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Life-forms and seasonal patterns in the pteridophytes in Zambia

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Abstract

146 species of pteridophytes occurring in Zambia were classified into Raunkiaer's life-form classes. The hemicryptophytes are dominant and include the most widely distributed species. The phanerophytes (tree-ferns and lianas) and the epiphytes are rather scarce and limited to or concentrated in the higher-rainfall areas in the northern part of the country. Simplified diagrams of periodicity were constructed for all Zambian pteridophyte species. Three major types of seasonal pattern of growth and dormancy were distinguished: the evergreen type, the poikilohydrous type, and the "summer--green" type. The first of them is connected with the local conditions of continuously wet non-zonal sites, while the two others clearly reflect the peculiarities of the zonal climate of Zambia.

INTRODUCTION

The aim of the present paper is to discuss some general aspects of pteridophyte seasonality in Zambia. The paper is based mainly on direct observations made during extensive collecting trips in 1971—1973; additional data from herbarium labels and the literature have also been used. Detailed ecological and chorological information on each individual species is being published in a separate account (Kornaś 1978 a), which may also be consulted for the nomenclature of taxa and their delimitation.

THE ENVIRONMENT

Zambia has a tropical continental climate (climatic type II of Walter 1971: 47, 58), with fairly abundant summer-rains and a prolonged winter drought (Fig. 1). The mean annual rainfall is between 1500 and

1000 mm in the north and gradually decreases to 635 mm in the south. The minimum temperatures are usually well above 0°C, even in the coolest months (June—July), and regular night frosts are known only

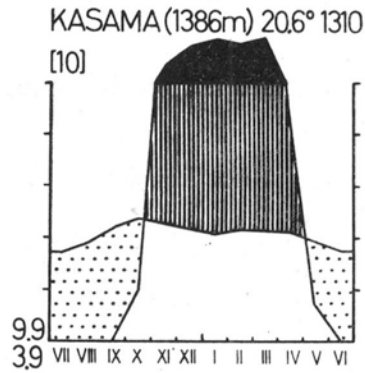


Fig. 1. Climatic diagram of a representative station in northern Zambia, drawn according to the method of H. Gaussen and H. Walter

Roman numerals designate the months (VII = July, VIII = August, etc.). The peaked line shows the mean monthly precipitation in mm (one scale interval = 20 mm). The flat line shows the monthly mean temperature in °C (one scale interval = 10°C). The drought period is dotted, the humid period vertically hatched (and shown in black, when mean monthly precipitation exceeds 100 mm). The heading includes the name of the station, the altitude above sea level (in m), the mean annual temperature (in °C), the mean annual precipitation (in mm) and the number of observation years (in square brackets). The upper figure at the bottom left indicates the mean daily minimum temperature of the coldest month, and the lower figure the lowest temperature ever recorded

in the south-westernmost part of the country (Davies 1971, Kornaś 1978 a). Under such conditions dry deciduous woodlands dominate as zonal vegetation types, and the water supply is the most important factor which determines the seasonal periodicity of growth and dormancy in plants, the rainy months being the main growing time, and the dry months the main resting period. In places, however, locally abounding in water, e.g. on river banks, near waterfalls, in swamps and around sources, plants are able to grow continuously, all the year round. Hence, two types of habitat exist, strongly contrasting in their periodicity of water supply and plant growth: the absolutely dominant zonal sites, severely affected by drought in the rainless months, and the very limited non-zonal mesic and hygric sites, sufficiently moist even in the dry season.

This situation is clearly reflected in the distribution, the life-form spectrum and the seasonal pattern of growth and dormancy in the pteridophytes. As pointed out by Kornaś (1974, 1976, 1978 a) and Dzwonko & Kornaś (1978), the pteridophytes are very unevenly distributed in Zambia, both in regard to the major features of their geographical ranges and to the local distributions in various plant community types. The mesophilous and hygrophilous species, by far the

most numerous and mainly of northern (Guineo-Congolian and Afro--montane) affinities are concentrated in the higher-rainfall areas and grow in the non-zonal vegetation types of wet evergreen forests, moist rocks (especially near the waterfalls), etc. The less numerous xerophilous species, often of southern geographical affinities, occur mainly in the initial plant communities on dry and sunny rocks. There are only very few pteridophyte species, which are able to grow in the zonal vegetation types of dry deciduous woodlands, and they are nearly absent from the low-rainfall areas in the southernmost part of the country.

THE LIFE-FORMS

Each of the 146 species of pteridophytes occuring in Zambia was analysed in regard to the location and protection of perennating organs during the dry season. The species were then classified into Raunkiaer's (1905) life-form classes as modified by Braun-Blanquet

Table 1

Biological spectrum of the pteridophyte flora of Zambia

	number of spp.	%
Epiphytic plants		
Epiphytes *	19	13.0
Terrestrial, amphibious or aquatic plants		
Phanerophytes **	5	3.4
Chamaephytes ***	8	5.5
Hemicryptophytes	95	65.1
Geophytes	11	7.5
Helophytes	2	1.4
Hydrophytes	5	3.4
Therophytes	1	0.7
Total	146	100.0

* occasional epiphytes not included
** perennating buds more than 1 m above the ground
*** perennating buds 25 cm — 1 m above the ground

(1932). The global biological spectrum of the pteridophyte flora of Zambia (Tab. 1) correlates very well with the general climate of the country. Nearly two thirds of all species represent the life-form of a hemicryptophyte. Some of them (e.g. *Adiantum patens* subsp. *oatesii, Blotiella crenata, Pteris friesii, Selaginella abyssinica, Tectaria gemmifera, Thelypteris denatata,* etc.) grow on the floor in wet evergreen forests, many

others, however, occur on rocks or in dry upland woodlands, and are evidently drought-resistant (e.g. *Actiniopteris radiata, Arthropteris orientalis, Mohria lepigera, Selaginella dregei,* etc.). This is particularly the case of the ferns in which the perennating buds are protected by a tunic-like structure consisting of rhizome scales and old stipe bases (e.g. *Actiniopteris pauciloba, Anemia angolensis, Aspidotis schimperi, Cheilanthes inaequalic, Pellaea longipilosa,* and others — see Fig. 4 - 15 in Kornaś 1978 b). Such features protect the plants very effectively also against the annual fires which occur regularly in upland woodlands and on rocky slopes. Nearly all of the common Zambian pteridophytes belong to this particular life-form.

The geophytes, which are rather uncommon among the pteridophytes, are fairly abundantly represented in Zambia. Some of them are again highly moisture-demanding (e.g. *Equisetum ramosissimum, Thelypteris confluens*), while the others are drought-resistant (and fire-resistant) and occupy the upland sites (*Pteridium aquilinum, Nephrolepis undulata, Ophioglossum vulgatum,* etc.). Both the hemicryptophytes and the geophytes occur in all parts of the country, including the low-rainfall areas in the south. The same is also true of the few members of two life-form classes attached to the aquatic or semiaquatic habitats: the hydrophytes (*Azolla pinnata* var. *africana, Ceratopteris cornuta,* etc.) and the helophytes (*Thelypteris interrupta,* etc.). The most unusual among Zambian pteridophytes is certainly *Selaginella tenerrima,* which seems to pass the unfavourable season in the form of spores and thus apparently represents the life-form of a therophyte.

The members of the three remaining life-form classes, the phanerophytes, the chamaephytes and the epiphytes, are evidently concentrated in or even restricted to the higher-rainfall areas in the north. This is most striking in the phanerophytes, all of which, three tree-fern species (*Cyathea dregei, C. manniana* and *C. thomsonii*) and two lianas (*Lygodium kerstenii, L. microphyllum*) have been found only within the 1100 mm annual isohyet (Fig. 2). Similarly distributed are also the chamaephytes with fairly high located perennating buds (regarded sometimes as nanophanerophytes): those with a short, erect, woody caudex (*Blechnum tabulare, Diplazium zanzibaricum* and *Marattia fraxinea,* Fig. 3) and those with a shrub-like habit (*Dicranopteris linearis*). The low herbaceous chamaephytes extend much further south (e.g. *Ampelopteris prolifera, Lycopodium cernuum,* both, however, occurring only in excessively wet sites). One species of this life-form, *Selaginella imbricata,* belongs to the most extreme xerophytes and is limited to the driest areas in southern Zambia.

