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The grasses of three Westindian islands, compared to North European grasses

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The Westindian islands St. Croix, St. Thomas and St. Jan, which were Danish until they in 1916 were sold to the United States, belong to the Virgin Islands group. Their total area amounts to 359 km². For the greater part the islands are rocky, with steep declivities, and slightly cultivated; only in St. Croix, of which the greater western part forms a large and slightly inclined plain, the sugar cane has been intensively cultivated, but the acreage of land under culture has been diminished during the latter years under American rule.

The climate of the islands is tropical. The average temperature of the hottest month (August) is 29,8° C, of the coldest (January) 23,8° C. The annual precipitation, measured on five stations during more than 50 years, gives an average of 1170 mm, falling chiefly in the months of September, Oktober and November, but the downpour is very irregular, both in the various years and in its distribution upon the months and upon the places (Tab. 1).

Table 1.

Precipitation (in mm) at St. Thomas 1852—1907 (after Will. Jantzen).

	Jan.	Febr.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year
Average .	64	41	51	58	113	103	91	113	138	155	132	80	1139
Maximum .	160	133	181	191	373	488	310	370	318	801	350	346	2034
Minimum .	14	0	8	9	14	10	14	16	39	41	22	17	639

Hence, the season unfavourable for plant growth is somewhat irregular and is not to be strictly defined.

For some years I have been working on a comprehensive flora of these islands with the purpose not only to give a list of all species present, but also to examine the biology of the species, trying, as it were, to give a biological diagnosis of each species. But it is a difficult task, numerous features of the plants being but unsufficiently known, or not at all. The sources from which information is drawn, are the published works of Eggers, of Britton & Wilson, Duss and others, next unpublished botanical notes by Eggers, Børge-

sen, Raunkiaer, Ostenfeld, and myself, and finally numerous herbarium and in alcohol preserved specimens in the Botanical Museum of the University of Copenhagen.

Here, some of the results of my investigations on the grasses of St. Croix, St. Thomas, and St. Jan, are presented. First, a list of all wild and naturalized species of Graminaceae found on the islands is given, with notes on the life form (in Raunkiaer's understanding) of each species. Next follow some general remarks on this tropical grass flora, and it is compared with a grass flora of a temperate climate.

List of grasses found on St. Croix, St. Thomas, and St. Jan.

Andropogon bicornis L. A caespitose Chamaephyte or Nanophanerophyte with branched culms.

Andropogon contortus L. A caespitose Chamaephyte (or Hemicryptophyte ? or Therophyte ?) (acc. to Hitchcock & Chase, and Duss) with branched culms. I have seen specimens which may be termed suffrutex : main shoot dead except its lower part (ab. 15 cm) from which new shoots arise.

Andropogon glomeratus (Walt.) B. S. P. A robust densely caespitose Hemicryptophyte (or, by branching culms, a Chamaephyte ?).

Andropogon leucostachyus H. B. K. A caespitose Hemicryptophyte (or, by branching culms, a Chamaephyte ?).

Andropogon pertusus (L.) Willd. A caespitose Chamaephyte, sometimes creeping by epigeous stolons and thereby « covering large acres along roadsides and in pastures » (Harris). Described from Timbuctu as an Hemicryptophyte (O. Hagerup).

Andropogon semiberbis (Nees) Kth. A caespitose Hemicryptophyte, partial rosette plant.

Andropogon sorghum Brot. An erect stout Therophyte.

Anthephora hermaphrodita (L.) Kze. A caespitose erect or ascending Therophyte or Hemicryptophyte (or, by branching culms, a Chamaephyte ?).

Aristida adscenscionis L. A caespitose Hemicryptophyte (or, by branched culms, a Chamaephyte ?) or a Therophyte. From Timbuctu this species is described as a Chamaephyte (O. Hagerup) but K. Gram says that in Sahara it is mostly a Therophyte but sometimes a Chamaephyte; in the West-Indies it seems as a rule to be hemicryptophytic.

