,5 μm de grosor. Conidióforos que surgen irregularmente sobre las hifas, simples, rectos o flexuosos, pardos; hasta de 10,5 μm de longitud por 2,5–5 μm de grueso. Conidios solitarios, acrógenos, limoniformes, elipsoidales o subglobosos, apendiculados, negros, lisos, constrictos en los septos, 30,5–41 $\times$ 25–28 μm . Los septos transversales y longitudinales de los conidios sólo son visibles cuando los conidios son jóvenes.

Holotipo: Sobre tronco muerto de *Bambusa* sp. Los Llanos de Padilla, Topes de Collantes, Sancti Spiritus, Cuba. 2. II. 1983, A. MERCADO 7019 (HAC).

Otros ejemplares examinados. Sobre tronco muerto no identificado, Monte de Jesús Delgado. 14. VII. 1982, A. MERCADO 6786 (HAC).

La especie *Pithomyces niger* presenta gran similitud con *P. pulvinatus*, respecto a la forma y coloración de los conidios, que en ambos casos pueden ser, principalmente, limoni-formes y de color negro o negruzco, pero en *P. niger* los conidios tienen dimensiones mucho menores que en *P. pulvinatus*, además de que, frecuentemente, poseen un apéndice que no se incluye en la descripción de *P. pulvinatus* (ELLIS 1971).

30. *Pithomyces sacchari* (Speg.) M. B. Ellis, Mycol. Pap., 76: 19 (1960)

Sobre hojas muertas. Campamento de Pioneros. 15. VII. 1982, A. MERCADO 6750 (HAC).

Colonias puntiformes, pardo oliváceas a pardo oscuras. Conidios de color pajizo o pardo, $15,2-25,4 (-27) \times (6,5-) 7,6-12,7 \mu\text{m}$.

31. *Pleurophragmium parvisporum*** (Preuss) Hol-Jech, Česka Mykol., 26 (4): 223-225 (1972)

Sobre ramas muertas no identificadas y sobre ramas muertas de *Nectandra coriacea* (Sw.) Gris. Los Llanos de Pédilla. 2. II. 1983, A. MERCADO 7048, 7049 (HAC).

Colonias dispersas, pardo pálidas a pardo oscuras. Conidióforos pardos a pardo oscuros, subhialinos hacia el ápice, hasta de $205 \mu\text{m}$ de longitud, $7,6-10,4 \mu\text{m}$ de grueso en la base, $4,5-5,2 \mu\text{m}$ en el resto. Conidios hialinos o subhialinos, $13-16,5 \times 4-5,5 \mu\text{m}$.

32. *Pseudobotrytis terrestris*** (Timonin) Subram., Proc. Indian Acad. Sci., Sect B, 43: 277 (1956)

Sobre pecíolo de la hoja muerta de *Roystonea regia* (H. B. K.) O. F. Cook. Los Llanos de Padilla. 2. II. 1983. A. MERCADO 7056 (HAC).

Colonias dispersas, pardas. Conidióforos pardos a pardo algo oscuros, hasta de $330 \mu\text{m}$ de longitud, $(4,5-) 5-6,5 \mu\text{m}$ de grosor cerca de la base. Conidios pardo pálidos, $7-8 \times 2,5-3,5 \mu\text{m}$.

33. *Pseudospiropes simplex* (Kunze ex Pers.) M. B. Ellis, Dematiaceous Hyphomycetes, C.M.I. Kew., p. 260 (1971)

Sobre ramas muertas no identificadas, pecíolo de la hoja muerta de *Roystonea regia* (H. B. K.) O. F. Cook y ramas muertas de *Coffea* sp. Los Llanos de Padilla. 2. II. 1983, A. MERCADO 7012, 7034, 7050 (HAC).

Colonias dispersas, pardo oscuras o pardo negruzcas. Conidióforos pardo oscuros, pálidos hacia el ápice, hasta de $120 \mu\text{m}$ de longitud, $5-6,5 \mu\text{m}$ de grosor. Conidios pardo dorados, $(28-) 33-40,5 (-49) \times 11-12,7 (-15,2) \mu\text{m}$.

34. *Rhinocladiella*** estado de *Dyctiotriciella manssoni* Schol-Schwarz, Antonie van Leeuwenhoek., 34: 122-135 (1968)

Sobre hojas muertas de *Roystonea regia* (H. B. K.) O. F. Cook. Los Llanos de Padilla. 2. II. 1983, A. MERCADO 7043 (HAC).

Colonias dispersas, oliváceas. Conidióforos pardo oliváceos, $33-90 \times 2,5-3 \mu\text{m}$. Conidios $2,5-4,5 \times 1,5-2 \mu\text{m}$. Los conidióforos de esta especie, según la descripción de ELLIS (1971) llegan hasta $60 \mu\text{m}$ de longitud y los conidios van de $4-6 \times 1-2 \mu\text{m}$. En el material cubano los conidióforos alcanzan hasta $90 \mu\text{m}$ de longitud, mientras que los conidios son ligeramente menores.

35. *Sporidesmium brachypus** (Ellis et Everh.) Hughes, Can. J. Bot., 36: 807 (1958)

Sobre ramas muertas de *Ocotea leucoxylon* (Sw.) Mez. y sobre pecíolo de la hoja muerta de *Roystonea regia* (H. B. K.) O. F. Cook. Los Llanos de Padilla. 2. II. 1983, A. MERCADO 7028, 7034 (HAC).

Colonias dispersas, pardo oscuras a negras. Conidióforos pardos, algo oscuros, $30-86 \times 5-6 \mu\text{m}$. Conidios ocráceos a pardo dorados, $56-76 \times 9,5-15 \mu\text{m}$.

36. *Sporidesmium coffeicola** M. B. Ellis, More Dematiaceous Hyphomycetes, C.M.I., Kew., p 87-88 (1976)

Sobre ramas muertas no identificadas y sobre ramas vivas y muertas de *Coffea* sp. Los Llanos de Padilla. 2. II. 1983, A. MERCADO 7004, 7010, 7047, 7051 (HAC).

Colonias dispersas, pardas a negras. Micelio inmerso en el sustrato. Conidióforos rectos o flexuosos, pardos, hasta de $115 \mu\text{m}$ de longitud, $2,5-4 \mu\text{m}$ de grosor, con 0-3 proliferaciones cilíndricas o lageniformes. Conidios estrechamente obpiriformes a obclaviformes, 2-3 (-4) septos; $13,5-20,3$ (-25) μm de largo, (3,5-) $4-5 \mu\text{m}$ de grueso, 2-3 μm en la base, con las dos células inferiores pardas y las superiores subhialinas.

Sporidesmium coffeicola solo reportado por ELLIS (1976) sobre hojas de *Coffea robusta* en el Oeste de Irán, se encontró en cuatro ocasiones en Topes de Collantes. Esta especie se lustra aquí, por presentar el material cubano algunas diferencias con el iraní, y por constituir el primer reporte para Cuba y para el Hemisferio Occidental. Los conidióforos en los especímenes cubanos son más largos y menos gruesos que lo planteado en la descripción inicial de esta especie. Los conidios también son más delgados, lo que influye en que su forma varíe y no sean piriformes sino estrechamente obpiriformes u obclaviformes y se encontraron algunos que podían presentar hasta 4 septos y $25 \mu\text{m}$ de longitud.

37. *Sporidesmium coronatum** Fuckel, Symb. mycol., Nachtrag 2: 77 (1874)

Sobre ramas muertas no identificadas, sobre ramas muertas de *Mikania* sp. y de *Zanthoxylum* sp. Los Llanos de Padilla. 2. II. 1983, A. MERCADO 7004, 7021, 7040 (HAC).

Colonias dispersas, pardo oliváceas a pardo oscuras. Conidióforos pardos, $25-78 \times 4-5 \mu\text{m}$. Conidios pardo pálidos, $36-71 \times 8-12,7 \mu\text{m}$.

38. *Sporidesmium leptosporum* (Sacc. et Roum) Hughes, Can. J. Bot., 36: 808 (1958)

Sobre ramas muertas no identificadas y sobre pecíolo de la hoja muerta de *Roystonea regia* (H. B. K.) O. F. Cook. Los Llanos de Padilla. 2. II. 1983, A. MERCADO 7023, 7056 (HAC).

Colonias dispersas, pardo oscuras. Conidióforos pardos, algo oscuros, hasta de $80 \mu\text{m}$ de longitud, (3,5-) $4-5 \mu\text{m}$ de grosor. Conidios subhialinos a ocráceos, frecuentemente pardo pálidos en la base; $33-53 \times 6-8 \mu\text{m}$.

39. *Sporidesmium tropicale* M. B. Ellis, Mycol. Pap., 70: 58-60 (1958)

Sobre tronco muerto de *Bambusa* sp., sobre ramas muertas de *Nectandra coriacea* (Sw.) Gris. y sobre el pecíolo de la hoja muerta de *Roystonea regia* (H. B. K.) O. F. Cook. Los Llanos de Padilla. 2. II. 1983, A. MERCADO 7019, 7049, 7055 (HAC).

Colonias dispersas, pardo negruzcas. Conidióforos pardos, hasta de $254\ \mu\text{m}$ de longitud, $5-6,5\ \mu\text{m}$ de grosor. Conidios pardos, $81-125 \times 11,5-15,2\ \mu\text{m}$.

40. *Sporidesmium vagum* C. G. et T. F. L. Nees ex Link, in Linne's Sp. Pl., Ed 4 (Willdenow's), 6 (2): 120 (1825)

Sobre ramas muertas no identificadas; sobre ramas muertas de *Ocotea leucoxydon* (Sw.) Mez, *Zanthoxylum* sp., *Gouania polygama* (L.) Radlk., *Coffea* sp., sobre tronco muerto y sobre el pecíolo de la hoja muerta de *Roystonea regia* (H. B. K.) O. F. Cook. Los Llanos de Padilla. 2. II. 1983, A. MERCADO 7004, 7010, 7019, 7028, 7033, 7034, 7037, 7040, 7046, 7048, 7050, 7051, 7052 (HAC).

Colonias dispersas, negras. Conidióforos pardos algo oscuros, $23-61 \times 5-7\ \mu\text{m}$. Conidios pardo a pardo algo oscuros, $125-240 \times 12-14\ (-16,5)\ \mu\text{m}$.

41. *Torula herbarum* f. *quaternella* Sacc., Ann. mycol., 11: 556-557 (1913)

Sobre rama muerta de malvácea. Los Llanos de Padilla. 2. II. 1983, A. MERCADO 7017 (HAC).

Colonias dispersas, pardo oscuras o negras. Conidios pardos, $11-16 \times 5-6,5\ (-7)\ \mu\text{m}$.

42. *Xenosporium berkeleyi* (Curtis) Pirozynski, Mycol. Pap., 105: 27-29 (1966)

Sobre ramas muertas de *Cenchrus* sp. Monte los Gallos. 13. VII. 1982, A. MERCADO 6806 (HAC); sobre tronco muerto de *Bambusa* sp. Los Llanos de Padilla. 2. II. 1983, A. MERCADO 7019 (HAC).

Colonias dispersas, negruzcas. Conidióforos pardos a pardo oscuros, $25-45 \times 6-7\ \mu\text{m}$. Conidios pardo dorados a pardo oscuros, $22-27\ \mu\text{m}$ de diámetro, con un "conidio secundario" que mide $5-7\ \mu\text{m}$ de diámetro.

43. *Xenosporium thaxteri* (Linder) Pirozynski, Mycol. Pap., 105: 30-33 (1966)

Sobre ramas muertas de *Cenchrus* sp. Monte los Gallos. 13. VII. 1982, A. MERCADO 6806 (HAC); sobre el pecíolo de la hoja muerta de *Roystonea regia* (H. B. K.) O. F. Cook. 2. II. 1983, A. MERCADO 7034 (HAC).

Colonias puntiformes, pardo oscuras a negruzcas. Conidióforos subhialinos a pardo pálidos, muy cortos, $5-7\ \mu\text{m}$ de grueso. Conidios al principio subhialinos, luego pardos a pardo algo oscuros, $44-53\ \mu\text{m}$ de diámetro; presentan 2-4 "conidios secundarios" de $6-7,6\ \mu\text{m}$ de diámetro.

44. *Zygosporium gibbum* (Sacc., Rouss et Bomm.) Hughes, Can. J. Bot., 36: 825 (1958)

Sobre hojas muertas. Monte los Gallos. 13. VII. 1982, A. MERCADO 6793 (HAC).

Colonias dispersas, pardo oscuras. Vesículas pedunculadas que surgen directamente de hifas del micelio, pardo oscuras, $10-12,7 \times 7,6-9\ \mu\text{m}$. Conidios hialinos, $3,5-5\ \mu\text{m}$ de diámetro.

En este espécimen el diámetro de los conidios puede ser ligeramente menor que el que se reporta para esta especie (ELLIS 1971) y más recientemente para Cuba (MERCADO 1984).

45. *Zygosporium mycophilum** (Vuill.) Sacc., *Annls mycol.*, 9: 256 (1911)

Sobre hojas muertas. Monte los Gallos. 13. VII. 1982, A. MERCADO 6793 (HAC).

Colonias dispersas, pardas. Vesículas sobre largos pedúnculos que surgen directamente de hifas del micelio superficial, pardas, $11-17 \times 6-7,6 \mu\text{m}$. Conidios elipsoidales, hialinos, lisos o finamente verrugosos, $6-7,5 \times 4-6,5 \mu\text{m}$.

46. *Zygosporium minus* Hughes, *Mycol. Pap.*, 44: 6-7 (1951)

Sobre hojas muertas. Monte los Gallos. 13. VII. 1982, A. MERCADO 6793 (HAC).

Colonias dispersas, pardo negruzcas. Conidióforos pardo pálidos o pardos, hasta de $35 \mu\text{m}$ de largo, $2-3 \mu\text{m}$ de grosor en la base. Vesículas pardo oscuras, $8-9 \times 5-6,5 \mu\text{m}$. Conidios hialinos, $6-7,6 \mu\text{m}$ de diámetro.

47. *Zygosporium oscheoides* Mont., *Ann. Sci. nat., Sér. 2*, 77: 121 (1842)

Sobre hojas muertas. Monte los Gallos. 13. VII. 1982, A. MERCADO 6793 (HAC); sobre ramas muertas de *Serjania diversifolia* (Jacq.) Radlk; sobre hojas muertas de *Panicum* sp., *Cecropia peltata* L., *Roystonea regia* (H. B. K.) O. F. Cook y sobre hojarasca. Los Llanos de Padilla. 2. II. 1983, A. MERCADO 7003, 7022, 7041, 7043, 7044 (HAC).

Colonias dispersas, parduscas o negras. Conidióforos pardos, pardo pálidos hacia el ápice, hasta de $45 \mu\text{m}$ de longitud, $2,5-3,5 \mu\text{m}$ de grosor en la base. Conidios hialinos o subhialinos, $7-10 \times 4,1-5 \mu\text{m}$.

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**RICCARDIA REYESIANA,
A NEW LIVERWORT FROM CUBA**

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Riccardia reyesiana is described from Cuba, as new to science. It is related to *R. sprucei* (Steph.) Meenks et De Jong.

This report is preliminary to the Hepatic Flora of Cuba (Hepáticas de Cuba) which is currently in preparation. The author studied the Aneuraceae Klinggr., a family in Cuba represented by two genera: *Aneura* Dum. and *Riccardia* S. F. Gray. While *Aneura sessilis* (Spreng.) Gott., Lindenb. & Nees is the only representative of its genus, there occur eleven *Riccardia* species on the island. In the present paper one of these *Riccardias* is described as new for science. It is dedicated to Sra. Deisi REYES MONTOYA (Santiago de Cuba), bryologist and one of the initiators of the projected Hepatic Flora of Cuba.

***Riccardia reyesiana* Meenks sp. nov.**

Plantae repentes vel erectes, virides, ad 1.3 cm longae, hyaline alatae (alae 1 vel 7 cellulatae). Ramificatio irregulariter bi- vel tripinnata; ramuli primarii oppositi, ad 5.5 mm longi, apice retusi vel emarginati. Thalli in sectione transversali bi- vel planoconvexi, 0.55-0.75 mm lati, 0.22-0.27 mm (celluli 7-10) crassi, margine acuti. Cellulae epidermales rectangulares, 15×12 -32-30 μm ; cellulae interiores isodiametricae, 15×15 -70 $\times$ 60 μm . Papillae hyalinae frequenter praesentes, obovatae, 40×8 -15 — 50 $\times$ 10-22 μm . Monoica. Inflorescentia archegonialis ad caulem, opposita. Calyptra obovata, ad 2.2×0.5 mm, cellulis externis asperis. Seta 4 cellularis lata in diametro. Valvae capsulae 700-780 μm longae, dimidio 185-270 μm crassae. Sporae 15-26 μm crassae. Elaterae 250-420 μm longae, dimidio 12.5-16.5 μm crassae. Ramuli masculi ad 1.2 mm longi, margine 1-5 cellulares lati, antheridiis usque ad 14 paribus suffulti. Speciem novam in honorem Deisi REYES MONTOYA dedicavi.

Typus: Cuba, prov. of Habana, Sierra del Rosario, Las Terrazas, NE del Estación Forestal; coll. PÓCS and REYES no. 9042/BH (HAC holo; EGR, VBI, BP, U).

The above species is most closely related to *Riccardia sprucei* (Steph.) Meenks et De Jong (1985: 22), a species also known from Cuba. In *R. reyesiana* the archegonial branches are present all along the axis, while those branches in *R. sprucei* only are to be found on the upper part of the axis. The spores

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of *R. reyesiana* are relatively large, up to 26 μm (maximum of *R. sprucei* 18 μm). Noteworthy is also the dorso-lateral wing of the antheridial branches which is 1–3 (5) cells wide and sometimes crenulate; this wing in *R. sprucei* narrow, only 1–2 cells wide and never crenulate.

Illustrations on *R. reyesiana* will be published in the Hepáticas de Cuba (ed. REYES, under preparation).

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NEW OR OTHERWISE INTERESTING SPECIES OF THE GENUS *BRYUM* (MUSCI, BRYACEAE) IN THE ANTARCTIC

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Bryum urbanskyi Broth. in Dryg. and *B. orbiculatifolium* Card. et Broth. are reported for the first time from the Antarctic botanical zone. Descriptions and illustrations of Antarctic material of both species are provided, together with brief notes on their ecology, taxonomy and distribution. *B. amblyodon* C. Muell., previously known only from the Melchior Archipelago, near the Antarctic Peninsula, as *B. inclinatum* (Brid.) Bland. var. *magellanicum* Card., is reported for the first time from King George Island, South Shetland Islands. A description, illustrations and notes on ecology, taxonomy and distribution are given for this species, including an Antarctic distribution map. *B. imperfectum* Card. and *B. inclinatum* (Brid.) Bland. var. *magellanicum* Card. are reduced to synonymy with *B. amblyodon* C. Muell.

Introduction

The genus *Bryum* is very prominent in the moss flora of the Antarctic and about fifteen species have been described or reported from this area. OCHI (1979) provided a critical taxonomic review of this genus in Antarctica and reduced several species to synonymy with cosmopolitan species such as *Bryum pseudotriquetrum* (Hedw.) Gaertn., Meyer et Scherb. and *B. argentum* Hedw. As in other areas, *Bryum* is taxonomically one of the most difficult of all moss genera, particularly because of the common occurrence of sterile plants and the considerable variability of the taxa.

The severe climatic conditions of the southern polar region are not favourable for the production of *Bryum* sporophytes, although some species in other genera e.g. *Andreaea*, *Dicranoweisia* and *Schistidium*, regularly produce fully mature capsules in these conditions (WEBB 1973). Even when *Bryum* species do fruit in the Antarctic, the capsules and spores often remain immature. However, fully mature sporophytes do occur infrequently and are particularly likely to be found on plants growing in microhabitats with favourable temperature conditions.

At present, the southern polar regions are being visited more frequently by professional bryologists. This is resulting in the rapid growth of knowledge about Antarctic bryology and the discovery of species which have not been previously known to grow there. During the Fourth Polish Antarctic Expedition 1979-1980 to King George Island, South Shetland Islands, the senior author discovered several species of mosses including a few species of *Bryum* which proved to be new to the Antarctic botanical zone as defined by GREENE (1964) and SMITH (1984). The first record of *B. dichotomum* Hedw. in Antarctica is reported by the present authors elsewhere (OCHI and OCHYRA 1986).

The present paper is a short account of further new records of *Bryum* in Antarctica. Two species, *B. urbanskyi* Broth. in Dryg. and *B. orbiculatifolium* Card. et Broth., are recorded



Fig. 1. *Bryum urbanskyi* Broth. in Dryg.: A – habit; B – leaves; C – axillary gemmae; D – mid-leaf and marginal cells; E – upper cells with margin; F – basal cells

for the first time from within the Antarctic botanical zone. *B. amblyodon* C. Muell., an older name for *B. inclinatum* (Brid.) Bland. *nom. illeg.*, is reported from the South Shetland Islands for the first time, which is the second record of this species from within the Antarctic botanical zone.

1. *Bryum urbanskyi* Broth in Dryg., Deutsch. Südpolar-Exp. 1901–1903 8 (Botanik): 89, tab. 8, fig. 1. 1906 (Fig. 1)

Type: Kerguelen — am Schwarzen See (Urbansky) (H-Br! — holotype)

Syn.: *Bryum anomobryoides* Card. et Broth., K. Svensk. Vet. Ak. Handl. 63 (10): 38, tab. 2, fig. 13, 1923. Types: "Patagonia occ.: Archip. Adelaide, Isla Atalaya, Puerto Cuarenta Dias (557); Fuegia: Lago Fagnano, ad saxa riparia irrorata" (Lectotype nova: "Herb. Cardot. *Bryum anomobryoides* Card. sp. nova. Patagonie: île Atalaya, rochers maritimes. Leg. C. SKOTTSBERG, 1908" — PC-Card!; Isolectotypes: S!, H-Br!).

Bryum laetevirens Card. et Broth., K. Svensk. Vet. Ak. Handl. 63 (10): 41, tab. 3, fig. 3, 1923. Type: "Patagonia occ.: Peel Inlet, Puerto Témpanos, ad rupes litoreas (555) (H-Br! — holotype; BM!, S-Möller!, PC-Card! — isotypes).

Plants slender in dense, green to yellowish-green above, brown to blackish below, slightly shiny tufts matted with brown radicles, 1.0–2.5 cm high. Stems elongate, unbranched or sparsely branched, red, bearing single, large, brown, broadly oblong or oblong-obovate brood bodies with 3–5, obtuse, well-developed leaf-like points in the upper leaf axils of sterile shoots. Leaves imbricate when dry, slightly spreading when moist, 1.0–1.3 mm long, 0.6–0.8 mm broad, reddish and narrowed at the base, ovate with an obtuse or acuminate apex, occasionally $\pm$ apiculate, concave; margins entire, plane or slightly recurved below, not bordered; costa usually ending below the apex or rarely percurrent. Laminal cells lax, thin-walled; upper cells rhomboid-hexagonal to oblong hexagonal, about 13–15 μ m wide, 30–40 μ m long; lower cells subquadrate to shortly rectangular, in regular rows from the costa to the margin, 15–20 μ m wide, 20–45 μ m long. Sterile.

Specimens examined: Antarctica, South Shetland Islands, King George Island, Admiralty Bay region — (1) Ezcurra Inlet, Dufayel Island: Gdynia Point, 62°09'45" S, 58°33' W, elev. 15 m; in moist crevices of andesite rocks in turfs of *Deschampsia antarctica* Desv., OCHYRA 1764/80 (KRAM-B, herb. H. OCHI); (2) Rembiszewski Nunataks between Viéville Glacier and Rybak Glacier, 60°09'30" S, 58°18' W, elev. 200 m; in swampy situation on gravelly ground at north foot of the highest nunatak, OCHYRA 2773/80 (KRAM-B, herb. H. OCHI); (3) Rakusa Point between Halfmoon Cove and Suszczewski Cove, 62°09'30" S, 58°27'30" W, elev. 4 m; in slightly moist situation at foot of basalt plug on soil amongst boulders, OCHYRA 2397/80 (KRAM-B, herb. H. OCHI; Bryophyta Antarctica Exsiccata No. 193).

Ecology. All Antarctic specimens of *B. urbanskyi* were collected in similar ecological conditions. The species seems to prefer moist or wet habitats and the best developed plants have been collected on wet, bare soil or gravel along melt water channels or rills and in wet depressions and hollows between boulders. The ecological requirements of *B. urbanskyi* are very similar to those showed by other species of this genus in the Antarctic, especially by very widespread and variable species *B. pseudotriquetrum* (Hedw.) Gaertn., Meyer et Scherb. The data about the ecology of *B. urbanskyi* from the other parts of its range are very scant and meagre, but judging from information available from labels on specimens collected in southern South America and on Îles Kerguelen, the habitats fit rather well with field observations made in the Antarctic.

Txonomy and geographical distribution. *Bryum urbanskyi* was described by BROTHÉRUS (1906) from material collected from Îles Kerguelen during the German South Polar Expedi-

tion under the command of E. von DRYGALSKI. The species was known only from the type locality until OCHI (1982), in a taxonomic revision of the subfamily Bryoideae in southern South America, found that *Bryum anomobryoides* and *B. laetevirens*, two species described by CARDOT and BROTHERUS (1923) from material from Patagonia and Tierra del Fuego, were conspecific with *B. urbanskyi*. At present, the species is known from several localities in southern Chile, reaching a northerly latitude of ca. 33°S, from Îles Kerguelen, and from the Antarctic. Due to imperfect knowledge of the true geographical range it is very difficult to refer *B. urbanskyi* to any of currently recognized floristic elements in the Southern Hemispheres. The species penetrates northward beyond the Valdivian region but here it appears to be restricted to higher elevations. Therefore, the best solution is to consider *B. urbanskyi* to be a subantarctic species. Since it occurs only within the South American and Indian Ocean sectors of the sub-Antarctic it can be included in the amphiatlantic subantarctic subelement (ENGEL 1978, OCHYRA and VÁŇA 1987). A similar distribution pattern is shown by *Hygrolembidium ventrosium* (Mitt.) Grolle among hepatics (OCHYRA and VÁŇA 1987), and by *Schistidium falcatum* (Hook. f. et Wils.) Bremer among mosses (OCHYRA and BELL 1984).

The taxonomic position of *B. urbanskyi* was discussed by OCHI (1972, 1982). Since all the material of the species is sterile the taxonomic position of *B. urbanskyi* remains uncertain. On one hand this species is similar to *Brachymenium exile* (Doz. et Molk.) Bosch et Sande Lac., judging from the habit and size of plants, shape and areolation of the leaves as well as the axillary gemmae. On the other hand, *B. urbanskyi* may be related to a species of *Bryum* from the subgenus *Anomobryum* such as *B. werthii* (Broth.) Ochi (Îles Crozet, South Africa), *B. harriottii* R. Brown ter. (New Zealand), *B. plicatum* (Card.) Ochi (Mexico), and *B. rotundifolium* Ochi (tropical South America) in which the laminal cells are neither linear nor linear-vermicular, but broader and shorter, being rhomboid or rhomboid-hexagonal in shape.

Although *B. urbanskyi* is known only in a sterile state it can be readily distinguished from all other bryaceous mosses growing in the Antarctic by its very thin-walled, short, rhomboid-hexagonal laminal cells, the presence of broadly oblong to oblong obovate axillary gemmae, and broadly ovate, shortly acuminate or obtuse, concave leaves. Antarctic plants do not differ significantly from South American ones and are especially similar to the habitat form described by CARDOT and BROTHERUS (1923) as *Bryum laetevirens*. The only difference in comparison with the type material of *B. urbanskyi* is in the size of plants, the type material being generally smaller than the Antarctic material.

2. *Bryum orbiculatifolium* Card. et Broth., K. Svensk. Vet. Ak. Handl. 63 (10): 42. 1923. (Fig. 2)

Type: "Patagonia occ.: Peel Inlet, ad terram glareosam, saepe irrigatam prope glaciem (540)" (Lectotype nova: "Expediitio suecica 1907-1909. 212. *Bryum orbiculatifolium* Card. sp. nova. Patag. occid. Peel Inlet, in [illeg.] glaciem. 16. 6. 1908. Leg. C. SKOTTSBERG" — S!; isolectotype — PC-Card!).

Syn.: *Bryum cymbifoliellum* Dixon in Christ., Res. Norw. Sci. Exp. Tristan da Cunha 1937-1938 48: 32, 1960. Types: "Tristan da Cunha: *Empetrum* heath, above Burntwood, ca. 1200 m, Nos. 784c, 785" (Lectotype nova: "Herb. H. N. DIXON. Ref. No. 784c. *Bryum cymbifoliellum* Dix. sp. nov. *Empetrum* heath, above Burntwood, c. 1200 m, Tristan da Cunha. Coll. CHRISTOPHERSEN and MEJLAND, 8 Jan. 1938. Comm. Bot. Mus., Oslo — BM-Dix!; Syntype: ditto, No. 785 — BM-Dix!).

Plants soft in dense, lustrous tufts about 1.0-2.5 cm high, light green above, brown below, with few rhizoids. Stems filiform, pale-yellowish to brown, unbranched or sparsely branched. Leaves imbricate, closely and evenly spaced almost all along the stem, slightly contorted in the upper part of the stem when dry, suborbicular to broadly oblong, narrowed

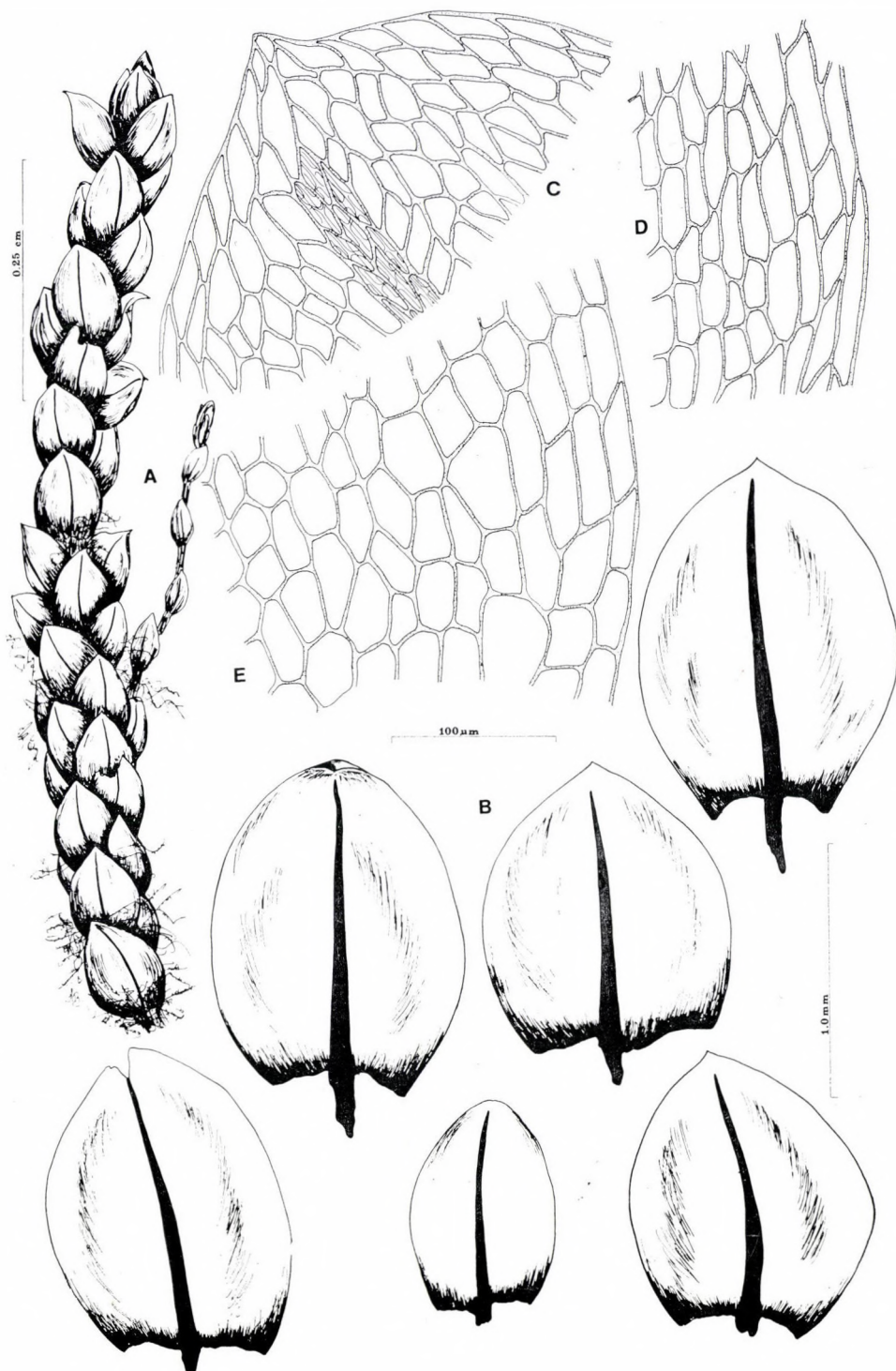


Fig. 2. *Bryum orbiculatifolium* Card. et Broth.: A - habit; B - leaves; C - leaf apex; D - mid-leaf and marginal cells; E - basal cells

at the base, not or scarcely decurrent, 1.0–1.3 mm long, 0.8–1.0 mm wide, strongly concave, obtuse and apiculate, sometimes cucullate; margins plane or sometimes slightly recurved below, entire; costa percurrent or shortly excurrent; upper cells rhomboidal to oblong-rhomboidal, rather thin-walled, 18–21 μm wide, 25–40 μm long, longer and narrowed in a few rows at the margin forming an indistinct border; lower cells subquadrate to shortly rectangular, width to length ratio about 1 : 1–3. Sterile.

Specimens examined: Antarctica, South Shetland Islands, King George Island, Fildes Peninsula, Lake Kitezh at Bellingshausen Station, 62°12' S, 58°58' W, elev. ca. 15 m; on wet gravelly ground on southern side of the lake associated with *Calliergon sarmentosum* (Wahlenb. Kindb. and *Campyliadelphus polygamus* (B.S.G.) Kanda, OCHYRA 2456/80 (KRAM-B, AAS, BM, H, herb. H. OCHI).

Ecology. *Bryum orbiculatifolium* thrives on wet bare ground, on gravel, on banks of lakes and in places inundated with melt water. It grows with mosses showing similar habitat requirements such as *Calliergon sarmentosum* (Wahlenb.) Kindb., *Campyliadelphus polygamus* (B. S. G.) Kanda, *Sanionia uncinata* (Hedw.) Loeske, and *Bryum pseudotriquetrum* (Hedw.) Gaertn., Meyer et Scherb. These habitats generally lack closed vegetation and only scattered patches of mosses are found amongst pebbles. It appears that the species grows in similar habitat conditions at the type locality in southern Chile.

Taxonomy and geographical distribution. *Bryum orbiculatifolium* is readily distinguished from all other Antarctic species of *Bryum* even when sterile. The species is characterized by its strongly concave, suborbicular leaves which are very obtuse or rounded, and finely apiculate frequently, and sometimes cucullate.

Bryum orbiculatifolium appears to be closely related to *B. cyclophyllum* (Schwaegr.) B. S. G., a widespread circumpolar species in the Northern Hemisphere. OCHI (1972) pointed out the differences between these two taxa: *B. orbiculatifolium* grows normally in dense tufts, the plants are rather densely foliated and lustrous, and the leaves are shortly apiculate. By contrast, *B. cyclophyllum* grows in much more lax tufts, the plants are not or only scarcely shiny and distantly foliated, and leaves are rounded without an apiculus.

Presently, *Bryum orbiculatifolium* is known only from two localities in the Magellanian and Valdivian regions of southern Chile extending northwards as far as lat. 48° S in Prov. Aysen (OCHI 1982). Additionally, the species occurs at higher elevations on Tristan da Cunha, where it was described as *Bryum cymbifoliellum* by DIXON (1960). However, OCHI (1982) found that these two species were conspecific. Thus, *B. orbiculatifolium* can be included in the group of amphiatlantic temperate species (ENGEL 1978, OCHYRA and VÁŠA 1984), which comprises species distributed mainly in temperate parts of the south Atlantic, i.e. in temperate South America, and South Africa and occasionally on Tristan da Cunha.

3.* *Bryum amblyodon* C. Muell., Linnaea 42: 293. 1879. (Fig. 3)

Type: "Argentina Tucumanensis, in via ab Tafi per Quebrada de Monteros cum *Bryo micro-pendulo*, 4–6. April 1872, leg. Lorentz" (Isotype — NY!).

Syn.: *Bryum inclinatum* (Brid.) Bland., Uebers Mecklenb. Moss. 6. 1809, *hom. illeg.*; non *B. inclinatum* (Hedw.) Dicks. ex With., Syst. Arr. Brit. Pl. ed. 4, 3: 818. 1801 [= *Distichium inclinatum* (Hedw.) B. S. G.].

Bryum stenotrichum C. Muell., Flora 70: 219. 1887.

* Recently Geissler (1984) found that *Bryum inclinatum* (Brid.) Bland. is identical to *B. imbricatum* (Schwaegr.) B.S.G. Thus, the latter name seems to be the oldest available name for the species which is called in this paper *B. amblyodon* C. Muell. See GEISSLER, P. (1984). Notulae Bryofloristicae Helveticae. Candollea 39 (2): 641–646.

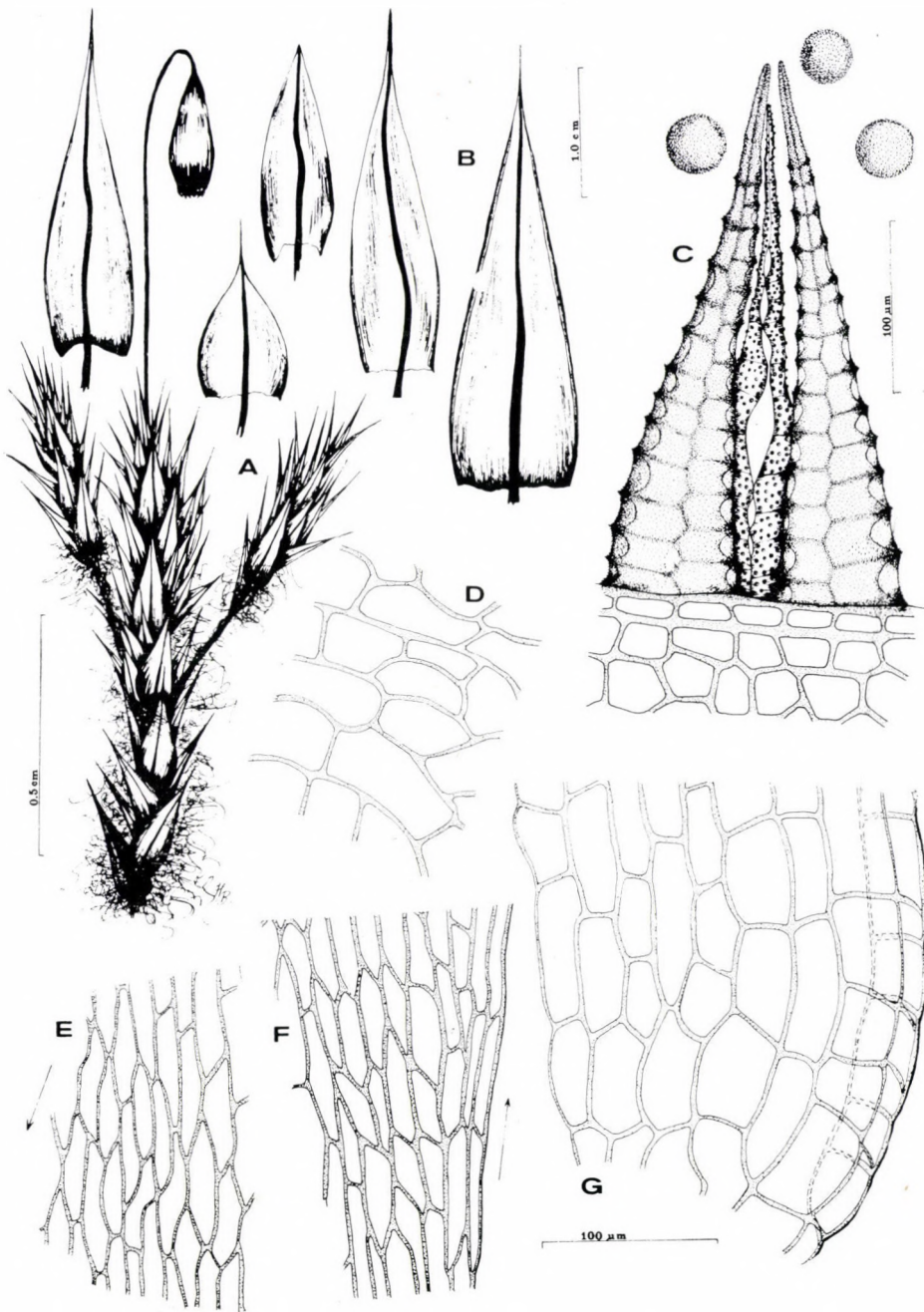


Fig. 3. *Bryum amblyodon* C. Muell.: A - habit; B - leaves; C - portion of peristome and spores; D - exothecial cells; E - mid-leaf cells; F - upper cells with margin; G - basal cells

Bryum inclinatum (Brid.) Bland. var. *magellanicum* Card., Rev. Bryol. 27: 41. 1900. Type: Détroit de Magellan: environs de Punta Arensa [Lectotype (selected here): "Herb. J. Cardot. Mousses du voyage de la Belgica. No. 59. *Bryum inclinatum* Br. eur. var. *magellanicum* Card. var. nov. Détroit de Magellan: environs de Punta-Arenas. Leg. RACOVITZA, 9 décembre 1897", — PC-Card !; isolectotype — PC-Card !; syntypes: ditto No. 62c, 63, 64 — PC-Card !], syn. nova.