The most prominent life-form in the pteridophytes of the humid tropics are the ephiphytes (Holttum 1938, Johansson 1971). They are fairly numerous also in the seasonally dry climate of Zambia, but

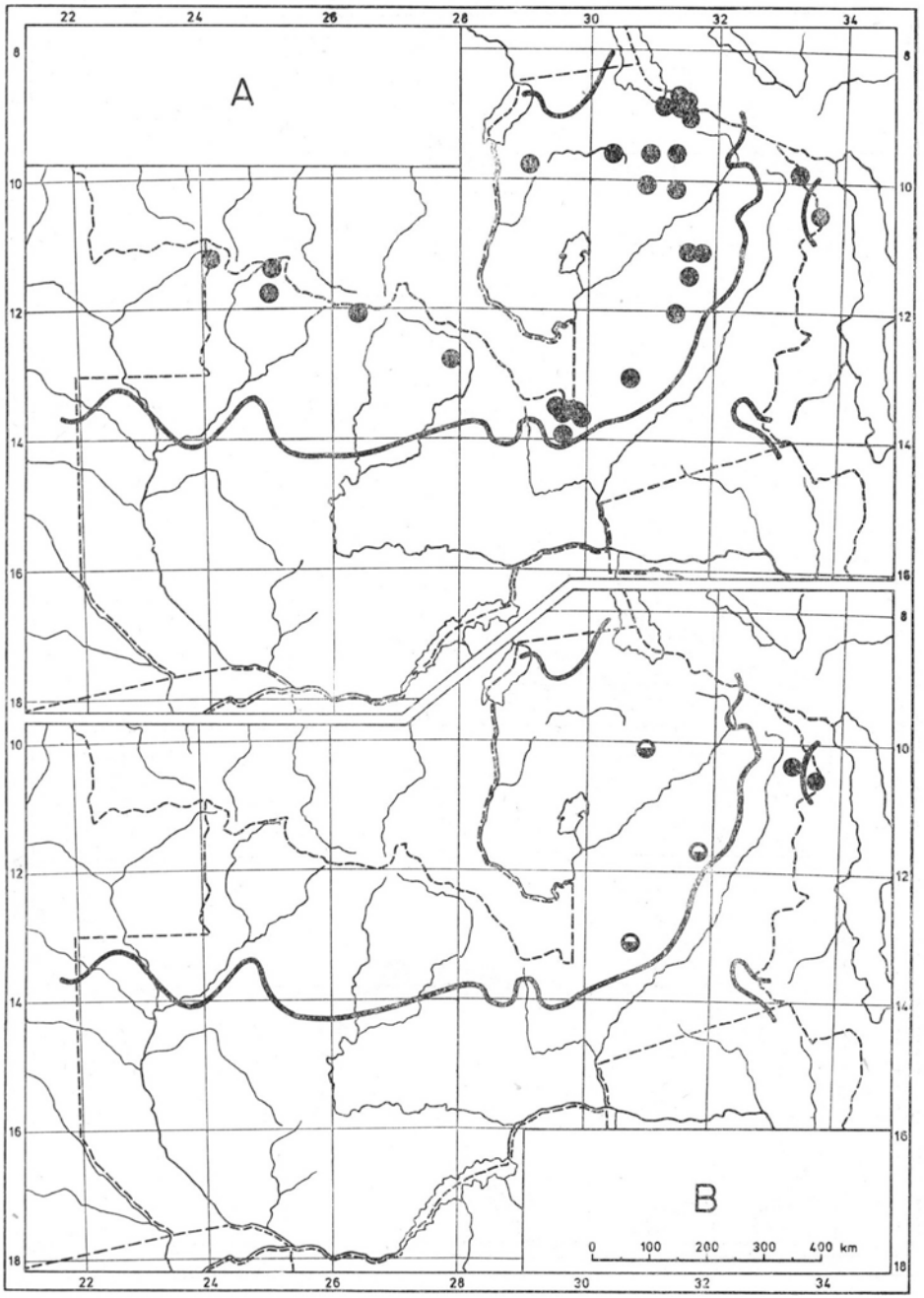


Fig. 2. Distribution of tree-ferns in Zambia

A — *Cyathea dregei*, B — *Cyathea manniana* (solid dots) and *C. thomsonii* (half-solid dots). Heavy line = 1100 mm annual isohyet

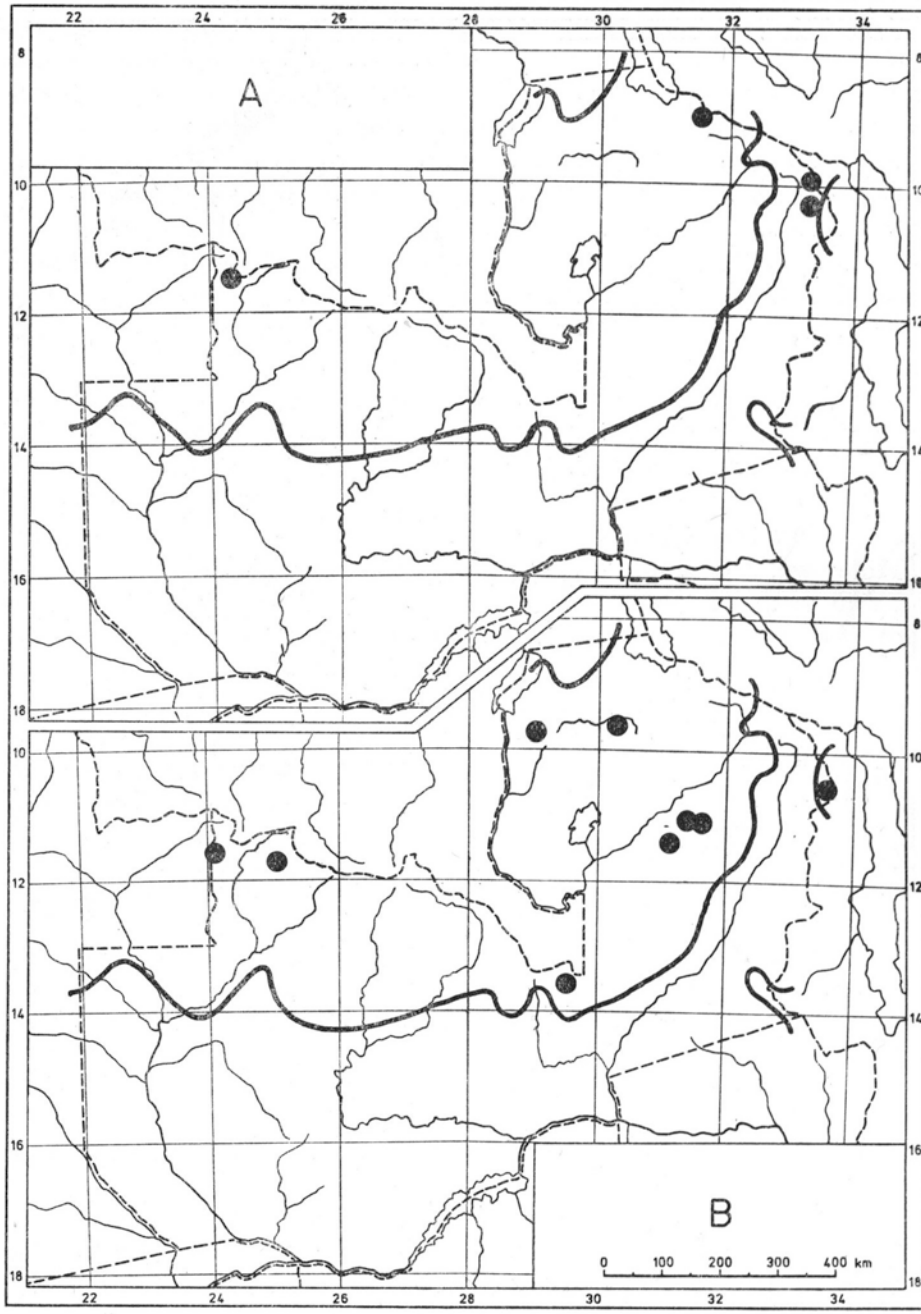


Fig. 3. Distribution of chamaephytic ferns with short woody caudex in Zambia
A — *Marattia fraxinea*, B — *Blechnum tabulare*. Heavy line = 1100 mm annual isohyet