Aristida cognata Trin & Rupr. Seems to be, biologically at least, a replica of A. adscenscionis.

Aristida Suringari Henrard. A densely caespitose Chamaephyte, when young may be a Therophyte or Hemicryptophyte.

Arundinaria capillifolia (Griseb.) Hack. A Microphanerophyte or Nanophanerophyte « climbing to a height of 15 m or more, repeatedly branching, swinging from the trees in great curtains, or festooning lower growth » (Hitchcock & Chase).

Axonopus compressus (L.) Beauv. An Hemicryptophyte, partial rosette plant, « under favourable conditions producing long leafy stolons » (Hitchcock & Chase), or may be sometimes a Therophyte.

Bambusa vulgaris Schrad. An arborescent Microphanerophyte. After flowering the whole tree is said to die, and new shoots arise from subterranean (or sometimes epigean) branched rhizomes. Hence, in years of flowering (which is said to be rare, Duss) Bambusa may be counted as a geophyte (or Chamaephyte, or Nanophanerophyte).

Bouteloua americana (L.) (Scribn.). A caespitose Protohemicryptophyte (or a Therophyte ?).

Cenchrus echinatus L. A Chamaephyte with epigeous stolons, or an Hemicryptophyte, often caespitose with ascending and often rooting stems, or a Therophyte.

Cenchrus pauciflorus Benth. A Chamaephyte with long epigeous and ramified stolons, or a Therophyte, or Hemicryptophyte.

Chloris ciliata Sw. A Therophyte or a caespitose Hemicryptophyte.

Chloris paraguaiensis Steud. A caespitose Hemicryptophyte, partial rosette plant, or a Therophyte.

Chloris radiata (L.) Sw. A Therophyte, or an Hemicryptophyte, partial rosette plant.

Chloris sagraeana A. Rich. A caespitose Hemicryptophyte (or, by branching culms, a Chamaephyte ?) or a Therophyte.

Cynodon dactylon (L.) Pers. A creeping or ascending Chamaephyte, or a Protochemicryptophyte. The runners are mostly epigeous, but sometimes hypogeous and then with buds in the earth's crust. Timbuctu-specimens were by O. Hagerup described as Hemicryptophytes or, more rarely, Chamaephytes, whereas K. Gram says that in Sahara the plants of this species always survive as Hemicryptophytes.

Dactyloctenium aegyptium (L.) Richt. A creeping Hemicryptophyte, forming a dense sod, or a Chamaephyte (?) or Therophyte; from Timbuctu described as a Therophyte (O. Hagerup).

Digitaria digitata (Sw.) Urban. A decumbent and rooting, or creeping, Chamaephyte, or a caespitose Protohemicryptophyte whose tufts emit decumbent stems.

Digitaria sanguinalis (L.) Scop. Seems to be, as to growth-form, a replica of the preceeding species.

Echinochloa colonum (L.) Link. A caespitose Protohemicryptophyte, or a Therophyte (or, by branching of the culms, a Chamaephyte ?); the stems procumbent and often rooting at the lower nodes.

Eleusine indica (L.) Gärtn. A caespitose Therophyte or Hemicryptophyte, partial rosette plant (or, by branching culms, a Chamaephyte ?)

Eragrostis amabilis (L.) Wight & Arn. A caespitose Therophyte.

Eragrostis Barrelieri Desv. A Therophyte (?).

Eragrostis ciliaris (L.) Link. A caespitose Therophyte, or a Protohemicryptophyte (or, by branching culms, a Chamaephyte ?). In Timbuctu the species is therophytic (O. Hagerup).

Eragrostis Elliottii S. Wats. A caespitose Hemicryptophyte, or a Therophyte.

Eragrostis glutinosa (Sw.) Trin. A caespitose Hemicryptophyte.

Eragrostis hypnoides (Lam.) P. B. S. A creeping Chamaephyte or Hemicryptophyte (?).