Bryum imperfectum Card., Rev. Bryol. 27: 44. 1900. Type: "XX^{me} débarquement" [later, Cardot (1901) wrote: "Détroit de Gerlache: XX^{me} débarquement, Terre de Danco, à l'entrée du chenal de Lemaire, sur des roches isolées au milieu d'un glacier, à 50 metres au dessus du niveau de la mer. (N^o 268b; 12 février 1898)] (Holotype — BR !), syn. nova.

Plants in dense, yellow-green, lustrous tufts, scarcely radiculose below, 1.0–1.5 cm high. Stems repeatedly branched by innovations. Leaves appressed to erect when dry, erect-patent when moist, larger and crowded in comal tufts at the stem tips, straight, 1.5–3.5 mm long, 0.8–1.2 mm wide, reddish at base, ovate to lanceolate to oblong-lanceolate, acuminate to longly acuminate; margins distinctly bordered with elongate and narrow cells and recurved; costa stout, reddish to reddish-brown at the base, yellowish above, long excurrent; upper cells oblong-hexagonal, 10–15 μ m wide, 40–60 μ m long, firm-walled becoming narrower and longer at the margins and forming a distinct unistratose border.

Synicous. Setae (0.8)10–30 mm long, brownish; capsules cernuous or pendulous, pale brown, elongate-ovate or narrowly ellipsoid, symmetrical, straight, 2.5–3.0 mm long, neck well developed, abruptly narrowed into seta; operculum convex, apiculate; exothecial cells at the mouth small, horizontally rectangular, below rectangular; outer peristome teeth pale yellow and only at the base slightly orange-yellow with narrow hyaline border, finely papillose processes with narrowly gaping perforations, more strongly papillose, cilia rudimentary or lacking; spores 18–26 μ m, finely and densely papillose.

Specimens examined: Antarctica — (1) South Shetland Islands, King George Island, Admiralty Bay region, Ezcurra Inlet, mountain ridge called Cytadela between Monsimet Cove and Zalewski Glacier, 62°11' S, 58°35' W, elev. 50 m; on bare earth in moist situation on scree slope with northerly aspect, OCHYRA 967/80 (KRAM-B, AAS, herb. H. OCHI); (2) Antarctic Peninsula region, Melchior Archipelago, Lysted Island, Sipple 335.1 (FH-Bartr); (3) Antarctic Peninsula, Danco Coast, Lemaire Island, 64°50' S, 62°48' W, elev. 50 m, on nunataks RACOVITZA 268b (BR-type of *Bryum imperfectum*); (4) Antarctic Peninsula region, Short Cut Island near Palmer Station, Anvers Island, 64°03' W, 64°47' S, growing on patch of mossy peat on rocks, G. T. PRANCE 28595 (KRAM-B, NY).

Ecology. In the Antarctic *Bryum amblyodon* grows on bare earth in slightly moist situations on scree slopes. This habitat agrees well with the descriptions and field observations from other localities in which this species occurs.

Taxonomy and geographical distribution. *Bryum amblyodon* C. Muell. appears to be the oldest available name for a moss which is commonly known as *Bryum inclinatum* (Brid.) Bland. The latter name, however, is an illegitimate homonym of *Bryum inclinatum* (Hedw.) Dicks. ex With. OCHI (1980) pointed out that *B. amblyodon* described from Argentina by MÜLLER (1879), agrees in all respects with the Holarctic populations and that this name antedates *B. stenotrichum* C. Muell., a name used recently by various, mostly American, authors (e.g. CRUM and ANDERSON 1981) since ANDREWS (1940) had found that the latter name is synonymous with *B. inclinatum* (Bid.) Bland.

South American populations and Antarctic ones of this species are usually referred to as *Bryum inclinatum* (Brid.) Bland. var. *magellanicum* Card., a variety described by CARDOT (1900, 1901) from material collected in Tierra del Fuego. The only characters distinguishing this variety from the type of *Bryum inclinatum* are the paler peristome teeth and less numerous lamellae (10–15 instead of 15–20). The characters of the variety are typical of the Antarctic

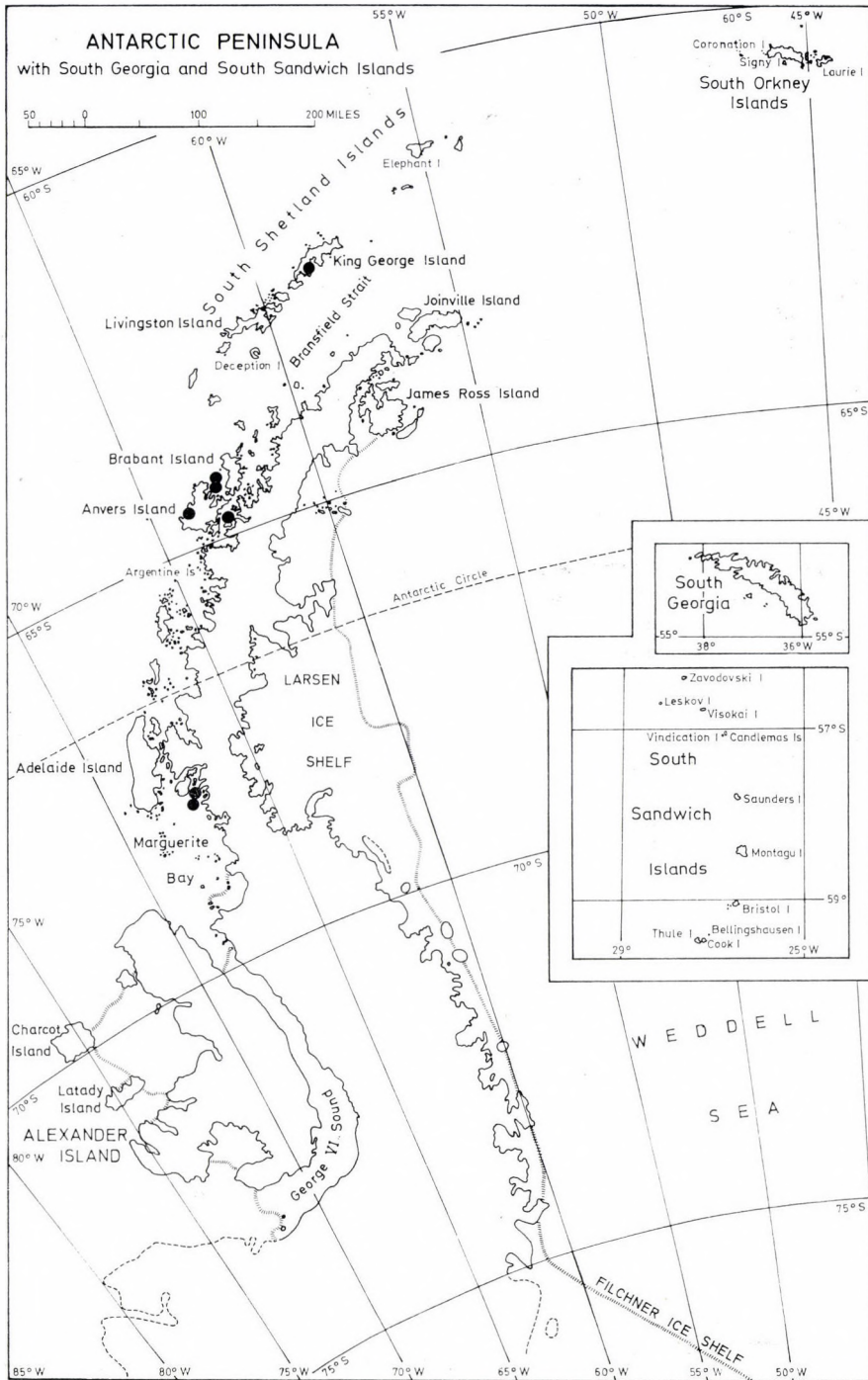


Fig. 4. The known distribution of *Bryum amblyodon* C. Muell. within the Antarctic botanical zone

plants and BARTRAM (1957) reported this species from the Antarctic as *B. inclinatum* var. *magellanicum*. However, the characters of the variety fall well within the range of variability of the species and, in consequence, this variety does not merit recognition as a distinct taxon and should be placed in synonymy with *B. amblyodon*.

On the basis of material collected by É. RACOVITZA during the course of the "Belgica" Expedition CARDOT (1900, 1901) described from the west coast of the Antarctic Peninsula *Bryum imperfectum*, a species closely related to *B. inclinatum* var. *magellanicum*. According to CARDOT it differs from the latter variety by its shorter setae, shorter and broader leaves, broader hyaline border of exostome teeth and imperfectly developed processes. Type material of *B. imperfectum*, however, coincides in all essential points with *B. amblyodon* and in consequence this species is reduced to synonymy with the latter. The critical characters of *B. imperfectum* fall excellently in a broad range of variability of these characters in *B. amblyodon*, and in fully mature capsules well developed processes with narrowly gaping perforations and rudimentary or none cilia may also be observed. However, some capsules in the type material of *B. imperfectum* are not fully mature and these really have imperfectly developed processes. Such underdeveloped capsules are also observed in other species of *Bryum* in Antarctica and this confirms rather well known fact that polar areas are too cold for producing fully mature capsules in the species of this genus.

When fully mature, *B. amblyodon* is readily distinguished from other species of this genus by the following combination of sporophyte and gametophyte characters: plants synoicous, cilia rudimentary or none, small spores, usually (17)20–30(35) μm , well-developed border and strong, long excurrent costa. It can be mistaken for *B. algovicum* Sendtn. ex C. Muell. as both species are synoicous. However, the latter has outer peristome teeth with obvious vertical and oblique lines joining transverse articulations which are lacking or very obscure in *B. amblyodon*.

Bryum amblyodon is a bipolar species with a few altimontane stations in the Bolivian Andes. It is widely distributed in the Northern Hemisphere extending southwards to Morocco and Algeria in North Africa, Central Asia, and California. It seems to be quite widespread in temperate South America including Patagonia, Tierra del Fuego and the Falkland Islands. BARTRAM (1957) reported this species from the Melchior Archipelago on the west coast of the Antarctic Peninsula reaching its southernmost locality on Lagoterrierie Island on lat. 67°53' (Fig. 4), in the northern part of Marguerite Bay. Apart from the South American sector of the Southern Hemisphere, *B. amblyodon* is known from Îles Kerguelen where it was reported as *Bryum gemmaceolum* C. Muell. (BROTHERUS 1906, OCHI 1972).

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TWO NEW SPECIES OF THE GENUS
ISIDOREA A. RICH. (RUBIACEAE)
FROM HISPANIOLA

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Two new species of the genus *Isidorea* A. Rich. were found in the rich collection of Eric Leonard EKMAN. One of them was discovered and recognized by him immediately in the field and named in the schedule as *I. veris* Ekman. It is related to *I. pungens* (Lam.) Robins. and lives in the Cordillera Central of Santo Domingo. The other species is an endemic to Gonave Island and named by the authors as *I. gonavensis*, a very narrow leaved taxon near to *I. leonardi* Urb. *Isidorea* (Rubiaceae) is a remarkable endemic genus of Cuba and Hispaniola with not less than 20 endemic species.

Introduction

The authors worked synchronically on the taxonomy of the genus *Isidorea* during the late seventieth. A more precise characterization of the genus and its delimitation from *Portlandia* and other related genera were elaborated by AIELLO (1979), with new combinations for some Cuban taxa of *Portlandia*. At the same time some new species of *Portlandia* were described (1977) and later transferred to *Isidorea* (1980) by BORHIDI, with the collaboration of M. MONCADA. The authors agreed in publishing jointly their further results concerning the taxonomy of the genus *Isidorea*.

Isidorea gonavensis Aiello et Borhidi sp. nova

Rami 4-angulares, glabri internodiis 0.5-2.0 cm longis ad ramulos brevissimis vel subnullis. Stipulae interpetiolares 4-10 mm longae, basi late triangulares et abrupte in spinas pungentes 5-7 mm longas excurrentes. Folia opposita subsessilia vel usque ad 2 mm longe petiolata, lanceolato-linearia, sub medio latissima, inferne breviter angustata, apice in spinam 1.5-2.5 mm longam contracta, 1.5-2.5 cm longa, 2-4 mm lata, nervo medio supra impresso, lateralibus supra obsoletis subtus nullis, crasse et rigide coriacea, supra nitida et pilis brevissimis basi callosis scabroso-hirtula subtus opaca et papilloso-scabridula margine valde revoluta. Pedicelli axillares, basi bracteis e basi triangulare pungenti-subulatis 3 mm longis obsiti 0-1 mm longi, brevissime puberuli. Calycis tubus obovatus lateraliter compressus, brevissime pilosulus, lobi 5, lanceolato-acuti, spinoso-mucronati, dorso uninervi 5-6 mm longi, 0.6-1 mm lati. Corolla albida, glabra 13-17 mm longa, tubus supra basin 2-2.5 mm crassus deinde valde ampliatus, angulatus, lobi 3-4 mm longi et 5 mm lati, late triangulares vel semiorbiculares, tubo 3-4-plo breviores, apice obtuse apiculati. Stylus 12 mm longus. Filamenta basi tubi adnata 5 mm longa. Antherae lineares apice acutae, 3-3.5 mm longae, medio tubi insertae.



Fig. 1. Type specimen of *Isidorea gonavensis* Aiello et Borhidi (EKMAN H 8664 in S)

Capsula obovata, loculicida, lateraliter leviter compressa, 6–7 mm longa et 5–6 mm lata, 4 mm crassa, semina 6–8 in quoque loculo.

Holotypus: Ile La Gonave, Pte. á Paquettes, Morne Fort-Fiel det. et leg.: E. L. EKMAN H 8664. 24. 7. 1927. S!

***Isidorea veris* Ekman ex Aiello et Borhidi sp. nova**

Rami teretes, brevissime pilosuli, demum glabri. Stipulae interpetiolares oblongo-triangulares, sensim attenuati, acuti, 3–5 mm longi glabri. Folia oblongo-elliptica, lanceolata vel oblanceolata, leviter asymmetrica, basi cuneata, apice in mucronem pungentem 1.5–2.5 longam contracta, 1.5–4 cm longa et 6–20 mm lata, nervo medio utrinque prominenti lateralibus 8–14 sub angulo 20–30° abeuntibus utrinque prominentibus et supra prominenter reticulatis, supra lucida subtus opaciora, utrinque calloso-punctulata, margine recurva, coriacea. Flores 2 axillares, pedicelli 5–9 mm longi, glabri. Calycis tubus obovatus, 2 mm longus, glaber, lobi 5, linear-oblongi, attenuati, acuti, apice curvati, 9 mm longi, glabri, 3-nervati et calloso-punctati. Corolla rubra, vel pallide rubra, 18–24 mm longa, e basi angusta abrupte ampliata deinde



Fig. 2. Type specimen of *Isidorea veris* Ekman ex Aiello and Borhidi (EKMAN H 15431 in S)

sensim latiuscula, tubus 14–20 mm longus; lobi 5, late triangulares, acuti, apiculati 4–6 mm longi. Stamina 5, in medio tubi corollae inserta; filamenta basi tubi adnata 5–7 mm longa, antherae lineari-lanceolatae 4–5 mm longae. Capsula obovata, 1 cm longa et lata, 5-carinata. Semina cc. 8 in quoque loculo.

Holotypus: EKMAN 15431. Hispaniola, Santo Domingo, Cordillera Central, Prov. de Samaná, Los Haitises, Boca del Infierno, limestone crags 25. 6. 1930. S!

Spec. examin. EKMAN 15069 Peninsula de Samaná, prov. de Samana Cábo Cabrón rough limestone near Pescado del Cariste. 22. 5. 1930. S!

I. gonavensis is related to *I. leonardi* Urb. which lives in the South-west Peninsula of Haiti near Port au Paix. *I. leonardi* differs from our species in having slender stem, glabrous leaves and calyx, shorter linear bracts and 4 seeds in each cells.

Isidorea veris Ekman ex Aiello and Borhidi is confined with *I. pungens* (Lam.) Robins. and *I. pedicellaris* Urb. et Ekm. *I. pungens* can be distinguished by its narrower lanceolate leaves, very short and wide corolla lobes. *I. pedicellaris* Urb. et Ekm. has similar leaves to those of *I. veris* but it differs clearly by having long pedicels and flowers up to 4 cm long.

Isidorea is remarkable genus from plant geographical point of view, which manifests the close floristic relations between East-Cuba and Hispaniola. (See BORHIDI 1985: 33.) The

genus is represented not less than 20 endemic species, mostly of very small-sized areas. The genus must have developed during a long dry period of the Middle of Tertiary, since all species of the genus have a well-defined xeromorphic character and leave on climatically or/and edaphically dry habitats.

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HISTOLOGICAL CHARACTERISTICS OF *CYTISUS COMMUTATUS* (WILLK.) BRIQ.

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This article describes the histology of the stem, root and leaves of *Cytisus commutatus* (Willk.) Briq. The arrangement and nature of the central cylinder and fundamental tissue is reported, together with the characteristics of the epidermis and the presence of a bundle sheath around the leaf bundles.

Introduction

Cytisus commutatus, a species of the Leguminosae endemic in the northern Iberian peninsula, has had an extremely eventful taxonomic history. First described by WILLKOMM (1881) as *Sarothamnus commutatus*, BLAKELOCK (1953), calls it *Cytisus ingramii* and MERINO (1905) *Sarothamnus purgans*. VICIOSO (1955) considered it to be an intergeneric hybrid between *Cytisus multiflorus* (L'Hér.) Sweet. and *Sarothamnus commutatus* Willk. LAÍNIZ RIBALAYGUA and LAÍNIZ (1958) denoted it to *Cytisus commutatus* (Willk.) Briq. subsp. *merinoi* Laínz RIBALAYGUA and LAÍNIZ. BELLOT (1966) treats *Cytisus commutatus* and *Cytisus ingramii* as synonyms for one and the same species and uses the two names indiscriminately. SAÑUDO (1973) found the chromosome number of *Cytisus ingramii* collected in Xuances (Lugo) to be $2n = 96$ and that of *Cytisus commutatus* from Mañaria (Vizcaya) to be $2n = 92, 96$. HORJALES (1978) likewise assumes only a single taxon to be involved, which he refers to as *Cytisus commutatus* (Willk.) Briq.

The distribution of the plant in Galicia (Spain) has been studied by ALVAREZ and HORJALES (1977). On the north coast it is found from Puentedeume (La Coruña) to Viveiro (Lugo), and inland its natural home seems to be the basin of the River Eume, with Guitiriz (Lugo) as its southernmost location and the Serra do Xistral (Lugo) limiting its extension to the east (Fig. 1). These are areas of ultrabasic rock (PARCA PONDAL 1966) whose typical oceanic temperate climate involves annual rainfall of 500-700 mm on the coast and up to 1250 mm at heights above 600 m. Actual rainfall is nevertheless not the only factor to be considered, since it is common for relative humidity to reach 98 or even 100% on days persistent fog (DÍAZ-FIERROS 1971).

The present article describes the histology of the stem, root and leaves of *Cytisus commutatus*.

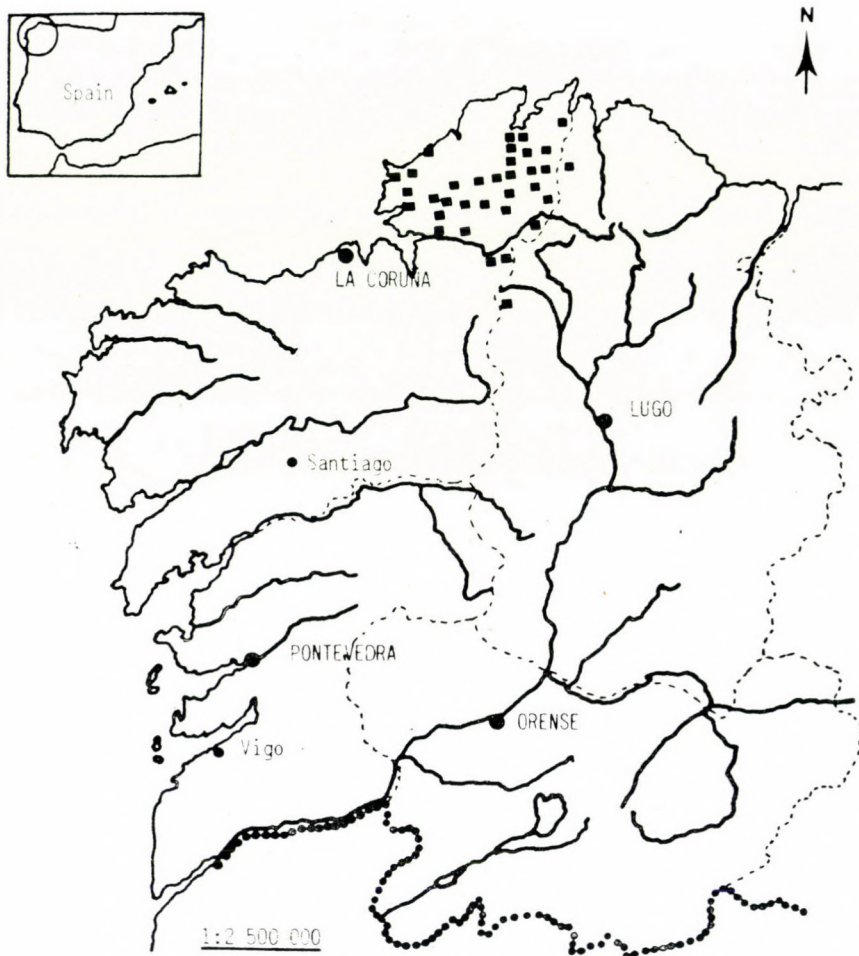


Fig. 1. Distribution of *Cytisus commutatus* (Willk.) Briq. in Galicia (N. W. Spain)

Material and methods

Cytisus commutatus (Willk.) Briq. was collected in Xestoso (La Coruña) in June, when the plant is in full flower. Roots, stems and leaves were fixed in F.A.A. (formalin-acetic-alcohol) (JOHANSEN 1940) embedded in paraffin wax and stained with safranine fast green (JENSEN 1962) and safranine hematoxylin (PUJILULA 1931).

Results

Stem anatomy

The stem of *Cytisus commutatus* has the structure of a typical dicotyledon (METCALFE and CHALK 1950, ESAU 1972, FAHN 1978). The epidermis consists of a single layer of isodiametric cells with a cutinized membrane. Unicellular cellulose-walled trichomes are com-

mon. The cortical cylinder is composed of chlorophyllous parenchyma as tissue fundamental and angular collenchyma as tissue of support, forming a continuous cylinder of various layers of living cells with cellulose walls thickened mainly at the angles. The primary-walled parenchyma cells are large and more or less polyhedral. These tissues carry out the essential vegetative functions requiring living protoplasm. The inmost layer of the cortex is an endodermis surrounding the central cylinder. It is easily distinguished in transverse sections (Fig. 2) and is formed by a compact layer of parenchyma cells with subdued Casparian bands.

The central cylinder corresponded of ectophloematic siphonostele bounded by various layer of clearly differentiated lignified cells forming a continuous ring of sclerenchyma separating the cortex from the central region. The vascular bundles are arranged in continuous concentric cylinders around the pith, with the phloem external to the xylem. The vessels are of large bore and are accompanied by fibres and parenchyma elements (Fig. 3). Spiral or annular thickenings are clearly recognizable in longitudinal sections. The parenchymatous

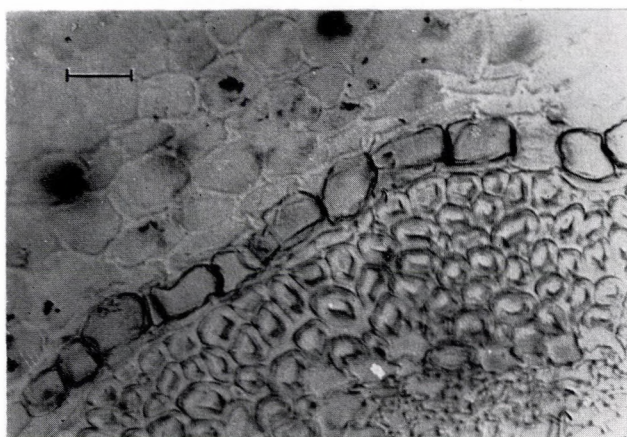


Fig. 2. Section of stem showing the endodermis and sclerenchyma fibres; bar scale 10 μ m

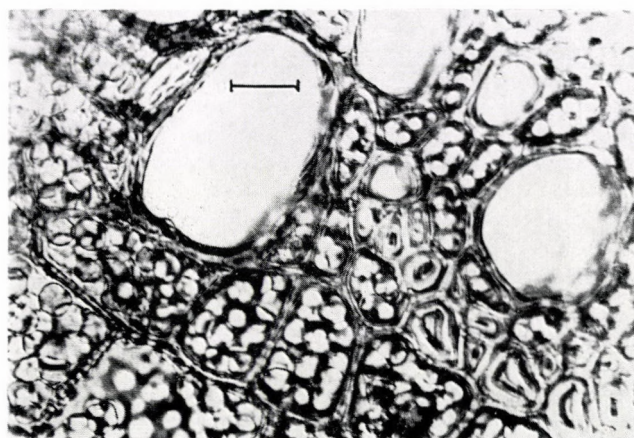


Fig. 3. Transversal section of xylem, showing vessels surrounded by fibres and parenchymatose cells; bar scale: 10 μ m

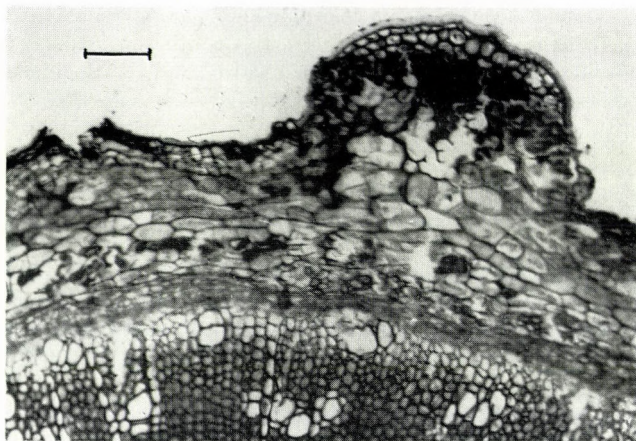


Fig. 4. Transverse section of young stem; bar scale: 50 μm

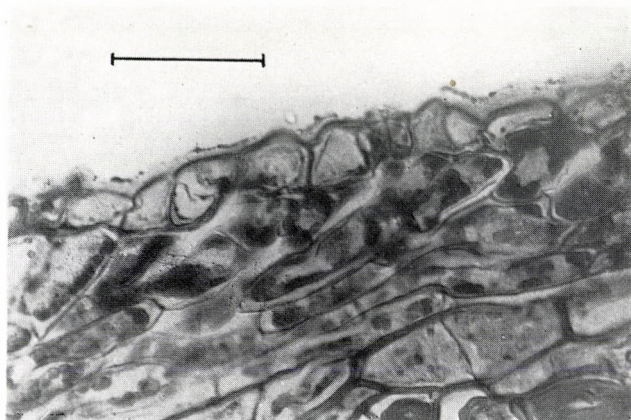


Fig. 5. Structure of the stem, showing highly cutinized epidermal cells, stomata and collenchyma; bar scale: 50 μm

cells of the phloem, like those of the medullary rays, have unlignified primary walls. The pith, surrounded by the vascular bundles, is more or less cylindrical and made up of roughly uniform parenchyma cells, with a certain number of fibres appearing in the peripheral region.

The stem of *Cytisus commutatus* exhibits pronounced ribs and stomas (Fig. 4), especially when young. In these cords the collenchyma is particularly well developed, and each contains a group of sclerenchyma cells forming a triangle pointing inwards (Fig. 5).

Root anatomy

The organization of the root is similar to that of the stem as regards secondary xylem and phloem. Suberin is deposited on the cellulose membrane of a layer of subepidermal cells, within which colourless cortical parenchyma is separated from the central cylinder by an endodermis which is more marked than in the stem. Immediately within the endodermis there is a multilayer pericycle from which lateral roots originate.

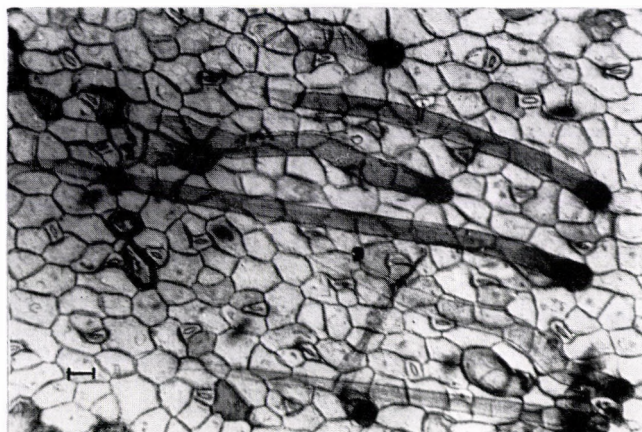


Fig. 6. Epidermis of the underside of a leaf, showing numerous trichomes; bar scale: 50 μ m

Leaf anatomy

The leaf of *Cytisus commutatus* has a dorsiventral structure. The single epidermal layer comprises various kinds of epidermal cells including stomatic guard cells with 3 or 4 subsidiary cells and non-glandular uniserial hairs consisting of a short basal cell and a long, pointed terminal cell (Fig. 6), though these hairs, abundant on the lower surface of the leaf, are absent from the upper surface. Except for the intercellular spaces between the guard cells of the stomata, the epidermis is a very compact tissue.

The palisade mesophyll is different of the spongy mesophyll, the cells of the former being long and arranged in various layers to form the principle specialized photosynthetic tissue. The spongy mesophyll contains large intercellular spaces facilitating gaseous exchange between the photosynthetic tissue and the exterior. In size, shape and arrangement, the spongy mesophyll cells are very like those of the inmost layer of palisade cells.

The leaves exhibit collateral bundles of various sizes, and bundle sheath of thick-walled lignified cells.

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ANATOMÍA DE MADERAS DE CUBA, I

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The most important anatomical features of the wood of 10 taxa belonging to different families of the Cuban flora were described in this paper.

Introducción

Como es sabido el conocimiento de la estructura interna del xilema secundario nos permite establecer algunas características que ayudan a la determinación de las especies, así como a su posible utilización, y de esta forma coadyuvan a incrementar la reforestación de nuestros bosques, de tal forma que se puedan ir reduciendo paulatinamente las importaciones y en algunos casos hasta suprimirlas.

Las características de los elementos que constituyen el tejido xilemático están relacionadas directamente con las propiedades de las maderas. LECLERCQ (1980) señaló que algunas propiedades de las maderas están condicionadas por sus estructuras anatómicas y mas específicamente por las proporciones de las dimensiones del tejido fibroso. Por ejemplo, el largo de las fibras ejerce una influencia negativa en la dureza, hienda o clivaje y densidad, mientras que contribuye satisfactoriamente al incremento de la flexión estática, tenacidad y compresión de la madera.

El grosor de la pared de las fibras contribuye por su parte a aumentar la dureza, densidad, tensión, flexión estática, compresión y clivaje o hienda, siempre que éste se relacione con el largo de las fibras y su proporción en el tejido.

KOLLMAN (1959) destacó que los poros o vasos pueden constituir zonas de mínima resistencia si éstos se encuentran distribuidos en forma anular, siendo importante considerar el diámetro y contenido de ellos en los procesos de preservación y secado de las maderas.

Por último otro de los elementos que influye en las características de las maderas es el parénquima axial, el cual aunque posee paredes finas y limenes amplios, lo que contribuye a la elasticidad de la madera, también es muy susceptible al ataque de xilófagos, por lo que se hace necesario conocer su abundancia y distribución.

La flora cubana con un alto endemismo, cuenta con mas de 3490 especies de plantas lignificadas (BORHIDI 1973, 1976) de las cuales cerca de 200 tienen interés forestal por las características de sus maderas. El presente trabajo constituye el primero de una serie que contribuirá al conocimiento de la anatomía del xilema de especies lignificadas y sus características, lo que en consecuencia permitirá un aprovechamiento racional mas efectivo de nuestros bosques. Simultaneamente estaremos contribuyendo así a la elaboración del Atlas Xilológico de plantas cubanas.

Tabla 1

Valores medios de los elementos y principales

Especies	Caracteres	Elementos de los vasos				Parénquima axial	
	Frecuencia/mm ²	Diam. tang en μ m	Pared en μ m	Platina de perforación	Largo en μ m	Diam. medio en μ m	± de células
<i>Dendropanax arboreus</i>	20	76	5	S y E	945	20	4-7
<i>Ochroma pyramidalis</i>	2	190	6	S	475	55	2-3
<i>Cinnamomum montanum</i>	13	97	8	E	445	17	2-6
<i>Talauma minor</i>	19	90	3	E	1100	20	6-9
<i>Swietenia mahagoni</i>	11	143	8	S	340	44	4-9
<i>S. macrophylla</i>	8	62	6	S	307	33	5-7
<i>S. macrophylla</i> × <i>mahagoni</i>	9	113	5	S	452	28	5-8
<i>Trichilia havanensis</i>	24	55	5	S	540	14	4
<i>Lysiloma Sabicu</i>	6	65	6	S	400	22	2-4
<i>Matayba apetala</i> ssp. <i>oppositifolia</i>	9	56	6	S	290	19	6

Leyenda de la tabla: S — simple; E — escaleriforme

Materiales y metodos

Para la descripción del tejido xilemático de las especies aquí trabajadas se confeccionaron probetas de tablillas de la xiloteca del Centro de Investigación Forestal (HBw), así como de troncos de maderas adultas de la xiloteca del Herbario de la Academia de Ciencias (HACw), las cuales están respaldadas por sus correspondientes ejemplares de herbario. Las probetas fueron ablandadas por cocción en agua destilada y posteriormente se realizaron los cortes histológicos con un micrótopo de deslizamiento a un grosor de 20-30 μ m. Los cortes obtenidos fueron deshidratados según las técnicas usuales y montados en portaobjetos con Euparal.

Para realizar las mediciones del largo de los elementos fibrosos se colocaron las astillas en una mezcla 1 : 1 de peróxido de hidrógeno al 30% y ácido acético glacial, y se calentaron a 80 °C durante dos horas aproximadamente.

Como en la mayoría de los casos los estudios se basaron en muestras de un solo árbol, las descripciones tienen gran utilidad desde el punto de vista práctico ya que contribuyen a los propósitos de identificación, sin embargo no muestran la variabilidad que suele encontrarse en las dimensiones de los elementos en diferentes individuos de una misma especie.

Los términos utilizados en las dimensiones y abundancia de los elementos son los propuestos por CHATTAWAY (1932) y por el Committee on the Standardization of Terms of Cell Size (1937 y 1939), mientras que las descripciones se realizaron según la terminología del Glosario Internacional de términos de Anatomía de la Madera, en versión castellana (COROTHIA 1963).

El largo de los elementos axiales se expresa con tres valores que corresponden al mínimo, medio y máximo respectivamente.

Las descripciones están dispuestas en orden alfabético de familias y géneros, e incluyen los sinónimos y nombres vulgares de las especies estudiadas.

Resultados

Los principales caracteres cuantitativos y cualitativos de cada una de las maderas investigadas se expresan en la Tabla 1.

caracteres observados en las especies estudiadas

Frecuencia/mm	Radios medulares				Fibras				
	Homogéneos	Heterogéneos	Excl. uniseriados	Uni y multiseriados	Fibras libriformes	Fibrotaqueidas	Diam. medio en μm	Pared en μm	Largo en μm
5		+		1-4	+		20	6	1335
4		+		1-7	+		14	3	2500
6		+		1-3	+		22	7	1220
11		+		1-3		+	16	5	1470
7		+		1-5	+		15	4	1035
7		+		1-3	+		16	5	996
8		+		1-3	+		18	5	810
15	+		+	1	+		18	4	894
9	+		+	1	+		22	6	1086
16	+		+	1	+		17	5	1010

ARALIACEAE

Dendropanax arboreus (L.) Dec. & Planch.

(*Aralia arborea* L.; *Hedera arborea* Sw.; *Schefflera arborea* Maza; *Gilibertia arborea* March.; *Sciadophyllum samydaefolium* Wr. ex Sauv.)

Nombres vulgares Víbona.

Anillos de crecimiento poco distinguibles, poroso-difusa, poros moderadamente numerosos, 20 poros/ mm^2 , mayormente solitarios y en múltiples radiales de 2-3 elementos, ocasional-

El parénquima axial es de tipo paratraqueal escaso, aunque ocasionalmente se observa también apotraqueal difuso. Las series del parénquima están formadas por 4-7 células, las cuales poseen diámetro medio en sección transversal de 20 μm (Fig. 1).

Los radios medulares son escasos, 5/mm, heterogéneos y de dos tipos: uniseriados y multiseriados con 3-4 series de ancho, éstos últimos con valor promedio de 48 μm de ancho.

Las fibras son de tipo libriforme, septadas, con formas poligonales a ovales y distribuidas radialmente. En sección transversal alcanzan un diámetro promedio de 20 μm , pared de 6 μm de grosor. La longitud promedio es corta, 925-1334-1750 μm de largo (Figs 2 y 3). mente en pequeños grupos. Diámetro tangencial promedio de los poros solitarios moderadamente pequeño, 64-76-86 μm , pared celular de 5 μm de grosor con puntuaciones areoladas ovales, opuestas y escaleriformes, y poros lineales. Platinas de perforación mayormente inclinadas, simples y escaleriformes.

Los elementos de los vasos son moderadamente largos, con longitud de 830-945-1000 μm . No se observan contenidos en estos elementos.

BOMBACACEAE

Ochroma pyramidalis (Cav. in Lam.) Urb.*(O. lagopus Sw.; Bombax pyramidale Cav.)***Nombres vulgares:** Lanero, Balsa, Ceibón lanero, Ceibón botija.

Anillos de crecimiento poco conspicuos, madera poroso-difusa, poros escasos, $2/\text{mm}^2$, mayormente solitarios, frecuentes múltiples radiales de 2-3 elementos. Diámetro tangencial promedio de los solitarios de tallas medianas, $130-190-200\ \mu\text{m}$, pared celular de $6\ \mu\text{m}$ de grosor, con puntuaciones areoladas circulares y alternas, poros alargados a modo de fisura. Platinas de perforación simples y ligeramente inclinadas. No presentan contenidos (Figs 4, 5 y 6).

Los elementos de los vasos son cortos, con longitud de $305-475-650\ \mu\text{m}$.

El parénquima axial es abundante y presenta dos patrones de distribución: para-traqueal vasicéntrico y apotraqueal en bandas. Las series del parénquima están constituidas por 2-3 células, con diámetro medio en sección transversal de $55\ \mu\text{m}$.

Los radios medulares son poco abundantes, $4/\text{mm}^2$, heterogéneos y de dos tipos: uniseriados y multiseriados de 5-7 series de ancho. Los multiseriados con ancho promedio de $256\ \mu\text{m}$.

Las fibras son de tipo libriforme, poligonales y están distribuidas irregularmente. El diámetro de éstas en sección transversal es de $14\ \mu\text{m}$, grosor de la pared $3\ \mu\text{m}$. Las fibras son muy largas y alcanzan dimensiones de $1650-2500-3200\ \mu\text{m}$ de largo.

LAURACEAE

Cinnamomum montanum (Sw.) Berchthold & Presl*(Phoebe montana (Sw.) Griseb.; Laurus montana Sw.)***Nombres vulgares:** Boniato blanco, Boniato del pinar.

Anillos de crecimiento conspicuos, madera poroso-difusa, poros moderadamente numerosos, $13/\text{mm}^2$, solitarios, en múltiples radiales de 2 elementos y en grupos pequeños. Diámetro tangencial promedio de los poros solitarios pequeños, $66-97-140\ \mu\text{m}$, grosor de la pared $8\ \mu\text{m}$, las cuales muestran puntuaciones areoladas poligonales y alternas con poros lineales. Platinas de perforación escaleriformes e inclinadas (Figs 7, 8 y 9).

Los elementos de los vasos son de tallas medianas, con longitud de $290-445-510\ \mu\text{m}$. No se observan contenidos en sus interiores.

El parénquima axial es de tipo apotraqueal difuso, estando constituidas las series de éste por 2-4-6 células, las cuales en sección transversal tienen un diámetro medio de $17\ \mu\text{m}$. En el interior de las células se observan contenidos de color carmelita oscuro.