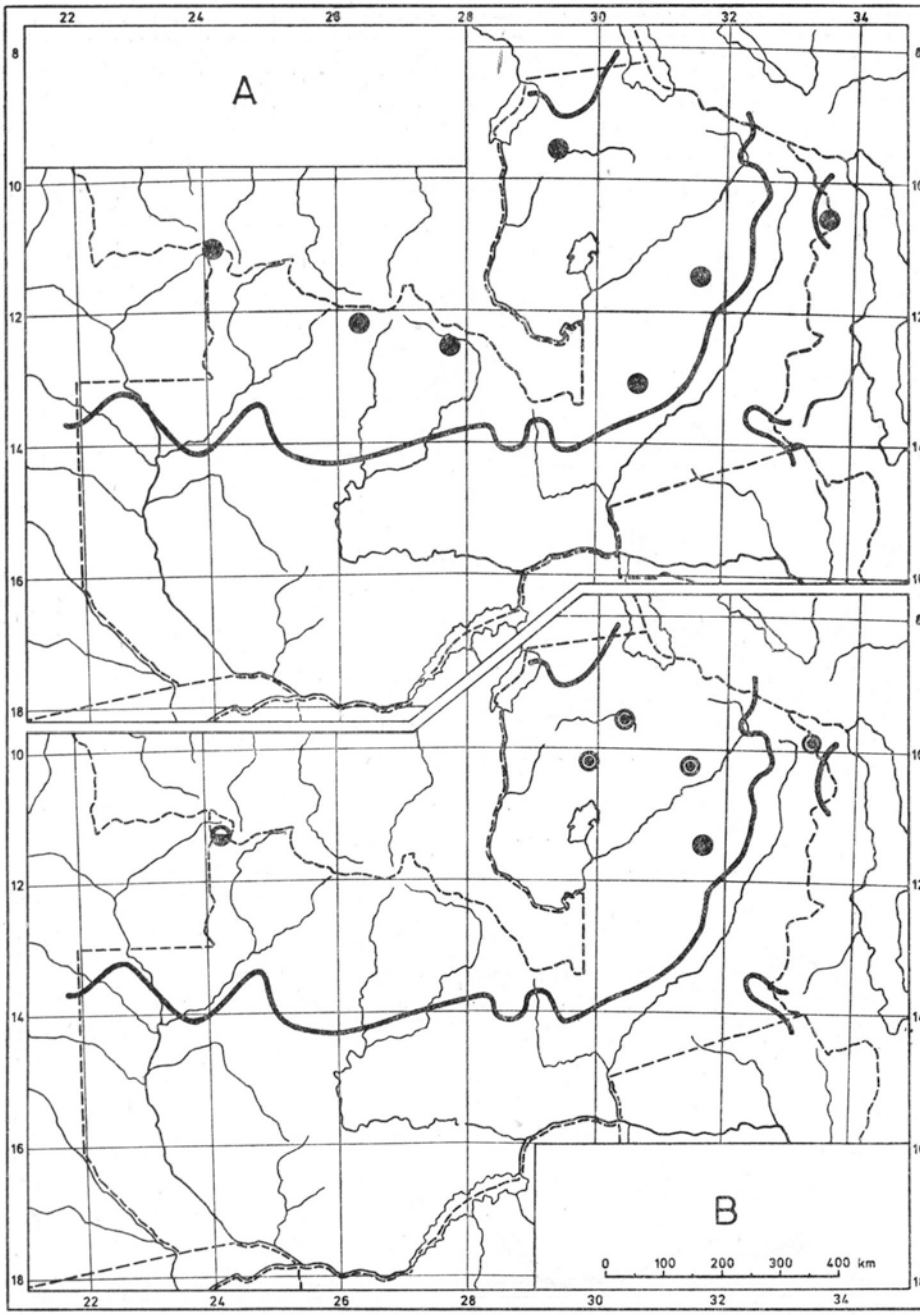


Fig. 4. Distribution of filmy ferns *(Hymenophyllaceae)* in Zambia

A — *Trichomanes pyxidiferum* var. *melanotrichum*, an epiphyte, B — *T. mannii* (half-solid dot) and *T. ramitrichum* (solid dot), both epiphytes, and *T. rigidum* (double circles), a terrestrial species. Heavy line = 1100 annual isohyet

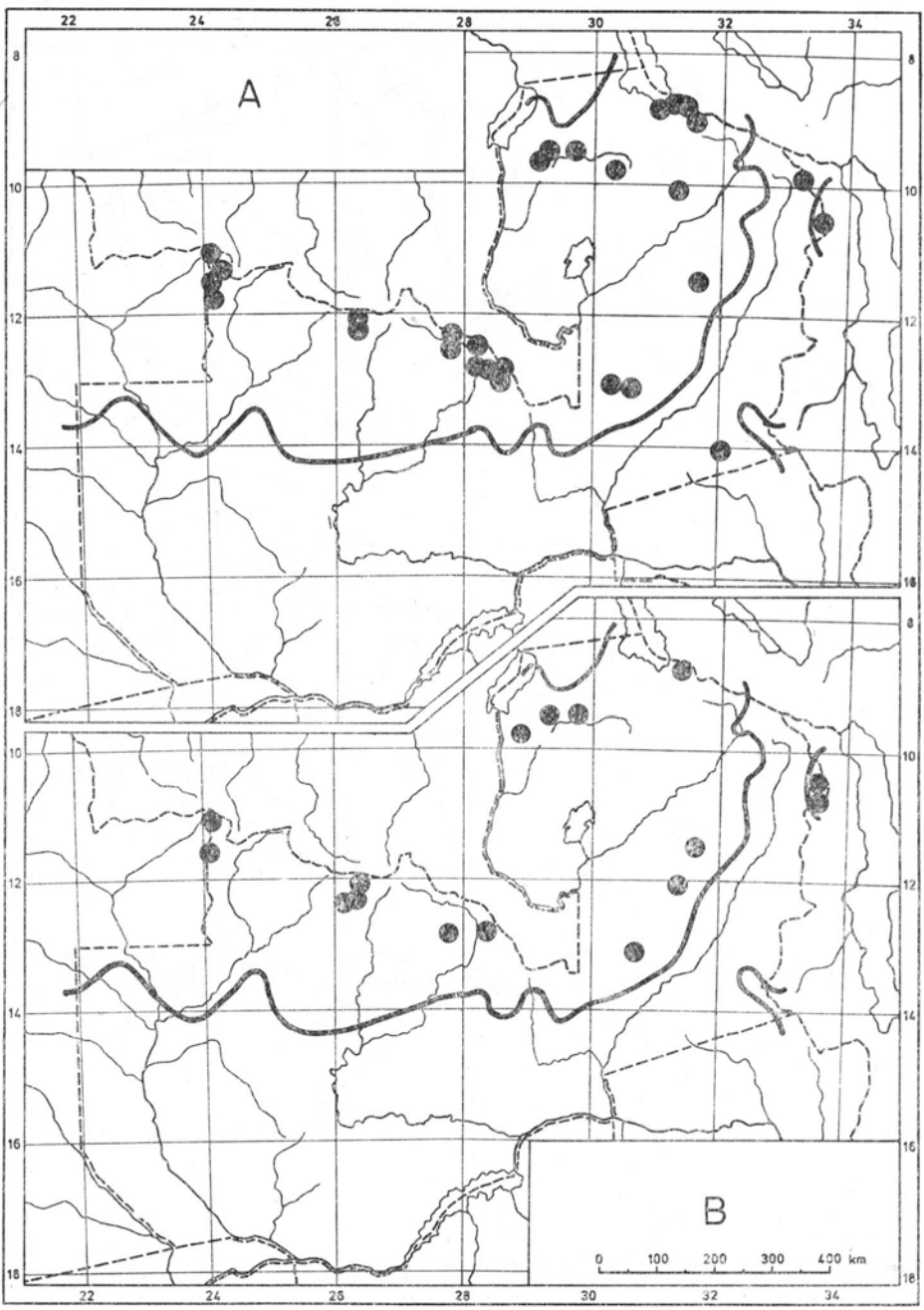


Fig. 5. Distribution of two epiphytic ferns in Zambia
A — *Pleopeltis excavata*, B — *Loxogramme lanceolata*. Heavy line = 1100 mm annual isohyet