Eragrostis pilosa (L.) Beauv. A caespitose Therophyte or Hemicryptophyte.

Eragrostis tephrosanthos Schult. A caespitose Therophyte or Hemicryptophyte.

Eriochloa punctata (L.) Desv. An erect Protohemicryptophyte.

Eustachys petraea (Sw.) Desv. A caespitose Protohemicryptophyte, « sparingly stoloniferous » (Hitchcock & Chase), or a Therophyte (?).

Gymnopogon foliosus (Willd.) Nees. An erect Chamaephyte (?) or Protohemicryptophyte (?).

Imperata contracta (H. B. K.) Hitchc. A caespitose Protohemicryptophyte.

Lasiacis divaricata (L.) Hitchc. A reclining and climbing Nanophanerophyte or Microphanerophyte, the bamboo-like woody culm erect or arching over

shrubs, until ab. 5 m long, much branched above — or sometimes a Chamaephyte.

Lasiacis Harrisii Nash. A Nanophanerophyte or Microphanerophyte climbing to a height of 5 m or more, or a Chamaephyte.

Lasiacis ligulata Hitchc. & Chase. A Nanophanerophyte or Microphanerophyte, « clambering to a height of 5 to 10 meters, the robust glabrous central cane as much as 1 cm in diameter ... » (Hitchcock & Chase).

Lasiacis patentiflora Hitchc. & Chase. As the preceeding species.

Lasiacis sorghoidea (Desv.) Hitchc. & Chase. As the preceeding species.

Leptochloa fascicularis (Lam.) Gray. A caespitose Helophyte or Protohemicryptophyte, sometimes whit short rooting stolons, or a Therophyte.

Leptochloa filiformis (Lam.) Beauv. A caespitose Therophyte or Protohemicryptophyte (or, by branching culms, a Chamaephyte ?).

Leptochloa virgata (L.) Beauv. As the preceeding species.

Olyra latifolia L. A Microphanerophyte or Nanophanerophyte, « bamboo-like in aspect, commonly 5 meters tall, the strong hollow culms sometimes 1 cm thick, erect and unsupported, the summit only arched (or weaker culms leaning among brush), the lower half to two thirds simple and naked, the short sheaths bladeless or nearly so, the elongate internodes ... branching from the upper nodes, the branches commonly fascicled, divaricate, often 1 m long, sometimes again branching « (Hitchcock & Chase).

Olyra pauciflora Sw. A caespitose Hemicryptophyte (?).

Oplismenus hirtellus (L.) Beauv. A creeping Chamaephyte with nearly meterlong epigeous and rooting, foliage-bearing stems.

Oryza sativa L. An erect Therophyte.

Panicum adspersum Trin. A Protohemicryptophyte ascending and rooting below (or, by branching culms, sometimes a Chamaephyte ?).

Panicum barbinode Trin. A robust Protohemicryptophyte, flowering culms erect, meterhigh or more, steril ones stoloniform and rooting, 1—2 m long.

Panicum diffusum Sw. A caespitose Protohemicryptophyte.

Panicum fasciculatum Sw. A caespitose Protohemicryptophyte (or, by branching culms, a Chamaephyte ?) or a Therophyte.

Panicum geminatum Forsk. A caespitose Protohemicryptophyte, spreading and sometimes stoloniferous.

Panicum ghiesbreghtii Fourn. A robust caespitose Protohemicryptophyte (?).

Panicum laxum Sw. A caespitose Protohemicryptophyte (or, by branching culms, may be sometimes a Chamaephyte ?); stems often decumbent and rooting.

Panicum maximum Jacq. A robust caespitose Protohemicryptophyte with « creeping rootstocks » (Hitchcock & Chase), 1—3 m high or more, when old with culms lignified and then may be a Micro- or Nanophanerophyte.

Panicum miliaceum L. An erect Therophyte.

Panicum reptans L. A Protohemicryptophyte (or Chamaephyte ?), usually prostrate or with a decumbent base, rooting at the lower nodes.