Los radios medulares son moderadamente numerosos, $6/\text{mm}^2$, heterogéneos y de dos tipos: uniseriados y multiseriados de 2-3 células de ancho. Los multiseriados poseen ancho medio de $27\ \mu\text{m}$ y se observa en ellos la presencia de células oleíferas.

Las fibras son de tipo libriforme, de formas cuadradas a poligonales y presentan tendencia a la distribución radial. En sección transversal alcanzan un diámetro medio de $22\ \mu\text{m}$, grosor de la pared de $7\ \mu\text{m}$. Las fibras son cortas, con longitudes de $650-1220-1550\ \mu\text{m}$.

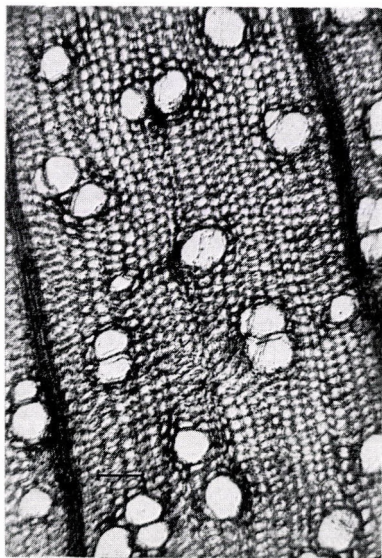


Fig. 1. *Dendropanax arboreus*, corte transversal, línea de escala: 100 μ m



Fig. 2. *Dendropanax arboreus*, corte tangencial, línea de escala: 100 μ m



Fig. 3. *Dendropanax arboreus*, corte radial, línea de escala: 100 μ m

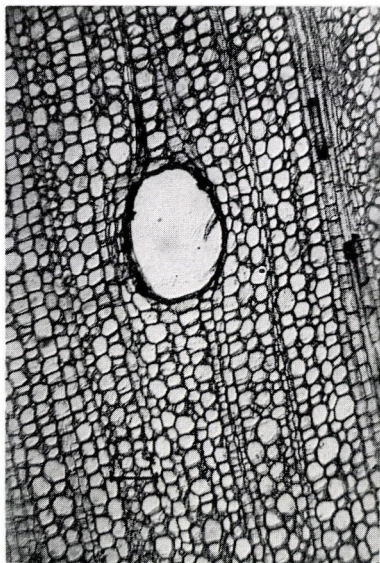


Fig. 4. *Ochroma pyramidalis*, corte transversal, línea de escala: 100 μ m

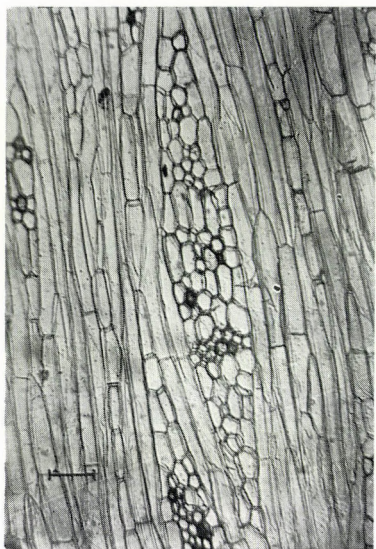


Fig. 5. *Ochroma pyramidalis*, corte tangencial, línea de escala: 100 μm



Fig. 6. *Ochroma pyramidalis*, corte radial, línea de escala: 100 μm

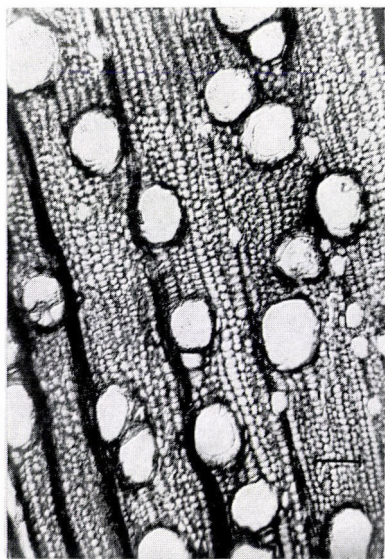


Fig. 7. *Cinnamomum montanum*, corte transversal, línea de escala: 100 μm



Fig. 8. *Cinnamomum montanum*, corte tangencial, línea de escala: 100 μm



Fig. 9. *Cinnamomum montanum*, corte radial, línea de escala: 100 μm

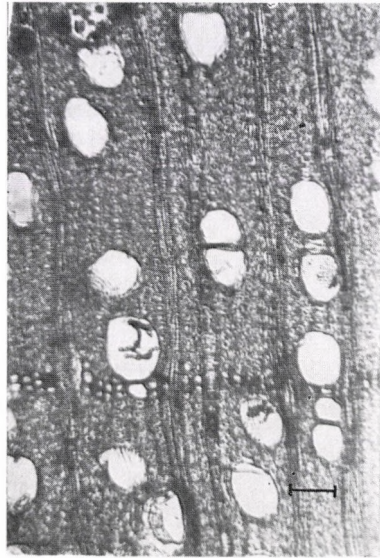


Fig. 10. *Talauma minor*, corte transversal, línea de escala: 100 μm

MAGNOLIACEAE

Talauma minor Urban

(*T. Plumieri* Griseb.; *Svenhedinia minor* Urban pp.)

Nombres vulgares: Azulejo, Marañón de costa.

Anillos de crecimiento conspicuos, formados por bandas de parénquima apotraqueal terminal; madera poroso-difusa, poros moderadamente numerosos, 19/mm², mayormente solitarios, frecuentes en múltiples radiales de 2 ó mas elementos. Diámetro tangencial promedio de los poros solitarios pequeño, 50–90–130 μm , grosor de la pared celular 3 μm , con puntuaciones areoladas escaleriformes. Platinas de perforación escaleriformes (Figs 10, 11 y 12).

Los elementos de los vasos son moderadamente a muy largos, con dimensiones de 980–1100–1280 μm de largo. Se observan contenidos de color carmelita rojizo.

El parénquima axial es de tipo apotraqueal terminal. Las series de éste están constituidas por 6–9 células, las cuales en sección transversal tienen un diámetro promedio de 20 μm .

Los radios medulares son muy numerosos, 11/mm², heterogéneos y de dos tipos: uniseriados y multiseriados de hasta 3 series de ancho. Los multiseriados con un ancho promedio de 47 μm .

Las fibras son del tipo fibrotraqueida, con formas poligonales y distribuidas irregularmente, aunque con cierta tendencia a la distribución radial. En sección transversal tienen un diámetro promedio de 16 μm y pared de 5 μm de grosor. Estas fibras son cortas y alcanzan longitudes de 1370–1470–1550 μm .



Fig. 11. *Talauma minor*, corte tangencial, línea de escala: 100 μm

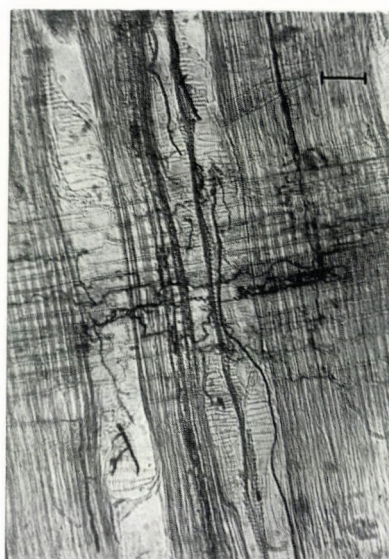


Fig. 12. *Talauma minor*, corte radial, línea de escala: 100 μm

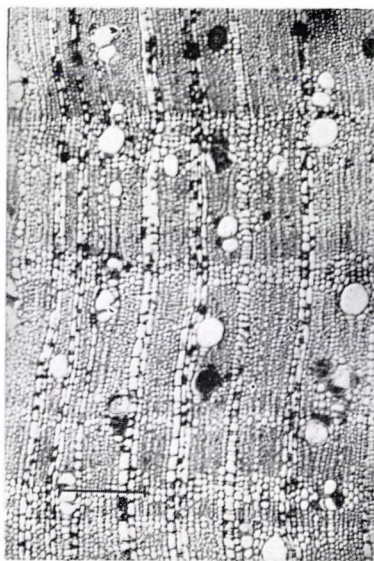


Fig. 13. *Swietenia mahagoni*, corte transversal, línea de escala: 500 μm

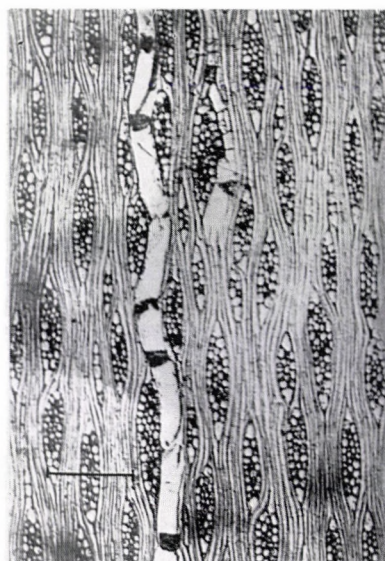


Fig. 14. *Swietenia mahagoni*, corte tangencial, línea de escala: 500 μm

MELIACEAE

Swietenia mahagoni (L.) Jacq.

Nombres vulgares: Caoba, Caoba de Cuba, Caoba Antillana.

Zonas de crecimiento presentes, madera con porosidad difusa, poros moderadamente numerosos, $11/\text{mm}^2$, solitarios y en múltiples radiales. Diámetro tangencial promedio de los poros solitarios de tallas medianas, $114\text{--}143\text{--}198\ \mu\text{m}$, grosor de la pared celular $8\ \mu\text{m}$ con puntuaciones areoladas redondas, alternas y con poros ovals ocasionalmente coalescentes. Platinas de perforación simples y ligeramente inclinadas (Figs 13, 14 y 15).

Los elementos de los vasos son moderadamente cortos, con largos de $330\text{--}340\text{--}409\ \mu\text{m}$.

El parénquima axial es de tipo paratraqueal vasicéntrico, frecuentemente se observa también parénquima inicial. Las series de éste están constituidas por 4–7–9 células, con diámetro promedio en sección transversal de $44\ \mu\text{m}$.

Los radios medulares son moderadamente numerosos, $7/\text{mm}^2$, heterogéneos y de dos tipos: uniseriados y multiseriados de 3–5 células de ancho. Los multiseriados con ancho promedio de $84\ \mu\text{m}$.

Las fibras son de tipo libriforme, a veces con septos muy finos, con forma poligonal y distribuidas irregularmente. En sección transversal tienen diámetro medio de $15\ \mu\text{m}$ y pared de $4\ \mu\text{m}$ de grosor. Las fibras son cortas y alcanzan valores de $875\text{--}1035\text{--}1175\ \mu\text{m}$ de largo.

Swietenia macrophylla King

Nombres vulgares: Caoba de Honduras.

Anillos de crecimiento conspicuos, madera con porosidad difusa, poros moderadamente escasos, $8/\text{mm}^2$, solitarios y en múltiples radiales. Diámetro tangencial promedio de los solitarios pequeño, $58\text{--}62\text{--}85\ \mu\text{m}$, pared celular de $6\ \mu\text{m}$ de grosor con puntuaciones areoladas diminutas, poligonales y alternas con poros ovals. Platinas de perforación simples y ligeramente inclinadas (Fig. 16, 17 y 18).

Los elementos de los vasos son moderadamente cortos, con valores de $239\text{--}307\text{--}405\ \mu\text{m}$ de largo.

El parénquima axial es mayormente de tipo paratraqueal vasicéntrico, aunque ocasionalmente se observa también con distribución terminal. Las series del parénquima están formadas por 5–7 células, las cuales poseen un diámetro medio en sección transversal de $33\ \mu\text{m}$.

Los radios medulares son moderadamente numerosos, $7/\text{mm}^2$, heterogéneos y de dos tipos: uniseriados y multiseriados de 2–3 series de ancho. Los multiseriados alcanzan un ancho medio de $35\ \mu\text{m}$.

Las fibras son de tipo libriforme, con formas poligonales y están distribuidas irregularmente. En sección transversal tienen un diámetro promedio de $16\ \mu\text{m}$ y pared de $4\text{--}5\ \mu\text{m}$ de grosor. Las fibras son muy cortas, con valores de $875\text{--}996\text{--}1275\ \mu\text{m}$ de largo y septos muy finos.

Swietenia macrophylla × **mahagoni** (Figs 19, 20 y 21)

Nombres vulgares: Caoba híbrida.

Anillos de crecimiento presentes, madera poroso-difusa, poros moderadamente escasos, $9/\text{mm}^2$, solitarios, en múltiples de 2 elementos y en conglomerados. Diámetro tangencial promedio de los solitarios de tallas medianas, $90\text{--}113\text{--}150\ \mu\text{m}$, pared celular de $5\ \mu\text{m}$ de grosor

con puntuaciones areoladas diminutas poligonales y alternas con poros ovales, ocasionalmente coalescentes. Platinas de perforación simples.

Los elementos de los vasos son de tallas medianas, con valores de 310–452–560 μm de largo.

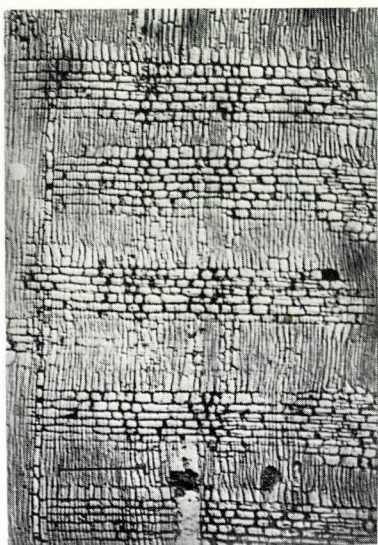


Fig. 15. *Swietenia mahagoni*, corte radial, línea de escala: 500 μm

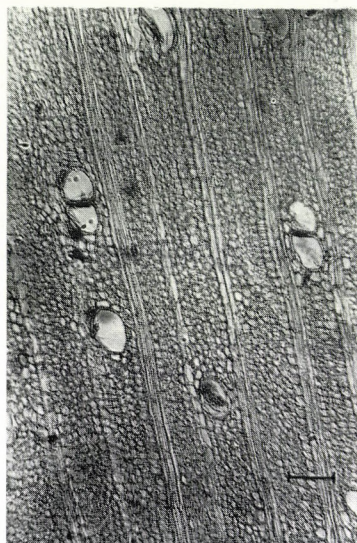


Fig. 16. *Swietenia macrophylla*, corte transversal, línea de escala: 100 μm

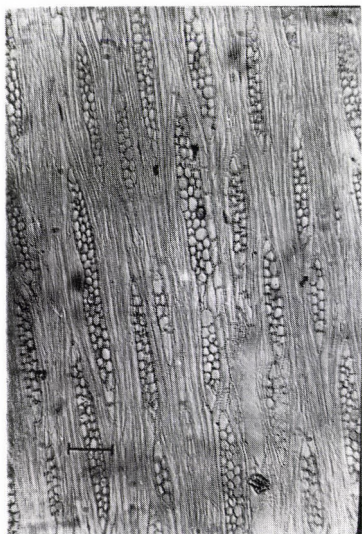


Fig. 17. *Swietenia macrophylla*, corte tangencial, línea de escala: 100 μm



Fig. 18. *Swietenia macrophylla*, corte radial, línea de escala: 100 μm

El parénquima axial es mayormente de tipo paratraqueal vasicéntrico, a veces se observa también con distribución terminal. Las series del parénquima están constituidas por 5-8 células, las cuales en sección transversal poseen un diámetro medio de $28\text{ }\mu\text{m}$.

Los radios medulares son numerosos, $8/\text{mm}^2$, heterogéneos y de dos tipos: uniseriados y multiseriados de 2-3 células de ancho. Los multiseriados alcanzan un ancho medio de $20\text{ }\mu\text{m}$.

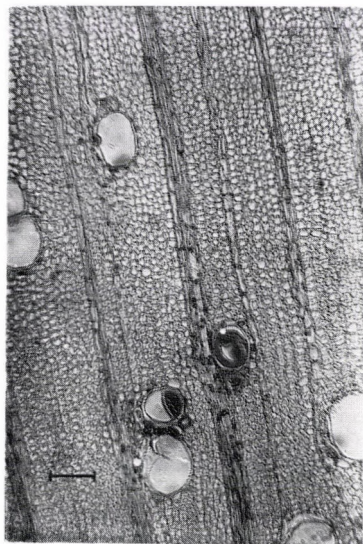


Fig. 19. *Swietenia macrophylla* × *mahagoni*, corte transversal, línea de escala: $100\text{ }\mu\text{m}$

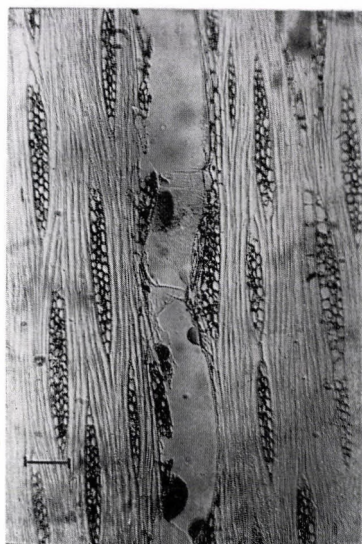


Fig. 20. *Swietenia macrophylla* × *mahagoni*, corte tangencial, línea de escala: $100\text{ }\mu\text{m}$

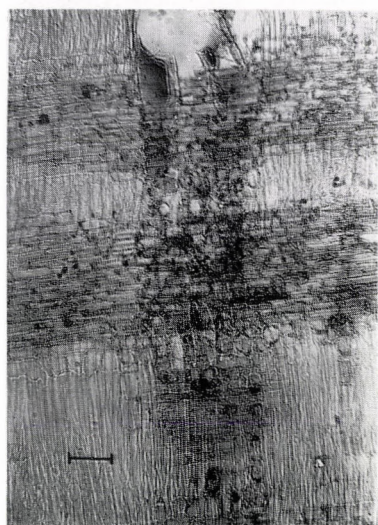


Fig. 21. *Swietenia macrophylla* × *mahagoni*, corte radial, línea de escala: $100\text{ }\mu\text{m}$

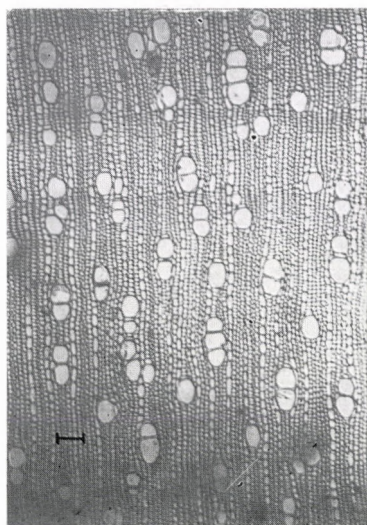


Fig. 22. *Trichilia havanensis*, corte transversal, línea de escala: $100\text{ }\mu\text{m}$

Las fibras son de tipo libriforme, con formas poligonales y están distribuídas irregularmente. En sección transversal tienen un diámetro medio de $18\ \mu\text{m}$ y pared de $5\text{--}6\ \mu\text{m}$ de grosor. Las fibras son muy cortas, con valores de $575\text{--}810\text{--}1125\ \mu\text{m}$ de largo y presentan algunos septos muy finos.

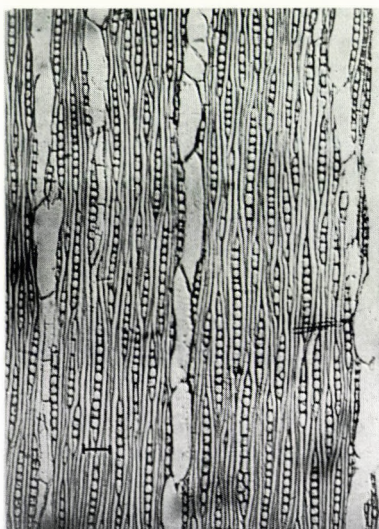


Fig. 23. *Trichilia havanensis*, corte tangencial, línea de escala: $100\ \mu\text{m}$



Fig. 24. *Trichilia havanensis*, corte radial, línea de escala: $100\ \mu\text{m}$

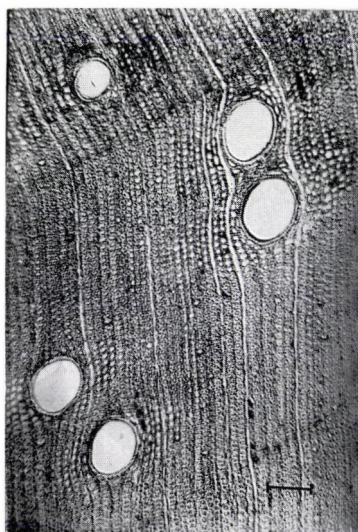


Fig. 25. *Lysiloma Sabicu*, corte transversal, línea de escala: $100\ \mu\text{m}$

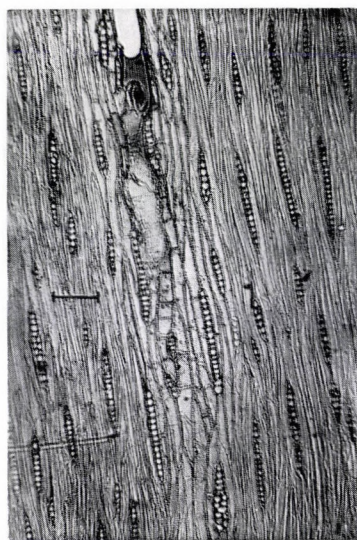


Fig. 26. *Lysiloma Sabicu*, corte tangencial, línea de escala: $100\ \mu\text{m}$

Trichilia havanensis Jacq. (Figs 22, 23 y 24)

Nombres vulgares: Siguaraya.

Zonas de crecimiento distinguibles, madera poroso-difusa, poros numerosos, $24/\text{mm}^2$, solitarios, en múltiples radiales de 2–5 elementos y en conglomerados de 3–4 células. Diámetro tangencial promedio de los solitarios pequeño, 48–55–62 μm , pared celular de 5 μm de grosor con puntuaciones intervasculares areoladas, circulares y alternas con poros alargados. Platinas de perforación simples.

Elementos de los vasos de tallas medianas, alcanzando valores de 430–540–610 μm de largo.

El parénquima axial es de tipo paratraqueal vasicéntrico, a veces formando bandas irregulares. Las series del parénquima están formadas por 4 células, las cuales en sección transversal tienen un diámetro promedio de 14 μm . Presentan contenidos de color naranja.

Los radios medulares son numerosos, $15/\text{mm}^2$, cercanamente homogéneos, aunque esporádicamente se distinguen los dos tipos de células. Los radios son exclusivamente uniseriados con un ancho medio de 21 μm .

Las fibras son de tipo libriforme, con formas poligonales y están distribuidas irregularmente. En sección transversal tienen un diámetro medio de 18 μm y pared celular de 4 μm de grosor. Las fibras son muy cortas, con valores de 633–894–1000 μm de largo. Se observan algunos septos muy finos.

El parénquima es de tipo paratraqueal confluyente, formando en ocasiones bandas. Las series están formadas por hasta 5 células, las cuales en sección transversal poseen un diámetro promedio de 20 μm .

Los radios medulares son numerosos, $15/\text{mm}^2$, cercanamente homogéneos, aunque, frecuentemente se observan los dos tipos de células. Los radios son exclusivamente uniseriados con ancho medio de 22 μm .

Las fibras son de tipo libriforme, con formas poligonales y están distribuidas irregularmente. En sección transversal tienen un diámetro medio de 16 μm , con pared de 4 μm de grosor. Las fibras son muy cortas, con valores de 525–985–1275 μm .

MIMOSACEAE

Lysiloma Sabicu Benth. (Figs 25, 26, y 27)

[*L. latisiliqua* (L.) Benth.; *Mimosa latisiliqua* L.; *Acacia formosa* A. Rich.]

Nombres vulgares: Sábicu, Jigüe, Sábicu amarillo, Zapatero, Bacona morada.

Anillos de crecimiento conspicuos, madera con porosidad difusa, poros moderadamente escasos, $6/\text{mm}^2$, solitarios, en múltiples radiales de 2 elementos y en grupos de 3–4 células. Diámetro tangencial promedio de los poros solitarios pequeño, 32–65–151 μm , grosor de la pared 6 μm , con puntuaciones areoladas ornadas, circulares y alternas con poros ovales. Platinas de perforación simples.

Los elementos de los vasos son de tallas medianas, con dimensiones de 230–400–490 μm de largo. Eventualmente se observan contenidos de color naranja-carmelitosos.

El parénquima axial es de tipo paratraqueal vasicéntrico y aliforme, que en ocasiones llega a ser confluyente. Las series están formadas por 2–4 células, las cuales en sección transversal tienen diámetro medio de 22 μm . Se observan frecuentemente células cristalíferas septadas con cristales poliédricos.

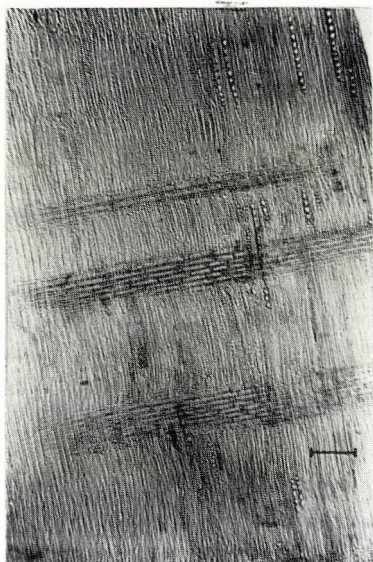


Fig. 27. *Lysiloma Sabicu*, corte radial, línea de escala: 100 μm

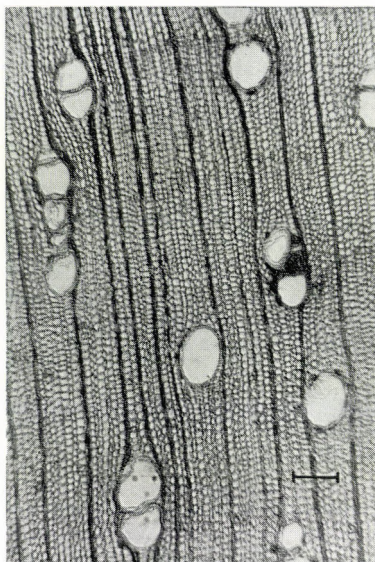


Fig. 28. *Matayba apetala* ssp. *oppositifolia* corte transversal, línea de escala: 100 μm

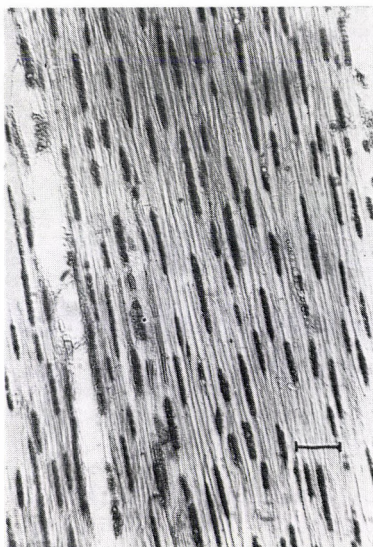


Fig. 29. *Matayba apetala* ssp. *oppositifolia* corte tangencial, línea de escala: 100 μm

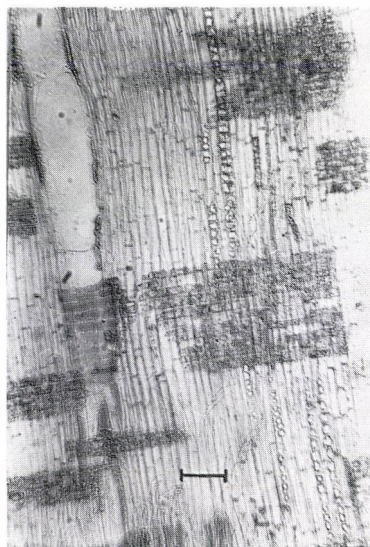


Fig. 30. *Matayba apetala* ssp. *oppositifolia* corte radial, línea de escala: 100 μm

Los radios medulares son numerosos, $9/\text{mm}^2$, homogéneos y exclusivamente uniseriados, éstos con un ancho medio de $16\ \mu\text{m}$.

Las fibras son de tipo libriforme, de formas poligonales y están distribuidas radialmente. En sección transversal tienen un diámetro promedio de $22\ \mu\text{m}$, y pared celular de $6\ \mu\text{m}$ de grosor. Las fibras son cortas, con valores de $950\text{--}1086\text{--}1100\ \mu\text{m}$ de largo. Se observan septos muy finos.

SAPINDACEAE

Matayba apetala (Macf.) Radlk. ssp. **oppositifolia*** (A. Rich.) Borhidi (Figs 28, 29 y 30)

(*Cupania oppositifolia* A. Rich.)

Nombres vulgares: Macurije.

Zonas de crecimiento presentes, madera con porosidad difusa, poros escasos, $9/\text{mm}^2$, solitarios, en múltiples radiales de 2 elementos y en grupos de 3 células. Diámetro tangencial promedio de los solitarios pequeño, $41\text{--}56\text{--}60\ \mu\text{m}$, grosor de la pared celular $6\ \mu\text{m}$, con puntuaciones areoladas circulares y alternas con poros ovales. Platinas de perforación simples e inclinadas.

Los elementos de los vasos son moderadamente cortos, con valores de $198\text{--}290\text{--}303\ \mu\text{m}$ de largo.

El parénquima axial presenta dos patrones fundamentales de distribución: apotraqueal en bandas irregulares y paratraqueal vasicéntrico. Las series de éste están formadas por 6 células, las cuales en sección transversal tienen diámetro medio de $19\ \mu\text{m}$.

Los radios medulares son muy numerosos, $16/\text{mm}^2$, homogéneos y uniseriados, con ancho medio de $23\ \mu\text{m}$.

Las fibras son de tipo libriforme, de formas cuadradas a poligonales y presentan distribución radial. En sección transversal estos elementos tienen diámetro medio de $17\ \mu\text{m}$ con pared de $4\text{--}5\ \mu\text{m}$ de grosor. Las fibras son cortas, con dimensiones de $675\text{--}1010\text{--}1575\ \mu\text{m}$ de largo.

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* *Matayba apetala* (Macf.) Radlk. ssp. *oppositifolia* (A. Rich.) Borhidi **comb. et stat. nova** hoc loco. Basionym: *Cupania oppositifolia* A. Rich. in Sagra, R. Hist. Nat. Cub. X. p. 292, t. 32 (1845).

ESTUDIO COMPARATIVO DE LA MADERA DE *BUCIDA* L. (COMBRETACEAE)

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The anatomy of the secondary xylem and some ecological features of the representants of genus *Bucida* L. in Cuba: *B. buceras* L., *B. ophitica* Bisse, *B. palustris* Borhidi, *B. spinosa* (Northrop) Jennings and *Bucida subinermis* Bisse are described. The relation between ecoanatomical aspects in these species are discussed.

Introducción

El género *Bucida* L. tiene distribución neotropical encontrándose exclusivamente en América Tropical y las Antillas.

LEÓN y ALAÍN (1953) reportaron la presencia en Cuba de las especies *B. buceras* L. y *B. spinosa* (Northrop) Jennings; sin embargo estudios posteriores realizados con vistas a la edición de la nueva obra Flora de Cuba, han hecho posible el descubrimiento de 3 nuevos taxones (BISSE 1974 y BORHIDI et MUÑIZ 1975): *B. subinermis* Bisse; *B. ophitica* Bisse y *B. palustris* Borhidi.

La madera de las especies de este género tiene amplio uso en la industria de la madera por su gran dureza y durabilidad (incluso en contacto directo con el agua). Por tal motivo decidimos realizar el estudio anatómico de la madera de las 5 especies antes mencionadas con el fin de ofrecer aquellas características que apoyan las propiedades físico-mecánicas, así como determinar si existen diferencias que permitan la identificación de cada una de ellas.

Materiales y métodos

Se confeccionaron pequeñas probetas de las 5 especies en estudio a partir de ejemplares de las xilotecas del Centro de Investigación Forestal (HBw) y del Instituto de Botánica de la Academia de Ciencias de Cuba (HACw), las cuales fueron ablandadas por cocción en agua destilada para su seccionamiento. Los cortes obtenidos a un grosor de 20-30 μ m fueron deshidratados y montados según las técnicas usuales en anatomía de maderas. El material disgregado se obtuvo de pequeñas astillas las cuales fueron calentadas en una mezcla de ácido acético y peróxido de hidrógeno al 30% en relación 1 : 1.

Para cada uno de los caracteres se realizaron 50 mediciones con excepción del largo de las fibras y largo de las series del parénquima axial de los que se realizaron 100 y 25 mediciones respectivamente. Los términos empleados en las clases de las dimensiones y abundancia de los elementos son los aprobados para las descripciones anatómicas (CHATTAWAY 1932 y Committee on Standardization of Cell Size 1937 y 1939). Para el grosor de la pared de las fibras seguimos los criterios de PÉREZ MOCOLLÓN (1973), basados en la relación lumen/diámetro medio.

Resultados

Zonas de crecimiento presentes. Porosidad difusa, poros numerosos en *B. ophitica* (24/mm²), moderadamente numerosos en *B. palustris* (19/mm²), *B. spinosa* (15/mm²) y *B. subinermis* (11/mm²) y moderadamente escasos en *B. buceras* (8/mm²).

Diámetro tangencial de talla media en *B. buceras* (115 µm), *B. subinermis* (115 µm), *B. palustris* (120 µm) y pequeños en *B. spinosa* (80 µm) y *B. ophitica* (60 µm). Diámetro radial de talla media en *B. buceras* (140 µm), *B. subinermis* (150 µm) y *B. palustris* (150 µm); moderadamente pequeños en *B. spinosa* (105 µm) y pequeños en *B. ophitica* (80 µm). Solitarios, múltiples radiales de hasta 4 células en *B. palustris* y *B. spinosa*; de hasta 3 células en *B. buceras* y de hasta 6 células en *B. subinermis* y *B. ophitica*. Presencia eventual de conglomerados de pocas células (generalmente de 4) en *B. palustris*, *B. ophitica*, *B. spinosa* y *B. subinermis*. Pared celular de 5–6 µm de grosor.

Elementos vasculares moderadamente cortos en *B. ophitica* (150–300–390 µm) y *B. spinosa* (125–306–426 µm). Talla media en *B. buceras* (300–460–750 µm), *B. subinermis* (230–415–671 µm) y *B. palustris* (325–490–780 µm). Punteaduras intervascuales alternas, ornadas, con bordes circulares de 5×5 µm de diámetro. Poros en forma de fisura con dimensiones de 4×1 µm, incluidos, ocasionalmente coalescentes.

Parénquima axial paratraqueal confluyente en *B. ophitica* y *B. subinermis*, aliforme confluyente en *B. buceras*, *B. palustris* y *B. spinosa*. Series con (2–4–7) células ó (306–445–590 µm) de longitud. Pared celular de (1,5–2–3 µm) de grosor; diámetro celular de 30 µm en *B. buceras* y *B. subinermis* 25 µm en *B. ophitica*; 20 µm en *B. spinosa* y 15 µm en *B. palustris*. Longitud celular (140–150–177 µm). Presencia de cristales.

Radios medulares numerosos en *B. buceras* (10/mm²), *B. subinermis* (8/mm²) y *B. palustris* (9/mm²) y muy numerosos en *B. spinosa* (16/mm²) y *B. ophitica* (13/mm²), simétricos; los uniseriados moderadamente altos en *B. spinosa* (96 µm) con 2–3–7 células y *B. ophitica* (90 µm) con 3–5–8 células altas; en *B. buceras* (120 µm) con 2–4–11 células, *B. subinermis* (100 µm) 3–6–13 células y *B. palustris* (170 µm) 2–6–14 células. Multiseriados muy altos con (345 µm) 1–14–21 células en *B. buceras*; (330 µm) 7–15–25 en *B. subinermis*, (371 µm) 9–14–27 células en *B. palustris*, (270 µm) con 8–12–17 células en *B. spinosa* y (256,4 µm) con 9–12–18 células en *B. ophitica*. El ancho es de 55 µm (2–3) células en *B. buceras*; 45 µm (2–3–4) células en *B. spinosa*; 48 µm (2–3) células en *B. subinermis*; 45 µm (2) células en *B. palustris* y 49 µm (2–3) células en *B. ophitica*. Los radios son mayormente homogéneos compuestos por células procumbentes con cristales muy abundantes, isodiamétricos, muy frecuentemente con extremos puntiagudos y en casi todos presentan núcleos orgánicos en su interior. Las dimensiones celulares para *B. buceras* 15 µm de ancho; 18 µm en *B. spinosa*; 15 µm en *B. subinermis*; 17 µm en *B. palustris* y 12 µm en *B. ophitica*. Altura de 17,4 µm en *B. buceras*; 26 µm en *B. spinosa*; 18 µm en *B. subinermis*; 21 µm en *B. palustris* y 20 µm en *B. ophitica*. La profundidad es de 73 µm en *B. buceras*, 47 µm en *B. spinosa*, *B. palustris* y 53 µm en *B. subinermis* y *B. ophitica*.

Fibras distribuidas irregularmente de forma poligonal, cortas en *B. buceras* (1075–1420–1650 µm), *B. spinosa* (910–1130–1465 µm), *B. subinermis* (875–1385–1750 µm) y *B. ophitica* (895–1155–1550 µm) y largas en *B. palustris* (1275–1600–1910 µm). Diámetro celular de 14 µm en *B. buceras* y *B. spinosa*; 16 µm en *B. subinermis*, 12 µm en *B. palustris* y 11 µm en *B. ophitica*.

Pared celular gruesa en *B. buceras* con 3,9 µm ($L/\varnothing = 0,44$), *B. spinosa* 4,5 µm ($L/\varnothing = 0,35$), *B. subinermis* 4,98 µm ($L/\varnothing = 0,37$) muy gruesas en *B. palustris* 5,8 ($L/\varnothing = 0,03$) y *B. ophitica* 4 µm ($L/\varnothing = 0,27$).

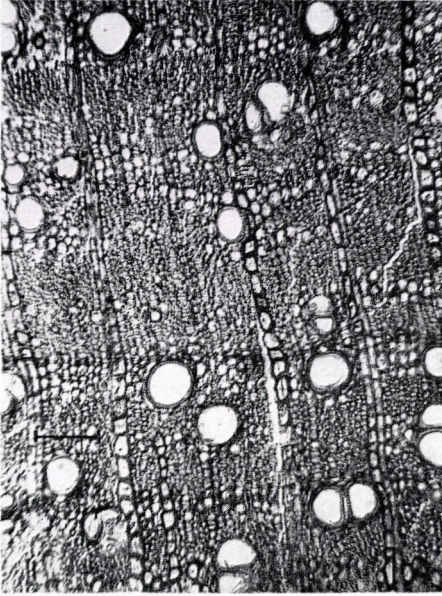


Fig. 1. Sección transversal de *B. ophiticola*
línea de escala: 100 μ m

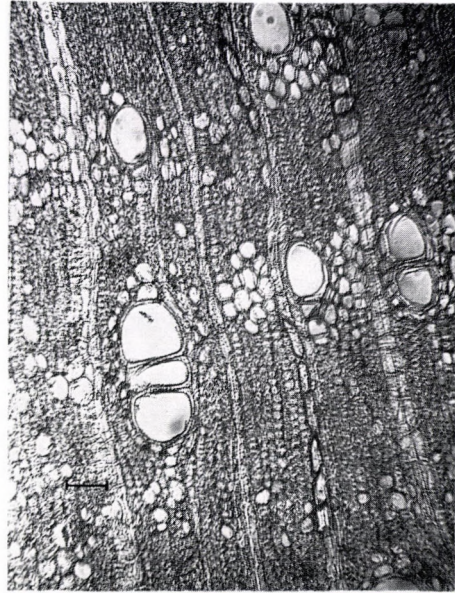


Fig. 2. Sección transversal de *B. subinermi*
línea de escala: 100 μ m



Fig. 3. Sección longitudinal tangencial de
B. spinosa línea de escala: 100 μ m



Fig. 4. Sección longitudinal radial de *B. ophiticola* línea de escala: 100 μ m

Discussion

La tabla 1 muestra que las maderas de las 5 especies de *Bucida* presentan una gran homogeneidad en sus estructuras, observándose sólo ligeras variaciones desde el punto de vista cuantitativo, las que sin lugar a dudas están dadas por diferencias ecológicas, relacionadas fundamentalmente en nuestra opinión con la cantidad de agua asimilable existente en el suelo.

Bucida palustris crece sobre turba (suelo ácido) en la Ciénaga de Zapata donde la humedad del suelo es alta; *Bucida subinermis* crece sobre mocarrero donde existen fluctuaciones anuales de agua y *Bucida spinosa* crece fundamentalmente en terrenos costeros, maniguas y suelos pedregosos-cenagosos pero más relacionados con agua salada, la que aunque en abundancia resulta fisiológicamente poco asimilable. *B. buceras* por su parte crece en las proximidades de ríos y costas, mayormente asociadas a aguas no saladas en movimiento y ricos en oxígeno, mientras que *B. ophiticola* lo hace sobre serpentina donde se manifiesta un estado de pseudoxeromorfía (VALES et al. 1982) debido a la permeabilidad de este suelo y sequía fisiológica por la alta concentración de iones pesados.