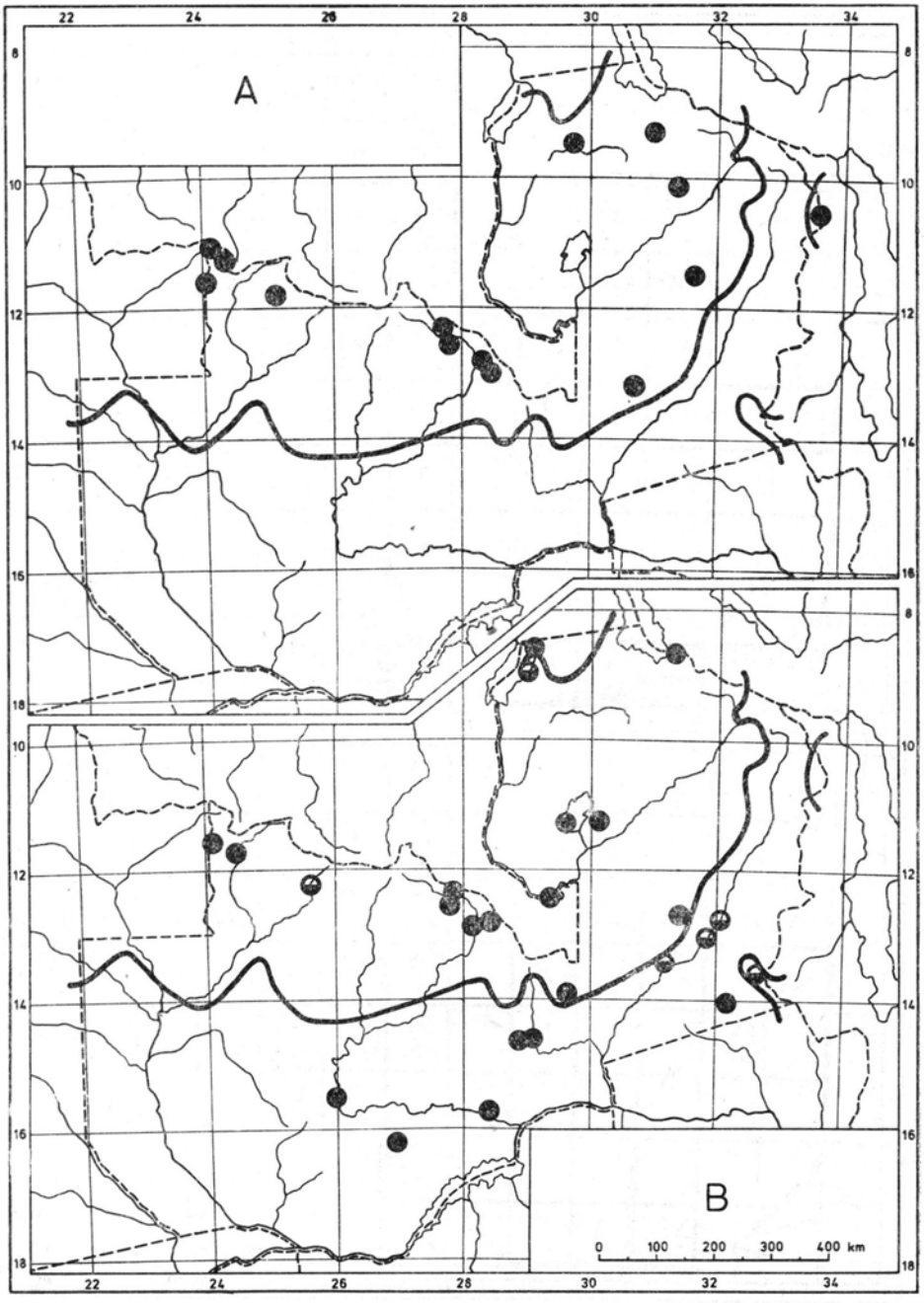


Fig. 6. Distribution of three epiphytic ferns in Zambia. A — *Asplenium thecifer-rum* var. *concinnum*, a species of evergreen forests, limited to the higher-rainfall areas, B — *Pyrrosia schimperana* (solid dots) and *Platycerium elephantotis* (half--solid dots), two riverside forest species, penetrating into the lower-rainfall areas. Heavy line = 1100 mm annual isohyet

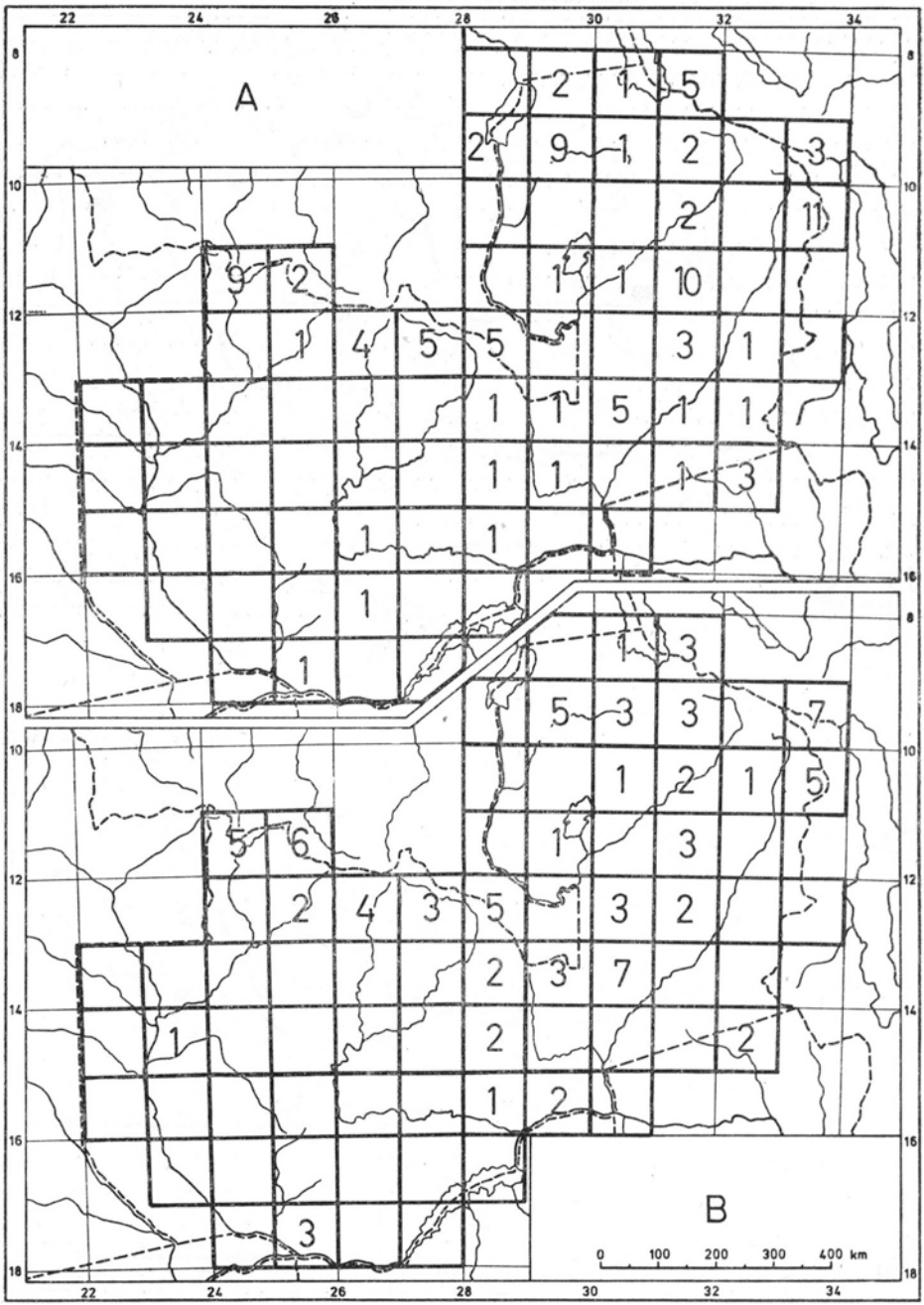


Fig. 7. Number of epiphytic pteridophyte species in 1°×1° squares in Zambia. A — typical epiphytes, B — occasional epiphytes

the majority of them is strictly confined to the higher-rainfall areas within the 1100 mm isohyet (Figs. 4—7). The following species have to be classified as typical epiphytes, occuring exclusively on tree branches or growing exceptionally also on rocks (*): **Arthropteris monocarpa, Asplenium mannii, *A. megalura, A. theciferum* var. *concinnum, Drynaria volkensii, *Loxogramme lanceolata, *Lycopodium verticillatum, *Microgramma lycopodioides, *Nephrolepis delicatula, Platycerium elephantotis, *Pleopeltis excavata, *P. macrocarpa, *Pyrrosia schimperana, P. stolzii, Psilotum nudum, *Trichomanes mannii, *T. pyxidiferum* var. *melanotrichum, T. ramitrichum, *Vittaria guineensis* var. *orientalis*. They are nearly all confined to the non-zonal evergreen forest communities, although a few of them also occur in dry deciduous woodlands on mist-affected hill tops (e.g. *Pleopeltis excavata*, Fig. 5A, and *P. macrocarpa*), and two most drough-resistant species, *Pyrrosia schimperana* and *Platycerium elephantotis* (Fig. 6B), penetrate far to the south, growing in the gallery forests along the rivers. Besides the typical epiphytes, ten other species establish themselves occasionally on tree trunks and branches in moist evergreen forests, but only in the higher-rainfall areas (Fig. 7B): *Asplenium aethiopicum, A. boltonii, A. dregeanum, A. formosum, A. protensum, Blechnum attenuatum, Cheilanthes farinosa, Elaphoglossum salicifolium* subsp. *petiolatum, E. spathulatum* and *Nephrolepis undulata*.