Panicum trichanthum Nees. A Chamaephyte or Nanophanerophyte, culms branched, 1—2 m high, clambering (?) (sometimes a Hemicryptophyte ?).

Panicum trichoides Sw. A spreading Chamaephyte (or Hemicryptophyte ?), stems ascending from a decumbent and rooting base.

Panicum utowanaeum Scribn. A slender caespitose Protohemicryptophyte.

Pappophorum alopecuroideum Vahl. A caespitose Protohemicryptophyte.

Paspalum Boscianum Flügge. An Hemicryptophyte or Chamaephyte ? (« a rather succulent annual, branching at the base and commonly from the middle nodes ..., culms ... ascending to widely spreading, sometimes rooting at the lower nodes ... [Chase]).

Paspalum conjugatum Berg. An extensively creeping Hemicryptophyte, partial rosette plant (or, by branching culms, a Chamaephyte ?).

Paspalum densum Poir. A caespitose Hemicryptophyte.

Paspalum distichum L. An extensively creeping Protohemicryptophyte with meterlong runners (or, by branching culms, a Chamaephyte ?).

Paspalum fimbriatum H. B. K. An erect Therophyte (or Protohemicryptophyte ?).

Paspalum laxum Lam. A caespitose Hemicryptophyte, partial rosette plant.

Paspalum molle Poir. A caespitose spreading Hemicryptophyte, partial rosette plant.

Paspalum notatum Flügge. An Hemicryptophyte, partial rosette plant, with a short stout woody horizontal rhizome, forming tough but not extensive sods.

Paspalum orbiculatum Poir. (doubtfull). An extensively creeping Hemicryptophyte, often forming dense mats.

Paspalum paniculatum L. A caespitose Protohemicryptophyte, culms ascending or sometimes decumbent at base and rooting.

Paspalum plicatulum Michx. A caespitose Protohemicryptophyte.

Paspalum secans Hitch. & Chase. An erect caespitose Protohemicryptophyte.

Paspalum vaginatum Sw. An extensively creeping Hemicryptophyte or Chamaephyte with meterlong runners which strike root in wet soil, but parts of them may be rootless, and long runners have been seen hanging down like festoons over rocks near the sea.

Paspalum virgatum L. An erect robust caespitose Protohemicryptophyte.

Pharus glaber H. B. K. A caespitose Protohemicryptophyte.

Saccharum officinarum L. A Nanophanerophyte (or Rhizome-Geophyte).

Setaria geniculata (Lam.) Beauv. A caespitose Protohemicryptophyte (or, by branching culms, a Chamaephyte ?) or may be sometimes a Therophyte.

Setaria rariflora Mik. A caespitose Protohemicryptophyte (or, by branching culms, a Chamaephyte?).

Setaria setosa (Sw.) Beauv. A caespitose Protohemicryptophyte (or, by branching culms, a Chamaephyte ?) or may be sometimes a Therophyte.

Spartina patens (Ait.) Muhl. A Rhizome Geophyte with long hard-scaly subterranean runners, in sand of seashores.

Sporobolus argutus (Nees) Kth. A caespitose Protohemicryptophyte (or, by branching culms, a Chamaephyte?) or a Therophyte.

Sporobolus indicus (L.) R. Br. A caespitose Hemicryptophyte, partial rosette plant.

Sporobolus Jacquemontii (Trin.) Kth. A caespitose Hemicryptophyte, partial rosette plant, or a Therophyte.

Sporobolus muralis (Rad.) Hitchc. & Chase. A Therophyte.

Sporobolus virginicus (L.) Kth. A Chamaephyte with long hard scaly epigeous runners, erect culms often branching, or a Protohemicryptophyte, or a Rhizome-Geophyte with runners subterranean.

Stenotaphrum secundatum (Walt.) Kze. An active Chamaephyte with extensively creeping epigeous runners rooting at the lower nodes or all over.