Las características xeromórficas han sido general asociadas por varios autores con elementos de los vasos estrechos, cortos y muy numerosos. VAN DER GRAAFF y BAAS (1974) destacaron también estrechamiento y acortamiento de los elementos de los vasos e incremento de la porosidad y radios medulares bajos con el incremento de la latitud; resultados similares aunque más atenuados con el incremento de la altitud fueron igualmente señalados por estos autores. METCALFE y CHALK (1950), señalaron que el incremento en el diámetro de los vasos y el decremento de los radios medulares puede ser fácilmente afectado por condiciones ecológicas.

En las especies investigadas no existen diferencias de latitud, por lo que las diferencias cuantitativas observadas deben estar en función de la disponi-

Tabla 1
Valores de los principales caracteres observados

	Elementos de los vasos					Fibras	
	Diám. tang. en μm	Diám. radial en μm	Largo total en μm	Pared en μm	Frecuencia en mm^2	Diám. medio en μm	Pared en μm
<i>Bucida palustris</i>	120	150	490	5-6	19	12	5,8
<i>Bucida buceras</i>	115	140	460	5-6	8	14	3,9
<i>Bucida subinermis</i>	115	150	415	5-6	11	16	5
<i>Bucida ophiticola</i>	60	80	300	5-6	24	11	4
<i>Bucida spinosa</i>	80	105	306	5-6	15	14	4,5

bilidad de agua y nutrientes del suelo. Las especies *B. palustris*, *B. buceras* y *B. subinermis* mostraron los elementos de los vasos más largos y anchos, así como las fibras más largas, mientras que *B. ophitica*, y *B. spinosa* alcanzaron valores de estos caracteres significativamente más pequeños como se observa en la Tabla 1.

Los radios medulares uniseriados y multiseriados mostraron también variaciones en la altura, lo que coincide con lo encontrado por VAN DER GRAAFF y BAAS (1974) y VALES et al. (1982), quienes destacaron una estrecha relación entre la altura de los radios medulares y el largo de los elementos de los vasos.

CARLQUIST (1977) definió los términos vulnerabilidad (diámetro medio de los elementos de los vasos dividido por la frecuencia de éstos por mm²) y mesomorfía (vulnerabilidad multiplicada por el largo de los elementos de los vasos) indicando que bajos valores de vulnerabilidad le ofrecen al sistema conductor capacidad de aseguramiento, en la cantidad de agua necesaria para el buen desarrollo de todos los procesos en el vegetal (decrece la posibilidad de la formación de burbujas de aire en los vasos) mientras que altos valores de mesomorfía son interpretados por él como indicadores de características mesomórficas en esas especies. La tabla 2 muestra los valores encontrados para los índices numéricos de vulnerabilidad (V) y mesomorfía (M) en las 5 especies de *Bucida*. En ella se observa que las hipótesis de CARLQUIST se cumplen para *B. buceras* y *B. subinermis* no así para *B. palustris* donde se obtuvo un valor relativamente bajo. Para *B. spinosa* se obtuvo un valor de vulnerabilidad más bajo que el encontrado para *B. buceras* y *B. subinermis*, lo que en cierta medida resulta lógico ya que al ser una especie que está más ligada al agua salada presenta situaciones similares a los manglares donde como es sabido las plantas están sujetas a una alta tensión de agua y fuertes presiones negativas. VAN VLIET (1979) estudiando especies de Combretaceae que forman parte de manglares, encontró valores de vulnerabilidad que oscila-

en las diferentes especies investigadas de *Bucida*

Largo en μm	Lumen/Diám. medio	Parénquima axial			Radios medulares			Frecuencia/mm
		Diám. medio en μm	Largo de las series en μm	Ancho de los multiseriados en μm	Ancho de los multiseriados en $\pm$ de células	Altura de los uniseriados en μm	Altura de los multiseriados en μm	
1600	0,03	15	590	45	2	170	371	9
1420	0,44	30	470	55	2-3	120	345	10
1385	0,37	30	476	48	2-3	150	330	8
1155	0,27	25	306	49	2-3	90	256	13
1130	0,35	20	390	45	2-4	90	270	16

ron de 13,2-35,5, lo que evidentemente no concordaba con las hipótesis de CARLQUIST para este tipo de vegetación.

Por último *B. ophitica* mostró los valores más bajos de ambos índices (2,9 y 810) lo que en nuestra opinión concuerda con las características ecológicas de las serpentininas donde se manifiesta una sequía fisiológica debido a la alta concentración de iones pesados en el suelo, así como el estado de pseudo-

Tabla 2

Valores de los índices numéricos V y M

Especies	(V) Vulnera- bilidad	(M) Meso- morfía
<i>Bucida palustris</i>	7,2	3508
<i>B. buceras</i>	16,1	7364
<i>B. subinermis</i>	12,2	5753
<i>B. spinosa</i>	6,08	1860
<i>B. ophitica</i>	2,9	810

xeromorfía señalado por VALES et al. (1982) como una combinación de caracteres morfológicos xeromórficos con un sistema conductor típico para especies mesomórficas.

Nuestros resultados del análisis de las hipótesis de CARLQUIST reflejan, como ha sido señalado ya por el propio CARLQUIST, BAAS (1976) y VAN VLIET (1979) que el papel del largo de los elementos de los vasos en la conducción del agua es completamente especulativo, debiendo analizarse más ampliamente ya que el largo de esos elementos puede estar en mayor o menor grado afectado por el crecimiento intrusivo de acuerdo a las concentraciones de nutrientes.

CHALK y CHATTAWAY (1934) señalaron que el largo de las células fusiformes cambiales se correspondía aproximadamente con el largo de las series del parénquima. Estudios posteriores (Süss 1967 y VALES 1982) han demostrado que las series del parénquima al igual que las fibras y los elementos de los vasos pueden tener alargamientos por crecimiento intrusivo. En la Tabla 1 se observa que con excepción de *B. ophitica* donde el largo del parénquima axial es casi igual al largo de los elementos de los vasos, en las otras especies el largo del parénquima axial es mayor que el largo de los elementos de los vasos, lo que implica que en estas especies ocurre un marcado crecimiento intrusivo de todos los elementos. Al parecer la alta concentración de nutrientes en el suelo en que crece *B. palustris* hace que sus elementos obtengan los mayores valores de largo (debido al crecimiento intrusivo), pero a la vez esta alta concentración y acidez del suelo afecta la capacidad de asimilación, de agua por la planta.

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KEY BASED ON LEAF EPIDERMAL ANATOMY FOR FOOD HABITS STUDIES OF HERBIVORES

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The microanatomical characteristics of 2 pine, 110 dicotyledon and 26 monocotyledon plant epidermis were described and ordered in a taxonomy key. Results are presented as a series of descriptions and accompanying photos. This key has been used for the diet analyses of wild herbivores on the bases of esophagus-, rumencontent and feces.

Introduction

Microhistological analyses of esophagus- (BRYANT et al. 1980), stomachcontent (HOLISOVA et al. 1982, MÁTRAI et al. 1983) and feces (SEXSON 1981) have been widely used for qualitative and quantitative estimation of herbivore diets. These methods are based on the characteristics of epidermal tissues preserved in the digestive tract. For the species identification of the epidermis tissues deriving from the digestive tract of herbivores a reference plant collection should be made in the original habitat. Species of the reference collection are first identified by classical taxonomic methods, then characteristics of the epidermis tissues of known plant species are described and ordered in a taxonomic key.

Taxonomic keys were prepared by STEWART (1965) and LIVERSIDGE (1970), LENSING (1980) to grass species of some areas of Africa.

The aim of this study is to describe a taxonomic key containing mainly of plant species of an artificially afforested pine habitat common in Hungary.

Study area

The study area was a part (64 ha) of the Research Area (3200 ha) of the Game Biology Research Station, University of Agricultural Sciences, situated 30 km East of Budapest, at the Gödöllő foothills. Elevation ranges from 100 to 250 m. Average annual rainfall and temperature are 569 mm, 9.9 °C respectively. Yearly fluctuation of rainfall and temperature is significant. Soil is chalky sand. This area is intensively used by red deer (*Cervus elaphus* L.) and roe deer (*Capreolus capreolus* L.) throughout the year.

The scotch fir (*Pinus sylvestris* L.) and the sourcherry (*Prunus serotina* L.) was introduced 10-12 years ago. The pine habitat (64 ha) is surrounded by old forests of acacia (*Robinia pseudoacacia* L.), oak (*Quercus* sp.) and aspen (*Populus* sp.). The plant community (Soó 1980) of *Cynodonti-Poetum angustifoliae* (48%), *Arrhenatheretum elatioris* (22%) and *Sisymbrium officinalis* (9%) spots amongst *Festuco vaginatae-Pinion*, *Astragalo-Festucetum rupicolae* (11%) and *Brometum tectorum* (6%) are present in undisturbed communities.

Materials and methods

Plant species consumed by large wild herbivores were preferred for the reference collection. All those plant species were collected which were seen to be grazed or browsed by roe or red deer. The original reference collection was later completed by those species which were found in the rumen contents of roe deer.

Leaves and stems were collected from each plant species. They were reserved in 30 per cent ethanol or 4 per cent formalin until elaboration could be carried out.

Epidermis fragments were prepared and stained by methods of SÁRKÁNY et al. (1957). Photos were made of each epidermis.

For the taxonomic key the plant species were arranged by their anatomical features of the abaxial epidermis.

Results

Key to 2 Pine, 110 Dicotyledon and 26 Monocotyledon species from Hungary based on the anatomy of the abaxial leaf epidermis

- A Cells of epidermis regularly shaped, stomata arranged in rows with their pores parallel to the longitudinal axis of leaves I
- B Cells of epidermis irregularly shaped, with smooth, slightly waved or lobed walls. Guard cells kidney-shaped DICOTYLEDONS
- I a Silica cells, hairs, papillae in the costal and intercostal zones may also be present. Guard cells mostly bone-shaped MONOCOTYLEDONS
- b Silica cells, hairs, papillae in the costal and intercostal zones absent. Stomata situated near to one another. Guard cells kidney-shaped *Pinus silvestris* L., *Pinus nigra* Arn.

B Dicotyledons

- 1 a Hairs present 2
- b Hairs absent 63
- 2 a Hairs unicellular 3
- b Unicellular and glandular hairs present 17
- c Unicellular and transversely septated (uniseriate) hairs present 27
- d Unicellular, uniseriate and glandular hairs present 30
- e Hairs uniseriate 35
- f Uniseriate and glandular hairs present 38
- g Fasciculate hairs present 48
- h Candelabra hairs resembling superimposed stellate hairs with 3–4 μ of wall-thickness and uniseriate stalked glandular hairs with multicellular heads present 50
- i Stellate hairs present 51
- j Peltate hairs present. Rays thin-walled, soft. Hairs forming a dense covering on the epidermis *Elaeagnus angustifolia* L.
- k Shaggy hairs with pointed apices accompanied by hooked ones. Thickness of walls 6–8 μ . Glandular hairs with uniseriate stalks and unicellular heads present (Fig. 1) ... *Picris hieracioides* L.
- l Hairs forming web-like covering 55
- m Uni- and multicellular papillae mostly on the ribes present. Cells with lobed walls *Saponaria officinalis* L.

- n Papillae and glandular hairs with uniseriate stalks and unicellular heads with a round bases min. 10 μ in diameter. Last haircells and heads often broken down. Epidermal cells lobed **Amaranthus retroflexus** L.
- o Glandular hairs present 58
- 3 a Epidermal cells lobed 4
- b Epidermal cells smooth- or slightly wavy-walled 11
- 4 a Hairs min. 10-times longer than the max. width 5
- b Smooth-walled hairs with pointed apices 4–10-times longer than the max. width 8
- c Hairs max. 4-times longer than the max. width occurring on the ribes with grooved surfaces and blunt apices 9
- 5 a Wavy-walled hairs with rounded apices on margins present. Width on the bases min. 80 μ **Mycelis muralis** (L.) Dun.
- b Hairs with pointed apices on the lamina everywhere present 6
- 6 a Soft hairs thin-walled, width at the bases max. 80 μ **Cynoglossum officinale** L.
- b Thickness of walls 2–6 μ 7
- 7 a Soft hairs smooth-walled with a max. 80 μ in diameter at the round bases **Anchusa officinalis** L.
- b Rigid hairs wavy-walled with a 10–20 μ in diameter at the polygonal bases. Hairs often broken near the bases and the short bits of hairs dark coloured occurring mostly on the lamina with a 8–12 μ in diameter **Melilotus albus** Desr. ap. Lam.
- 8 a Stem epidermis of short, more or less square cells forming a ring around stomata. On the lamina stomata situated close one to another **Prunus** sp.
- b Stem epidermis and lamina have not any features as above. Hairs thin-walled, width on the bases max. 20 μ **Lepidium campestre** R. Br.
- 9 a Smooth, thin-walled hairs. Bases min. 20 μ wide **Viola arvensis** Murr.
- b Hairs wavy-walled 10
- 10 a Hairs thin-walled **Taraxanum officinale** Webb
- b Thickness of walls: 3–4 μ **Veronica hederaefolia** L.
- 11 a Smooth-walled hairs min. 10-times longer than the max. width with pointed apices on the ribes. Means wall-thickness 8 μ **Crataegus monogyna** Jacq.
- b Hairs with blunt apices 5–10-times longer than the max. width 12
- c Hairs with blunt apices max. 5-times longer than the max. width 13
- d Hairs varying in length 14
- 12 a Rigid, smooth-walled hairs with bases forming a ring of 16 μ in diameter on means **Populus $\times$ robusta**
- b Soft, wavy-walled hairs, bases not as above **Gleditsia triacanthos** L.
- 13 a Diacytic type of stomata. Wavy-walled hairs with a thickness of 4 μ on means **Dianthus giganteiformis** Borb.
- b Paracytic type of stomata. Smooth-walled hairs with a thickness of 8 μ on means **Salsola kali** L.
- c Hexacytic type of stomata. Smooth-walled hairs on the ribes with a thickness of 2 μ on means **Vinca minor** L.
- 14 a Hairs smooth-walled 15
- b Hairs wavy-walled with a thickness of 2 μ on means **Anthriscus silvestris** Hoffm.
- 15 a Hairs on the ribes with a thickness of 4 μ on means **Rhamnus catharticus** L.
- b Hairs over all on the lamina 16
- 16 a Hairs with harsh surfaces and a wall-thickness of 2 μ on means seated on pedestals of several epidermal cells and situated more or less in parallel bands **Selinum carvifolia** L.
- b Hairs with plain surfaces and thin or 4–8 μ thickness of walls ... **Echium vulgare** L.

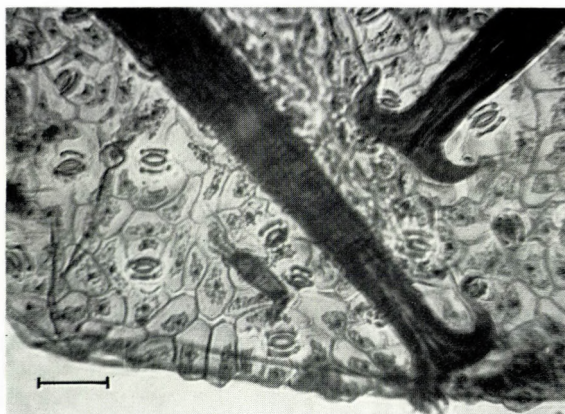


Fig. 1. *Picris hieracioides*, leaf, abaxial surface, bar scale: 50 μm

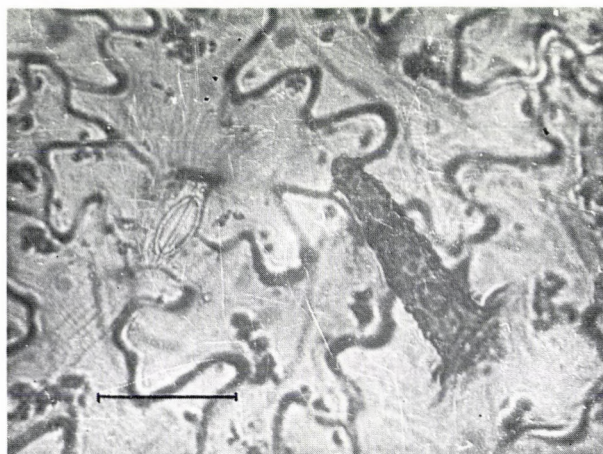


Fig. 2. *Salvia nemorosa*, leaf, abaxial surface, bar scale: 50 μm

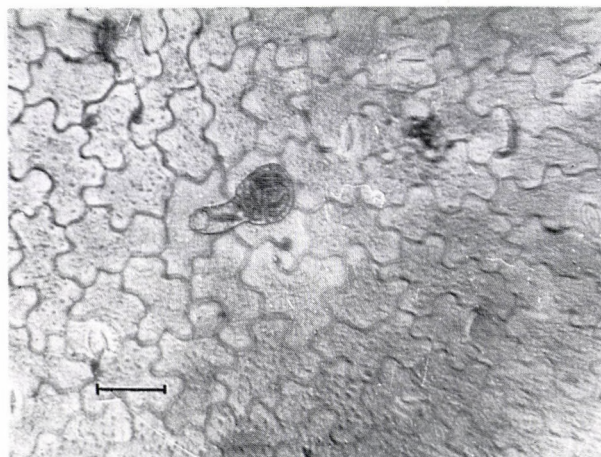


Fig. 3. *Solanum nigrum*, leaf, abaxial surface, bar scale: 50 μm

- 17 a Epidermal cells with lobed walls 18
 b Epidermal cells with smooth or slightly waved walls 22
- 18 a Glands of smaller and larger sizes, width of the latter 40–80 μ at the bases equal the complete length of the smaller ones, and segmented stalks and unicellular heads. Smaller glands with unicellular heads and usually unicellular stalks. Soft covering hairs thin, smooth-walled. Width at the bases 8–16 μ wide **Geranium phaeum** L.
 b All glands of equal sizes 19
- 19 a Short stalked glands with heads composed of cells radialized, covering by cuticle sharply separated from the epidermal cells. Smooth-walled clothing hairs with a bases forming a ring of 30–40 μ in diameter **Convolvulus arvensis** L.
 b Glands with unicellular heads and smooth-walled clothing hairs present 20
- 20 a Glands with unicellular stalks 21
 b Uniseriate stalked glands. Clothing hairs of 2 distinct sizes: thickness of longer 8 μ on means with a min. 5-times dimension of the shorter ones **Geum urbanum** L.
- 21 a Glands with spherical heads. Clothing hairs with a 20–24 μ in diameter at the polygonal bases. Thickness of walls 4 μ on means. Bases with short hairs-remainders occurring often on the lamina **Vicia tetrasperma** Schreb.
 b Glands with conical heads often consisting of 2 layers of cells. Smooth-walled clothing hairs 4–10-times longer than the bases-width occurring mostly on the ribes **Quercus cerris** L.
- 22 a Glands with multicellular heads 23
 b Glands with unicellular heads 27
- 23 a Heads composed of cells radialized covering by cuticle sharply separated from the epidermal cells 24
 b Headcells not as above 25
- 24 a Thin-walled clothing hairs soft, smooth, fairly enlarged at the round bases. Hairs forming a dense covering on the epidermis **Cannabis sativa** L.
 b Few thick and smooth-walled hairs with a bases not as above **Acer campestre** L.
- 25 a Glands with unicellular stalks. 26
 b Glands with multicellular stalks. Thin, smooth-walled clothing hairs 4–10-times longer than the max. width with rough surfaces occurring mostly on the ribes **Sambucus nigra** L.
- 26 a Clothing hairs of varying length thin, wavy-walled with dotted surfaces surrounded by a rosette of more epidermal cells at the bases **Knautia arvensis** Coult.
 b Glands with spherical, multicellular heads and narrowed, unicellular stalks. Smooth-walled clothing hairs of varying length with capitate or sharp-pointed apices and rounded bases **Urtica dioica** L.
 c Glands, each having an ellipsoidal, multicellular, club-shaped head and unicellular stalk with parallel walls. Clothing hairs rigid with regularly waved walls, a width of 8 μ on means and a bases forming a girdelle of 20–24 μ in diameter **Trifolium arvense** L.
- 27 a Epidermal cells with lobed walls. Thin, wavy-walled hairs with rounded apices and rough surfaces, 4–10-times longer than the bases-width (Fig. 2) ... **Salvia nemorosa** L.
 b Epidermal cells with smooth or slightly waved walls 28
- 28 a Diacytic type of stomata. Thin-walled hairs with blunt apices 29
 b Type of stomata not typical. Thin, wavy-walled hairs smooth, sometimes branched, with blunt apices, 2–10-times longer than the max. width .. **Pimpinella saxifraga** L.
- 29 a Rigid hairs wavy-walled with dotted surfaces, 2–10 times longer than the max. width **Silene otites** Wib. ssp. **hungarica** Wrigley
 b Soft hairs wavy-walled with plain surfaces, max. twice longer than the bases **Tunica prolifera** Scop.

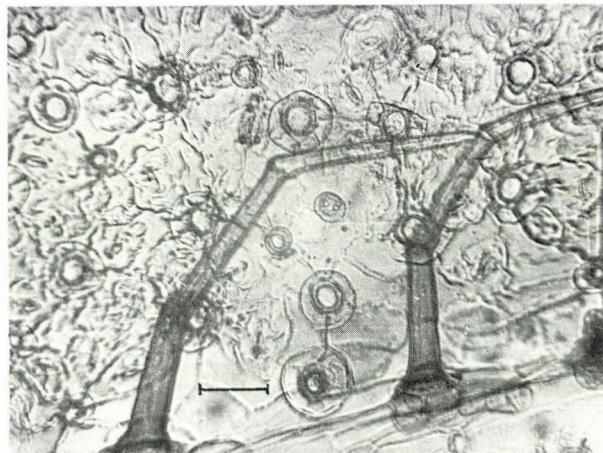


Fig. 4. *Teucrium chamaedrys*, leaf, abaxial surface, bar scale: 50 μm

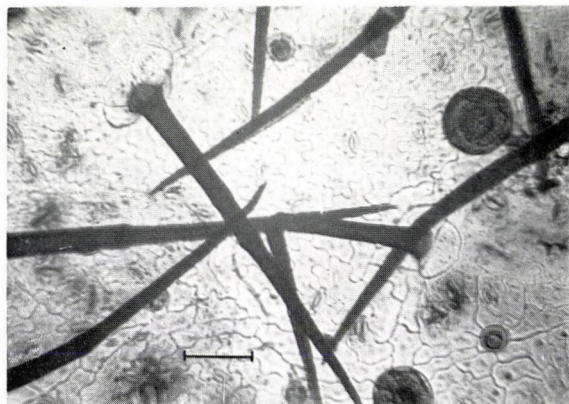


Fig. 5. *Leonurus cardiaca*, leaf, abaxial surface, bar scale: 50 μm

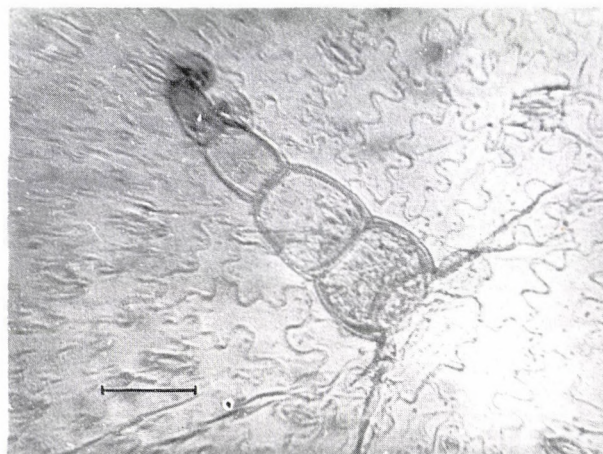


Fig. 6. *Cucubalus baccifer*, leaf, abaxial surface, bar scale: 50 μm

- 30 a Epidermal cells with lobed walls 31
 b Epidermal cells with smooth or slightly waved walls. Smooth walled clothing hairs with pointed apices, rounded bases, knobbed at the transverse septa. Thickness of walls 4–8 μ . Glands with short unicellular stalks and multicellular heads **Ballota nigra** L.
- 31 a Glands consisting of smaller and larger sizes, width of the latter at the bases at least the complete length of the smaller ones, with smooth walls and constrictions at the transverse septa. Smaller glands with unicellular stalks and 3–4 cellular heads. Clothing hairs with rounded apices (Fig. 3) **Solanum nigrum** L.
 b Glands with unicellular stalks and uni- or multicellular heads. The latter composed of cells radialized, covering by cuticle sharply separated from the epidermal cells. Smooth walled clothing hairs with pointed apices 32
 c Glands with unicellular stalks and heads 33
- 32 a Glands with spherical heads. Segmented hairs with knobbed transverse septa, many times longer than segmentless hairs. Thickness of walls: 1–2 μ **Galeopsis tetrahit** L.
 b Glands with elongated heads. Clothing hairs with 3–4 μ wall-thickness and dotted surfaces. The short segmentless hairs fitted to the lamina **Thymus glabrescens** Willd.
- 33 a Thin-walled clothing hairs. Segmentless, rigid hairs with striated surfaces and commonly broken near the bases sometimes shortly branched. Segmented hairs soft. Contents flowed from glands sometimes forming web-like covering on the lamina **Crepis rhoeoifolia** M. B.
 b Wall-thickness of clothing hairs 4–8 μ 34
- 34 a Soft clothing hairs with plain surfaces. Width of glandheads more or less twice greater than that of the stalks (Fig. 4) **Teucrium chamaedrys** L.
 b Erect clothing hairs with dotted surfaces. Segmented hairs many times larger than segmentless ones. Width of glandheads not or slightly greater than that of the stalks **Calamintha clinopodium** Fritsch
- 35 a Thin-walled bicellular hairs each having a short basal and a much longer terminal cell 36
 b Hairs consist of varying length of cells. Diacytic type of stomata 37
- 36 a Rigid terminal cells pointed **Amorpha fruticosa** L.
 b Soft terminal cells frequently broken away from the basal cells **Robinia pseudoacacia** L.
- 37 a Smooth walls hairs soft, knobbed at the transverse septa with circle-shaped bases. Thickness of walls: 3–4 μ . Hairs min. 10 times longer than the max. width **Lychnis coronaria** Desr.
 b Thin, waved walls hairs with rounded apices and markedly short basal cells 5–10 times longer than the max. width **Silene nutans** L.
- 38 a Epidermal cells with lobed walls 39
 b Epidermal cells with smooth or slightly waved walls 46
- 39 a Hairs min. 10 times longer than the max. width 40
 b Hairs (2) 5–10 times longer than the max. width 41
 c Hairs of varying length 44
- 40 a Glands with unicellular stalks and multicellular heads composed of cells radialized covering by cuticle sharply separated from the epidermal cells. Soft, smooth-walled clothing hairs with rounded apices knobbed at the transverse septa. Thickness of walls 4–8 μ **Fraxinus ornus** L.
 b Glands as above and with unicellular heads. Rigid, smooth-walled clothing hairs with pointed apices (Fig. 5) **Leonurus cardiaca** L.



Fig. 7. *Veronica spicata*, leaf, abaxial surface, bar scale: 50 μ m

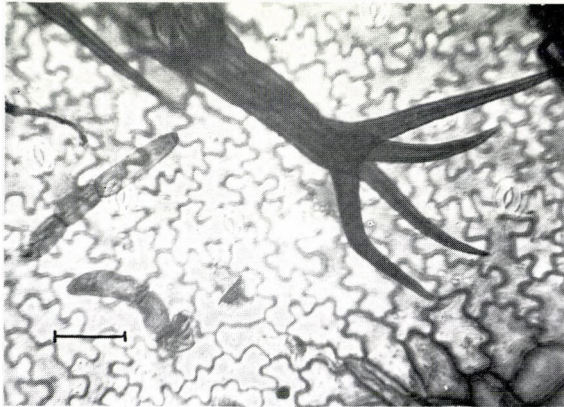


Fig. 8. *Leontodon hispidus*, leaf, abaxial surface, bar scale: 50 μ m

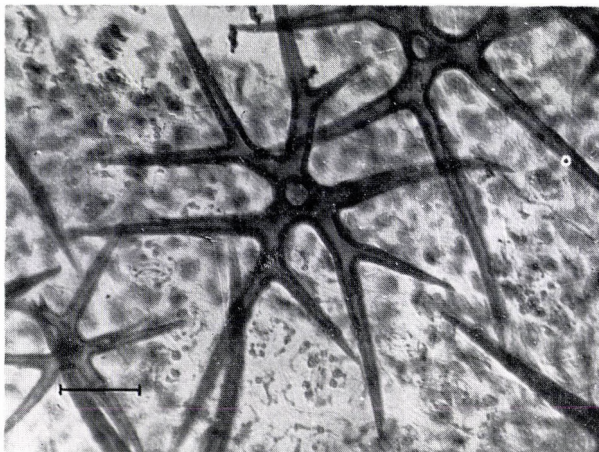


Fig. 9. *Berteroa incana*, leaf, abaxial surface, bar scale: 50 μ m

- c Glands of two forms: with unicellular stalks, bicellular, ellipsoidal heads and multicellular stalked with unicellular heads. Clothing hairs smooth-walled, knobbed at the transverse septa with 4–12 μ wallthickness occurring mainly on the stems **Artemisia annua** L.
- 41 a Glands and clothing hairs of similar length, knobbed at the transverse septa 42
- b Glands many times shorter than the clothing hairs. Clothing hairs smooth-walled with pointed apices 43
- 42 a Smooth, thin-walled hairs. Width on the bases 30–40 μ ... **Melandrium album** Garcke
- b Waved walls hairs with 2–4 μ of wallthickness. Width on the bases min. 40 μ (Fig. 6) **Cucubalus baccifer** L.
- 43 a Biseriate stalked glands with unicellular heads each having two blunt apices. Hairs with knobbed walls at the transverse septa and prolonged terminal cells **Ambrosia elatior** L.
- b Glands with unicellular stalks and unicellular, flash-shaped heads. Clothing hairs with angular bases and markedly short basal cells. Thickness of walls: 2–4 μ **Stenactis annua** Nees
- 44 a Each glands many times shorter than clothing hairs 45
- b Glands consisting of smaller and many times larger sizes, width of the latter min. 24 μ on the bases with thin, slightly-waved walls and rounded apices. Smaller glands with unicellular stalks and bicellular heads (Fig. 7) **Veronica spicata** L.
- 45 a Glands with unicellular stalks and bicellular heads. Slightly-waved walls clothing hairs with blunt apices and dotted surfaces. Thickness of walls: 5–8 μ **Veronica officinalis** L.
- b Glands with unicellular heads and uni- or multicellular or multiseriate stalks. Smooth, thin-walled clothing hairs knobbed at the transverse septa with prolonged terminal cells and markedly short basal cells. Biseriate hairs occurring on the stems often broken near the bases **Solidago virga-aurea** L.
- 46 a Glands similar to the clothing hairs. Smooth-walled hairs of varying length with rounded apices knobbed at the transverse septa. Hairs on the ribs mainly consisting of two cells of similar sizes. Thickness of walls 2 μ on means. Diacytic type of stomata **Gypsophila paniculata** L.
- b Multicellular stalked glands with unicellular heads many times shorter than the clothing hairs 47
- 47 a Thin, waved-walls clothing hairs knobbed at the transverse septa with prolonged terminal cells. Hairs 5–10 times longer than the min. 40 μ bases-width with markedly short cells near the bases **Erigeron canadensis** L.
- b Soft, smooth-walled hairs of varying length with blunt apices and dotted surfaces. Thickness of walls: 1–2 μ , width on the bases min. 30 μ . Sometimes biseriate cells near the round bases **Cichorium intybus** L.
- 48 a Unicellular stalked hairs 49
- b Multiseriate stalked hairs. Glands occurring on the lamina with multicellular stalks and unicellular heads. Epidermal cells with lobed walls (Fig. 8) **Leontodon hispidus** L.
- 49 a Epidermal cells with lobed walls. Desmocytic type of stomata **Turritis glabra** L.
- b Epidermal cells with straight walls **Arabis hirsuta** Scop.
- 50 a Epidermis slightly hairy. Epidermal cells with waved walls **Viburnum lantana** L.
- b Hairs forming a dense covering on the lamina. Epidermal cells with lobed walls **Verbascum phlomoides** L., **Verbascum lychnitis** L.
- 51 a Stellate hairs with unicellular stalks. Epidermal cells with straight or slightly-waved walls 52
- b Stellate hairs with multicellular stalks and smooth walled arms 54

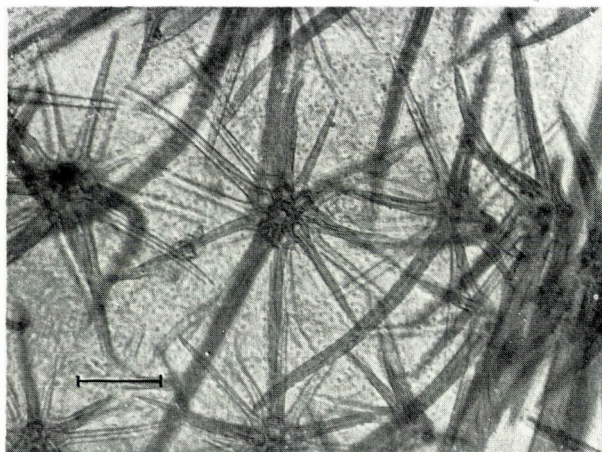


Fig. 10. *Potentilla arenaria*, leaf, abaxial surface, bar scale: 50 μ m

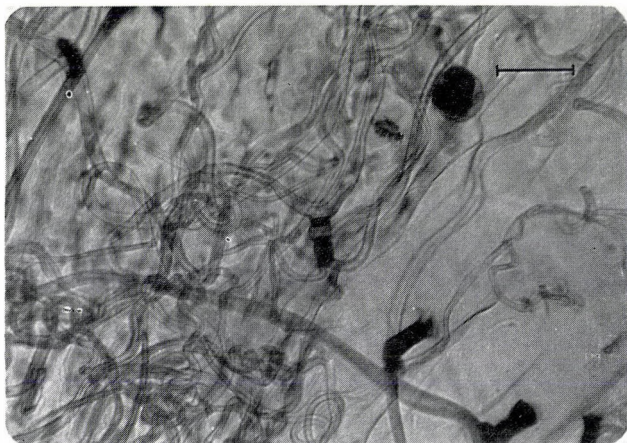


Fig. 11. *Artemisia vulgaris*, leaf, abaxial surface, bar scale: 50 μ m

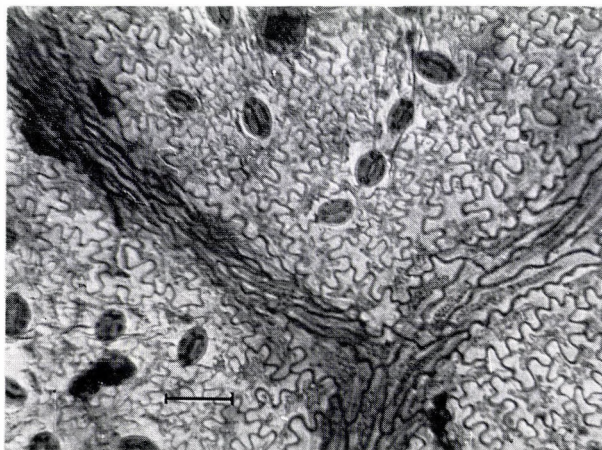


Fig. 12. *Fraxinus excelsior*, leaf, abaxial surface, bar scale: 50 μ m

- 52 a Multiarmed stellate hairs with round bases 53
 b Two-armed stellate hairs with angular bases *Cornus sanguinea* L.
- 53 a Smooth-walled hairs commonly with branched arms. Thickness of walls: 2–4 μ (Fig. 9)
 *Berteroa incana* DC.
 b Waved walled hairs not as above. Thickness of walls: 6–8 μ
 *Erysimum erysimoides* Cr., *Erysimum diffusum* Ehrh.
- 54 a Smooth-walled stellate hairs each having one arm many times longer than the others.
 Glands with multicellular stalks and heads present. Epidermal cells with lobed walls
 (Fig. 10) *Potentilla arenaria* Borkh.
 b Stellate hairs with filiformed arms. Thick-walled simple unicellular hairs min. 10 times
 longer than the width of bases also present *Rubus* sp.
- 55 a Short stalked hairs with two arms 56
 b Short stalked hairs with one arm. Epidermal cells with straight walls 57
- 56 a Hairs with unicellular, calix-like stalks. Epidermal cells with straight walls
 *Xeranthemum annuum* L.
 b Hairs with multicellular, rectangular stalks. Epidermal cells with lobed walls (Fig. 11)
 *Artemisia vulgaris* L.
- 57 a Multicellular stalked hairs. Simple segmented and segmentless hairs also present.
 Segmented soft hairs thin walled with marked constrictions, blunt apices, round,
 min. 80 μ bases-width. Rigid, sharply pointed segmentless hairs on the margins common
 *Carlina vulgaris* L.
 b Hairs of varying length with uni- and multicellular stalks. Glands with spherical heads
 also present *Centaurea rhenana* Bor., *Centaurea micranthos* Gmel.
- 58 a Epidermal cells with lobed walls. Glands with unicellular stalks and multicellular heads
 composed of cells radialized, covering by cuticle sharply separated from the epidermal
 cells (Fig. 12) *Fraxinus excelsior* L.
 b Epidermal cells with straight or slightly waved walls 59
- 59 a Glands with unicellular bases 60
 b Glands with bicellular, ellipsoidal bases, unicellular stalks and heads. Stomata arranged
 in regular lines on the stems *Rumex acetosella* L.
- 60 a Glands with unicellular stalks and heads 61
 b Glands with soft, multicellular stalks 62
- 61 a Glands with short stalks and large distended spherical heads (Fig. 13)
 *Chenopodium album* L., *Chenopodium glaucum* L.
 b Erect glands with long, rectangular stalks 8–10 μ in diameter and heads in the same
 sizes. Stomata arranged close one to another (Fig. 14) *Quercus rubra* Michx.
- 62 a Glands with unicellular heads. Stalks of varying length, width on the bases 24 μ , heads
 of similar size (Fig. 15) *Sambucus ebulus* L.
 b Glands with obconical, 3–4 headcells. Stalks with 6–8 μ in diameter
 *Sanguisorba minor* Scop.
- 63 a Epidermal cells with lobed walls 64
 b Epidermal cells with straight or slightly waved walls 68
- 64 a Epidermal cells arranged in rows 65
 b Epidermal cells irregularly arranged 66
- 65 a Diaeytic type of stomata (Fig. 16) *Silene cucubalus* Wib.
 b Type of stomata not as above *Asperula taurina* L.
- 66 a Dezmocytic type of stomata (Fig. 17) *Vicia sepium* L.
 b Paracytic type of stomata *Nigella arvensis* L.
- 66 c Type of stomata not as above 67
- 67 a Stainless circles near one to another in the guard cells *Ligustrum vulgare* L.