THE SEASONAL PATTERNS

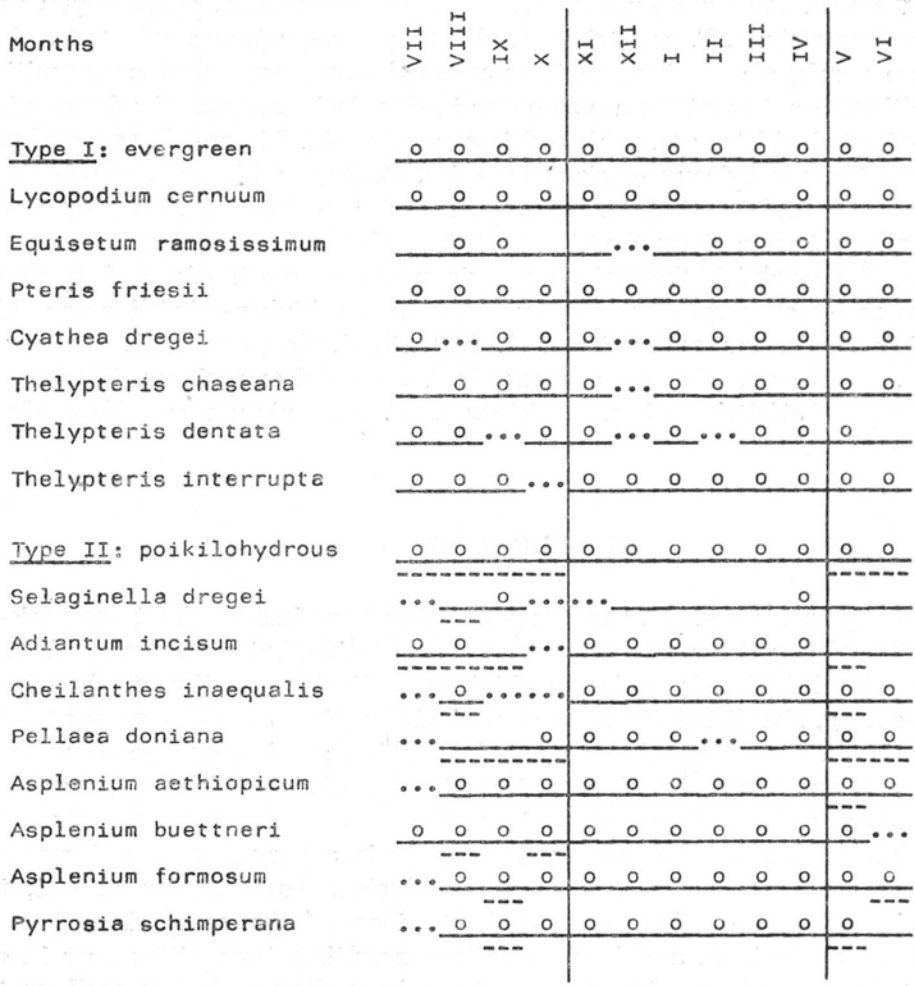
Up to the present, nearly nothing has been known about the periodicity of growth and dormancy in the pteridophytes in seasonally dry areas of Africa. In order to obtain a preliminary notion of these phenomena, simplified diagrams of periodicity (Braun-Blanquet 1932: 47) were constructed for all 146 Zambian species, on the grounds of field notes and the information from herbarium labels. These data proved to be rather abundant for the common species, and scarce but significative for the rare ones, and only in a very few cases they were too fragmentary for any sound conclusion. As a matter of fact, the diagrams give only an approximate idea of the seasonal rythms of species. Regional and local variations resulting from differences in climate and soil conditions, must have been disregarded as well as the possible existence of various ecotypes within individual species. Nevertheless, the data available seem to be sufficient for some generalization.

Three major types of seasonal pattern may easily be distinguished in the pteridophytes in Zambia (Tab. 2, 3), the evergreen type (I), the poikilohydrous type (II), and the "summer-green" type (III), as well as

a very rare "summer-dormant" type (IV). Types II and III clearly reflect the pecularities of the zonal climate of Zambia with its long unfavourable dry season. Type I is obviously connected with the local conditions of

Tab. 2

Seasonal pattern of growth and dormancy in the pteridophytes in Zambia



—— leaves present

=== leaves present in the dormant stage

\+ leaves occasionally present in special habitats

o sporangia present

••• no data available

continuously wet non-zonal sites. Type IV, represented by a single species only, seems to result from the abnormal life conditions on periodically flooded river banks.

Type I: evergreen: Seasonal pattern imperceptible. No drought dormancy. The plants are actively growing and bearing assimilating

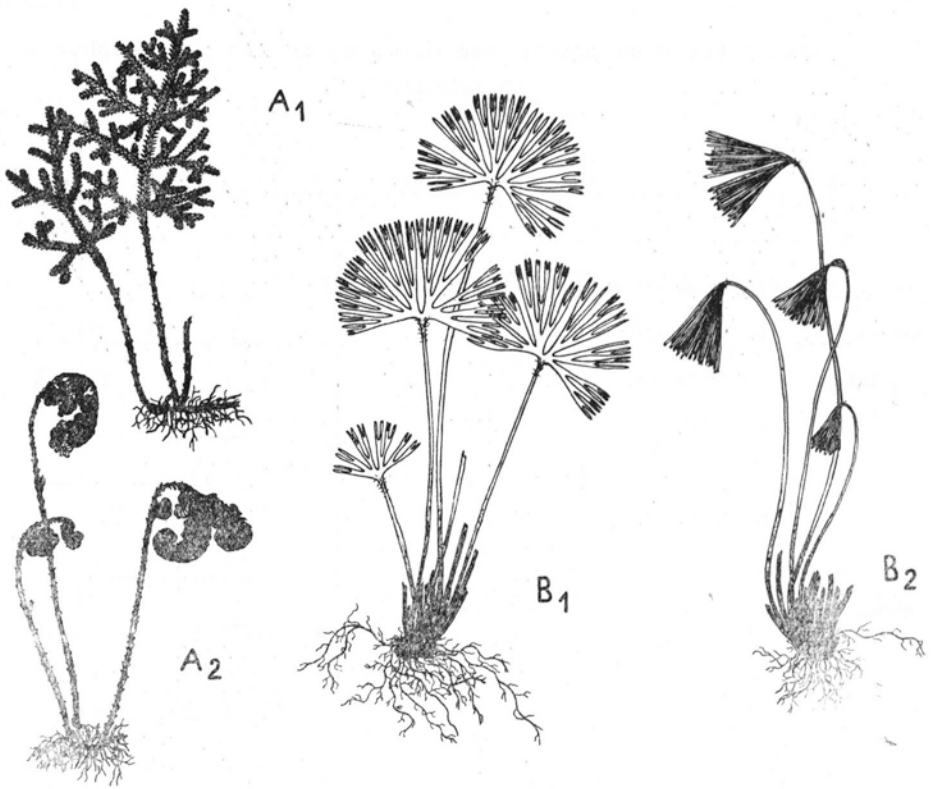
Tab. 3

Seasonal pattern of growth and dormancy in the pteridophytes in Zambia

Months	VII	VIII	IX	X	XI	XII	I	II	III	IV	V	VI
Type III a: "summer-green"							o	o				
Type III b: "summer-green"					o	o	o	o	o	o	o	
Ophioglossum thomasii							o	o				
Ophioglossum costatum							o	o	o			
Elaphoglossum petiolatum			+					o	o	o	o	
Asplenium pumilum		+						o	o	...	o	
Mohria lepigera							o	o	o	o	o	
Athyrium schimperi							o	o	o	o	o	
Pleopeltis excavata						o	o	o	o	o	o	
Dryopteris inaequalis	+			+		o	o	o	o	o	o	
Selaginella abyssinica						o		o	o	o	o	
Adiantum philippense	+	+	+			o	o	o	o	o	o	
Dryopteris athamantica						o	o	o	o	o	o	o
Anemia angolensis						o	o	o	o	o	o	o
Oleandra distenta			+		o	o	o	o	o	o	o	
Aspidotis schimperi						o	o	o	o	o		
Arthropteris orientalis		+		+		o	o	o	o	o	o	o
Doryopteris concolor	+				o	o	o	o	o	o	o	o
Type IV: "summer-dormant"	o	o	o	o	o						o	o
Osmunda regalis	o	o	o	o	o				+	+	o	o

organs (fronds, shoots), usually with sporangia, all the year round. Assimilating organs drought-sensitive, delicate, hygromorphic or mesomorphic.