Tragus alienus (Spreng.) Schult. A Therophyte or a caespitose Hemicryptophyte or, by short decumbent and rooting epigeous branches, a Chamaephyte. Specimens from Timbuctu are described by O. Hagerup as mostly therophytic, very few individuals persisting.

Uniola virgata (Poir) Gris. A robust caespitose Hemicryptophyte.

Valota Eggersii (Hack.) Hitchc. & Chase. A slender caespitose Hemicryptophyte, partial rosette plant.

Valota insularis (L.) Chase. A caespitose Hemicryptophyte, partial rosette plant (or, by branching culms, a Chamaephyte ?), stoloniferous (Duss).

In order to compare these tropical grasses, 95 species in all, to grasses of a country with a temperate climate, I choose Denmark as representing the latter. Denmark has on its 42,927 square kilometers — more than 119 times the area of the three Westindian islands together ! — 112 wild and naturalized grass species (Raunkiaer, Exkursions-Flora, 1934).

Not a single species is common for the Westindian islands and Denmark, and from Tab. 2 it may be seen how the subfamilies of the grasses are represented in the two floras; only Agrostideae and Festuceae are represented in both floras.

Table 2.

Number of species of different subfamilies of grasses growing on the three Westindian islands and in Denmark.

	St. Croix, St. Thomas, St. Jan	Denmark
Andropogoneae	8	0
Zoysieae	2	0
Paniceae	49	0
Oryzeae	2	0
Phalarideae	0	2
Agrostideae	8	17
Aveneae	0	16
Chlorideae	14	0
Festuceae	10	56
Hordeae	0	21
Bambuseae	2	0
Number of species	95	112

Taxonomically very distinct from each other the two grass-floras show also several morphological and biological differences. The Westindian grasses comprise a number of Fanerophytes, some few (3) erect, but of climbing species 6; these are all without special climbing apparatus, and keep themselves upright between bushes by their patent or divaricate branches. — Further about half a score of Westindian grasses are creeping, often by meterlong runners, especially on sandy beaches or loamy places near lagunes. Other grasses are stoloniferous — Climbing grasses are not found in Northern Europe, and creeping ones are rare.

Bisexual flowers in one-flowered spikelets and often surrounded by 5 glumes, are common in the West-Indies, and the spikelets are very often arranged in long one-sided spikes (or racemes with short pedicels) of which several form a digitate inflorescence, rare in temperate countries.

From the ordinary position of the alternate leaves, close together below but above with long internodes between, there are deviations in some Westindian grass-genera, where long and very short internodes alternate. Here some examples.

Dactyloctenium aegyptium has ordinary single leaves, but nodi on the creeping runners are as a rule double where these strike root, one nodus close above the other, each with its leaf, the leaves being then nearly opposite and subtending opposite branches. — *Cynodon dactylon* has single leaves only under the inflorescence. The greater part of the erect shoots has leaves in twos : two nodi close together with two leaves nearly opposite, the upper sheath closely clasping the culm and often a little longer than the lower sheath which is clasping the upper; the two blades nearly horisontal and close together or opposite. Now and then a single leaf may be found between the pairs. The runners of *Cynodon* as a rule have nodi and leaves in threes, but only the lowest one subtends a lateral shoot. — *Sporobolus virginicus* has leaves in twos like *Cynodon*. — *Stenotaphrum secundatum* has, except the uppermost leaves, all leaves in twos. Ramification is rather rich and takes place mostly from both axils, hence is nearly dichasial, but because of the prophylls being dorsal all leaves and all lateral shoots are in the same plan, thus differing from the dichasium. — Also *Chloris radiata*, *Eustachys petraea*, and *Eleusine indica*, have leaves in twos.

After these somewhat casual remarks on morphology let us consider the life forms of the Westindian grasses, here looking apart from other biological features such as flowering and fruiting.