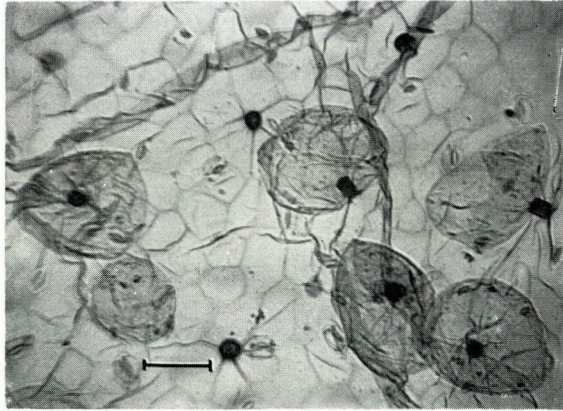


Fig. 13. *Chenopodium glaucum*, leaf, abaxial surface, bar scale: 50 μm

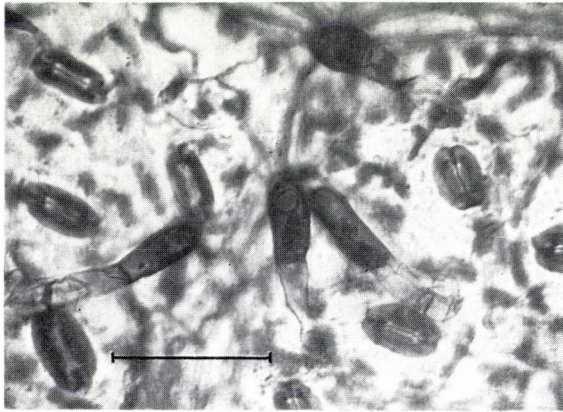


Fig. 14. *Quercus rubra*, leaf abaxial surface, bar scale: 50 μm

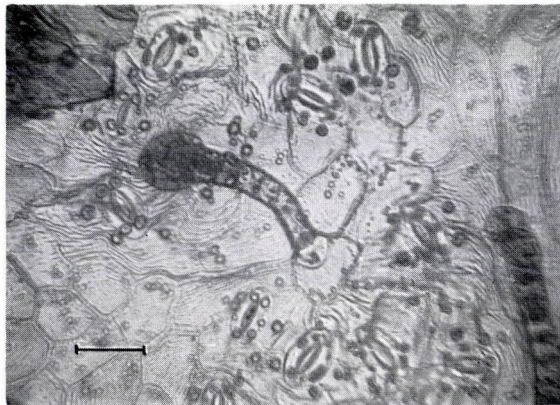


Fig. 15. *Sambucus ebulus*, leaf, abaxial surface, bar scale: 50 μm

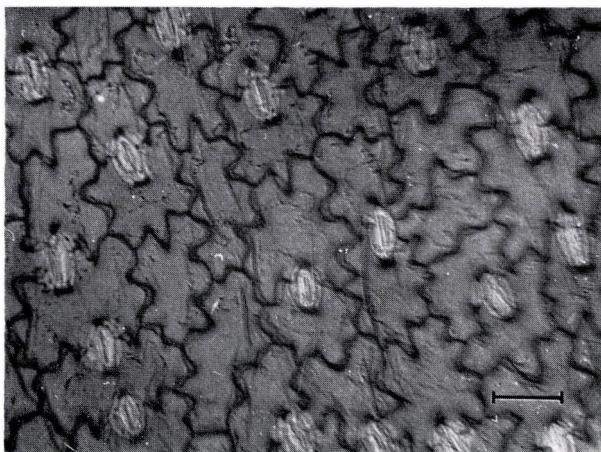


Fig. 16. *Silene cucubalus*, leaf, abaxial surface, bar scale: 50 μm

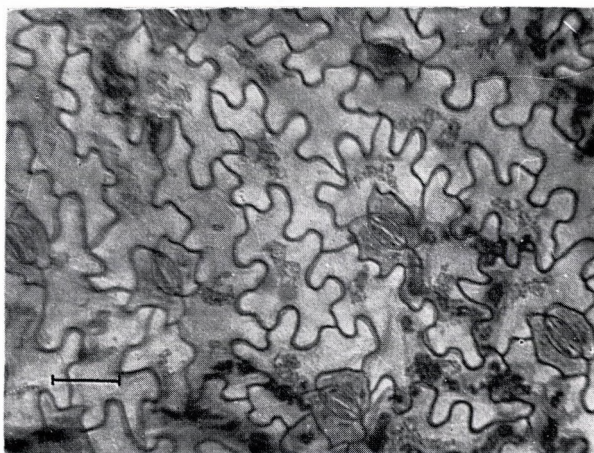


Fig. 17. *Nigella arvensis*, leaf, abaxial surface, bar scale: 50 μm



Fig. 18. *Viscum album*, leaf abaxial surface, bar scale: 50 μm

- b Epidermis not as above
Astragalus glycyphyllos L., **Campanula persicifolia** L., **Lactuca serriola** Torr., **Lactuca quercina** L., **Petroselinum hortense** Hoffm., **Thalictrum minus** L.
- 68 a Type of stomata typical 69
- b Type of stomata not as above 70
- 69 a Diacytic type of stomata. Epidermal cells more or less in regular square or rectangular forms **Viscaria vulgaris** Bernh.
- b Paracytic type of stomata (Fig. 18) **Viscum album** L.
- 70 a Small stained circles near the stomata
..... **Euonymus europaeus** L., **Euonymus verrucosus** Scop.
- b Epidermis not as above
Berberis vulgaris L., **Chondrilla juncea** L., **Dictamnus albus** L., **Polygonum aviculare** L., **Seseli leucospermum** W. et K., **Seseli varium** Trev., **Seseli osseum** Cr. em. Simk., **Tragopogon orientalis** L.

I a Monocotyledons

- 1 a Macrohairs present 2
- b Macrohairs absent 14
- 2 a Walls of macrohairs sinuous. Prickle hairs and silica cells absent. Cell walls of epidermal cells wavy (Fig. 19) **Carex hirta** L.
- b Walls of macrohairs smooth. Silica cells present 3
- 3 a Prickle hairs present 4
- b Prickle hairs absent 10
- 4 a Macrohairs present in intercostal zones 5
- b Macrohairs absent from intercostal zones 9
- 5 a Bicellular microhairs and papillae present. Thickness of macrohair walls 3–4 μ ; their proximal ends markedly narrowed. Microhairs with minute basal cells much shorter than apical cells **Cynodon dactylon** Pers.
- b Bicellular microhairs and papillae absent 6
- 6 a Prickle hairs in intercostal zones present 7
- b Prickle hairs from intercostal zones absent. Macrohairs soft. Long cells in intercostal zones hexagonal with smooth walls **Bromus mollis** L.
- 7 a Long cells in intercostal zones rectangular with sinuous walls 8
- b Long cells in intercostal zones elliptical-shaped with smooth walls. Short macrohairs soft **Poa nemoralis** L.
- 8 a Macrohairs consisting of similar kinds: rigid with rounded apices
..... **Alopecurus pratensis** L.
- b Macrohairs consisting of different kinds: soft, thin-walled in intercostal zones; rigid, thick-walled in costal zones **Brachypodium silvaticum** Beauv.
- 9 a Prickle hairs present in intercostal zones. Macrohairs soft and rigid
..... **Brachypodium pinnatum** Beauv.
- b Prickle hairs absent from intercostal zones. Macrohairs erect, rigid
..... **Apera spica-venti** Beauv.
- 10 a Silica cells present in intercostal zones 11
- b Silica cells absent from intercostal zones. Long cells in intercostal zones smooth-walled 12
- 11 a Cell walls of long cells in intercostal zones wavy. Long, soft and shorter, rigid macrohairs present in costal zones **Stipa capillata** L.
- b Cell walls of long cells in intercostal zones smooth. Rigid macrohairs absent from costal zones **Bromus sterilis** L.

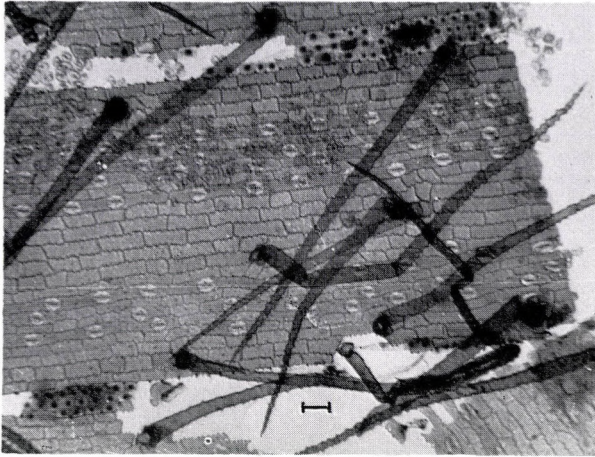


Fig. 19. *Carex hirta*, leaf, abaxial surface, bar scale: 50 μm

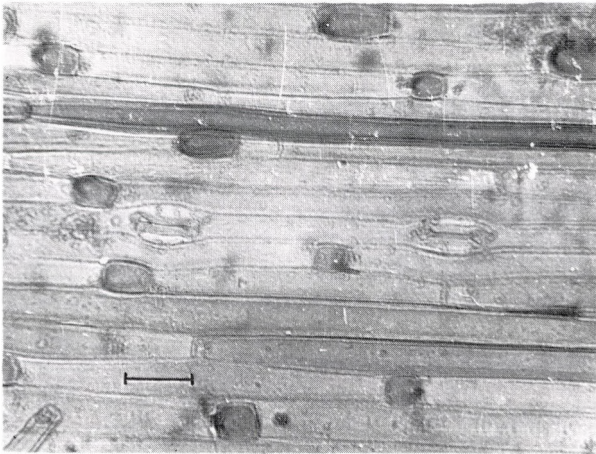


Fig. 20. *Arrhenatherum elatius*, leaf, abaxial surface, bar scale: 50 μm

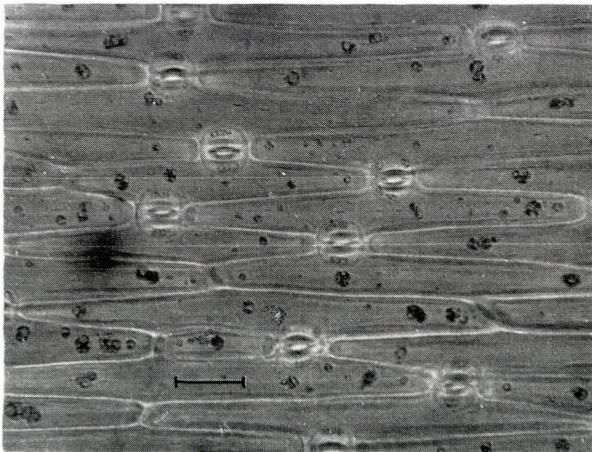


Fig. 21. *Asparagus officinalis*, leaf, abaxial surface, bar scale: 50 μm

- 12 a Macrohairs soft 13
 b Macrohairs rigid. Long cells rectangular **Triticum aestivum** L.
 13 a Long cells rectangular **Melica transsylvanica** Schur
 b Long cells hexagonal **Bromus tectorum** L.
 14 a Lamina divided into longitudinal zones 15
 b Lamina undivided. Prickle hairs, silica cells absent 25
 15 a Silica cells present in intercostal zones 16
 b Silica cells absent from intercostal zones 18
 16 a Prickle hairs present 17
 b Prickle hairs absent. Long cells thin-walled, sinous in intercostal zones. Subsidiary cells prominently triangular **Zea Mays** L.
 17 a Long cells smooth-walled, elliptical in intercostal zones **Poa pratensis** L.
 b Long cells wavy walled, rectangular in intercostal zones .. **Agropyron repens** Beauv.
 18 a Prickle hairs present in intercostal zones 19
 b Prickle hairs absent from intercostal zones 21
 19 a Bicellular microhairs present 20
 b Bicellular microhairs absent. Cell walls of long cells in intercostal zones thin, wavy (Fig. 20) **Arrhenatherum elatius** (L.) C. Presl.
 20 a Papillae present. Bicellular microhairs with much smaller basal cells narrowed at the proximal end. Prickle hairs with pointed apices in costal zones, with rounded ones in intercostal zones. Silica cells saddle-shaped **Calamagrostis epigeios** Roth.
 b Papillae absent. Bicellular microhairs with similar cells. Silica cells dumbbell-shaped **Setaria viridis** Beauv.
 21 a Long cells in intercostal zones hexagonal 22
 b Long cells in intercostal zones rectangular 23
 22 a Bicellular microhairs with similar cells present. Silica cells dumbbell-shaped
 **Setaria glauca** Beauv.
 b Bicellular microhairs absent. Elongated silica cells with nodular walls
 **Dactylis glomerata** L.
 23 a Cell walls of long cells in intercostal zones smooth 24
 b Cell walls of long cells in intercostal zones wavy **Poa compressa** L.
 24 a Silica cells rectangular, wavy-walled **Bromus erectus** Huds.
 b Silica cells square, smooth-walled **Bromus inermis** Leyss.
 25 a Epidermal cells rectangular **Muscari racemosum** Mill.
 b Epidermal cells hexagonal (Fig. 21) **Asparagus officinalis** L.

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ALKALOID BIOSYNTHESIS OF *CORYDALIS CAVA* CALLUS TISSUES AND THE INFLUENCE OF GROWTH REGULATORS ON THE ALKALOID FORMATION

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Tissue cultures from the tuber of *Corydalis cava* were prepared. Different proportions of regulators (0-5 mg/l, 2,4-D, IAA, NAA and Kinetin) were added to study the inner differentiation and the alkaloid biosynthesis in the 3 years old callus tissues. Alkaloid crystals and starch grains were detected in different cultures using Dragendorff reagent. The formation parenchymateous cells and transport tissues were also different.

Medium MS (Murashige-Skoog) containing 2 mg/l IAA and 0.5 mg/l Kn proved to be optimal for the formation of the total of alkaloids. IAA augmented the formation of alkaloids as compared to 2,4-D and Kn. The composition of alkaloids spectra are also influenced with hormones. There were detected bulbocapnin, corydalin and unknown alkaloids in different cases used HPLC technique with additional method.

Keywords: Tissue culture, *Corydalis cava*, Bulbocapnin, Corydalin

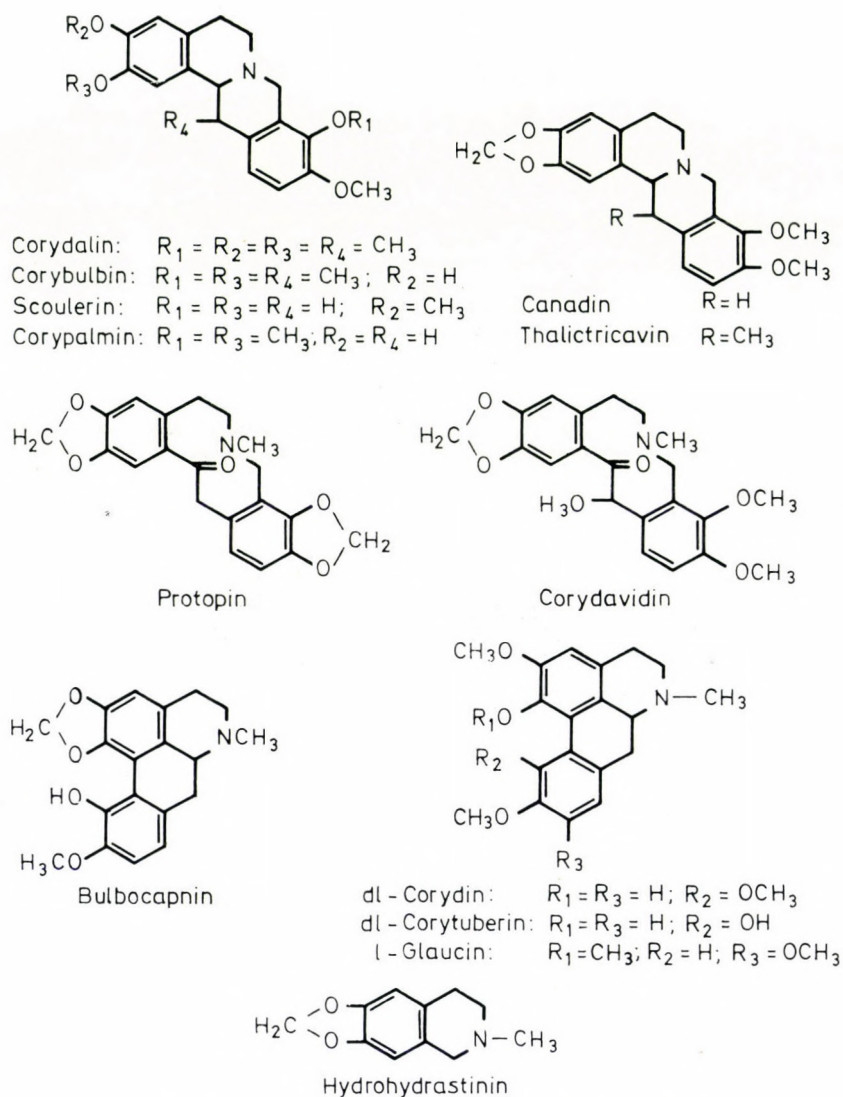
Introduction

Callus culture of the tuber of *Corydalis cava* (L.) Schweig. et Körte (Papaveraceae) an early spring plant was collected by authors in order to study the formation of alkaloids and investigate the formation of calluses.

In the tuber HOANG (1981) have found nearly 5% alkaloid content which is a high level in Center-European plants. The tuber is official in the Japanese Pharmacopoeia (KARIYONE 1973). Nearly 20 alkaloids can be found in it: bulbocapnin, tetrahydropalmatin, corydalin as well as protopin are of the greatest importance (VERZÁR-PETRI and HOANG 1978) (Fig. 1).

Many scientists have investigated the potential use of plant tissue cultures in the field of synthesizing alkaloids under different conditions. Organogenetic potential and biosynthesis have been studied by adding precursors or hormones to the medium (TABATA 1977). An important aspect of this study is that the cultured tissues exhibit often changes in their metabolites not observable in the parent plant (GORDON 1976).

Following these ideas the authors have investigated the differentiation processes and the localization of the alkaloids in the *Corydalis* tuber tissue cultures. Other experiments were carried out in order to determine the alkaloid formation of callus cultures influenced by growth hormones.

Fig. 1. Structure of the main alkaloids of *Corydalis*

Materials and methods

Culture technique

The 3 years old callus tissues originated from the tuber of *Corydalis cava* were cultured on Murashige-Skoog medium (MS) and on MS-2 (medium without glycine) supplemented with different concentrations and proportions of 2,4-D, IAA, NAA and Kn. All the cultures were maintained in darkness at 26 °C and 70% relative air humidity.

At the end of the 8th week of the growth period the fresh and dry weights of the calluses were determined in eprouvette, and the growth activity of the tissues were counted with methods of SZŐKE et al. (1979)

1. Fresh weight of tissue in grams
2. Dry weight of tissue in milligrams

$$GV = \frac{P_t - P_0}{P_0}$$

(P_t = weight of the tissue at the end of the experiment

P_0 = starting weight of the tissue culture [NICKEL 1956])

The growth value was calculated for both the fresh and dry weight of the tissue.

4. Contents of dry material of the tissue in per cent
5. Growth speed of tissues viz., the daily growth of the fresh weight of the tissues (MARÓTI 1976). In the experiments performed with the application of growth stimulators the final weight of the callus was used in the calculations.

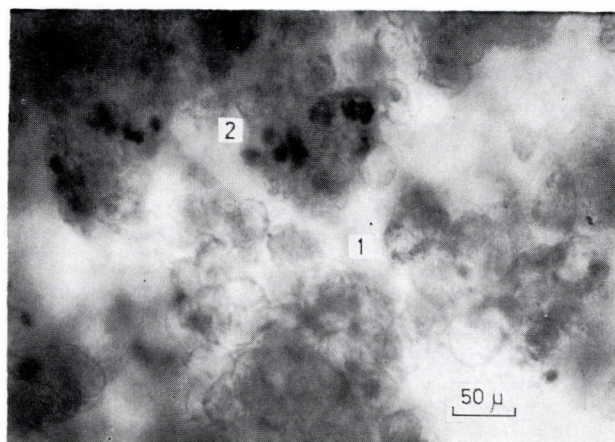


Fig. 2. Histochemistry of transverse section of callus tissue cultured on medium containing 1 mg/l 2,4-D and 1 mg/l kinetin painted with Dragendorff-R

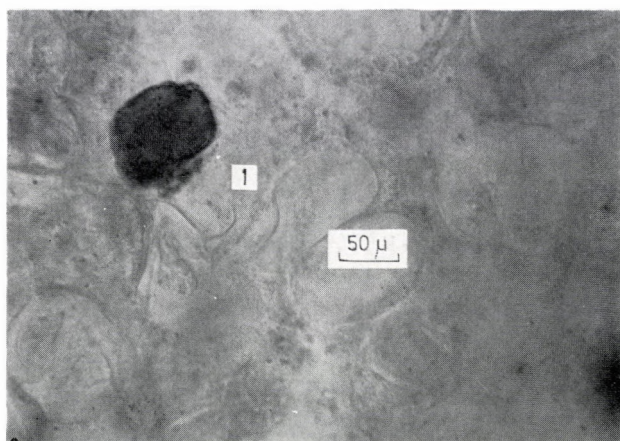


Fig. 3. Histochemistry of transverse section of callus tissue cultured on medium containing 1 mg/l IAA and 0.5 mg/l kinetin painted with Dragendorff-R

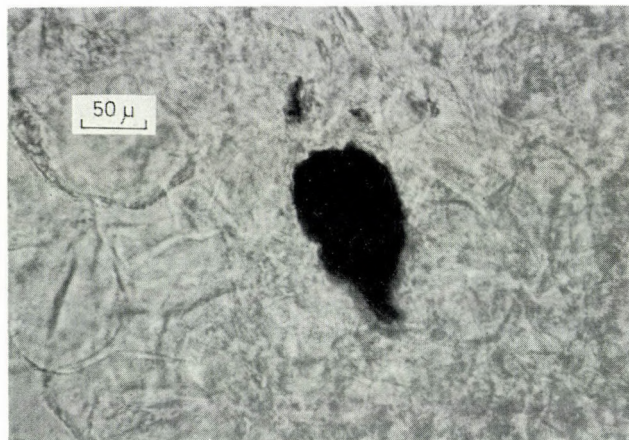


Fig. 4. Histochemistry of transverse section of callus tissue cultured on medium 0.5 mg/l Kn and 1 mg/l IAA painted with toluidin blue

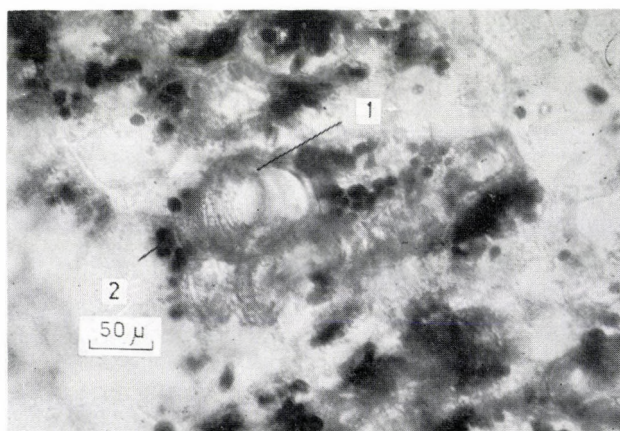


Fig. 5. Histochemistry of transverse section of the tuber of the plant painted with Dragen-dorff-R

Transverse section preparations were made from fresh tissue cultures for microscopic examinations. The alkaloids were detected with histochemical method using modified Dragen-dorff reagent or painted with toluidin blue (VERZÁR-PETRI 1972).

Chemical analysis

The callus tissues collected after eight weeks of incubation were lyophilized, powdered and subjected to extraction with organic solvent.

The tissues were alkalized with 25% NH_4OH and then 5 ml acetone:ethanol (7 : 3) was added to the solution. Afterwards the tissues were extracted with homogenizator, the extracts were centrifugated for 10 minutes at 4000 rpm. The organic extracts were evaporated and the residues were dissolved in 2% H_2SO_4 . The acidic solution was basified with 25% NH_4OH to pH 8–9 and the basic components were chaed out with CHCl_3 .

The estimation of total alkaloids was carried out on a Spektromom 195 spectrophotometer, the optical density was measured at 496 nm. The total alkaloid content was calculated using a Corydalin calibration curve.

The components of alkaloid were estimated by HPLC analysis carried out on Liquechrom 307, a RP-C 18 column with methanol-0.2% diammonium hydrophosphate (65 : 35). Data of preparing are as follows: The main alkaloids were detected with additional technique.

Acknowledgements are expressed to Prof. NISHIOKA FUKUOKA Japan for the test material sendd.

Results

The callus tissues produced from the tuber of *Corydalis cava* grow well in darkness in the nutrient medium influenced by various hormone concentrations. Externally there were no signs of organogenesis in either of the experimental variants.

During the histochemical examinations the presence of crystals, was observed in the individual idioblast which gave positive alkaloid reaction with Dragendorff reagent.

The most typical picture was seen using the Kn/2.4-D combinations. The tissues are very interesting in case of the culture containing 1 mg/l Kn and 1 mg/l 2.4-D. In the gradually loosening tissue many starch grains can be found, and yellow alkaloid crystals appear in special cells (Fig. 2).

In cultures grown on Kn/IAA nutrient medium secretory cells appear (Figs 3, 4). Similar ones can also be observed in the tissue of intact tuber (Fig. 5). Cultures grown on an MS nutrient medium with 0.5 mg/l Kn and 1 mg/l IAA ratio are more congested, their cells are well rounded and Dragendorff positive cells are at several places (Table 1).

Table 1
Size of cells in the different tissue cultures

Hormone rations		Elongated cells			Rounded cells		
Kinetin	2.4-D	per cent	length in μm	width in μm	per cent	length in μm	width in μm
mg/l							
0.5	0	26	94	52	74	47	39
0.5	0.5	20	87	46	80	53	42
0.5	1	8	97	62	92	52	43
0.5	2	20	103	58	80	53	44
0.5	5	38	106	63	62	59	49
1	0	18	87	47	82	51	43
1	0.5	14	100	56	86	52	43
1	1	44	92	56	56	59	50
1	2	20	90	57	80	51	43
1	5	20	91	61	80	60	52
2	0	38	95	64	62	60	51
5	0	4	78	63	96	49	38
5	0.5	2	107	66	98	44	36
5	1	16	90	61	84	66	57
5	2	12	79	53	88	49	40
5	5	32	112	56	68	54	45

It may be concluded that the different hormon ratios produce more or less differentiated tissue cultures that are very different from one another in their characteristics. In this plant species alkaloid crystals were found in both the intact organs and the derived tissue cultures.

Tables 2 and 3 show the results of the callus tissues grown in darkness in the basic medium (MS) with various auxin and kinetin concentrations. The callus tissues grow most intensively with the following concentrations of 2,4-D, IAA and kinetin: 1 mg/l Kn and 1 mg/l of 2,4-D or 1 mg/l of Kn and $2 \pm \text{g/l}$ of IAA. Applying a larger amount of kinetin and 2,4-D or kinetin and IAA concentration the cultures grew only a little or not at all. In cases like these the tissues became more solid and their dry weight increased considerably.

In Table 4 results of growth of callus tissues are shown grown in darkness. In the period during 8 weeks the fresh and dry weight of the callus tissue considerably increased. The dry material content of the callus tissues is the highest between the first and second weeks. On the end of the growth period the water content increases in the cells (enlargement, expansion) so that the dry material content of the tissues gradually decreases.

Table 2

The effect of — kinetin and 2,4-D — growth regulators on the growth of Corydalis cava callus cultures

Serial number of experimental variants	Concentration, mg/l		Fresh-weight of callus, g/culture	Dry weight of callus, mg/culture	Content of dry material, %	Growth rate, mg/day	Growth value (GV) relating to	
	Kn	2,4-D					fresh weight	dry weight
1	0	0	1.7237 ± 0.0278	84.12	4.88	27.85	9.54	7.67
2	0	0.5	2.3945 ± 0.0123	101.53	4.24	39.84	13.64	9.47
3	0	1	2.5035 ± 0.0165	105.61	4.18	41.71	14.30	9.85
4	0	2	2.4198 ± 0.0282	96.31	3.98	40.29	13.79	8.93
5	0	5	1.8505 ± 0.1964	77.12	7.17	30.12	10.31	6.95
6	0.5	0	2.0789 ± 0.1015	104.57	5.03	34.20	11.71	9.78
7	0.5	0.5	2.4112 ± 0.0104	112.84	4.68	40.13	13.74	10.63
8	0.5	1	2.3538 ± 0.0349	108.04	4.59	39.10	13.39	10.14
9	0.5	2	2.4209 ± 0.0590	94.90	3.92	40.31	13.80	8.78
10	0.5	5	2.3661 ± 0.0552	96.77	4.09	39.33	13.46	8.98
11	1	0	2.0960 ± 0.0812	106.06	5.06	34.51	11.81	9.93
12	1	0.5	2.4927 ± 0.0911	106.69	4.28	41.59	14.24	10.00
13	1	1	2.5052 ± 0.1297	103.46	4.13	41.81	14.31	9.66
14	1	2	2.1527 ± 0.1304	89.55	4.16	35.52	12.16	8.23
15	1	5	2.0070 ± 0.0784	90.50	4.51	32.92	11.27	8.33
16	2	0	2.1429 ± 0.0850	101.79	4.75	35.34	12.10	9.49
17	2	0.5	2.1473 ± 0.1583	95.98	4.47	35.42	12.12	8.89
18	2	1	2.4234 ± 0.1650	104.45	4.31	40.35	13.81	9.77
19	2	2	2.4147 ± 0.0880	100.69	4.17	40.19	13.76	9.38
20	2	5	2.0972 ± 0.0957	89.13	4.25	34.53	11.82	8.19
21	5	0	1.0516 ± 0.1252	63.09	6.00	15.86	5.45	5.50
22	5	0.5	1.5130 ± 0.1679	72.77	4.81	24.10	8.25	6.50
23	5	1	1.3353 ± 0.1393	68.76	5.15	20.92	7.16	6.10
24	5	2	1.9570 ± 0.1667	86.69	4.43	32.02	10.96	7.94
25	5	5	2.0211 ± 0.1303	85.49	4.23	33.17	11.35	7.81

Table 3

The effect of — kinetin and IAA — on the growth of Corydalis cava callus cultures

Serial number of experimental variants	Concentration, mg/l		Fresh-weight of callus, g/culture	Dry-weight of callus, mg/culture	Content of dry weight, %	Growth rate, mg/day	Growth value (G.V.) relating to	
	Kn	IAA					fresh weight	dry weight
1	0	0	1.7555 ± 0.0816	101.29	5.77	26.85	5.97	10.42
2	0	0.5	1.9375 ± 0.1447	107.14	5.53	30.10	6.69	11.08
3	0	1	1.7241 ± 0.1051	102.24	5.93	26.29	5.84	10.53
4	0	2	1.8215 ± 0.0836	110.93	6.09	28.03	6.23	11.51
5	0	5	1.8248 ± 0.0883	106.02	5.81	28.08	6.24	10.96
6	0.5	0	1.8139 ± 0.0486	106.48	5.87	27.89	6.20	11.01
7	0.5	0.5	1.8025 ± 0.0900	105.27	5.84	27.69	6.15	10.87
8	0.5	1	2.0612 ± 0.0703	120.58	5.85	32.32	7.18	12.60
9	0.5	2	2.0751 ± 0.0611	116.21	5.60	32.56	7.24	11.10
10	0.5	5	2.2955 ± 0.2625	125.10	5.45	36.49	8.11	13.11
11	1	0	1.7303 ± 0.0520	108.85	6.27	26.40	5.87	11.28
12	1	0.5	1.8114 ± 0.0301	108.86	6.01	27.85	6.19	11.28
13	1	1	2.2281 ± 0.1343	128.78	5.78	35.29	7.85	13.52
14	1	2	2.4071 ± 0.3045	128.30	5.33	38.48	8.56	13.47
15	1	5	2.3482 ± 0.0739	126.57	5.39	37.43	8.32	13.28
16	2	0	1.8211 ± 0.0689	108.85	5.96	28.02	6.23	11.28
17	2	0.5	1.9588 ± 0.0643	111.46	5.69	30.48	6.78	11.57
18	2	1	2.1718 ± 0.0937	120.10	5.53	34.28	7.62	12.55
19	2	2	2.3121 ± 0.0871	122.54	5.30	36.79	8.18	12.82
20	2	5	1.7136 ± 0.0430	106.07	6.19	26.10	5.80	10.96
21	5	0	0.5697 ± 0.2427	35.10	6.16	5.67	1.26	2.96
22	5	0.5	2.0106 ± 0.0678	116.82	5.81	31.40	6.98	12.18
23	5	1	1.4682 ± 0.1926	81.78	5.57	21.72	4.83	8.22
24	5	2	1.4678 ± 0.2872	82.64	5.63	21.71	4.83	8.32
25	5	5	1.8365 ± 0.2442	102.29	5.57	28.30	6.29	10.54

The daily growth of callus tissues grown in basic medium in darkness related to the fresh weight has two intensive periods. The lower maximum value occurs as early as in the second week while the higher one appears in the seventh week. The most intensive growth period is between the sixth and seventh weeks.

Other experiment has been performed to examine the effects of growth regulators on the alkaloid biosynthesis and component formation of callus tissue.

Plant growth regulators are known to bring about morphogenetic and biochemical changes in cells and tissue. The biochemical changes that occur due to the hormonal stimuli may have profound influence on the metabolic events leading to the synthesis of secondary products (VERZÁR-PETRI and HOANG 1978, BAUMANN et al. 1982, STOCKLING et al. 1982).

In the present study alkaloids were synthesized in cultured *Corydalis cava* tissues. Growth regulators, such as 2,4-D, IAA, NAA and Kn were found to influence the formation of alkaloids in the tissue cultures on the different hormones tested, IAA augmented the formation of alkaloids as compared to 2,4-D and Kn.

Table 4

Growth dynamics of the callus tissue of Corydalis cava grown on the basis medium (MS) in dark

Incubation period (week)	Fresh-weight of callus, g/culture	Dry-weight of callus, mg/culture	Content of dry material, %	Growth value (G.V.) according to		Growth rate, mg/day
				fresh-weight	dry-weight	
0	0.0499 ± 0.0073	2.2920	4.5930			
1	0.0959 ± 0.0081	7.2021	7.5100	0.9218	2.1423	6.5714
2	0.1521 ± 0.0083	10.3276	6.7900	2.0481	3.5059	10.8600
3	0.2441 ± 0.0156	13.4320	6.9200	2.8898	4.8604	9.2476
4	0.4755 ± 0.0234	29.9090	6.2900	8.5290	12.0493	15.2000
5	0.6391 ± 0.0406	36.3390	5.6860	11.8076	14.8547	16.8300
6	0.8041 ± 0.0705	42.9469	5.3410	15.1144	17.7377	19.1400
7	1.3050 ± 0.0650	65.7067	5.0350	25.1523	27.6678	25.6100
8	1.4698 ± 0.1070	72.7551	4.9500	28.4549	30.7430	25.3500

Table 5

The effect of growth regulators on the total alkaloid and component formation of Corydalis cava callus tissues

Medium	Hormone concentration, mg/l				Content of total alkaloid mg/g dry weight	Main components mg/g total alkaloid	
	Kn	2.4-D	IAA	NAA		bulbocapnin	tetrahydropalmatin
MS-2	1	1	—	—	0.125	20.3722×10^{-3}	—
	0.5	1	—	—	0.460	18.2721×10^{-3}	—
	1	0.5	—	—	0.330	6.1488×10^{-3}	1.6991×10^{-3}
	0	0	—	—	0.510	4.3074×10^{-3}	—
	0.02	—	2	—	0.180	—	3.2997×10^{-3}
	0.20	—	2	—	0.495	—	17.7635×10^{-3}
	0.50	—	2	—	0.755	—	43.3807×10^{-3}
	1.00	—	2	—	0.962	16.4223×10^{-3}	17.9144×10^{-3}
MS	0.02	—	2	—	0.680	6.7653×10^{-3}	19.4167×10^{-3}
	0.20	—	2	—	0.752	—	11.8981×10^{-3}
	0.50	—	2	—	1.021	—	10.8737×10^{-3}
MS	0.50	—	1	1	0.418	—	7.8554×10^{-3}
	0.50	—	—	2	0.481	—	9.5416×10^{-3}

MS = Murashige-Skoog medium

MS-2 = without glycine (2 mg/l)

Our experiments also showed that the influence of growth regulators depends not only on the characteristics of each, but also on their combination and proportion. In the same medium (MS) 2.4-D and Kn in certain combinations were found to be inhibitory to alkaloid synthesis, but IAA and Kn in some combination were found to favour the formation of the alkaloids (Table 5). In this case not only IAA, but Kn also influenced the alkaloid synthesis

positively in the cultured tissues of *Corydalis cava*. The data show that in the 2 mg/l concentration of IAA when it was held constant and the concentration of Kn was raised (from 0.02 mg/l to 1 mg/l), the total alkaloid content significantly increased (from 0.180 mg/g to 0.962 mg/g).

The tissue cultures were cultured in MS and MS-2 (without 2 mg/l glycine) with the same concentration of IAA and Kn. The total alkaloid content of callus tissues cultured in the MS medium was higher than that of the callus tissue cultured in the MS-2 medium. Glycine was found to be favourable for alkaloid synthesis in the cultured tissues of *Corydalis cava* (Table 6).

Table 5 shows the effect of growth regulators (2,4-D IAA, NAA and Kn) on the formation of the alkaloid components in *Corydalis cava* callus tissues cultured on the medium MS and MS-2. In case of cultures grown on MS-2 medium with various concentrations of 2,4-D and Kn, the main component was bulbocapnin. Medium MS-2 containing 1 mg/l 2,4-D, naftilacetic acid and 1 mg/l Kn was found to be optimal for the formation of bulbocapnin (Fig. 6).

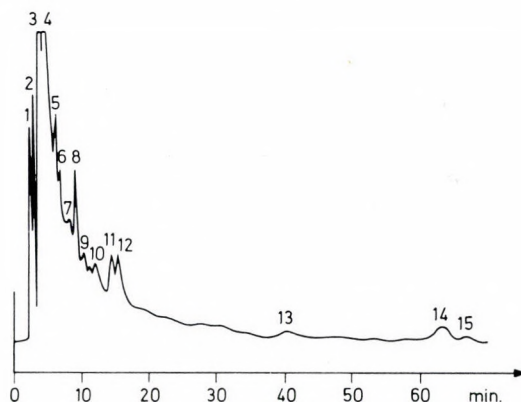


Fig. 6. HPLC chromatogram of the callus culture grown in the MS medium containing 2 mg/l IAA and 1 mg/l Kn (11) bulbocapnin, (12) tetrahydropalmatin on a RP-C 18 column with methanol/0.2% diammonium-hydrogenphosphate mixtures (65 : 35)

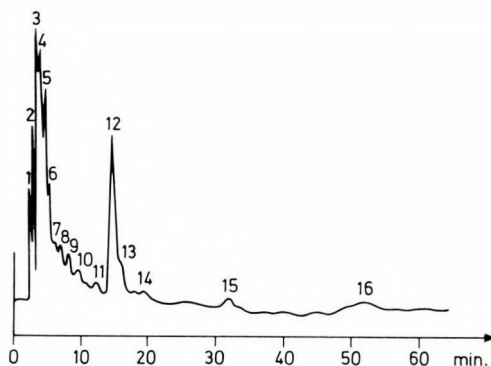


Fig. 7. HPLC chromatogram of the callus culture grown in the MS medium containing 1 mg/l Kn and 1 mg/l 2,4-D, (12) bulbocapnin, (13) tetrahydropalmatin, (15) protopine on a RP-C 18 column with methanol/0.2% diammonium-hydrogenphosphate mixtures (65 : 35)

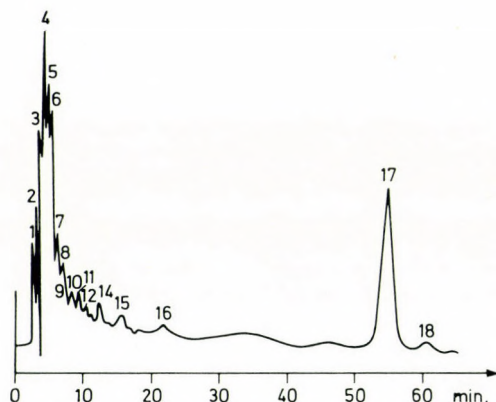


Fig. 8. HPLC chromatogram of the callus culture grown in the MS-2 medium containing 2 mg/l IAA and 0.5 mg/l Kn, (15) tetrahydropalmatine, (16) corydaline (17) unknown component, on a RP-C 18 column with methanol/0.2% diammonium-hydrogenphosphate mixture (65 : 35)

In case of cultures grown on medium MS and MS-2 containing various IAA, NAA and Kn concentrations the main component was tetrahydropalmatin. Its content increased when larger concentrations of Kn added (Fig. 7). In medium MS-2 containing 2 mg/l IAA and various concentrations of Kn however, when the concentrations of Kn reached 1 mg/l, the content of tetrahydropalmatin decreased and bulbocapnin appeared.

Medium MS containing 2 mg/l IAA and 0.5 mg/l Kn was found to be optimal for the formation of the total of alkaloids. In addition to tetrahydropalmatin, large amount (24%) of an unknown component was detected (Fig. 8).

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EXTRACELLULAR CELLULASE AND XYLANASE PRODUCTION OF *PLEUROTUS* SPECIES

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Of the extracellularly produced enzymes of mycelium cultures of 15 *Pleurotus* species the author followed the trend of activity of cellulase (C_x and C_1) and xylanase in response to various carbon sources. On the basis of the data of the analysis series he established that the changes of the C_1 -enzyme could be described by a maximum or ascending curve. The values of C_x obtained by viscosimetry were characterized by an increase in time. The fact that in the culture medium containing sugar measurable quantities of enzyme were not produced in any case proves the inducible nature of the C_x enzyme. The temporal relation between the C_1 and C_x activities could in most cases be proved on all three complex carbon sources. The data suggest that the curve and maximum, respectively, of the C_1 activity precedes the descent of the C_x activity.

The xylanase activity which plays a primary role in the decomposition of hemicelluloses shows an increasing tendency in the cultures. In the sugar-containing culture medium low and decreasing activities indicate the inducible nature of the enzyme. The data presented in the paper, besides filling a gap concerning the production dynamics of enzyme groups of decisive importance in the nutrition of the *Pleurotus* species, may contribute to the chemotaxonomic characterization of the species.

Introduction

Classing the *Pleurotus* species among the white rot fungi indicates that in the course of decomposing the substrates (generally lignocelluloses) of fungi they are able to utilize both the lignin and the cellulose (RYPÁČEK 1966). In the nutrition of the *Pleurotus* species enzymes of exocellular activity play a determinative role. The enzyme group secreted is multicomponent, the cellulases and xylases are important components.