This type is dominant among the pterodophytes in the humid tropics. In Zambia it includes as much as about 40% of species. All of them, however, are strictly limited to special habitats with abnormally favour-



Figs. 8—14. Poikilohydrous pteridophytes from Zambia in the active stage (1), and in the dormant stage (2)

Fig. 8. A — *Selaginella imbricata* (1 — Kornaś Pl. Afr. 1986, KRA; 2 — Kornaś Pl. Afr. 3926, KRA) B — *Actiniopteris radiata* (1 — Kornaś Pl. Afr. 3689, KRA; 2 — Kornaś Pl. Afr. 1983, KRA). ×0.5

able soil-moisture conditions: floors of wet evergreen forests (*Asplenium protensum, Blotiella crenata, Cyathea dregei, Histiopteris incisa, Lygodium microphyllum, Marattia fraxinea, Pteris friesii, Thelypteris chaseana, Th. dentata,* etc.), river banks (*Ampelopteris prolifera, Dicranopteris linearis, Equisetum ramosissimum,* etc.), wet grasslands and swamps (*Lycopodium cernuum, Thelypteris interrupta,* etc.), and aquatic habitats (*Salvinia molesta,* etc.). Nearly three quarters of these species are concentrated in wet evergreen forests, and most of them are rare or very

rare and confined to the higher-rainfall areas in northern Zambia. There are only two species of epiphytes (*Psilotum nudum, Lycopodium verticillatum*) which may tentatively be assigned to this group.

Fig. 9. *Pellaea doniana* (1 — Kornaś Pl. Afr. 0409, KRA; 2 — Kornaś Pl. Afr. 1896, KRA). ×0.5

Type II: poikilohydrous. Seasonal pattern well pronounced, although rather irregular and directly dependent upon the weather conditions. The plants retain their assimilating organs, usually with sporangia, all the year round. They grow actively only it the rainy weather

and become dormant in every dry spell. The assimilating organs are usually rather tough and xeromorphic (although, exceptionally, they may be delicate and hygromorphic, as in *Asplenium mannii* and *Tricho-*

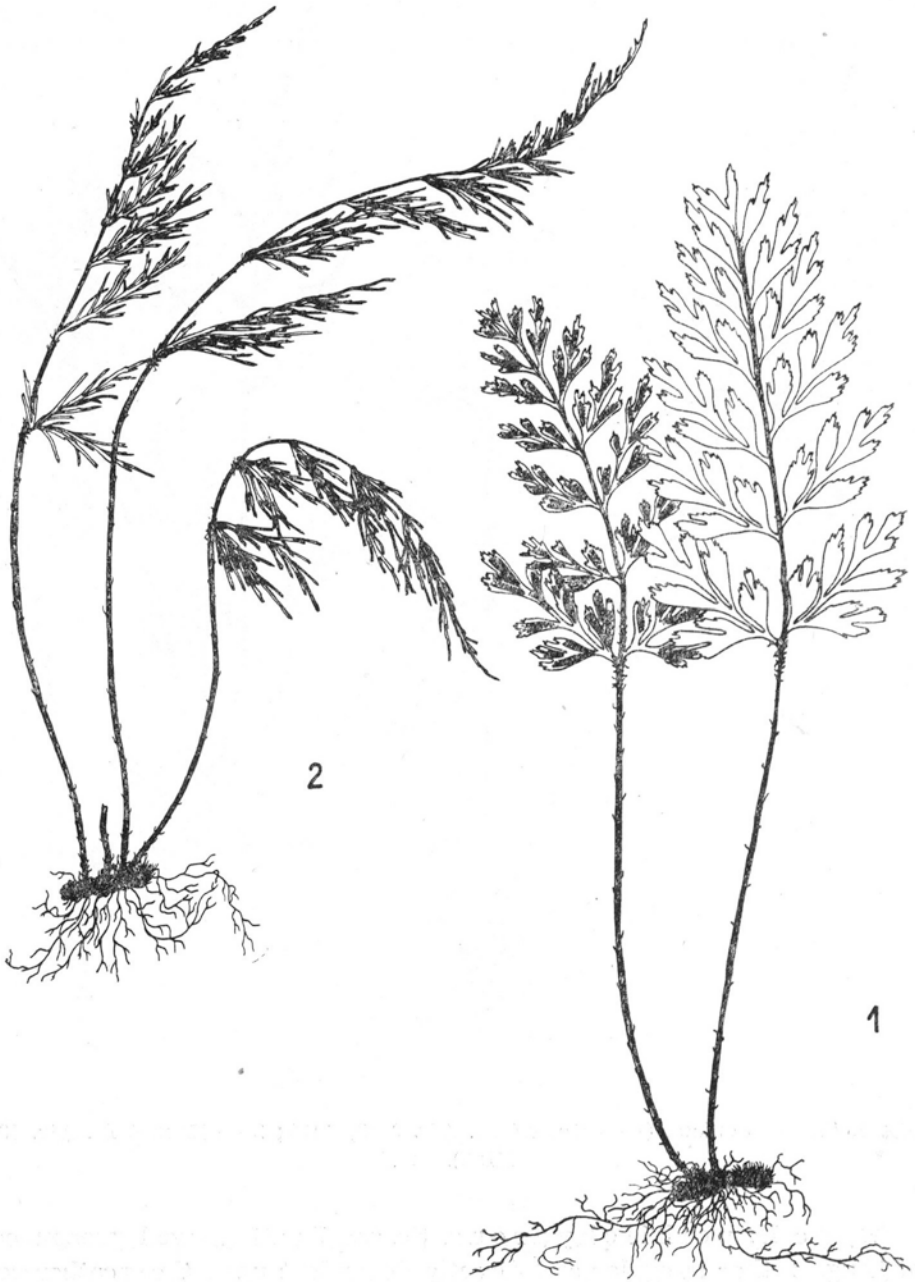


Fig. 10. *Asplenium buettneri* (1 — Kornaś Pl. Afr. 0408, KRA; 2 — Kornaś Pl. Afr. 0368, KRA). ×0.5

manes spp.). They curl up and remain alive through the drought, and unfold again * after being wetted (Figs. 8—14).

The poikilohydrous pteridophytes occur either on rocks, especially in the warm arid climatic zones (W a l t e r 1971: 314, 398), or as epiphytes in the humid tropics. In Zambia about 20% of species clearly belong to this group. About one quarter of them grow on dry rocks and rocky slopes (*Cheilanthes inaequalis, Selaginella dregei, S. imbricata,* etc.), and about three quarters occur in wet evergreen forests, either epiphytically (*Asplenium mannii, A. megalura, A. theciferum* var. *concinnum, Loxogramme lanceolata, Trichomanes pyxidiferum* var. *melanotrichum, Vittaria guineensis* var. *orientalis,* etc.), or on the forest floor (*Asplenium formosum, Pellaea doniana, Trichomanes rigidum,* etc.). Only a few poikilohydrous epiphytes with extremely xeromorphic structure are able to establish themselves in dry evergreen forests and on tree rows along the rivers (*Platycerium elephantotis, Pyrrosia schimperana).*

T y p e I I I: "summer-green". Seasonal pattern well pronounced and regular. The plants are actively growing and producing sporangia only in the rainy season; they lose their assimilating organs and become dormant in the dry season. The assimilating organs are usually mesomorphic; they die at the onset of drought, but often remain attached to the plants for some months, forming a kind of protective structure around the renewal buds. In a few species, however, the fronds are articulated and regularly shed when dry (articulated stipes in *Arthropteris* spp., *Elaphoglossum* spp., *Microgramma lycopodioides, Oleandra distenta, Pleopeltis excavata,* etc.; articulated pinnae in *Adiantum philipense, A. poiretii, Nephrolepis* spp. and *Pellaea* spp.; deciduous lamina in *Drynaria volkensii*).