The life forms in the sense of Raunkiaer is said to express the plant's adaptation to the unfavourable season. But, as stated above, in the Westindian islands the unfavourable season, that is the dry season, is somewhat irregular. A dry period may occur at nearly every season of the year, or in some years and in some places it may not occur at all. Hence it is but natural that the life form may change from one year to another, that f. i. a Therophyte in good years may survive as an Hemicryptophyte, or a Hemicryptophyte as a Chamaephyte, and so on.[1] — In the list above are given the life forms of the species, and their variations. A special detail has been a little puzzling : as the culms of several species are branching often rather high up, the buds of such branches may in good, i. e. moist years, be able to survive « the unfavourable season », and then the plant must be considered a Chamaephyte. But being uncertain whether such upper lateral buds really sur-

[1] The same thing has been described by O. Hagerup from Timbuctu and by K. Gram from Sahara, and is also mentioned by Raunkiaer (l. c. p. 556) who says that it shows that the life form system employed by him is well suited to reflect the external conditions, since changing environment causes changing life form of the species.

vive I have given the words « or, by branching culms, a Chamaephyte » a question mark and put them in brackets.

Table 3.

Percentage of life forms (Biological spectra).

	Number of species	F	Ch	H	G	HH	Th
1	904	61	12	9	3	1	14
2	95	10	16	54	1	1	18
3	168 unities	8	25	45	1	0,6	21
4	147 unities	8	15	51	1	0,7	24
5	112	—	—	51	13	5	31
6	1084	7	3	50	11	11	18

1: The whole flora of St. Croix, St. Thomas, and St. Jan (after Raunkiaer).
2: The grasses of the same islands; for each species is counted but one life form, considered the most important.
3: The same, but all possible life forms counted.
4: As 3, but without regard to „Chamaephytes by branching culms".
5: The grasses of Denmark.
6: The whole flora of Denmark (after Raunkiaer).

In table 3, line 2, is given the percentages of the « main » life form of the Westindian grasses, in line 3 all possible life forms are counted, in line 4 the same but with the exclusion of « Chamaephytes by branching culms ». It is seen that 2 and 4 agree fairly well, the majority of Westindian grasses being hemicryptophytic but with many Therophytes and not few Chamaephytes. The few HH (Helo- and Hydrophytes) are accounted for by the scarceness of fresh water in the islands, but it is curious that but one grass species is geophytic *(Spartina patens)*, another *(Sporobolus virginicus)* is casually a geophyte. — Line 3, the spectrum including « Chamaephytes by branching culms » might perhaps be termed a spectrum of moist years ? but with its many Chamaephytes and relatively few Hemicryptophytes it does not agree with the other two, and, since the West-Indies do not belong to a region characterized by numerous Chamaephytes, it may rather show that it is not likely that branching culms are of importance for the life form.

A comparison of the grass spectra 2 and 4 with the spectrum of the whole flora of the three islands shows that the grasses have much fewer Fanerophytes than the whole flora but that on the other hand Hemicryptophytes are much more numerous. There must be something in the nature of grasses which tends to make them Hemicryptophytes and makes it difficult to become Fanerophytes. The Danish grass flora is, in percentage of Hemicryptophytes and Therophytes, surprisingly

similar to the Westindian, but differs in having several Geophytes and no Fanerophytes.

Finally, if we compare the Westindian grass spectrum 2, on one side to the whole flora of the three Westindian islands, on the other side to the whole flora of Denmark, we find that the Westindian grass spectrum is much more like a temperate than a tropical flora spectrum — indeed, if we make it up numerically in subtracting the values of 1 and 2 and of 2 and 6, and adding the differences, we get a difference of 40 between Westindian grasses and Denmark's flora, but a difference of 105 between the Westindian grasses and the flora of the islands where the grasses have grown.

This seems to show that grasses adapt themselves to climate in their own way. It would, indeed, be more remarkable if they did not do so, and of course differences in adaptation between the families are of no consequence for the biological spectra and their use. But they characterize the families. Thus the grasses seem to be specially characterized by a tendency for hemicryptophytic life.

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