In the literature (RODIONOVA 1981, HIGHLEY and KIRK 1979) 1,4- β -D-glucan-4-glucanhydrolase (E.C. 3.2.1.4., syn.: C_x), 1,4- β -glucan-4-glucohydrolase (E.C. 3.2.1.74.), 1,4- β -D-glucocellobiohydrolase (E.C. 3.2.1.91., syn.: C_1) and β -glucosidase (E.C. 3.2.1.21.) are made responsible for the cellulose decomposition. The cellulose decomposing enzymes are particularly active in the lower fungi (*Trichoderma* spp., *Sporotrichum pulverulentum*). Hence the research is mainly concerned with the enzymes of these organisms. Wood-rotting fungi — including *Pleurotus* species — were tested for cellulase activity by GINTEROVA (1980). The cellulose and the carboxymethylcellulose induce high activity, while the cellobiose does not do so (BUCHT and ERIKSSON 1968). Recent data (CHURILOVA et al 1979, LAUSTER 1975) also emphasize the inhibitory effects of cellobiose and glucose.

The activity of xylanases in the cultures of wood-rotting fungi on culture media containing xylane or glucose is considerable (LYR 1959, FLANNINGAN and GILMOR 1980). On the basis of a number of data it can be supposed that the decomposition of xylanase is, in fact, carried out by a system with at least two components, though this question has not been examined yet for higher fungi.

Present paper gives account of a work done as a part of a comprehensive analysis series; exocellular cellulose and xylase production of mycelium cultures of 15 *Pleurotus* species, as well as some fundamental characteristics of the cellulase (C_x) enzyme as a function of various carbon sources were studied.

Material and method

The study included the following *Pleurotus* species: *P. calyptratus* (Lindbl in Fr.) Sacc., *P. candidissimus*, *P. cornucopiae* Paul ex Fr., *P. cystidiosus* O. K. Miller, *P. elongatipes* (Peck), *P. eryngii* (DC. ex Fr. Quel.), *P. euosmus* (Berk. apud Hussey) Sacc., *P. eryngii* var. *ferulae* Lanzi, *P. florida* (= *P. floridanus* Sing.), *P. japonicus* (Kawamura) Sing (= *Lampteromyces japonicus* (Kawamura) Sing., *P. mutilus* Fr. Gill [= *Clitocybe josserandii* (Sing.) Sing], *P. ostreatus* (Jacq. ex Fr.) Kummer, *P. passeckerianus* Pilát, *P. pulmonarius* (Fr.) Quel., *P. sapidus* Kalchbr. The carbon sources of the basic culture medium (VETTER 1983) used (at a concentration of 10 g/l):

Variant	Carbon source
A	crushed straw
B	crushed corn cob
C	crushed oak-wood
D	sugars: maltose (20 g/l) glucose (10 g/l)

The $C_x/1,4\text{-}\beta\text{-D-glucan-4-glucanhydrolase}$ (E.C. 3.2.1.4.) activity in the filtrate of the culture medium was measured every 3 minutes during 15 minutes of reaction at 40 °C in OSTWALD's viscosimeter, using the viscosimetric method of RODIONOVA et al. (1966). From the time of outflow of reaction mixture and water the reciprocal value of the relative viscosity, then the average difference of the reciprocals of relative viscosities measured at different times were calculated, and latter referred to 1 ml of the culture medium filtrate.

The values of C_1 activity were obtained by titrimetric determination of the quantity of sugar released from cellulose MN 300 dust while decomposing at 40 °C over a given time (after BILAJ 1973).

For the measuring of the activity of xylanase the reducing sugar content produced at 40 °C in a given time from xylane substrate prepared from maize stalk was determined. The value of activity was expressed with the reducing sugar content released in 1 hour by 1 ml culture medium. The enzyme activities were measured in 3-4 replications for each variant; in the tables generally the arithmetic mean ($\bar{x}$) and the standard error (s) are given.

Results

The C_x -activity values of the species examined are summed up in Table 1.

a) Cellulase was produced by every species. The lowest activities were measured in the culture media of *P. florida* and *P. passeckerianus*, and relatively low values were obtained with those of *P. ostreatus*, *P. cornucopiae* and *P. cystidiosus*. A larger group of the species is characterized by a gradual increase in activity from the first sampling onwards. For example, the activity values for *P. calyptratus* ranged from 0.181 to 1.20, for *P. euosmus* from 0.232 to 1.560 (on culture medium A), from 0.078 to 1.05 (on culture medium B) and from 0.099 to 0.3 (on culture medium C). Changes of different absolute value but similar tendency were measured for *P. elongatipes*, *P. mutilus* and *P. japonicus* (Fig. 1). Latter species also produced the most active enzyme, since the activity rose from 0.120 to 2.49 (on culture medium A). *P. candidissimus* shows an unambiguous maximum curve on culture medium B, while the changes in activity on culture media A and C are somewhat different from that. Increasing tendency is

Table 1

Exocellular cellulase (C_x) activities of the *Pleurotus* species examined on culture media with four different carbon sources. The unit of activity:

$d\frac{1}{\eta}\bigg|dt$, that is the change in the reciprocal value of relative viscosity produced by 1 ml culture medium in 3 minutes

	Samples															
	1				2				3				4			
	culture medium				culture medium				culture medium				culture medium			
	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D
<i>Pleurotus calyptratus</i>	0.181	0.059	0.042	0.004	0.272	0.178	0.027	0.003	0.652	0.520	0.002	0.005	1.200	1.030	0.165	0.002
<i>P. candidissimus</i>	0.024	0.008	0.027	0.003	0.475	0.708	0.132	0.004	0.363	0.492	0.126	0	0.515	0.330	0.095	0
<i>P. cornucopiae</i>	0.001	0	0.002	0.001	0.054	0.024	0.020	0.004	0.046	0.030	0.069	0	0.040	0.050	0.035	0
<i>P. cystidiosus</i>	0.054	0.004	0.003	0.001	0.056	0.010	0.011	0.022	0.039	0.031	0.011	0	0.110	0.078	0.100	0
<i>P. elongatipes</i>	0.072	0.083	0.163	0.006	0.248	0.298	0.306	0.001	0.339	0.084	0.232	0.012	0.403	0.929	0.106	0.004
<i>P. eryngii</i>	0.003	0.006	0.013	0.003	0.087	0.019	0.029	0	0.023	0.025	0.065	0	0.129	0.038	0.546	0.004
<i>P. eryngii</i> var. <i>ferulae</i>	0.066	0.004	0.005	0.003	0.052	0.034	0.028	0.001	0.016	0.006	0.053	0.003	0.208	0.035	0.274	0.008
<i>P. euosmus</i>	0.232	0.078	0.099	0.007	0.472	0.372	0.207	0.007	0.849	0.896	0.209	0.008	1.560	1.050	0.300	0.007
<i>P. florida</i>	0.002	0.002	0	0	0.058	0.047	0.011	0.005	0.072	0.035	0.039	0	0.039	0.072	0.027	0
<i>P. japonicus</i>	0.120	0.352	0.630	0.366	0.420	0.427	0.770	0.125	0.422	0.975	1.390	0.117	2.490	1.920	1.740	0.005
<i>P. mutilus</i>	0.090	0.150	0.150	0.009	0.170	0.207	0.070	0.049	0.295	0.142	0.057	0	1.150	0.415	0.240	0.010
<i>P. ostreatus</i>	0.014	0.023	0.003	0	0.098	0.117	0.013	0.003	0.055	0.163	0.031	0.048	0.330	0.294	0.090	0
<i>P. passeckerianus</i>	0.004	0.004	0.004	0.005	0.012	0.001	0.001	0.005	0.004	0.002	0.004	0.015	0.050	0.030	0.080	0.079
<i>P. pulmonarius</i>	0.012	0.013	0.006	0.002	0.122	0.133	0.063	0.012	1.388	1.230	—	0.013	1.250	1.280	0.360	0
<i>P. sapinus</i>	0.079	0.077	0.153	0.007	0.310	0.160	0.208	0.002	0.275	0.219	0.150	0.021	0.365	0.290	0.115	0.009

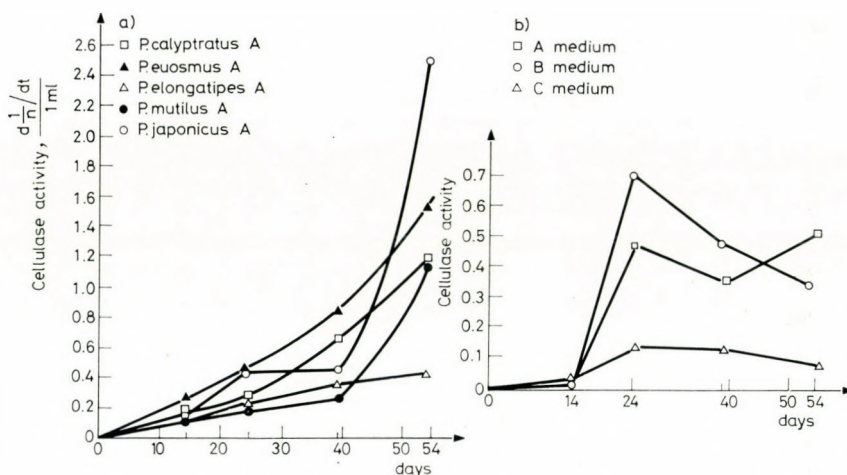


Fig. 1. (a) Changes in the cellulase activities of several species. (a) Cellulase (C_x) activity. (b) Cellulase activity of *P. candidissimus* in various culture media.

shown by *P. eryngii* and *P. eryngii* var. *ferulae*; rapid increase from the second to the third sampling is characteristic of *P. pulmonarius* (0.122–1.38) on culture media A and B.

b) Characterization of activities shown on different culture media. In comparing the activities according to the culture media used, the numerical values of "average" activities irrespective of the species may give a clearer picture:

Culture medium	Sampling			
	1.	2.	3.	4.
A	0.056	0.193	0.322	0.583
B	0.057	0.182	0.322	0.499
C	0.047*	0.081	0.176	0.266

* Without the outstandingly high value of *P. japonicus*

that is: on the **straw** (A) and **corn cob** (B) culture medium the average activities are very close or equal to one another at each time of sampling. The average activity on culture medium C (41–54%) is about half of that obtained on culture media A and B, respectively. In the case of the D (maltose-glucose) culture medium — with the exception of two species, *P. japonicus* and *P. passeckerianus* — very low, zero or just measurable activities were obtained. For *P. passeckerianus* the value of activity only rose from 0.05 to 0.079, but the true exception is represented by *P. japonicus*, as its activity — 0.366 on the first sampling — dropped to 0.005 by the time the last sample was taken. It seems thus, that this fungus has a considerable basic activity even on maltose-glucose culture medium.

Data of C_1 activity are available for the 2nd to 4th samples of 10 *Pleurotus* species (Table 2).

a) **Changes in time.** When reckoning with average values irrespective of the species, very close values are obtained for the three times of sampling. An analysis by species reveals various tendencies of changing. Curves of maximum character are shown by *P. euosmus*,

Table 2

Exocellular C₁ activity of 10 Pleurotus species on culture media containing straw (A), corn-cob (B) and oak-dust (C), respectively, as carbon source
(Activity: mg released sugar/ml culture medium × hour)

		Samples								
		2			3			4		
		culture medium			culture medium			culture medium		
		A	B	C	A	B	C	A	B	C
<i>Pleurotus calyptratus</i>	$\bar{x}$	0.078	0.082	0.055	0.056	0.122	0.052	0.100	0.094	0.085
	s	0.008	0.060	0.005	0.018	0.029	0.005	0.004	0.005	0.019
<i>P. cystidiosus</i>	$\bar{x}$	0.155	0.116	0.053	0.060	0.044	0.056	0.081	0.092	0.070
	s	0.070	0.010	0.009	0.014	0.008	0.000	0.012	0.009	0.010
<i>P. elongatipes</i>	$\bar{x}$	0.134	0.117	0.084	0.132	0.089	0.086	0.078	0.185	0.030
	s	0.010	0.030	0.007	0.038	0.015	0.008	0.006	0.029	0.002
<i>P. eryngii</i>	$\bar{x}$	0.070	0.057	0.029	0.049	0.032	0.029	0.073	0.055	0.100
	s	0.003	0.007	0.008	0.070	0.008	0.011	0.004	0.003	0.021
<i>P. eryngii</i> var. <i>ferulae</i>	$\bar{x}$	0.061	0.032	0.072	0.122	0.103	0.134	0.036	0.018	0.049
	s	0.004	0.011	0.035	0.012	0.005	0.012	0.023	0.023	0.016
<i>P. euosmus</i>	$\bar{x}$	0.132	0.090	0.104	0.091	0.098	0.110	0.072	0.053	0.052
	s	0.019	0.046	0.012	0.021	0.012	0.005	0.025	0.007	0.009
<i>P. japonicus</i>	$\bar{x}$	0.142	0.132	0.137	0.140	0.139	0.171	0.317	0.226	0.207
	s	0.056	0.003	0.016	0.030	0.012	0.023	0.009	0.039	0.014
<i>P. mutilus</i>	$\bar{x}$	0.095	0.086	0.063	0.104	0.073	0.070	0.157	0.110	0.089
	s	0.110	0.001	0.003	0.009	0.001	0.003	0.031	0.012	0.010
<i>P. passeckerianus</i>	$\bar{x}$	0.038	0.029	0.026	0.122	0.112	0.129	—	—	0.025
	s	0.011	0.009	0.010	0.007	0.014	0.006	—	—	0.010
<i>P. sapidus</i>	$\bar{x}$	0.116	0.101	0.108	0.082	0.072	0.086	0.054	0.054	0.035
	s	0.010	0.012	0.008	0.010	0.025	0.013	0.020	0.016	0.000

P. eryngii var. *ferulae*, *P. passeckerianus*, *P. sapidus*, *P. elongatipes*. The activity is increasing in the case of *P. mutilus*, *P. calyptratus*, *P. japonicus* (with very high absolute values).

b) **Evaluation of the effect of culture medium.** Averages of the activities measured, irrespective of the species:

Culture medium	Sampling		
	2	3	4
A	0.102	0.096	0.107
B	0.084	0.088	0.098
C	0.073	0.092	0.064

that is: culture medium A is of the highest activity, though the differences are small. Samples 3 and 4 are characterized by balanced activities. Lowest of all are the activities produced in culture medium C; in sample 4 e.g. the ratio is: A : B : C = 1.0 : 0.91 : 0.69.

The data of exocellular xylanase activity are contained in Table 3. All species examined produced xylanase enzyme. One of the groups of species is characterized by either a maximum activity or an activity curve with a plateau. Characteristic maximum is reached by the activity of *P. eryngii* and *P. eryngii* var. *ferulae* (Fig. 2), while the activities of *P. ostreatus*, and on culture media A and B of *P. pulmonarius* are less so; in the last sample the activity decreases

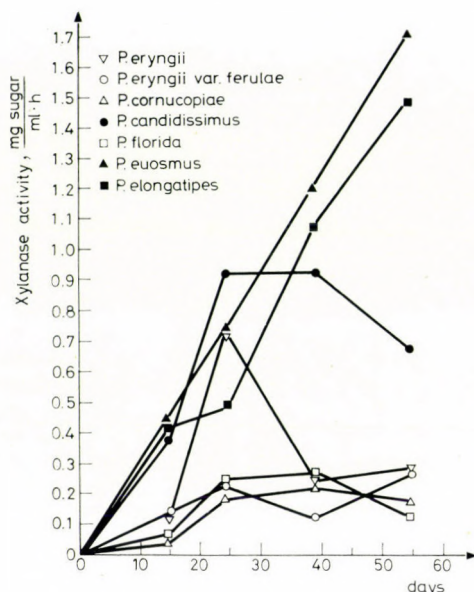


Fig. 2. Changes in the xylanase activities of several species in culture medium A.

as in the case of *P. cornucopiae*, *P. candidissimus* and *P. florida*, but not so much in the case of *P. mutilus*. The other large group is characterized by increasing activities (*P. japonicus*, *P. passeckerianus*, *P. sapidus*). *P. cystidiosus* can hardly be placed in either group, since on culture media A and C the curve shows an ascending character, while on culture medium B the activity reaches outstanding maximum on the 2nd sampling.

For most species there are no great differences between the activities of the culture media, but e.g. in the case of *P. elongatipes* the activity of culture medium C, with *P. calyptratus* that of B, while in the case of *P. euosmus* the activity of the A culture medium exceed considerably those measured in the others. The values of average activity per sample, irrespective of the species:

Culture medium	Sampling			
	1	2	3	4
A	0.260	0.557	0.641	0.757
B	0.296	0.572	0.504	0.554
C	0.346	0.450	0.594	0.601

show that the C culture medium induces a higher initial activity which, however, by the time of the second sampling is lower than in the other two culture media, and in the last sample its value is between the average activity values of culture media A and B. With all samples and culture media taken into consideration, difference of any importance is only shown by the A culture medium of the last sample, though even there it is only due to the extremely high values of two or three species that increase the average. The situation is different with the maltose-glucose (D) culture medium where any activity could only be measured in a

Table 3

Exocellular xylanase activities of the Pleurotus species examined on four kinds of carbon sources
(Activity: mg released sugar/ml filtrate x hour)

		Samples															
		1				2				3				4			
		culture medium				culture medium				culture medium				culture medium			
		A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D
<i>Pleurotus</i>	$\bar{x}$	0.545	1.520	0.328	0	0.843	0.525	0.431	0.229	0.834	0.750	0.603	0	1.000	0.735	0.469	0
<i>calypttratus</i>	s	0.356	0.070	0.017	0	0.058	0.049	0.019	0.050	0.025	0.103	0.015	0	0.080	0.026	0.044	0
<i>P. candidissi-</i>	$\bar{x}$	0.376	0.056	0.369	0.245	0.904	0.797	0.780	0.321	0.925	0.813	0.672	0	0.670	0.728	0.624	0
<i>mus</i>	s	0.000	0.054	0.078	0.000	0.051	0.061	0.048	0.020	0.080	0.056	0.050	0	0.100	0.070	0.065	0
<i>P. cornuco-</i>	$\bar{x}$	0.049	0.031	0.020	0.193	0.172	0.165	0.165	0.188	0.211	0.164	0.209	0.060	0.170	0.133	0.164	0
<i>phiae</i>	s	0.006	0.002	0.003	0.020	0.030	0.015	0.022	0.012	0.012	0.010	0.011	0.009	0.020	0.020	0.010	0
<i>P. cystidiosus</i>	$\bar{x}$	0.123	0.097	0.137	0.224	0.561	1.830	0.234	0.277	0.519	0.816	0.264	0.245	0.502	0.738	0.350	0
	s	0.025	0.004	0.018	0.025	0.034	0.067	0.023	0.034	0.090	0.037	0.075	0.052	0.035	0.068	0.077	0
<i>P. elongatipes</i>	$\bar{x}$	0.441	0.477	0.917	0.121	0.489	0.565	0.986	0	1.070	0.654	1.590	0.200	1.490	1.220	1.340	0
	s	0.009	0.019	0.019	0.000	0.003	0.011	0.072	0	0.080	0.031	0.060	0.137	0.100	0.080	0.070	0
<i>P. eryngii</i>	$\bar{x}$	0.113	0.071	0.134	0	0.743	0.238	0.169	0.187	0.247	0.175	0.194	0.235	0.272	0.125	0.328	0
	s	0.021	0.002	0.006	0	0.210	0.011	0.006	0.000	0.012	0.013	0.007	0.091	0.014	0.006	0.110	0
<i>P. eryngii</i>	$\bar{x}$	0.123	0.057	0.075	0	0.207	0.120	0.153	0	0.116	0.055	0.158	0	0.240	0.089	0.504	0
<i>var. ferulae</i>	s	0.004	0.003	0.002	0	0.082	0.013	0.058	0	0.027	0.001	0.010	0	0.040	0.003	0.006	0
<i>P. euosmus</i>	$\bar{x}$	0.441	0.258	0.638	0	0.726	0.726	0.798	0	1.200	1.080	1.090	0.185	1.740	1.120	1.150	0.164
	s	0.006	0.168	0.021	0	0.199	0.090	0.035	0	0.040	0.020	0.020	0.000	0.120	0.130	0.130	0.090
<i>P. florida</i>	$\bar{x}$	0.042	0.029	0.023	0	0.237	0.169	0.194	0.272	0.252	0.166	0.181	0	0.108	0.138	0.156	0
	s	0.005	0.006	0.004	0	0.010	0.015	0.022	0.035	0.040	0.030	0.015	0	0.010	0.011	0.020	0
<i>P. japonicus</i>	$\bar{x}$	0.261	0.582	0.749	0	0.648	0.932	0.814	0	0.637	0.750	1.129	0.593	1.337	0.910	0.734	0.254
	s	0.050	0.025	0.079	0	0.103	0.009	0.039	0	0.056	0.045	0.175	0.021	0.116	0.056	0.067	0.076
<i>P. mutilus</i>	$\bar{x}$	0.528	0.634	0.564	0	1.250	1.264	0.674	0.579	0.823	0.811	0.734	0.755	1.096	0.912	0.738	0.213
	s	0.334	0.401	0.026	0	0.063	0.052	0.011	0.070	0.037	0.043	0.031	0.055	0.039	0.152	0.111	0.036
<i>P. ostreatus</i>	$\bar{x}$	0.104	0.100	0.044	0.254	0.296	0.298	0.159	0.140	0.325	0.336	0.191	0	0.270	0.226	0.229	0
	s	0.032	0.014	0.002	0.034	0.065	0.045	0.033	0.010	0.044	0.057	0.033	0	0.020	0.030	0.012	0
<i>P. passecke-</i>	$\bar{x}$	0.032	0.048	0.034	0.780	0.080	0.106	0.140	0.503	0.100	0.057	0.294	0.239	0.234	0.136	0.370	0.080
<i>rianus</i>	s	0.002	0.003	0.001	0.055	0.044	0.036	0.004	0.000	0.009	0.013	0.028	0.018	0.013	0.087	0.073	0.000
<i>P. pulmona-</i>	$\bar{x}$	0.299	0.037	0.176	0	0.318	0.314	0.245	0	0.965	0.199	0.482	0	0.738	0.302	0.905	0
<i>rius</i>	s	0.015	0.010	0.018	0	0.040	0.011	0.009	0	0.010	0.005	0.023	0	0.028	0.010	0.055	0
<i>P. sapidus</i>	$\bar{x}$	0.428	0.454	0.997	0.095	0.886	0.544	0.827	0	1.400	0.737	1.120	0	1.490	0.840	0.955	0
	s	0.008	0.049	0.012	0.031	0.059	0.066	0.092	0	0.080	0.213	0.020	0	0.160	0.040	0.075	0

few cases. Decreasing tendency characterizes the activities of *P. passeckerianus*, *P. cornucopiae* and *P. ostreatus*. The xylanase activity of *P. cystidiosus* on the D culture medium is steady in three samples and only decreases by the time of the last sampling. Hence it seems that on maltose-glucose culture medium most species do not produce xylanase, though some of them are even then able to produce enzymes of measurable activity (*P. passeckerianus*, *P. cystidiosus*, *P. cornucopiae*); this production shows a tendency decreasing in time.

Discussion

Of the presence and functioning of an enzyme system which decomposes the carbon-hydrates information is supplied by the data of C_x -, C_1 - and xylanase activities.

The temporal changes of the C_x activity are characterized by an increasing tendency for almost all species examined. A cellulase activity of increasing character up to the 28th day was pointed out by GALÁDOVA and NECESANY (1980) in the surface and especially in the submerged cultures of *Fomes fomentarius*, where ECHBALTALAB et al. (1976) measured maximum curve. As for the C_x activity of the individual species, with all culture media taken into consideration *P. japonicus* was the biggest producer [this confirms the experimental results of GINTEROVA (1980) obtained with a different method].

The values of C_x activity on the straw and cob culture medium generally were very close to each other. The activity of the crushed oak variant was on the average about half of those of variants A and B. The fact that on the maltose-glucose culture medium none of the species — except for *P. japonicus* — produced any considerable, in most cases not even demonstrable quantities of enzyme proves the inducible nature of the C_x enzyme, confirming the notion generally accepted in the literature. *P. japonicus*, which is anyway different from the other *Pleurotus* species in many physiological (enzymatic) parameters, seems to reduce only gradually its C_x production on maltose-glucose culture medium.

According to the data of the C_1 activity (Table 2) some species show maximum others ascending curves. The activities displayed on straw and cob media are more or less the same, while on oak-dust they are always lower. As regards the C_1 - C_x order of succession in the mechanism of cellulose decomposition, according to literary data (FEDOROV and STAYCHENKO 1971) the C_1 activity precedes in time the C_x activity. Our examination data undoubtedly appear to confirm this dynamism of the enzyme activity for *P. elongatipes*, *P. sapidus*, *P. euosmus*, *P. cystidiosus*, *P. eryngii* var. *ferulae*, *P. passeckerianus* and *P. candidissimus*. With the other species this correlation either is not definite (*P. calyptratus*, *P. eryngii*), or the curves of the activities run parallel (*P. japonicus*, *P. mutilus*), with a possible higher rate of increase for C_x .

On the basis of the activities of the xylanase enzyme the temporal changes are best characterized by the maximum curve or the curve with a plateau (*P. eryngii* or *P. candidissimus* are typical examples of this), or by a steadily increasing activity (*P. elongatipes*, *P. euosmus*). The summarized data — averages independent from species — increase. The culture media show no substantial differences in enzyme activity. In some cases the activity measured on the C medium is the highest. Interesting question is the activity of culture medium D. The activity, though pointed out for 7 species, dropped in every case to zero after the first or second sampling; hence the rate of enzyme synthesis seems to decrease rapidly (*P. cornucopiae*, *P. passeckerianus*). In the case of *P. japonicus*, on the other hand, enzyme activity — and not at all negligible at that — could only be detected in the 3rd and 4th samples. On the basis of the data of culture media the inducibility of the enzyme can be regarded as a proved fact for most species, as it was pointed out by BIELY et al. (1980) for *Saccharomyces*.

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DINÁMICA DEL CRECIMIENTO Y CAMBIOS BIOQUÍMICOS DEL FRUTO DE PIÑA [*ANANAS COMOSUS* (L.) MERR.] CULTIVAR ESPAÑOLA ROJA EN CUBA

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Changes of some physical and chemical indices of the pineapple fruit were studied in different phases of its development. Fruit samples were measured and weighed during 11 weeks of the maturation and ripening process. Content of total soluble matter and titrable acidity were analyzed and their relation was calculated. Obtained results permit to define the optimal period of harvesting fruits of the cv. Española Roja.

Introducción

Los cambios asociados a la maduración e índices de calidad han sido estudiados en numerosos frutos durante el período final de la maduración, pero relativamente pocos han investigado esto a fondo desde la floración hasta la senectud.

Se han realizado varias investigaciones donde se analizan los cambios que ocurren en los parámetros físicos y bioquímicos del fruto de piña en distintos momentos de su desarrollo ante condiciones ecológicas variables. Estos estudios han sido efectuados en distintos cultivos pero la mayor información se tiene en el cv. Cayena Lisa en trabajos realizados en Hawaii y Costa de Marfil (KERNS 1936, GORTNER 1965, SINGLETON 1965, SINGLETON y GORTNER 1965, GORTNER y SINGLETON 1965, GORTNER et al. 1967, DULL 1971, TEISSON 1973) y en el cultivar Kew en la India (LODH et al. 1972).

El comportamiento de los frutos de piña del cultivar Española Roja en este sentido no había sido reportado antes de la realización de este experimento, por lo cual se hacía necesario estudiar los cambios que ocurrían en los frutos durante su desarrollo en las condiciones de Cuba y especialmente en el cultivar Española Roja que es el más plantado en el país. Esto permite conocer y caracterizar — a través de indicadores físicos y químicos — el proceso de desarrollo del fruto en este cultivar.

Este estudio se ha realizado con el objetivo de obtener información sobre la dinámica del crecimiento de los frutos, sobre las etapas de desarrollo y sobre los pronósticos de maduración y cosecha de los mismos no solo por apreciación visual, sino también por medio de indicadores físicos y químicos.

Materiales y métodos

Para la realización de este estudio se emplearon frutos de piña del cv. Española Roja, provenientes de un experimento situado en la Estación Experimental Agrícola de Tapaste, Habana; el cual fue plantado sobre un suelo ferralítico rojo compactado (HERNÁNDEZ et al. 1975).

El diseño experimental utilizado fue de bloques al azar con 4 repeticiones. Las plantas utilizadas recibieron una fertilización sólida antes de la siembra y a los seis meses de plantada con la fórmula 10-6-18 (N, P, K) a razón de 30 g/planta.

A partir del tercer mes de plantada se realizaron también, mensualmente, aspersiones foliares con urea al 20%, K_2SO_4 al 2% y $FeSO_4$ al 0,5% hasta el oncenavo mes.

La inducción de la floración se realizó cuando las plantas tenían un año de edad, utilizando como inductor solución acuosa saturada en gas acetileno a razón de 50 ml/planta, realizándose dos aplicaciones en horas de la noche con tres días de intervalo entre ellas.

Se siguió la evolución que experimentaban los frutos durante su desarrollo, estudiándose el comportamiento de algunos índices físicos y químicos del fruto desde finales de la floración hasta el fruto totalmente maduro. Con este fin se efectuaron muestreos en diferentes etapas durante la pre-maduración y maduración del fruto.

Los muestreos fueron realizados sistemáticamente, con intervalos regulares de 7 días desde la semana 13 hasta la 23 después de la inducción floral (desde los 93 hasta los 163 días después de la inducción de la floración).

En cada caso se tomaron 24 muestras compuestas de un fruto cada una y se analizaron individualmente. Se escogieron 6 frutos representativos de cada parcela. Los frutos cosechados en cada semana fueron transportados al Laboratorio de Bromatología del Instituto de Ciencia Agrícola y procesados inmediatamente.

Tabla 1

Comportamiento de los datos climáticos desde la siembra del vástago hasta la cosecha del fruto

Datos climáticos	meses	Ene	Feb	Mar	Abr	May	Jun
Precipitaciones (mm)		—	—	—	—	—	—
(Acumuladas en el mes)		0	5,4	16,1	42,3	252,5	117
		11,4	—	—	—	—	—
		—	—	—	—	—	—
Temperaturas medias (°C)		24,5	21,8	24,8	25,4	26,4	26,9
(Promedios mensuales)		22,7	—	—	—	—	—
		—	—	—	—	—	—
Humedad relativa (%)		71,4	68,5	66,0	65,2	73,8	73,3
(Promedios mensuales)		79,0	—	—	—	—	—
		—	—	—	—	—	—
Datos climáticos	meses	Jul	Ago	Set	Oct	Nov	Dic
Precipitaciones (mm)		196	386	207	80	22	43
(Acumuladas en el mes)		322,7	103,9	155	109,6	47,6	2,0
		—	—	—	—	—	—
		26,3	26,2	26,0	25,1	24,2	20,3
Temperaturas medias (°C)		27,1	27,7	27,7	25,0	23,7	22,6
(Promedios mensuales)		—	—	—	—	—	—
		83	85	87	84	81	77
Humedad relativa (%)		78,6	76,7	79,2	79,0	77,0	76,0
(Promedios mensuales)		—	—	—	—	—	—
		—	—	—	—	—	—

Se observó de forma general la evolución de la coloración de los frutos durante su desarrollo.

En cada muestreo se midió el peso del fruto con corona y sin corona, y por diferencia entre ambos, se calculó el peso de la corona. Se midió la altura o largo de cada fruto y el diámetro o ancho y se calculó la relación largo/ancho en cada caso.

Se determinaron, semanalmente, los sólidos solubles totales, la acidez titulable y la relación sólidos solubles/acidez. La acidez se expresó en g ácido cítrico/100 ml jugo.

Los métodos utilizados para medir los diferentes índices fueron los clásicos establecidos.

El experimento fue realizado en el período de noviembre-enero, el cual está comprendido en el intervalo de noviembre-abril (meses secos) donde se cosecha la fruta con una calidad óptima.

Durante el desarrollo del experimento se registraron las precipitaciones acumuladas mensualmente, las temperaturas medias y la humedad relativa y se calcularon los promedios mensuales de estas últimas desde la siembra del vástago hasta la primera cosecha del fruto (tabla 1).

Resultados y discusión

Crecimiento del fruto y de la corona. Comportamiento de los índices físicos.

Dimensiones del fruto

El aumento de las dimensiones del fruto fue gradual; mostrándose siempre desde los primeros momentos, que al fruto era más alto que ancho, no observándose la inversión en el crecimiento señalada por TEISSON (1973) para el cultivar Cayena Lisa. Esta diferencia encontrada en los resultados no se debe atribuir a diferencias en la dinámica de crecimiento entre los dos cultivares, sino que se podría explicar ya que nuestros experimentos no abarcaron los estadios de desarrollo muy precoces donde Teisson observó tal inversión.

Las curvas teóricas calculadas para estos parámetros se muestran en la Fig. 1. Tanto el largo (l) como el diámetro (d) presentan curvas similares.

La relación entre el largo y el ancho del fruto fue siempre mayor que 1 y varió muy poco del primero al último muestreo ya que ambas magnitudes aumentan en la misma proporción. Esta tendencia en el comportamiento de los datos coincide con lo observado por SINGLETON (1965) en Hawaii para el cv. Cayena Lisa.

Pesos

El peso completo de los frutos aumentó significativamente ($P = 0,05$) en cada semana, alcanzando valores desde 0,486 kg al inicio hasta 1,638 kg al final del experimento (entre las semanas 13 y 23 posteriores a la inducción floral).

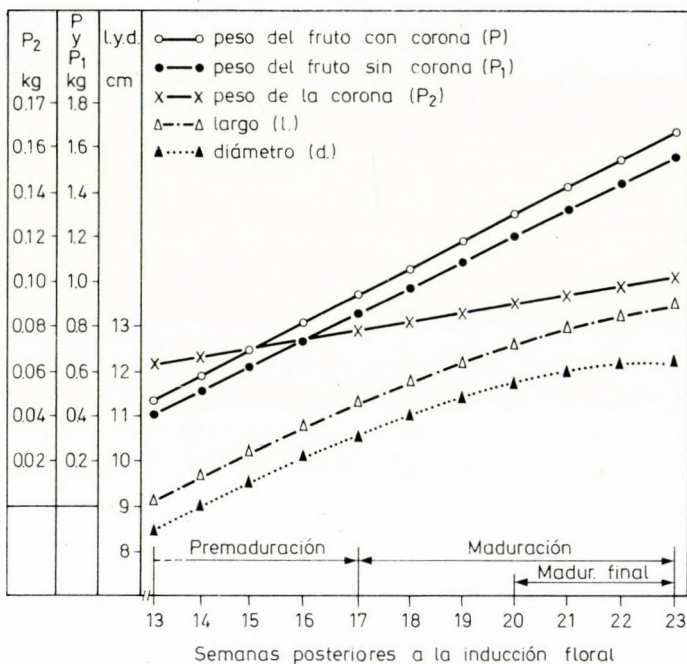
El peso de la corona se incrementó desde alrededor de 0,06 kg hasta aproximadamente 0,1 kg en el mismo intervalo de tiempo, aunque sus oscilaciones semanales no fueron significativas en la mayoría de los casos.

El peso completo de la fruta y el peso sin corona presentan curvas similares con un aumento gradual en el peso, mientras que el peso de la corona presenta aumentos mucho más discretos.

Las curvas teóricas calculadas para los pesos y las ecuaciones de regresión obtenidas se muestran en la Fig. 1.

En todos los casos los datos experimentales obtenidos se ajustan de forma satisfactoria a las curvas teóricas calculadas.

Evolución de algunos parámetros químicos durante el desarrollo del fruto. Comportamiento de los índices químicos.



Regresion calculada y coeficiente de correlación:

$$Y_P = 0.0169x - 1.0971$$

$$r_P = 0.9947^*$$

$$Y_{P1} = 0.0163x - 1.1085$$

$$r_{P1} = 0.9922^*$$

$$Y_{P2} = 0.0006x - 0.0082$$

$$r_{P2} = 0.6580^*$$

$$Y_L = 0.1626x - 0.0004x^2 - 2.6929$$

$$r_L = 0.9738^*$$

$$Y_d = 0.2066x - 0.0006x^2 - 5.7506$$

$$r_d = 0.9913^*$$

* $P < 0.01$

Fig. 1. Evolución de algunos parámetros físicos durante el desarrollo del fruto

Contenido de sólidos solubles totales (brix)

Como es conocido, el % de sólidos solubles totales es un indicador del contenido de carbohidratos.

El comportamiento del brix del jugo se mantuvo casi estable durante los primeros muestreos, encontrándose un valor mínimo a las 14 semanas posteriores a la inducción floral. No se observaron diferencias significativas en los datos obtenidos en los diferentes muestreos desde la semana 13 hasta la 17 después de la inducción floral. A partir de ese momento se observó un incremento rápido y significativo ($P = 0,05$) hasta la maduración de la fruta, notándose un aumento mucho más marcado en las últimas 4 semanas de la maduración, es decir, a partir de la semana 20 después de la inducción floral.

La curva teórica calculada para este parámetro y la ecuación de regresión obtenida se presentan en la Fig. 2. Los datos experimentales obtenidos se ajustan satisfactoriamente a las curvas teóricas calculadas.

Contenido de ácidos titulables

El contenido de ácidos titulables (calculados como ácido cítrico) se incrementa a medida que a fruta alcanza un mayor grado de desarrollo, aunque se mantiene relativamente bajo hasta a semana 17 después de la inducción floral. Posteriormente se incrementa rápidamente hasta alcanzar un máximo en la semana 21 (2 semanas antes de que el fruto esté totalmente maduro), a partir de este momento comienza a disminuir.

El coeficiente de correlación entre el contenido de acidez y el número de semanas después de la inducción floral fue altamente significativo. La ecuación de regresión resultante fue de 3er grado. La curva teórica calculada para este parámetro se muestra en la Fig. 2.

El comportamiento del fruto de piña del c.v. Española Roja, en lo que se refiere al contenido de sólidos solubles totales y acidez titrable, se asemeja a lo observado por SINGLETON y GORTNER (1965) para el cv. Cayena Lisa, aunque los cambios observados no coinciden cronológicamente, ni los valores obtenidos tampoco. Esto es lógico ya que cada cultivar tiene sus características específicas.

Relación sólidos solubles totales/acidez

El coeficiente de correlación encontrado entre la relación brix/acidez y el número de semanas posteriores a la inducción floral fue altamente significativa.

Al analizar la significación de los coeficientes de regresión de los distintos grados según el método de regresión polinómica de GAUSS-DOOLITTLE, se obtuvo una alta significación para el coeficiente de segundo grado. La ecuación de regresión resultante y la curva teórica calculada se muestra en la Fig. 2.

La relación brix/acidez disminuye muy marcadamente durante las primeras semanas, alcanza un valor mínimo en la semana 18 después de la inducción floral y continúa aumentando después hasta la maduración completa donde alcanza valores aproximadamente iguales a los valores iniciales.

Es de destacar que el aumento de la relación brix/acidez después de haber alcanzado un mínimo en la semana 18 posterior a la inducción floral, coincide con la aparición de los primeros tonos amarillos en el centro de los ojos y de los tonos marrones en los bordes.

Los incrementos en la relación brix/acidez son más marcados a partir de las semanas 20 y 21 después de la inducción floral, es decir, de 2-3 semanas antes de la maduración completa del fruto.

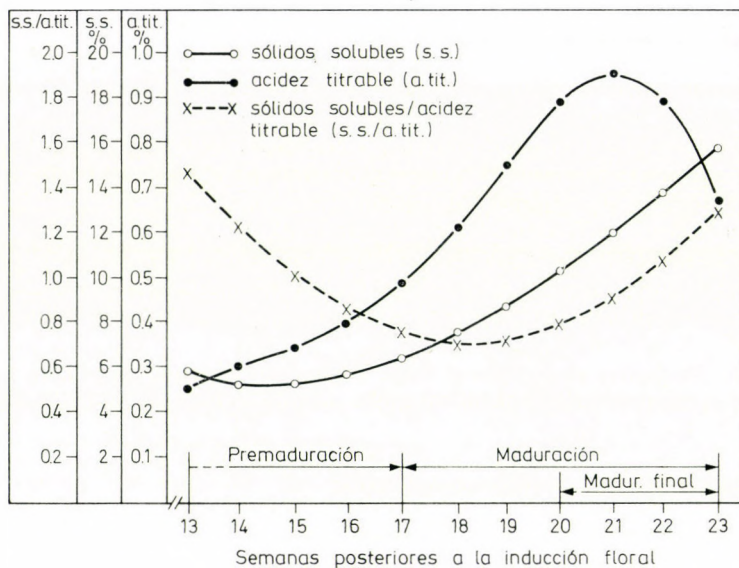
Los cambios observados en la relación brix/acidez como fue señalado por SINGLETON y GORTNER (1965) podrían fácilmente inducir a malas interpretaciones referentes al sabor o gusto del fruto en desarrollo.

Muchas semanas antes de la completa madurez del fruto, éste tiene una adecuada relación brix/acidez. No obstante, la calidad podría ser pobre a causa del bajo contenido de azúcares y ácidos.

Aunque la relación brix/acidez puede ser un indicador útil de la calidad comparando frutos de diferentes áreas en el mismo estado de madurez, obviamente, no puede servir como índice de calidad para frutos en diferentes estados de madurez.