The members of this group seem to be particularly well adapted to the seasonally dry climate of Zambia. They are fairly diverse and numerous (about 40% of species) and occupy a wide range of habitats, from seasonal pools (*Isoëtes* spp., *Marsilea* spp.), wet dambos and seepage areas on rocks (*Ophioglossum* spp.) to the dry upland sites. They occur especially often on the ground in the forests and woodlands, some species being attached to moist habitats (*Adiantum patens,* subsp. *oatesii, A. Poiretii, Asplenium pumilum, Athyrium schimperi, Dryopteris concolor, Dryopteris inaequalis, Elaphoglossum petiolatum* subsp. *salicifolium, Selaginella abyssinica,* etc.), the other being able to grow

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* It has to be checked, however, in how many species the assimilating organs are really able to resume their photosynthetic function after having endured by dry season. In some species this is certainly the case (e.g. *Cheilanthes farinosa, Platycerium elephantotis, Pyrrosia schimperana* and *Selaginella imbricata),* while in some others the surviving fronds serve possibly only prolonged spore dispersal (like the overwintering fronds in some ferns of the temperate zone — F a r r a r 1976).

even in dry deciduous woodlands of the miombo type. To the latter group belong the most common of all Zambian ferns (*Anemia angolensis, Arthropteris orientalis, Aspidotis schimperi, Nephrolepis undulata, Pel-*

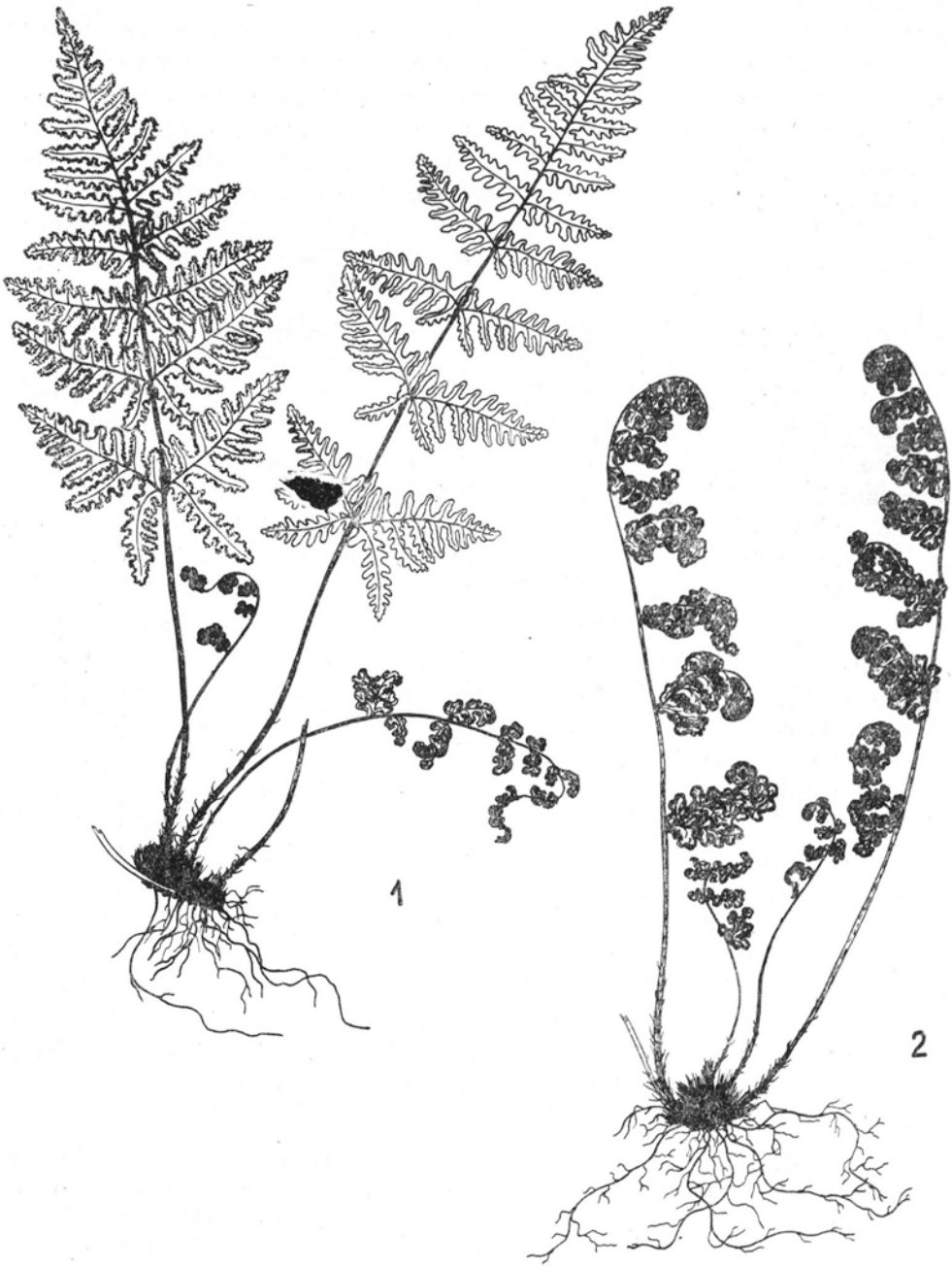

Fig. 11. *Cheilanthes farinosa* (1 — Kornaś Pl. Afr. 3958, KRA; 2 — Kornaś Pl. Afr. 0483, KRA). ×0.5

laea longipilosa, Pteridium aquilinum, etc.). The drought dormancy in them proved to be an extremely useful pre-adaptation for surviving the recurrent fires on the upland sites (K o r n a ś 1978 b). Only a few epiphytes exhibit the "summer-green" habit and prolonged drought dormancy (*Drynaria volkensii, Pleopeltis excavata,* etc.). On the other hand, there is a fairly large number of pteridophytes with such seasonal pattern on rocky slopes (*Mohria caffrorum, M. lepigera,* etc.), but most of them show some tendency towards the poikilohydrous habit, thus forming a transition between types II and III (*Actiniopteris radiata, Adiantum incisum, Cheilanthes leachii, Pellaea boivinii, P. pectiniformis,* etc.).

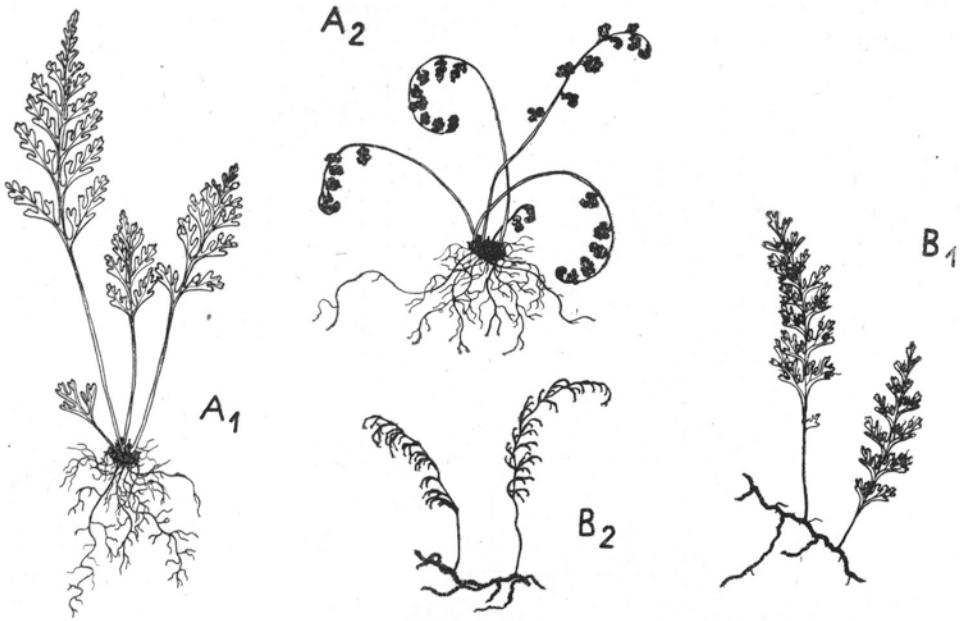

Fig. 12. A — *Asplenium theciferum* var. *concinnum* (1 — Kornaś Pl. Afr. 1759, KRA; 2 — Kornaś Pl. Afr. 1727, KRA), B — *Trichomanes pyxidiferum* var. *melanotrichum* (1 — Kornaś Pl. Afr. 3739, KRA; 2 — Kornaś Pl. Afr. 3589, KRA). ×0.5

T y p e IV: "s u m m e r - d o r m a n t". Seasonal pattern regular. Plants dormant and leafless in the rainy season, actively growing and producing sporangia during the dry months.