Los datos obtenidos con respecto a los parámetros químicos estudiados no solo ampliará nuestro conocimientos sobre algunos cambios bioquímicos básicos ocurridos durante el desarrollo del fruto, sino que sugieren la existencia de estados reconocibles en el desarrollo químico del fruto.

La existencia de estados discretos determinados durante el desarrollo del fruto ha sido señalado por SINGLETON y GORTNER (1965) para el cv. Cayena Lisa y por GORTNER et al. (1967) mientras estudiaba la base bioquímica para la terminología hortícola. LODH et al. (1972) observó también la existencia de estados definidos en el cv. Kew en la India.



$$Y_{s.s.} = -0.5095x + 0.026x^2 + 30.5008$$

$$r = 0.9822^*$$

$$Y_{a.tit.} = 1.7718x - 0.0231x^2 + 0.0001x^3 - 50.3999$$

$$r = 0.9825^*$$

$$Y_{s.s./a.tit.} = -0.1422x + 0.0005x^2 + 9.9609$$

$$r = 0.9067^*$$

* $P < 0.01$

Fig. 2. Evolución de algunos parámetros químicos durante el desarrollo del fruto

Sin embargo, estos estados no habían sido observados ni definidos para el cv. Española Roja antes de la realización de estos experimentos.

El aumento rápido observado en el brix y en la acidez a partir de la semana 17-18 después de la inducción floral, el cambio de dirección en la relación brix/acidez en la semana 18 y la coincidencia de la aparición de los primeros tonos amarillos en el centro de los ojos al comenzar a aumentar la relación brix/acidez indican o sugieren la existencia de uno de los estados fisiológicos discretos en el desarrollo químico del fruto de piña.

Estos son cambios asociados con el período o estado de la maduración ("maturation").

El incremento muy notable del brix 3 semanas antes de la maduración completa (semana 20 después de la inducción floral), el aumento de la acidez hasta alcanzar un máximo 2 semanas antes de la madurez completa (semana 21 después de la inducción floral) y el incremento en la relación brix/acidez en las semanas 20-21 posteriores a la inducción floral (de 2-3 semanas antes de la maduración completa), indican la existencia de otro de los estados discretos en el desarrollo químico del fruto. Esta parece ser la etapa o estado final de la maduración ("ripening").

Basándonos en los resultados experimentales señalados anteriormente, podemos hacer un análisis de la evolución del desarrollo del fruto de piña del cv. Española Roja de acuerdo con la terminología propuesta por GORTNER et al. (1967) para el cv. Cayena Lisa y, establecer las diferentes etapas de crecimiento del fruto de piña del cv. Española Roja en las condiciones de Cuba para una época comprendida en el período óptimo de cosecha.

Así, estos períodos o etapas serían:

Pre-maduración:

Período de desarrollo del fruto anterior al comienzo del proceso de maduración. Esta etapa comienza después de la terminación de la floración y se extiende hasta aproximadamente la semana 17 posterior a la inducción floral (6 semanas antes de que el fruto se colorea totalmente). Se caracteriza esta etapa por un aumento considerable de las dimensiones del fruto.

El brix se mantiene bastante estable en este período aunque presenta un mínimo. La acidez también se comporta bastante estable y sus valores son bajos.

Maduración ("maturation"):

Período de desarrollo del fruto durante el cual el fruto emerge de la etapa incompleta para adquirir su completo crecimiento y su máxima calidad comestible.

Esta etapa está comprendida entre la semana 17 hasta la 23 después de la inducción floral, es decir, el período de las 6 semanas anteriores a que el fruto se colorea totalmente.

El comienzo de esta etapa se caracteriza por un aumento notable en el brix y un aumento en la acidez. Durante esta etapa se observa también un máximo en el contenido de ácido y un mínimo en la relación brix/acidez.

En este período comienza también a colorearse el fruto, apareciendo los tonos amarillos en el centro de los ojos y los tonos marrones en los bordes que fueron aclarándose hasta que aparecieron los todos naranjas.

Maduración final o completa ("ripening"):

Etapla terminal de la maduración durante la cual el fruto adquiere su total desarrollo y su máxima calidad comestible y estética.

Esta etapa está incluida dentro de la etapa de maturation. El ripening que está comprendida entre las semanas 20 y 23 posteriores a la inducción floral (período de 2 o 3 semanas antes de que el fruto alcance su completa madurez).

En esta etapa ocurren fundamentalmente cambios químicos y se caracteriza por un incremento muy notable en el brix, por el máximo alcanzado por la acidez, por el incremento marcado de la relación brix/acidez y por el aumento marcado en el contenido de azúcares totales y sacarosa.

Al final de esta etapa el fruto está totalmente coloreado presentando una coloración amarilla bien definida en el centro de los ojos y naranja intenso en los bordes.

Las etapas antes descritas se encuentran señaladas en la Fig. 2.

Conclusiones

El comportamiento de los índices físicos y químicos observados durante el desarrollo del fruto de piña indica que para el cultivar Española Roja existen también varios estados discretos reconocibles durante el desarrollo del fruto. Este comportamiento permite caracterizar — a través de indicadores físicos y químicos — las diferentes etapas del crecimiento del fruto de piña para el c.v. Española Roja en las condiciones de Cuba para una época com-

prendida en el período óptimo de cosecha. Las etapas descritas son: pre-maduración, maduración y maduración final o completa.

Las ecuaciones de regresión calculadas para los parámetros físicos y químicos medidos podrían utilizarse para controlar el estado de desarrollo de las plantaciones comerciales.

El período óptimo de cosecha para la exportación en fresco hacia mercados lejanos está comprendida entre la semana 20 y 21 posteriores a la inducción floral, donde el fruto ha alcanzado un peso mayor a 1 kg e índices aceptables en su calidad interna, alcanzando posteriormente durante su transportación una coloración externa aceptable.

El período óptimo de cosecha para el consumo local y la industria conservera está comprendido entre las 22 y 23 semanas posteriores a la inducción floral, en este momento el fruto ha alcanzado índices óptimos en su calidad.

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ACIDIFICATION OF SOIL AND DECAY OF SESSILE OAK IN THE "SÍKFŐKÚT PROJECT" AREA (N-HUNGARY)*

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This paper presents a discussion of the results obtained from the investigation of dying sessile oaks in the research area "Síkfőkút Project" (N-Hungary). The aluminium and other toxic heavy metals becoming water soluble in acidic forest soils decrease the absorbing capacity of root-systems of trees primarily through the destruction of mycorrhiza-fungi. This, in the end, causes the trees to die in a state of water and nutrient circulation stress. The paper offers a new complex ecological diagram showing the different way of tree-dying except the natural catastrophies and aging. The bold line indicates the proved indirect path of death of sessile oaks caused by air pollution.

Introduction

The causes of the accelerating forest decay that started in recent years are being studied with a huge apparatus all over the world. This problem is approached from two major directions (with many transitions between them):

1. The primary cause of tree decay and disease is an epidemic generated by some pathogenic microorganism, a fungus, less frequently a fungus and a bacterium together or perhaps a virus (theories of epidemics). If pathogenic fungi get into the water and nutrient carrying vascular tissues of a deciduous tree, the disease is called tracheomycosis.

2. The primary cause of tree decay and disease is a change in some abiotic or biotic environmental factor that passes the tolerance level of a tree ("ecological theories"). Supporters of this theory link forest decay all over the world to the deterioration of environmental quality caused by human activity (e.g., incorrect forestry, air pollution, acid deposition, etc.).

Decay of forests in Hungary

The process of decay of sessile oak in Hungary speeded up in the late 1970's. This tree species constitutes 15.5% of the present forest stock in the country (SALI 1979). But according to the reconstructed vegetation map the communities *Quercetum petraeae-cerris* and *Quercus petraeae-Carpinetum* — in which the *Quercus petraea* trees occur with a 50-60% frequency — once covered 30% of the country's territory (JAKUCS 1980). That is, sessile oak is

* "Síkfőkút Project" No. 105.

one of the most important aboriginal tree species in Hungary. Decay can also be observed in the case of *Quercus robur*, *Alnus glutinosa*, *Fagus silvatica* and in planted pine species. According to the forest survey of 1982–83, decay was found in 11% of the present forest area in Hungary, of which 7.5% concerned sessile oak. Between 1981 and 1983, altogether 1.2 million m³ timber perished of which 900 000 m³ was made up of *Quercus petraea* (IGMÁNDY et al. 1984, SOLYMOS 1985).

The decay of oak occurs regardless of community, forest type, sprout or seedling origin of trees, in natural or planted stands and appears in every age-group. No correlation can be established with elevation above sea level or exposition. Unequivocal is, however, the relationship between the frequency of decay and the type of soil. Tree decay is far more intensive on deep, clayey, and slightly acidic brown forest soils or on shallow pseudo-podzols formed over acidic bedrocks (andesite, quartzite, riolite, shale, etc.) than in forests growing on soils rich in bases over lime and dolomite bedrock.

The external signs of the process of decay of sessile oak in Hungary are: yellowing of leaves, diminished leaf area, fewer leaves developing in the first stage of the vegetation period, withering of apical shoots, dropping first of smaller, later of larger branches, cracking of bark on tree trunks followed by peeling off. The process may sometimes last 1–2 years (in such cases, characteristic “suckers” may appear on the trunk or larger branches). It may also take place abruptly, within 2–3 weeks, with the dry brown leaves often remaining on the tree till autumn. The dead tree remaining in the forest is felled usually by strong winds without its roots that remain in the ground (see: Plate I).

The rate of decay, changes in structure and alterations in certain factors in the Síkfőkút forest

Since 1972, continuous and complex ecological research has been going on in the framework of MAB program in a stand of the climazonal oak forest community covering the foothills of the Northern Hungarian Mountains (“Sík-főkút Project”). The research project was intended to explore among other things structure, production, path of energy flow and element cycles of the forest (JAKUCS 1973, 1978, JAKUCS et al. 1981). Besides several papers, some of the results have published in a book (JAKUCS ed. 1985).

In the one hectare central plot of the Project area each tree was numbered in 1972 and the distribution of trunks and leaf cover was charted. There were 690 70–75-year-old, healthy *Quercus petraea* standing in 1973. Up to 1978 (a period of 6 years) 16 trees died (owing to damage by wind and natural death) which means an annual 0.4% average. The speeding up of the



PLATE I. Dying (a), deceased (b) individual of *Quercus petraea*, peeling of bark (c) and fall of tree from the soil without its roots (d) in the "Síkfőkút" research area

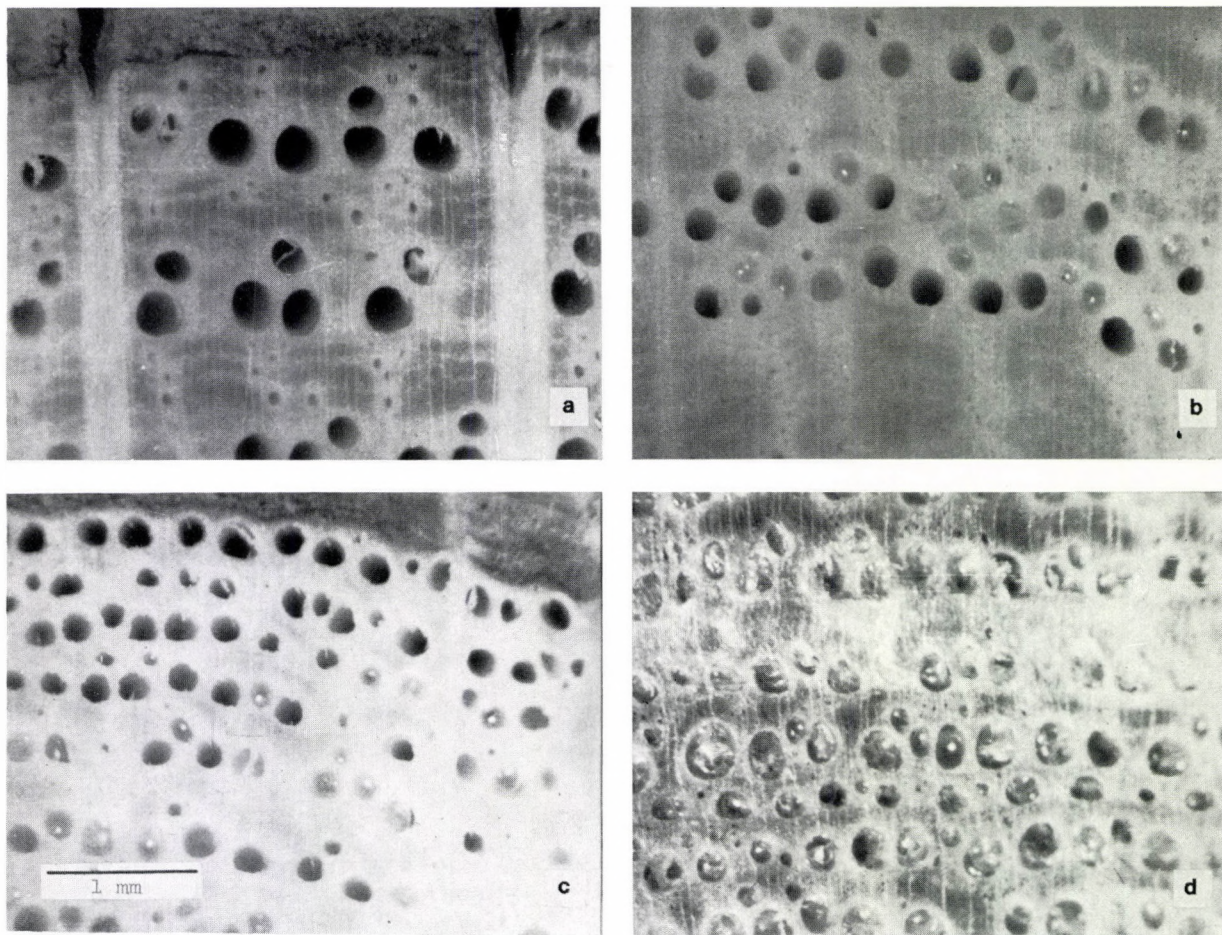


PLATE II. Obstruction of sapwood in the healthy (a), diseased (b, c) and dead (d) oaks (These segments are adjacent to the bark.)

Table 1

The number of Quercus petraea trees deceased in the central hectare and quarter-hectares of the "Sikfőkút Project" between 1972 and 1985 as well as the number of trees showing the signs of disease in 1985 and the number of trees fallen by August 30, 1985

Identification of quarterhectares	Number of trees in 1972	Number of deceased trees								Total		Diseased trees in 1985	Fallen trees
		1972-78	79-80	81	82	83	84	85	number	%			
A	206	10	42	8	6	15	10	12	103	50.0	13	34	
B	152	2	15	5	4	9	12	10	57	37.5	28	15	
C	184	3	34	2	3	10	9	33	94	51.0	12	32	
D	148	1	19	10	3	7	23	13	76	51.3	8	11	
Total hectare	690	16	110	25	16	41	54	68	330	47.8	61	92	
<i>Quercus cerris</i>	124								6	4.8	—	—	
Forest/hectare	814								336	41.2	61	92	

tree decay has been traced since 1978 (Table 1). Up to August, 1985 47.8% of sessile oaks died and symptoms of the disease were observed in 16.9% of the still living trees. 28% of the dead trees have fallen, the rest are still standing. In the same one hectare area, there were 124 *Quercus cerris* in 1972. Of them 6 (4.8%) trees have died in the past 13 years mainly because of storm damage. No signs of disease are visible in the remaining ones.

A remarkable change has taken place in the shrub level since 1979. 32% of shrubs taller than 1 m have withered. Almost all *Quercus petraea* of shrub-size have disappeared, and the number of *Cornus mas* and *Acer campestre* shrubs was halved. The shrubs and saplings shorter than 1 m are also diminishing in number (KÁRÁSZ et al. 1986).

Due to the decay of trees, the whole structure, pattern, and population diversity of species is in a process of transformation. The former stable radiation balance, albedo, and interception of radiation and precipitation have also altered. Significantly more solar energy enters the forest in the place of decayed trees or group of trees in a mosaic-like fashion than before and the internal parts of the forest get warmer and drier (NAGY, JUSTYÁK 1986). The soil is covered even in mid-summer by an ever thicker layer of forest litter containing almost intact leaves of the previous year, a fact that points to a disorder in decomposition (TÓTH 1985). The forest compensates for the missing foliage cover by the more intensive growth of the taller, tree-like shrubs (e.g. *Acer campestre*) as well as by the increased size of canopy of the still healthy trees (mainly *Quercus cerris*). The 8.29 ha/ha leaf area index of the forest in 1972-76, has, however, decreased by cca. 2 ha/ha.

The detailed input-output element budgets indicated as early as 1973-76 that the soil in the forest was acidifying. With respect to Ca and Mg, the

Table 2

*Results of chemical analysis of two soil profiles
(In 1973 analysis was performed by M. Kovács, 1976 by P. Stefanovits,
and in 1985 it was repeated by I. Berki)*

Soil profile 1

Depth (cm)	1973						1985				
	0-10	10-30	30-50	50-75	75-100	100-120	0-10	10-30	30-50	50-100	100-140
1. $pH_{(H_2O)}$	5.0	4.8	5.2	5.2	5.5	5.7	6.3	5.2	5.6	5.9	6.1
2. $pH_{(KCl)}$	4.4	4.1	4.2	4.3	4.5	4.7	4.9	3.3	3.5	4.1	4.3
3. 1 - 2.	0.6	0.7	1.0	0.9	1.0	1.0	1.4	1.9	2.1	1.8	1.8
4. y_1	29.0	30.7	18.5	14.5	13.1	10.6	15.0	42.0	17.5	12.0	11.2
5. y_2	3.7	10.9	3.6	1.9	0.3	0.1	0	28.0	4.0	0.5	0.5
6. Organic matter (%)	3.2	2.6	0.7	0.2	—	—	3.3	1.2	0.3	0.7	0.5
7. Exchangeable cations (me/100 g)											
Ca ²⁺	12.2	10.2	18.1	19.8	22.8	23.3	19.4	6.7	9.2	22.2	20.2
Mg ²⁺	2.0	2.9	5.1	8.6	5.5	5.5	4.6	3.4	3.8	8.8	8.2
K ⁺	0.6	0.3	0.3	0.3	0.3	0.3	1.4	0.5	0.4	0.6	0.6
Na ⁺	0.1	0.1	0.2	0.2	0.4	0.3	0.06	0.06	0.09	0.2	0.3
S-value	14.9	13.6	23.8	26.0	28.9	29.6	25.5	10.7	13.5	31.8	29.3
Ca ²⁺	82.1	75.0	76.4	76.2	78.8	78.7	76.2	62.6	[68.3	69.8	68.9
Mg ²⁺	13.4	21.7	21.5	21.5	19.0	18.7	18.0	32.0	27.9	27.6	28.0
K ⁺	3.8	2.4	1.4	1.5	1.1	1.1	5.5	4.8	3.2	1.9	2.1
Na ⁺	0.7	0.9	0.7	0.9	1.1	1.5	0.3	0.6	0.6	0.7	1.0

Soil profile 2

Depth (cm)	1976					1985				
	0-10	10-25	25-40	40-70	70-100	0-10	10-25	25-40	40-70	70-110
1. $pH_{(H_2O)}$	5.3	4.7	5.2	6.2	6.0	6.0	5.1	5.1	5.3	5.6
2. $pH_{(KCl)}$	4.6	3.8	4.0	6.0	5.4	4.9	3.4	3.4	3.8	4.0
3. 1. - 2.	0.7	0.9	1.2	0.2	0.6	1.1	1.7	1.7	1.5	1.6
4. y_1	28.0	38.3	22.0	15.3	11.1	18.5	37.0	27.0	17.0	15.0
5. y_2	1.1	17.2	4.4	—	—	0.2	18.5	12.0	2.5	0.9
6. Organic matter (%)	5.4	2.7	2.2	1.8*	1.2*	3.6	1.4	1.0	0.5	0.7

* Fe and Mn concretions disturb the oxidimetric distribution of organic matter.

The organic matter content was calculated from the organic carbon concentrations determined by TOC analyser.

element-balance of the ecosystem was markedly negative, whereas it was positive in the case of S, Cl, Zn and other heavy metals throughout 4 years (JAKUCS et al. 1981, JAKUCS 1985). Then, we indicated that the process of acidification would soon be manifested by the transformation of flora in the forest.

Table 2 presents the finding of two soil profiles digged earlier and analysed again in 1985. It is clear from this Table that the pH value in the 10–40 (–50) cm deep soil layer densely interwoven by roots decreased by 0.4–0.8 unit in a period of about 8–10 years. Especially remarkable is the increase in the values of exchange acidity (y_2). As a consequence of acidification, the S values, the total concentration of exchangeable cations are decreasing in these layers as well as the exchangeable Ca^{2+} ion concentration. The Ca quantity in percentage of the S-value is cca. 10% less than formerly (BERKI 1986).

As regards the tree decay in the Síkfőkút Project area, detailed studies are conducted concerning the seasonal change of the available soil water content, the effects caused by phytophagous organisms, the possible propagation of the pathogenic organisms and parasites of weakness by vectors e.g., bark beetles and metallic wood borers, etc. The present paper offers our findings in three such parts of our research, where data were obtained through a comparative analysis of healthy and diseased trees, of their rhizospheres and of the soils close to the roots in the same area.

A comparative chemical analysis of soils, roots and leaves

On June 22, 1983, we took 5 samples each of the soil around 2 healthy trees and 2 trees showing disease symptoms at a distance of 1.5 m from the trunk and at a depth of 10–40 cm. Then we mixed the soil samples belonging to one tree. Simultaneously we took samples also of roots with a diameter less than 1 mm and also of those with a diameter of 1–5 mm in 5 places in the case of each tree. Mixed leaf samples were collected after the trees were felled.

In the chemical analysis soil pH was measured in KCl and also in distilled water suspension (1 : 2.5), and the values of hydrolytic (y_1) and exchange acidity (y_2) were estimated too. $\text{NH}_4\text{—N}$ and $\text{NO}_3\text{—N}$ were determined — in a 1% KCl extract — by means of steam distillation, whereas P content — in a Ca-lactate extract — by molybdenum-blue method. Exchangeable Ca, Mg, Al were extracted with M KCl (1 : 2.5), exchangeable Mn with 0.05 M EDTA (1 : 2). In these two soil extractions Fe concentration was also measured. Zn concentration was determined after extraction with 0.5 M HCl (1 : 100). After igniting at 600 °C and subsequent solution in HCl the cation content of the plant samples were measured with an atom-absorption spectrophotometer.

According to data in Table 3, the soil in the proximity of the trees' root systems (10–40 cm) is acid (in accordance with values measured at the same levels in Table 2). The pH values measured in distilled water suspension and in KCl suspension differ with more than 1 unit. Accordingly, very high levels of hydrolytic (y_1) and exchange acidities (y_2) can be measured. Compared with healthy trees, the pH of the soil close to the roots of diseased trees decreases only slightly, while the y_1 and y_2 values are significantly higher.

If the nutrient concentrations of soils in contact with the root systems of healthy and diseased trees are compared, it is found that Ca, Mg, K and P concentrations are 2–3 times lower around the roots of diseased trees than around those of healthy ones. The concentrations of $\text{NH}_4\text{—N}$, Mn, Zn and Fe are about the same while those of $\text{NO}_3\text{—N}$ and Al higher in soil surrounding the roots of diseased trees. Studying the relationship between acidification Al^{3+} concentration, and $\text{NO}_3\text{—N}$ intake, BEREZOVSKIJ et al. (1976) pointed

Table 3

*The chemical analysis of soil in contact
with the root-system of tree at depth 10–40 cm
(means of two mixed samples)*

	Healthy	Diseased
	trees	
pH _{distilled water}	5.01	4.84
pH _{KCl}	3.83	3.67
y_1	48.62	54.90
y_2	25.50	39.29
$\text{NH}_4^+\text{—N}$, mg/100 g	1.904	1.523
$\text{NO}_3^-\text{—N}$, mg/100 g	0.038	0.191
Exchangeable Ca, mg/g	2.113	0.788
Exchangeable Mg, mg/g	0.534	0.420
Exchangeable Al, mg/g	0.454	0.721
Exchangeable Mn, mg/g	1.329	0.965
Zn_{HCl} , mg/g	0.060	0.048
Fe_{KCl} , mg/g	0.003	0.003
Fe_{EDTA} , mg/g	0.739	0.768

Table 4

*The mole ratios of Ca/Al and
Mg/Al in soils in contact with
healthy and diseased trees*

	Healthy	Diseased
	tree	
Ca/Al	3.137	0.738
Mg/Al	1.310	0.648

Table 5*Element concentration in the fractions of healthy and diseased trees (in mg/g)*

	Healthy tree			Diseased tree		
	leaf	root (1-5 mm)	thin root (1 mm)	leaf	root (1-5 mm)	thin root (1 mm)
Ca	5.654	12.582	6.176	4.301	11.857	7.114
Mg	2.573	2.258	1.686	1.851	1.740	1.562
K	5.311	1.142	1.941	5.205	8.831	5.458
Al	0.053	0.453	1.065	0.072	0.770	1.485
Fe	0.163	0.189	0.387	0.222	0.232	0.445
Mn	2.287	0.417	0.496	1.358	0.658	0.616
Zn	0.019	0.017	0.023	0.016	0.017	0.020
Na	0.197	0.304	0.389	0.199	0.205	0.274

out that a high Al^{3+} concentration developing at low pH values may block the intake of NO_3^- .

In relation to plant damages caused by soil acidity ULRICH (1983) regards the changes in the molar ratios of Ca/Al and Mg/Al as essential. According to him, tree growth is depressed if the Ca/Al gramm molecule ratio falls below 2. Below 0.4–0.5, the danger of Al-toxicity is very great and below 0.15 all plants suffer grave damage. According to our findings (Table 4) the Ca/Al ratio is 3–4 times smaller at the roots of diseased trees than in soils in contact with the roots of healthy trees. When our results are compared with the limit values established by ULRICH, the Ca/Al ratio indicates damage caused by Al in diseased trees. The relative accumulation of Al in the proximity of the roots of diseased trees is also manifested in the Mg/Al ratio.

The distribution of elements in the different parts of a tree (leaf, root and thin root fractions) changes significantly in the disease (Table 5). From this point of view, the elements studied can be categorized in three groups:

1. A large-scale accumulation in the root system is characteristic of Ca, Al, Fe and Zn; their concentration in the underground fraction increases in response to the disease. Al and Fe concentrations increased in the leaves too.

2. The concentration of Mg and Mn is highest in the leaves. Compared with healthy trees, their concentration remarkably decreases in the leaves of diseased trees. At the same time, however, a decrease in Mg concentration and an increase in Mn concentration occur in their root fractions.

3. A different concentration distribution is characteristic of potassium in healthy and diseased trees. While in healthy trees its concentration is highest in the leaves, in diseased trees most potassium is contained in the roots. In this fraction of diseased trees, K concentration is 8 times higher

Table 6
*Concentration ratios of different elements in the fractions
of examined trees*

		Ca/K	Ca/Al	Mg/Al
Healthy tree,	leaf	1.065	106.670	48.538
	root	11.018	27.719	4.986
	thin root	3.182	5.805	1.585
Diseased tree,	leaf	0.826	59.669	25.899
	root	1.343	15.676	2.262
	thin root	1.303	4.787	1.054

than in that of healthy ones, but their thin root fraction also contains this element at nearly 3 times higher concentration.

BARTUSKA and UNGAR (1980) found similar Al, Mg, Mn and Ca distribution in the leaf, trunk and root fractions of *Betula nigra* in the 3.2–4.7 soil pH interval, but they found a very large concentration of Al in the roots, ten times larger than in the soil. The Ca/Al and Mg/Al ratios are narrower in the fractions of diseased trees and they dramatically decrease in direction from the leaves to the thin root fraction as a result of the large-scale accumulation of Al in the roots and thin roots (Table 6).

A greater degree of accumulation of some of the studied elements in the root and thin root fractions of the diseased trees compared with those of the healthy ones as well as their transport from the roots (the site of intake) was to some extent hampered.

Changes in the thin roots and the mycorrhiza

There are several references in literature to the fact that damages leading to the death of trees may also originate from the rizosphere. The thin roots covered by large surface mycorrhiza play a crucial role in the water and nutrient supply of plants but they may transfer phytotoxic materials that occur in the soil or are deposited into the soil from external sources. The attack of phytopathogenes can be more intensive if the quantity of the symbiotic mycorrhiza fungi also playing a role in defense is decreased due to some factor (MARX 1973, WINGFIELD 1968, etc.). Therefore, we examined comparatively the thin roots and their mycorrhiza of healthy and diseased oaks.

In order to characterize the thin roots (diameter ≤ 1 mm) of healthy and diseased trees, the length of roots and the total length of lateral roots was measured, while the number of root tips and quantity of active and passive

Table 7*The characteristics of thin roots of healthy and diseased trees (June, 1983)*

Sample	Length of thin roots (cm)		Number of root tips		Quantity of mycorrhiza		Quantity of active mycorrhiza	
	1.	2.	1.	2.	1.	2.	1.	2.
Lökbérc								
healthy	39.8	414.5	117.7	1219.7	94.7	986.7	35.0	373.2
diseased	19.0	116.9	53.7	333.8	37.0	222.4	9.7	56.9
Síkfőkút								
healthy	30.9	189.2	95.0	575.9	77.7	470.5	24.6	149.0
diseased	27.2	148.3	58.0	318.1	41.0	224.2	10.0	53.9

Quantities under (1.) for root segment (5 cm), the values under (2.) for 1000 cm³ of soil.

mycorrhiza were also studied. Active and passive mycorrhizae were separated according to HARVEY et al. (1976). Root samples for these investigations were taken from two decaying oak forest stands in the Bükk Mountains (Síkfőkút, Lökbérc). From each place three healthy and three diseased trees were sampled. From under the sample trees, 10×10×20 cm soil monoliths were taken in three radial directions at every 20 centimeters. After thorough washing, 10 5 cm long segments of 1 mm diameter were cut from the root samples from each tree and their quantitative parameters were measured. The results were expressed for the 5 cm long segments and also for 1000 cm³ of soil (FOGEL 1980, MAJŠTRIK 1975). Table 7 show that the above quantitative parameters differ markedly between healthy and diseased trees. The total length of thin roots of healthy trees is greater both for 5 cm segment and for the 1000 cm³

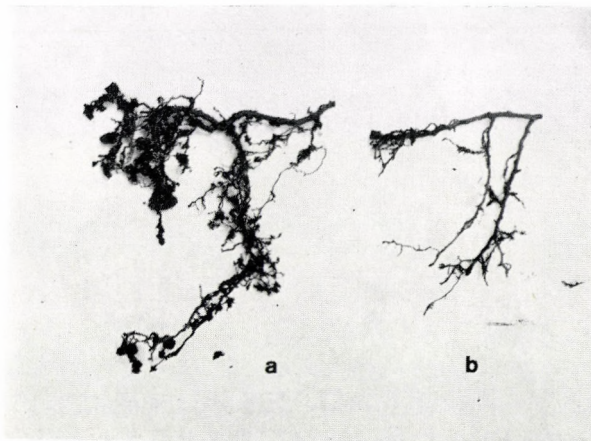


Fig. 1. Thin roots of healthy (a) and diseased (b) sessile oaks from the soil layer of 25 cm

soil volume compared with the corresponding values of diseased trees. This holds good for both sample areas, though the difference in Lökbérc samples was more expressed. Here, the total length of the thin roots of healthy trees was 414.5 cm in 1000 cm³ soil, whereas in decaying trees it was 116.9 cm. The above difference is adequately rendered by Fig. 1 which presents a root segment both from a healthy and a diseased tree. The thin roots of decaying trees had significantly fewer side-roots, fewer primary and secondary roots started from the 5 cm segment compared with that of healthy trees. That is why the system of thin roots of the diseased trees are less dense but lanker. The primary and secondary side-root of thin roots often break off in the case of decaying trees and circular wounds are left behind.

There is also a difference between healthy and decaying trees with respect to the number of root tips and the quantity of active and passive mycorrhiza. Thus, in the Lökbérc sample area there were 1220 root tips found in 1000 cm³ soil around healthy trees, while there were only 334 root tips in decaying trees. According to our findings, 80.6% (Lökbérc) and 82.7% (Síkfőkút) of the root tips of healthy trees were covered by mycorrhiza (both active and passive). The diseased sample trees can be characterized by lower mycorrhiza density (67.6% in Lökbérc and 70.9% in Síkfőkút). In addition, decaying trees have a lower ratio of active mycorrhiza. In healthy trees 37.5% (Lökbérc) and 32.2% (Síkfőkút) of the root tips with mycorrhiza were active,

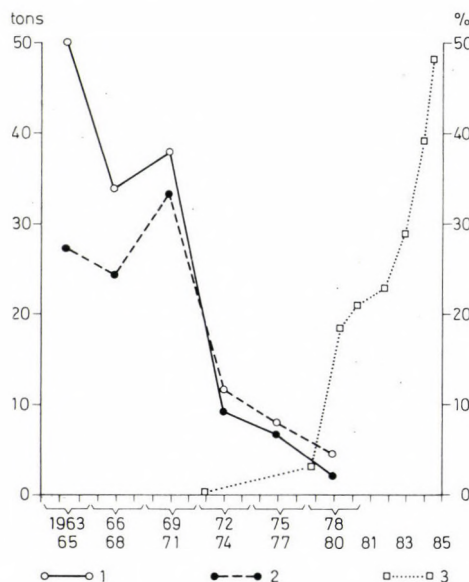


Fig. 2. Quantities of mycorrhiza fungi grown in natural conditions and brought to Budapest markets (3-year averages in tons) and the scale of tree decay in the Síkfőkút sample area (%) (data from KONECSNI and JAKUCS)

1 = *Boletus edulis*, 2 = *Cantharellus cibarius*, 3 = deceased sessile oaks

while in diseased trees only 24 to 26%. Our results correspond with studies carried out on other species by BLASCHKE (1981), HÜTTERMAN (1983), GEHRMAN, ULRICH (1983), ULRICH (1983), and VOGELMAN (1982), according to which the thin roots of sick trees are damaged, their quantity decreases and the symbiotic mycorrhiza relationship is disrupted.

Also striking is the phenomenon that exactly the fructification of symbiotic mushrooms living in protocoooperational or mutualist relationship with tree roots has radically decreased in the Hungarian forests in the past 10 years. The mycelia of these fungi may closely associate — especially in hot and dry periods — with the thin roots of trees resulting in a three to fourfold enlargement of the water and nutrient absorbing surface of the tree. In the case of saprophytic mushrooms (growing on forest litter) no decrease in fructification could be observed yet. Figure 2 shows the quantities of the edible mushrooms *Boletus edulis* and *Cantharellus cibarius* collected in forests and brought to the Budapest markets up to 1980 (KONECSNI 1982) and a comparative trend of oak decay in our research area. A similar disappearance of mushrooms has been reported in some other countries in Europe (WINTERHOFF, KRIEGLSTEINER 1984, GULDEN, HOILAND 1985).

The obstruction of trachea

The sapwood in the trunk cross-section of decaying or dead sessile oaks is quite visible discoloured. With the use of a strong magnifying glass it is easily noticeable that the water carrying vessels, the trachea, are partially or fully blocked.

Researchers who have regarded large-scale forest decay in the recent years as an epidemic caused primarily by a pathogenic fungus (tracheomycosis) are also familiar with the phenomenon of trachea obstruction. In their view, trees affected by mycotic infections defend themselves by blocking their tracheae with diverse products in order to prevent pathogenic fungi from spreading all over the vessel system with the flow of water. The excreted gel-like materials, bubbles and tyloses, however, simultaneously block the flow of water too in the sapwood consequently the leaves and the tree may even die (SHIGO and MARX 1977, SHIGO 1979, PEARCE and RUTHERFORD 1981, SAVVIN 1981, etc.).

In the course of research on the decay of oaks in Hungary, we have found tracheae blocked by different materials in a great number of trunk cross-sections. In order to learn more about their significance, the following examinations were carried out.

From the trunks of 5 healthy, 5 decaying and 5 dead trees in the Sikkókút project area trunk cross-sections were cut at 1.3 m above ground. The

surfaces of the slices were cut smooth with a microtom. Then the tracheae in the sapwood adjacent to the bark cca. 150–400 tracheae in one tree were examined under a stereo microscope. 1063 tracheae were counted and evaluated in the 5 healthy trees, 1262 in the decaying 5 trees and 917 in the dead 5 trees (a total of 3242 tracheae cross-sections).

The stereo microscope showed perfectly the empty (that is, water and nutrient permeable) tracheae and these blocked by different materials (see Plate II). Most of the blocked tracheae were filled with tyloses viscous gels, colloids and acellular bubbles (the latter being comparable to honeycombs filled with honey). In dead trees, tracheae were occasionally filled entirely with an impermeable mass of mycelia.

Our findings were summed up in Table 8. The mean values show that there are relatively few blocked tracheae in the healthy trees and there are about twice as many in the decaying trees. In the dead trees, the percentage of unblocked tracheae is only 10 to 20% at best. Calculating the results with variance analysis the differences are acceptably significant.

These investigations support the idea that the stoppage disrupt the water and nutrient transport in the trees and that it is a total blocking of water and nutrient flow that results in the death of the tree.

However, the question often discussed in the literature arises whether the obstruction of tracheae occurs owing to the tree's defense against tracheo-

Table 8

*The percentages of trachea stopped
and the comparison of means*

Tree repetition	Healthy	Diseased	Dead
1	7.8	17.6	74.4
2	17.7	36.3	97.5
3	18.3	24.8	92.5
4	20.5	29.8	81.0
5	17.3	47.7	97.1
$\bar{x}$	16.3	31.2	88.6

	Healthy	Diseased	Dead
Healthy	—	*	***
Diseased	14.9	—	***
Dead	72.3	57.4	—

* $\text{LSD}_{5\%} = 12.7\%$

** $\text{LSD}_{1\%} = 17.8\%$

*** $\text{LSD}_{0.1\%} = 25.2\%$

mycotic infections or it is a results of the decreasing water supply itself. If the trachea cross-sections in the sapwood are examined moving from the bark towards the heartwood, it becomes obvious that the tracheae that became part of the heartwood in the course of the previous years are filled with similar materials in healthy trees just as in decaying or dead trees.

Before shedding their leaves in the autumn, deciduous trees of the temperate zone are not capable of preventing the occurrence of embolisms in the water column caused by the negative pressure created by transpiration. So, the innermost parts of the sapwood are blocked permanently (that is, sapwood becomes heartwood). We can assume that a completely analogous process takes place in the tracheae of the sapwood in the course of oak decay. That is water supply may be interrupted and air bubbles may form not as a defense against pathogenes but because of a damage of the water and nutrient absorbing roots. In defense against the spreading of air bubbles, the trees block the tracheae at the beginning of the vegetation period or in summer.

A hiatus in the water column is such a damage that causes the water and nutrient circulation of the tree to get into stress. In situations like the sudden increase in transpiration (e.g., in the heat of summer) the formation of air bubbles and the obstruction of tracheae by tyloses, gels etc.) may take place with increasing frequency due to the negative transpiration pressure.

If the tracheae of the sapwood are still partially permeable, the agony of the tree may take a longer time. A few water sprouts may appear here and there, but the tree is incapable of regeneration. Blocking materials are not produced in the dead tree, only fungi and other microorganisms may propagate secondarily in the empty tracheae starting the process of decomposing the organic matter.

The above examinations also prove that the damage is started in the soil-root relationship where the primary obstruction of water and nutrient intake occurs. The obstruction phenomenon taking place in the tracheae of the sapwood is the defense of the tree against embolism forming in the water-carrying elements.

An ecological interpretation of forest degradation

The possible ways leading to the decay of trees in forests are presented in a complex ecological diagram (Fig. 3). Elemental calamities (e.g. lightning, fire, frost, storm, etc.) or death resulting from competition due to natural aging or diseases have been omitted. In the diagram the milieu factors which qualify as effective are unified with those of the tolerance-spectrum of trees qualified as receptive. We have indicated also the forms of human activity inducing unfavorable effects environmental pollution, incorrect forestry. On the

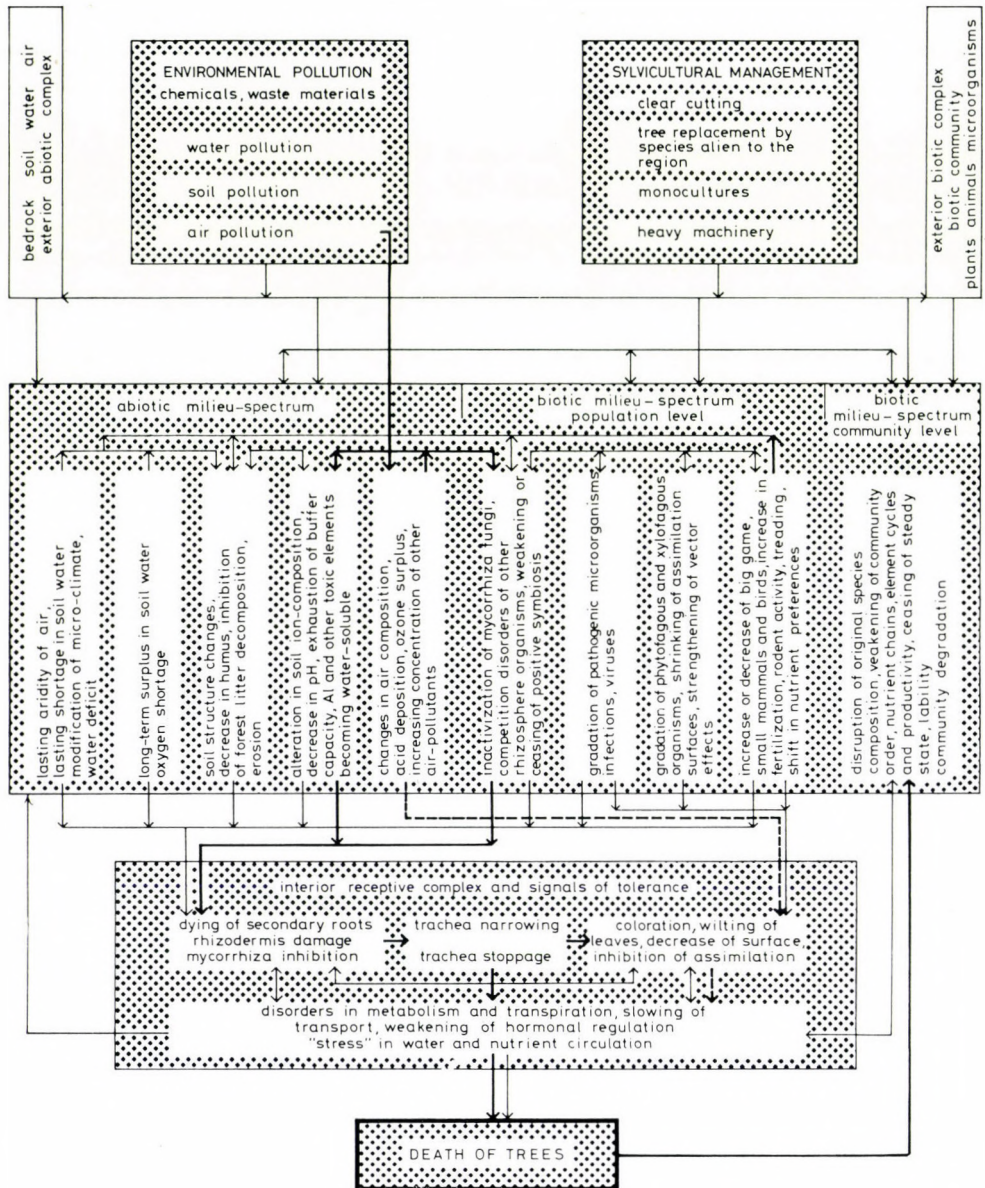


Fig. 3. An Ecological Interpretation of Decay of Forest Trees with Respect to the Relationship between the Effective Milieu-Spectrum (Damaging Effects) and the Receptive Tolerance-Spectrum (Damages Caused) (JAKUCS 1985)

- > dominant system of interdependences in present-day forest decline (in Hungary)
- - -> direct effects of air pollution
- > other influences which, depending on place and time-promote tree decline, or, occasionally, become a primary cause

basis of this diagram, one can pinpoint, as a working hypothesis, some possible primary effects leading to tree or forest decay in a given area and critical points of the presumable effect-reception links can be experimentally identified. Theoretically, this ecological diagram seems to be applicable in any part of the world and — perhaps with minor modifications — it can be used to point out links leading to the death of any living organisms (not only trees).

In principle, any one of the factors qualified as effective in the diagram can destroy a tree by itself. For example, pathogenic microorganisms or phytophagous caterpillars can reduce the leaf area of a tree to a degree that a water and nutrient "stress" is brought about. Similar damages may be caused by processes deriving for example from incorrect forestry, which drastically alters the naturally regulated composition of living populations in the forest.

All these effective and receptive links and the damages they cause to trees (extending over smaller or larger areas) have long been well known. The present-day cases of forest degradation have an essential new feature in common: they emerge simultaneously all over the northern hemisphere with nearly the same symptoms involving vast areas and gathering speed. That is why attention of researchers exploring the relevant factors was attracted to environmental and air pollution inflicting vast territories with increasing speed. (On our diagram causal processes regarded as effective are marked by thick continuous and broken lines.)

It has become common knowledge that large-scale industrialization and an increasing pace of burning fossile fuels resulted in an increasing emission of sulphur and nitrogen oxides into the atmosphere. These are oxidized into sulphuric and nitric acids already in the air while sometimes they travel thousands of kilometers away from the spot of emission. Of the materials transported through the atmosphere from far away or close by and entering the trees in forests and their soils through wet or dry deposition, SO_2 , NO_x , and Cl_2 (and also some heavy metals and artificial chemicals having, so far never circulated in the ecological systems) trigger off complicated and mostly accumulative processes in the dynamically balanced element circulation which has been under ecological regulation for ages.

Air pollution — especially in the vicinity of emission sources — can be directly damaging to living organisms such as trees. For example, entering the stomates it can set off auto-oxidation processes in the course of which free radical reactions may emerge. In the end, these may oxidate, e.g., the unsaturated fatty acids of cell membranes. Membrane permeability altered in this way may disturb the regulation of great many physiological functions (e.g., assimilation, dissimilation, water and nutrient circulation, etc.). Mostly in evergreen (coniferous) trees direct effects through several years accumulating these phenomena of radical pathology (PÓLYA 1979, MATKOVICS-SZÖLLÖSY

1976, SHIMAZAKI et al. 1980, TANAKA—SUGAHARA 1980, LIZADA—YANG 1981, SCHLEE—KOCH 1982) may lead to a decrease in the production or to death (SCHÜTT 1982, MATERNA—JANČARIK 1982, BAUCH 1983, WENTZEL 1983). Conversely the annual new foliage of deciduous trees receives the direct acidifying effects with a "tabula rasa". Detrimental effects of ozone can also be grouped with direct effects.

Although the direct damages are of grave economic and ecological consequences, a more decisive role is attributed to the indirect effects of the so called acid rains (this notion also includes compounds received by way of dry deposition), which may destabilize a whole population, community (forest) or the entirety or parts of the biosphere.

In the course of these indirect influences, the hydrogen ions in the dilute acidic solution entering the soil are exchanged other sorts of cations, a phenomenon which may lead mainly to the exclusion of some principal nutrient elements as Ca, Mg and K. Depending on the genetic soil conditions, the soil is acidifying quickly or more slowly. The buffer capacity of the soil is disrupted, the solubility and mobility of certain toxic metals (Mn, Cu, Zn, Cd, Al) and thus their availability for living organisms dramatically increases. Partly the acids themselves destroy the water and nutrient absorbing secondary and thin roots of trees, partly the toxic heavy metals and Al ions enter the organism (ULRICH et al. 1979, ULRICH 1983). The quick acidification of the soil inactivates or stops the mycorrhiza relationships. In the meanwhile, other organisms of the rhizosphere are also damaged and thus the processes of mineralization and decomposition are also hampered.

Especially in the long and hot vegetation periods, the diminishing tree roots cannot get into deeper parts of the soil while the transpirational demand of the tree is growing. Since there is a shortage of available water, the vitality of the organisms falls back. After all, the water and nutrient absorption and transport is hampered in the roots. Due to the negative pressure caused by transpiration, water columns may break and air blocks may form. The organism reacts to these effects and to the appearance of toxic materials by stopping up its water carrying vessels (tracheae) but, by doing so, it rules out the possibility of starting circulation again.

In this state of water and nutrient "stress" (depressed vitality) other possibly effective factors (e.g. pathogenes or parasites of weakness) launch a secondary attack on the weakened tree more easily enhancing the tree's state of "stress" and its death may come soon, sometimes with spectacular speed.

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BOOK REVIEWS

Editor: G. FEKETE

D. B. ROODYN (ed.): Subcellular Biochemistry. Vol. 10. Plenum Press, New York, 1984

The tenth volume of the Subcellular Biochemistry successfully covers a wide range of biological topics, all of which can be described in terms of fundamental molecular biology. The topics covered include structural, chemical and functional analysis of various cell membranes, nucleocytoplasmic RNA transport, the role of myo-inositolphosphate in cellular metabolism, cytoskeletal changes during fertilization and evolutionary aspects of human chromosomes.

The plastid envelope membranes provide a flexible boundary between the plastid and the surrounding cytosol. In Chapter 1. *The Plastid Envelope Membranes: Their Structure, Composition, and Role in Chloroplast Biogenesis*. R. DOUCE, M. A. BLOCK, and J. JOYARD survey the assembly of the envelope membrane and the turnover of various lipid and protein constituents of this membrane entity. The biogenesis of the plastid envelope membranes is also discussed from an operational point of view.

G. A. PESCHEK deals with the structural and functional aspects of the respiratory electron transport in various cyanobacteria (Blue-Green Algae). (*Structure and Function of Respiratory Membranes in Cyanobacteria*.) Detailed morphological analysis, comments on the problems of isolating membranes from cyanobacteria, kinetics of respiratory electron-transport, oxidative phosphorylation and bioenergetic regulation are the topics of this very interesting chapter.

By describing the major advances that have been made in this field, R. SETANDREU, E. HERRERO, J. P. MARTINEZ-GRACIA and G. LARRIBA help us to further understand the structure and biogenesis of the yeast cell wall. Processes, such as the genesis and location of enzymic complexes responsible for polymer formation, mechanism of polymerisation, secretion and interaction of polymers are discussed in relation to the formation of the yeast cell wall.

Sacharomyces cerevisiae has been used as the main object of this study, but the characteristics of other yeast cells are also described in a comprehensive way. (*Biogenesis of the Yeast Cell Wall*.)

In Chapter 4, a new interesting metabolic cycle is proposed to enlighten the role of a less known phosphateester, the myo-inositol phosphate in cell metabolism. (*Myo-Inositol Phosphates and Their Role in Cellular Metabolism: A proposed Cycle Involving Glucose-6-Phosphate and myo-Inositol Phosphates*.) In this review, B. B. BISWAS, B. GHOSH and A. L. MAJUMDER specifically stress the metabolism of myo-inositol phosphates, the regulation of their synthesis and degradation in both plant and animal cells. The authors are particularly interested in studying the role of their newly proposed metabolic cycle during germination and formation of seeds.

A general view of the most interesting advances that have been made in current understanding of nucleocytoplasmic RNA transport is also given in this volume. (*Nucleocytoplasmic RNA Transport*.) In P. S. AGUTER's excellent review, the biological significance of RNA transport, as well as related experimental procedures are discussed in order to create useful picture of the mechanism and regulation of this complex series of events.

In Chapter 6 (*The Supramolecular Organisation of the Cytoskeleton during Fertilization*), G. SCHATTEEN gives an excellent overview of the structural and biochemical changes that occur during cytoskeletal formation. In this chapter, fertilization is used as a model for the study of cellular motility, since the beating of the sperm tail is a good example of the sliding of adjacent microtubules. In Chapter 7, H. N. SEUÁÑEZ discusses some evolutionary aspects of the human karyotype, contributing to a clearer understanding of how our chromosomes have been altered and transmitted as far as their phylogeny may be traced into the past. (*Evolutionary Aspects of Human Chromosomes*.)

As a series, Subcellular Biochemistry has long established the highest standards in its multidisciplinary approach to this vitally important subject. Volume 10 includes an extensive book notices section that gives detailed accounts of numerous new books in biochemistry and cell biology. It is an essential reference work for biochemists and cell biologists.

ANNA H. NAGY

W. WIESSNER, D. G. ROBINSON, R. C. STARR (eds): *Compartments in Algal Cells and their Interaction*. Springer Verlag, Berlin-Heidelberg-New York-Tokyo. 1984. 241 pp.

The ultrastructure of eukaryotic cells is characterized by compartmentation, e.g., by the existence of special areas surrounded by membranes. These areas have special functions in cell metabolism and are partially endowed with their own genetic apparatus which is different from the nuclear one. The successful functioning of the cells depends on a highly organized cooperation and interaction between these compartments.

In plant cells we deal with a number of systems subjected to a pronounced compartmentation. The first is the eukaryote-characteristic, nucleocytosol compartment which is divided by the nuclear envelope separating the nucleus and the cytosol. In addition to the nucleocytosol compartment, plant cells dispose of the chloroplasts and also of mitochondria as well as a number of other organelles: flagellae, GOLGI apparatus, different vacuoles and microbodies.

In the book entitled "Compartment in Algal Cells and Their Interaction" the cooperation between the nucleus and the cytoplasm and between different organelles on structural and functional levels has been illustrated.

The book collects the materials of a symposium (Göttingen, September, 1983) entitled as above, presenting the proceedings of the meeting and contains all the papers presented.

The first article "The cytological view-point of functional compartmentation" gives an overall picture of cell compartmentation, the cytological definition of a compartment and connection between compartmentation and morphogenesis.

In four articles ("Organization and capacity of the chloroplast genome in algae", "Structure and expression of chloroplast and nuclear genes in *Chlamydomonas reinhardtii*", "Interactions between compartments in *Acetabularia* during gene expression" and "Aspects of translational coordination during chloroplast development") the molecular organization, expression and interaction of chloroplast and nuclear genomes in unicellular algae are presented. These papers combine the classical genetic studies with molecular approaches.

In the article "Control of genes expression during the early phase of chloroplast development" an additional control mechanism in chloroplast development is presented. An early light-induced protein as a nuclear coded signal plays a role in the expression of chloroplast genes.

In two articles ("Genom and gene organization of the cyanelle DNA from *Cyanophora paradoxa* in relation to the common organization in chloroplast" and "The organelle versus endosymbiont problem of *Cyanophora paradoxa*") comparative analyses of cyanellar and chloroplast genom structure and gene organization are presented which help understand the plastic ancestry and give new concepts about how to trace plastid evolution.

From articles, the development of flagellar apparatus, its interactions with cell organelles as well as control system of its regeneration and shortening in green algae, are presented.

The discussion of other organelles, the studies of structure, function and interaction of the contractile vacuole complexes, the extra-organelle cytoplasm of resting cells for concentration of free Ca^{2+} , the mitochondria, GOLGI apparatus, microbodies and also different vacuoles, comprise the main part in the book.

The last four articles deal with the cytological aspects of symbiosis between eukaryotic unicellular organisms and blue-green prokaryotic photosynthesizing endosymbionts, with main hypotheses trying to explain the development of the eukaryotic cell. It can be concluded that symbiosis formation is still an important, powerful factor in evolution.

At the end of the book, the formation and function of heterocysts as clear-cut examples of intercellular compartmentation are discussed.

I. GYURJÁN

J. I. GOLDSTEIN, D. E. NEWBURY, P. ECHLIN, D. C. JOY, CH. FIORI, E. LIFSHIN: *Scanning Electron Microscopy and X-Ray Microanalysis. A Text for Biologists, Materials Scientists, and Geologists*. Plenum Press, New York and London, 1981. ISBN 0-306-40768-X, pp. xiii + 673, with numerous tables and figures

The volume is based on the lectures presented at the SEM-X-ray course held annually at Lehigh University (U.S.A.). Its expressed aim is to provide the student with the fundamentals of the topic. At this point the authors should not be taken very seriously — the book offers much more than any other multi-authored textbook in this field. All the core and bore of a textbook is there, however, as the sub-title indicates, biologists are also catered for.

The first eight chapters (over four hundred pages) are devoted to a material which many biologically-minded people usually evade if possible, like the theoretical aspects of electron optics, radiation sciences, signal processing, not to mention the frightening amount of calculations involved. However, if hardships of life would force someone to face such problems the help is at hand here, often with worked examples or with the result of one particular solution at least.

Chapters 10–13 should be thoroughly understood by every biologist even contemplating to turn to a specialist to have some SEM and/or X-ray microanalysis work performed. Curiously enough, this is also the part where the seasoned professional will find many useful tricks of the trade, especially in the field of the all-important specimen preparation.

To sum up, for many biologists the book can be a textbook and a handbook as well. At this juncture it must be mentioned that the authors intend to elaborate on topics not covered in this book in a companion volume. As the tentative title suggests (*Advanced Topics in Scanning Electron Microscopy and Microanalysis*) a treatise on present trends such as data and image processing with computers, etc. is yet to come. Undoubtedly, I am not the only person looking forward to its arrival.

T. PÁTKAI

R. R. HENKE, K. W. HUGHES, M. J. CONSTANTIN and A. HOLLENDER (eds): *Tissue Culture in Forestry and Agriculture*. Plenum Press, New York and London, 1985, 390 pp.

Biotechnology is a nowadays frequently heard term, because it has become one of the most important lines and fields of the biological research. And that is only too understandable, since we are confronted with a pressing problem of these days — or rather more of our future: the need of satisfying the increased food- and energy requirements of the ever growing population. The fulfilment of these demands might be achieved through the knowledge acquired of the rules of biology, partly by increasing the quantity and quality of organic matters of plant origin with the application of biotechnologies. The possibilities of the biotechnology and the related prognoses are disbelieved by some, while others have blind faith in them. It is therefore important to know whether this almost "fashionable" conception covers realities or will shipwreck the biological research. For this very reason the works and reports published by competent authors on the present stage and prospective practical results of the tissue culture technology are of great value. The book in question is one of them.

The book was published by the Council for Research Planning in Biological Sciences, Inc. (Washington D. C.) as Vol. 32 of the series *Basic Life Sciences* (General Editor: A. HOLLAENDER), with the usual careful get-up of the Plenum Press. The work contains the material of the Symposium on Propagation of Higher Plants Through Plant Tissue Culture III held at the University of Tennessee (Knoxville) between 9 and 13 September 1984. This symposium as well as the two previous ones (1978, 1980) and most of the subjects were patronized or even fully financed by the USA Department of Agriculture Forest Service (USDA), Department of Energy (DOE) and the National Science Foundation (NSF), which shows the interest of management organs for the practice of cultivation.

The work is composed of two parts. The seven chapters of the largest first part contain lectures on the general principles, based and applied research of plant tissue cultures delivered by known authors or collectives of the special field on the basis of their investigations with various plant species. The smaller part of the book is formed by the contents of the 49 posters presented.

Very interesting new aspects of research are thrown up in Chapter 1 which calls attention to the stress of plant that has so far been neglected or at least overlooked. Namely, it may explain biochemical phenomena that have been incomprehensible up to this day.

Chapter 2 discusses the phenomena of regeneration. One of the three papers claims that today only the morphology of the regeneration process is known, and its exact inductors are only searched after. The other two publications point out that e.g. in the case of Grami-

neae from 13 species intact plants have been regenerated by somatic embryogenesis, though the microscope and electron microscope ontogeny of their somatic embryogenesis is not yet fully known.

In Chapter 3 papers on development mechanisms are found. The authors demonstrate the stages of embryogenesis, the inducers of them, the genetic, physiological and morphological effects of certain biochemical factors on the example of alfalfa, tomato and soybean.

Chapter 4 surveys the application of development systems in two papers. One of them shows the somatic embryogenesis as applied to clone propagation on the example of *Daucus* (carrot), taking into consideration the size, weight, treatment, etc. of the embryoids. The other publication discusses the possibility, advantages and results of using continuously producing "bioreactor" in the mass reproduction of plants. Beside the techniques and apparatus (fermentor, phytostat, etc.) used so far successfully for mass reproduction in 43 genera of plants, this apparatus will certainly be important in biotechnological experiments with plants.

In Chapter 5 three publications analyse the genetic variability and stability, taking into consideration the initial material of plant tissue cultures (inocula), the fact and circumstances of culturing, and the expected results. Some of the authors mainly deal with the problem of male sterility, while others with the question of symbiotic nitrogen fixation, taking into account the possibility of the so-called "somaclonal" variation of plants.

Chapter 6 contains four papers on the reproduction of woody plants in tissue culture. From about 51 genera commercially important tree species, and from 16 genera mostly tropical fruit-bearing woody plants have so far been reproduced with tissue culture methods. By vegetative microreproduction good results were obtained with conifers (*Pinus*, *Cupressus*) and coffee-shrubs (*Coffea*) too. It is the authors' general opinion that with the tissue cultures of woody plants the optimum inocula, the technique of culturing and the economic efficiency represent the greatest problem, that is — among others — the reason why the exact, reproducible results are relatively few. Still, the results attained so far make it likely that artificial afforestation by tissue culture will give twice as many plants in the tropics than in the temperate zone, and the efficiency of "clone afforestation" will surpass that of a natural reforestation.

In Chapter 7 four papers deal with the improvement of forest through tissue cultures. A survey is given of the improvement and widening of the genetic material of forest trees by tissue cultures, and of the maintenance of their gene stock; of certain tree species made resistant and of their vegetative reproduction, as well as of the general principles of developing resistance. A group of authors gives comparative data of the laboratory, greenhouse and outdoor parameters of some tree species. A paper discusses the destruction of tropical forests due to contamination, its effects, and the future role of tissue cultures in this respect.

In the smaller — about a quarter — part of the book the contents of the exhibited posters are found. The short summaries offer a clear view of the possibility and present stage of the vegetative micropropagation in tissue cultures of some 50 plant species.

To sum it up, the book gives up-to-date information of the principles of plant tissue culture, and of its application to higher plants by means of technological manipulation. Its realistic evaluation of the possibilities of biotechnology emphasizes that while the exact inducers of plant development are hardly known as yet, vegetative propagation through clones is already a quick and reliable method by which both genetic stability and variability can be achieved. The application of the "bioreactor", with the stress effects which act on the plant taken into account may help in attaining practical results. A further merit of the book is that it calls attention to the reproducibility of woody species by tissue cultures, which opens up new vistas concerning mass propagation of woody (and forest) plants, and thereby in nature conservation as well.

The book is completed with the list of those taking part at the symposium (c. 300 persons), subject and name indexes, and with the usual introductory parts (dedication, acknowledgements, preface). On the basis of what have been told the work is recommended to botanists, horticulturists, agronomists and forester beyond those directly engaged in tissue culture work.

M. MARÓTI

JENNINGS, D. H. and RAYNER, A. D. N. (eds): The Ecology and Physiology of the Fungal Mycelium. Symposium of the British Mycological Society held at Bath University 11–15 April 1983. Cambridge University Press, 563 pp., 1984

The book, the 8th volume of the Symposium series published by the British Mycological Society, contains the material of the symposium held at Bath University on April

11–15, 1983. The volume discusses the ecology, physiology and genetics of fungal hyphae in a uniform framework thereby offering an opportunity to acquire a deeper knowledge of the mycelial form of life. The book consists of 23 chapters written by mycologists, ecologists and geneticists of name.

In the first chapter GREGORY calls attention to the importance of studying the vegetative mycelium, and to the regrettable fact that there is a considerable backlog in this field as proved if only by the very succinct treatment of the question in most hand-books on mycology. The chapter gives then a historical survey of the progress of knowledge concerning the vegetative mycelium, the manifold function of the fungal mycelium, pointing out that the vegetative mycelium is the most important part of the mushroom.

In Chapters 2 and 3 TRINCI and BUTLER give an excellent view of the germination of fungal spores, the growth rate of germ-tube and vegetative hyphae, of their types of branching, and of the mechanism of thallus formation.

Of the sexual hypha fusion NGUYEN and NIEDERPRUEM, whereas of the vegetative hypha fusion AYLMOORE and TODD, supply valuable information (Chapters 4 and 5). The latter chapter is the first to complete the information with both light- and electron microscopic photographs.

The relationship between the secondary metabolism and the morphogenesis of the vegetative mycelium is discussed by MOSS (Chapter 6).

The mechanism of water flow within the mycelium is described by JENNINGS in Chapter 7.

In connection with the morphogenesis of *Serpula lacrimans*, WATKINSON points out that the nitrogen content of the nutrient influences the growth rate of the thallus, the extent of cellulose decomposition, and the amount and differentiation level of the mycelium formed (Chapter 8).

Attention is called to the distribution, role and importance of hypha bundles in decomposing *Basidiomycetes* found in the leaf-litter and humus layer of deciduous forests in the temperate zone, a rather neglected area of research, — by THOMPSON (Chapter 9).

When explaining the mycorrhizal relations, READ emphasizes that they are important to know if the functional and regulatory processes of the ecosystem are to be cleared up (Chapter 10).

FRANKLAND's case study deals with the autoecology of *Mycena galopus*, a litter-decomposing *Basidiomyceta* (Chapter 11).

The relationship between the distribution of *Basidiomycetes* mycelia in the deciduous forests of the temperate zone and the abiotic factors of the micro-environment is the subject of BODDY's paper (Chapter 12).

In Chapter 13, RAUDASKOSKI and SALONEN discuss the relationship between vegetative mycelial development and basidial fruiting body formation. In Chapter 14, LYSEK speaks of the physiological and ecological importance of rhythmic growth.

ESSER and his collaborators point out that the senescence of *Podospora anserina* can be induced with mitochondrial plasmid, and consider its possible importance in genetic engineering (Chapter 15).

In connection with the mycelium of *Endothia parasitica*, a fungal pathogen of plants, ANAGNOSTAKIS emphasizes the role of nuclear and cytoplasmic genes in determining the morphology and virulence of the fungus (Chapter 16).

ANDERSON deals with the variations observed in *Rhizoctonia solani* and with the importance of heterokaryosis (Chapter 17).

In Chapter 18, RAYNER and WEBBER survey the types of interspecific mycelial interactions.

Chapter 19 contains an interesting paper by NORDBRING-HERTZ on 3 nematophagous fungi in which the importance of the lectin-carbon dioxide relation is enlightened.

The interspecific responses of mycelia in the *Aspergillus* species and the mitochondrial inheritance are dealt with by CROFT and DALES in Chapter 20.

The last three chapters discuss the intraspecific interactions; valuable data also useful for the practice are presented by BRASIER on *Ceratocystis ulmi* (Chapter 21) and by ANAGNOSTAKIS on *Endothia parasitica* (Chapter 22). RAYNER et al. (Chapter 23) deal with the questions related to the somatic incompatibility, physiology and ecology of the higher wood-decomposing fungi.

The rich material of figures and photographs help a better understanding of the text. Each chapter is followed by a detailed list of references that are useful for all who want to get a deeper insight into the topic.

J. A. TÓTH

KAROL STARMACH: *Chrysophyceae und Haptophyceae*, in: Ettl, H., Gerloff, J., Heynig, H., Mollenhauer, D. (red.): *Süßwasserflora von Mitteleuropa*. Band 1. G. Fischer Verlag, Jena. 1985. 515 pp.

The author of the latest volume of the series "Süßwasserflora von Mitteleuropa" is STARMACH, the internationally recognized expert on the subject. He is one of the editors and author of several volumes of the determination book series written on the aquatic flora of Poland (*Flora Ślaskowa* Polska). His book on the class of *Chrysophyceae* has run to two editions in Poland (1968, 1980).

The editors' preface is followed by a taxonomic key for 20 classes of algae from the *Cyanophyceae* to the *Cryptophyceae*. After each class the number of the relevant volume of the series is given in brackets. The taxonomic key compared to those in the previous volumes has changed, since the algae in them are placed in 13 classes, while in the new conception they belong to 20 classes.

After the author's preface a list of contents is given.

The first chapter of the book supplies general information characterizing the morphology and organization of the *Chrysophyceae* class. On the basis of electron microscope examinations is the submicroscopic structure of the cell made known. Of the processes of cell division and reproduction and the types of life cycle the author speaks in a concise manner. The morphological characteristics of the species in the class *Haptophyceae* are described likewise on the basis of EM studies. Then the reader is acquainted with the distribution and ecology of the *Chrysophyceae* species and with the proposed methods of examination. The last section of the chapter deals with the systematization of the two classes, development of their taxonomic arrangement, and lists the subclasses, orders and suborders.

On the basis of the classification a total of 972 species are described in the second chapter of the book:

Chrysophyceae

<i>Heterochrysophycidae</i>				
<i>Chromulinales</i>	50	genera	296	species
<i>Ochromonadales</i>	48	„	462	„
<i>Acontochrysophycidae</i>				
<i>Chrysarachniales</i>	2	„	4	„
<i>Stylococcales</i>	14	„	68	„
<i>Chrysosaccales</i>	4	„	7	„
<i>Phaeoplacales</i>	2	„	6	„
<i>Craspedomonadophycidae</i>				
<i>Monosigales</i>	16	„	88	„
<i>Haptophyceae</i>				
<i>Isochrisidales</i>	13	„	30	„
<i>Prymnesiales</i>	7	„	11	„

The description of the major characteristics of classes is followed by the taxonomic key for subclasses and orders. Within the orders taxonomic keys for the suborders, then for the families and genera are found. With each genus-key the author gives a drawing of a characteristic species whereby the taxonomic key is made vividly descriptive and exact determination easier. After the characterization of the genera the author lists in most cases the relevant literature increasing thereby the value and usefulness of the book. Within the genera taxonomic keys for an detailed descriptions of the species are given. The taxonomic key of species is based on electron microscope morphology. In several cases, e.g. with the species *Mallomonopsis*, *Mallomonas*, *Synura*, *Spiniferomonas*, the basis of exact identification is formed by the scales which are reliably examined only by electron microscope. Detailed morphological characterization of the species, information on their habitats, and a drawing (or even drawings) of each species make the work complete.

An appendix contains the morphological characters of *Chrysophyceae* cistae and a description of cistae in several genera.

The book is closed by a list of literature (486 works) and an index. The 1051 figures, including some EM photos, mean in fact more than 3000 drawings of algae.

Unfortunately, though it does not reduce the value of the work, the book was printed on a paper of inferior quality compared to the former volumes, and so the drawings do not reach the high typographical level that we got used to with the earlier volumes. And it would have

required only a bit of thoughtfulness to choose the same colour and quality of the jacket as for the volumes published in 1983.

The clear structure of Starmach's work, the detailed morphology, the precise descriptions of species and the enormous bulk of drawings resulted in a determination book that every specialist can reliably use. Apart from the algologists, the work is recommended to systematists, hydrobiologists, and to biologists engaged in water management. Besides, Starmach's book is indispensable in the university teaching.

K. T. KISS

JOANNA Z. KADUBOWSKA: Conjugatophyceae I. Chlorophyta VIII. Zygnemales, in: Ettl, H., Gerloff, J., Heynig, H., Mollenhauer, D. (red.): Süßwasserflora von Mitteleuropa. Band 16. G. Fischer Verlag, Jena. 1984. 532 pp.

A new volume has been added to the series "Süßwasserflora von Mitteleuropa". The author is KADUBOWSKA, an expert in the order of *Zygnemales* known all over the world, who in 1972 wrote a determination book on the family *Zygnemaceae* in the Polish series *Flora Slodkowodna Polski* (red. STARMACH and SIEMINSKA).

After the preface and the list of contents a taxonomic key to 13 classes of algae from *Cyanophyceae* to *Cryptophyceae* is given.

In the first chapter of the book we are acquainted with the major characteristics of the order of *Zygnemales*. The structure of plasmodesmae and cell-walls, the types of diagonal cell-walls, the cell-wall thickenings in the *Zygnemales* species, further the characteristic shapes of chromatophores in the different genera are described in detail. Concise information is supplied on the metagenesis characteristic of the order (*Lebenszyklus*). The author gives full description of the major types of conjugation, of ladder-, lateral and terminal conjugation, which are of decisive importance in identifying the species. In the section that deals with the generative cells we learn about the types of gametangium, the morphological features of conjugation channels, and about the different types of zygote. The general part of the book is closed with information on the occurrence and distribution of the *Zygnemales* species and with a description of the methods of collecting, propagating, examining and determining them.

The second, systematical chapter of the book begins with the taxonomic key of the 12 genera in the order of *Zygnemales*. Identification is based on the shape and number of chromatophores, number or absence of pyrenoids, the gametangium, the zygote, and on the shape and position of the conjugation channel.

Within the genera *Mougeotia*, *Zygnema* and *Spirogyra* species groups (Sektionen) are separated. After a general characterization of the genera the taxonomic key of species groups and species follows. Besides the key a detailed morphological description and drawings help in the exact identification of the species. Naturally, it is of the reproductive organs, pieces of plasmodesma in the state of conjugation and zygotes rather than of the habitus that drawings are found here in the first place, since they form the reliable basis of determination in the case of *Zygnemales* species. There are also data of occurrence for each species.

The most populous genera are: *Spirogyra* (381 species), *Mougeotia* (138 species) and *Zygnema* (137 species). In the other genera the number of species ranges from 1 to 43. The identification book describes a total of 784 species.

The book is made complete with a bibliography (227 works), an index and 798 figures.

Unfortunately, though it does not detract from the value of the work, the book appeared on a paper of poorer quality compared to the previous volumes, and the colour and quality of the jacket do not agree with those of the former volumes either. In the case of a series attention should have been paid to such particulars.

The logical structure of KADUBOWSKA's determination book, the exact descriptions of species, the morphological details and the rich material of drawings resulted in a work safely recommended to every algologist. Systematists, hydrobiologists and those working in the practice of water management can make good use of the book. Besides, the book can be used in university education and in all fields where the knowledge and exact identification of the species in the order of *Zygnemales* is important.

K. T. KISS

DAKOV, M. et al. (eds): Chervena kniga na N. R. Bulgariya. Tom. 1. Rasteniya (Red data book of the People's Republic of Bulgaria. Volume 1. Planta). Izdatelstvo na Bulgarskata Akademiya na Naukite, Sofiya 1984. 447 pp.

Two decades have elapsed since the IUCN recognizing the irreparable losses of gene reserves disappearing with the extinguished species started the series of Red Data Books. Since then many books have been published each presenting the rare plants and animals threatened to be eradicated in a country or continent. Bulgaria published the first volume of the red book planned to run to two volumes in the autumn of 1984.

The editorial board includes scientists of name such as the professors S. NEDIALKOV, I. BONDEV, B. BOTEV, M. MARINOV, Tz. PESHEV, V. VELCHEV. The members of the editorial board for the first volume on plants (V. VELCHEV, I. BONDEV, S. KOZHUHAROV, B. KUZMANOV, M. MARKOVA) co-ordinated the activity of a team of 34 authors in the course of writing up the subject.

In the book of large format 763 of the 3560 species of the vascular flora of Bulgaria are described. A particularly large number of species is found in it from the genera *Verbascum*, *Alchemilla*, *Centaurea*, *Viola* and *Silene*. Naturally, the number of species endemic in Bulgaria (124) and of those endemic in the Balkan Peninsula and also found in Bulgaria (105) is high. Through changes in the vegetation over the centuries many of the once frequent plants have become relics by now; of these 50 are included in the book.

The plants beginning with the *Lycopodiaceae* are grouped by the family and within it in a generic order. On each page two species are characterized. The authors with a praiseworthy consistency give the most important particulars in 9 groups of information, each containing 15–30 lines on an average.

Under the headword biological type the plants are placed in one of the following groups: tree, shrub, sub-shrub, evergreen, annual, biennial, perennial herbaceous plants. Within the concept of threatened position 3 categories are set up: extinct (31 species), disappearing (158 species), rare (574 species). The geographical distribution is described in detail. The Bulgarian area of each species is shown on a separate map. The ecological characterization of habitats and data concerning the populations are given under the same headword. Beside the period of flowering and fruit ripening the generative and vegetative reproduction and the possibility and way of regeneration are also discussed.

Remarks on the factors influencing adversely or threatening the survival of plants and on the measures taken to protect the species are found under 3 headwords. They name the nature conservation areas where the populations of the different species can safely develop and survive due to a strict prohibition on admittance. The reader is also informed of the plants to be placed in the botanical garden of the Bulgarian Academy of Sciences in Sofia and of the seeds to be collected for the seed bank in the course of the gene preservation work already in process. The characterizations are completed by literary references.

The description of taxonomic characters concerning the species was no task of the book. The plants can be identified by 82×82 mm pictures equally given for each species, of which 155 are coloured the others black-and-white. The pictures often contain drawings of characteristic details, e.g. the spikelets of grasses, the urticula of sedges, the involucre bracts of centaurea or other plant parts are shown beside the pictures of habit. The artistic paintings and drawings are the works of D. VLAEV. In each picture a coloured pictogram indicates the degree of danger threatening the plant.

The uniform size of the pictures and the absence of descriptions prevent, however, the comparison of the measurements of plants; with a few words, or indication of scale, or with a simple pictogram it could have been made possible.

The style of the book is simple, clear, easy to read, obviously meant not only for specialists but for everyone fond of nature. Researchers and tourists, teachers and students may equally profit by reading it.

At the end of the volume 56 coloured photos delight the eye. The use of coated paper would have greatly increase the value of the photos.

Two maps make the book complete (works by V. VELEV). The first represents the floristic division of Bulgaria. The other is no less interesting: it contains the list and shows the locations of 180 nature conservation areas in Bulgaria.

To sum it up: the reader takes a useful, well composed book of fine get-up in hand. Though it appeared in a limited edition (10 000 copies) the book is hoped to reach many, and good use will be made of its content.

M. NAGY

L. ORLÓCI and N. C. KENKEL: *Introduction to Data Analysis with Examples from Population and Community Ecology*. International Co-operative Publishing House, Fairland, Maryland, USA. 1985, 340 pp.

This book came out as the first volume of the series "Statistical Ecology Monographs". In fact, this is the first textbook published by ICPH, all the others contain technical papers, reviews and bibliographies. As such, this book meets a long need, namely a successful combination of conventional univariate statistics with multivariate techniques. This sort of synthesis seems quite novel in the literature of statistical ecology.

The title reflects well the contents. A wide variety of methods have been discussed, including some more recently proposed approaches to the analysis of ecological data. Three main problem areas are addressed: exploration of data structure, estimation of population parameters and hypothesis testing. The descriptions are always problem-oriented, many examples help the reader find the way from theory to practice. The material is divided into 15 chapters and, in addition, a glossary, an author index and a subject index facilitate our orientation. A ninety-page appendix provides listings of BASIC programs designed to perform most techniques of data analysis discussed in the text. Sample runs are also provided, these may prove useful as a check of program implementation. As a matter of fact, the whole book can be considered as a "program output", since the text was processed and printed using a microcomputer. This explains the unusual large format of the volume.

It seems worth summarizing the contents to illustrate the general utility of this book. The first chapter discusses data types in brief and emphasizes the importance of careful planning in ecological surveys. Then, the authors give a short historical review of the development of methods and equipment used in biological data management. The next chapter describes data sources, variables, transformation functions and the methods of handling measurement errors. Chapter IV is devoted to the methods and aims of describing populations: distributions and population descriptors, including entropy and various moments, are discussed. Sampling problems get into focus in the next chapter. Then, the authors turn to the problems of estimation in various sampling designs. Chapter 7, "Measuring commonness and probability", represents the first step towards an introduction to hypothesis testing. Sampling distributions and confidence limits are considered in detail.

Resemblance functions used in comparisons between variables, individuals or groups are presented in Chapter 8. The formulation of hypotheses and their testing comprise the main part of the next chapter, which is the longest one in the book. The methods introduced here include the KOLMOGOROV-SMIRNOV test, *t*-tests, various versions of ANOVA, canonical correlation, homogeneity tests and the comparison of nested character hierarchies. Chapter 10 describes selected models of regression analysis. The determination of rank order of characters is discussed in the next chapter. Finally, the multivariate methods of data exploration are described. Four chapters are devoted to this topic. Algorithms for component analysis, multi-dimensional scaling, cluster analysis, analysis of concentration and discriminant analysis are among the many methods introduced here.

Although the text has been suggested by the authors for use primarily at university courses, I feel that it is very useful also as a handbook. Therefore, this volume is very highly recommended for all students of population and community ecology who wish to analyze their data in an objective manner.

J. PODANI

EBBINGHAUS, H. D., FLUM, J., THOMAS, W.: *Mathematical Logic*. Undergraduate Text in Mathematics. Springer-Verlag, New York-Berlin-Heidelberg-Tokyo, 1984. ix + 216 pp.

The book begins with a successful introductory chapter. In the sections of this chapter two simple mathematical proofs are presented as illustrations for methods of proof used by mathematicians. By these examples some questions which lead us to the main topics of the book are raised. There is an example from group theory (we require the axioms of group theory, then prove the existence of a left inverse), and an example from the theory of equivalence relations is also given. The proved theorem, after the statement of three axioms of the theory of equivalence relations, is that for all x and y , if there is a u such that $x R u$ and $y R u$, then for all z , $x R z$ if and only if $y R z$.

The following chapters contain an introduction to first-order logic, a proof of GÖDEL's completeness theorem (Ch. 5) and a short digression into model theory which shows that first-order languages have some deficiencies in expressive power.

The prerequisites from set theory that are necessary to overcome the above difficulties are explained and then the relation between logic and set theory is treated in a thorough manner.

GÖDEL's (first and second) incompleteness theorems are treated at the end of chapter 10 in connection with several related results.

As an alternative to first-order logic some other logical system is considered, such as second-order and infinitary logics.

In the final chapter some results are presented in connections with LINDSTRÖM's theorems which show that there is no logical system that extends first-order logic and at the same time shares all its advantages.

This book is translated from *Einführung in die mathematische Logik* published by Wissenschaftliche Buchgesellschaft in 1978.

Some sections have been revised for the translation and some exercises have also been added.

B. TÓTHMÉRÉSZ

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