This rather unexpected kind of seasonal pattern, found only in *Osmunda regalis,* is apparently correlated with the seasonal changes of water level in the rivers. The sites occupied by *Osmunda* in Zambia seem to be regularly flooded during the rains and to emerge in the rainless half of the year.

According to G a m s (1938: 383), the evergreen habit (type I) has to be regarded as evolutionary primitive in the pteridophytes, which

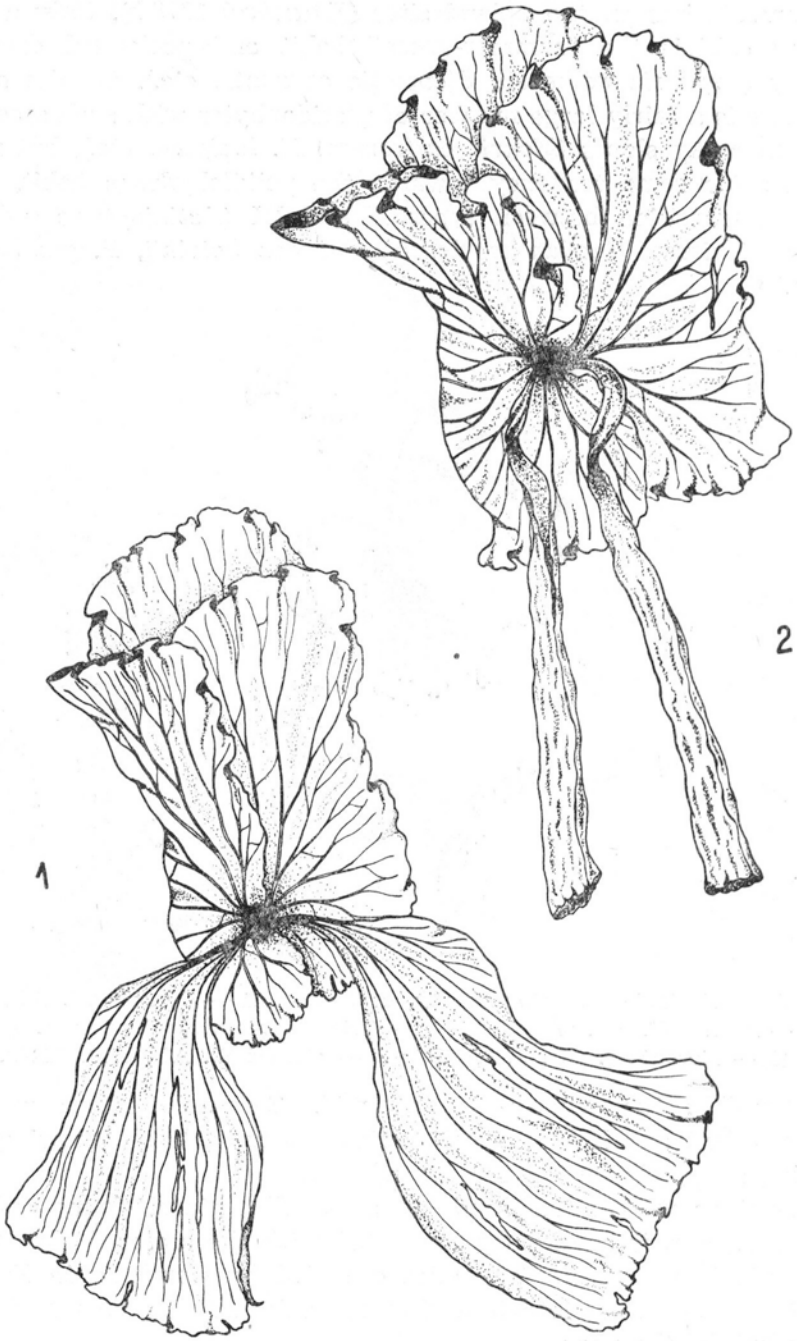

Fig. 13. *Platycerium elephantotis* (1 — Kornaś Pl. Afr. 1146, KRA; 2 — Kornaś Pl. Afr. 4030, KRA). ×0.2

apparently originated under the humid tropical climate. Both, the poikilohydrous habit (type II) and the "summer-green" habit (type III) represent two alternative strategies in colonizing the seasonally dry areas (or dry microhabitats, as in the case of the epiphytes).

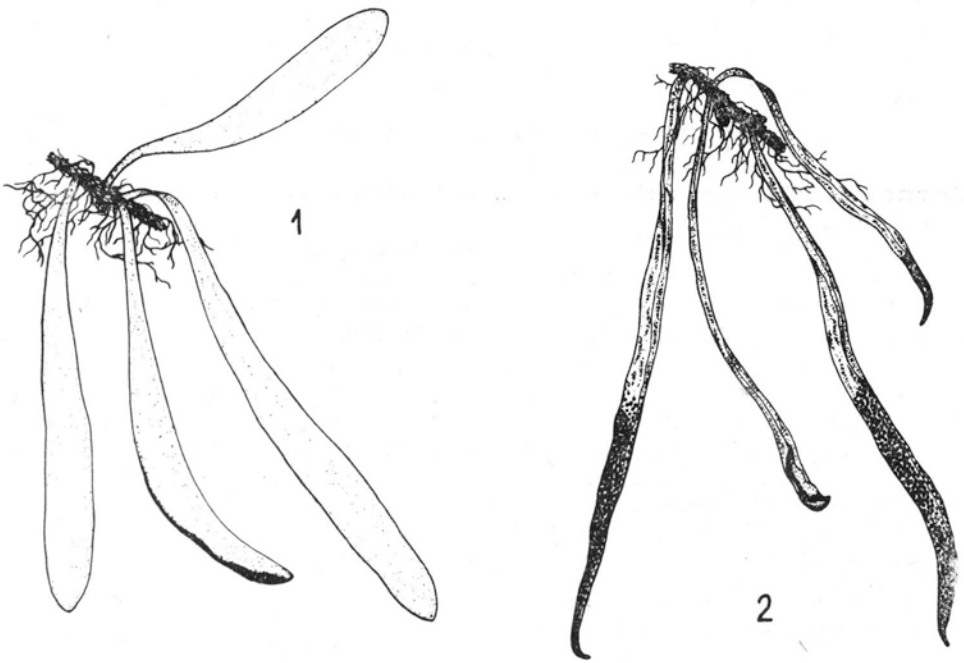

Fig. 14. *Pyrrosia schimperana* (1 — Mutimushi 16, KRA; 2 — Kornaś Pl. Afr. 3451, KRA). ×0.5

Many aspects of periodicity in the pteridophytes in Zambia are still completely unknown. Data on spore release and germination, on the development of gametophytes and sexual reproduction are urgently needed to understand the complete life cycles of individual species.

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Formy życiowe i rytmika sezonowa paprotników w Zambii

Streszczenie

146 gatunków paprotników, rosnących w Zambii, podzielono na klasy form życiowych zgodnie z systemem Raunkiaera. Klasą dominującą okazały się hemikryptofity, do których należą m.in. gatunki rozpowszechnione najszerzej. Fanerofity (paprocie drzewiaste i liany) oraz epifity są reprezentowane niezbyt licznie i ograniczone głównie do obszarów o wyższych opadach atmosferycznych na północy kraju. Skonstruowano uproszczone diagramy fenologiczne dla wszystkich paprotników zambijskich. Wyróżniono na tej podstawie trzy główne typy rytmów sezonowych: typ wiecznie zielony, typ poikilohydryczny i typ zielony latem, w okresie deszczowym. Typ wiecznie zielony związany jest z niezonalnymi siedliskami stale wilgotnymi, podczas gdy dwa pozostałe, znacznie szerzej rozmieszczone, odzwierciedlają właściwości zonalnego klimatu Zambii.