

The Underground Forests of Africa:

a preliminary review

by

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“Evolution in *Ficus* is from the thick to the thin” — E. J. H. Corner *in litt.* 27. ii. 74.

‘Evolution in Barotseland is from the thin to the thin’. Abbrided summary of this paper.

Summary

The growth-form of the geoxylic suffrutex, which has massive, woody, underground axes but only annual or short-lived shoots above ground is described. The species considered are all related to large forest or woodland trees or lianes and occur in genera with no herbaceous members. They are confined to tropical and subtropical savanna regions. Their distribution and ecology are considered. Geoxylic suffrutices are most diversified in Africa, where they have independently evolved in 31 families. Very few occur in the Sudanian Region and they are rare there. Most are endemic to the climatically similar Zambezi Region where they are centred on the Kalahari Sands which cover much of the upper Zambezi basin and its periphery. Arguments are developed which suggest that the growth form of the geoxylic suffrutex has evolved, not primarily in response to fire, nor to frost, as has been previously supposed, but as a response to the unfavourable edaphic conditions provided by extremely oligotrophic, seasonally waterlogged sandy soils in a region of extremely low relief.

Introduction

Corner's fruitful hypothesis, that the proto-Angiosperm was of pachycaul construction with an unbranched or sparsely branched stem, monopodial growth, massive apical meristem, wide pith and cortex, sparse secondary xylem, very short internodes and large compound leaves, illuminates the early adaptive radiation of the vegetative architecture of the Angiosperms and has inspired a number of important detailed studies (e.g. Hallé & Oldeman, 1970; Mabberley, 1974 a, b).

The further diversification of the leptocaul descendants of pachycaul plants, however, has received much less consideration. The purpose of this short account is to draw attention to a group of *geoxylic suffrutices*, which, despite their short stature and quasi-herbaceous habit are closely related to large forest or woodland trees or lianes, and, despite their exiguous subaerial parts, usually have massive woody subterranean structures. Most of them are trees which, for some reason, now live underground. It is interesting to enquire how this has come about.

Geoxylic suffrutices with this kind of phylogenetic relationship to large woody plants are almost confined to those parts of the tropics with a markedly seasonal distribution of rainfall, and where the prevalent vegetation is ‘savanna’ in which woody plants and grasses occur together in various proportions. The term savanna is used here in the general sense of Chapman & White (1970: 82) and not as a precise classificatory unit. Today savanna vegetation is everywhere subjected to extensive man-made fires and consists largely of pyrophytic species. It has probably always been subjected to natural fires which were formerly less frequent and more localized. Some authors, e.g. Exell & Stace (1972), believe that the suffruticose

habit in savanna regions has evolved largely as a response to fire. Fire has certainly played a part in the evolution of the geoxylic suffruticose habit, but its relative importance and significance seem to have been misunderstood.

The distribution of geoxylic suffrutices within the savanna regions of the world is very uneven. Their greatest concentration is in south-central Africa on the Kalahari Sands which cover most of the Upper Zambezi basin and its periphery. Since other elements in the Zambezian flora also show a similar distribution, White (1965) recognized a Barotse centre of endemism, which takes its name from the ancient Kingdom of Barotseland, situated near its heart.

Within the Barotse centre the most characteristic habitat of these suffrutices is a sparse open grassland which burns much less fiercely than most savanna vegetation. They are scarce or absent from the more fiercely burning types. This fact, and their localized distribution within the fireprone savanna regions, suggests that their origin should be sought not exclusively in relation to fire but that other factors should be considered.

A few suffrutices, which occur on Kalahari Sand, also extend their range into the Highveld grassland of the Transvaal, and a few others are endemic there. This is a part of Africa where frost is severe, a fact which led Burt Davy, writing at a time (1922) when the flora of Barotseland was completely unknown, to suggest that the suffruticose habit had been moulded in response to frost.

For the majority of suffruticose species occurring in the Zambezian Region speciation appears to be complete. Either their geographical ranges overlap with those of closely related large woody species, with which they presumably share a common ancestor, or they are taxonomically isolated and have no very close relatives. For a significant minority, however, speciation is incomplete. Within a single species some populations are suffruticose, whilst others are trees, shrubs or lianes. By studying these species, together with non-suffruticose species in the same general area, which have proceeded part-way towards the suffruticose habit, or show, perhaps sporadically, some of the attributes suffrutices must acquire, it is possible to reconstruct the probable ancestry of this particular growth form.

Evidence is presented in this paper which suggests that, in Africa, the geoxylic suffrutex originated primarily as a response to extremely unfavourable edaphic conditions, but that for some species, at least occasionally, fire is necessary for vigorous growth. The suffrutex is better adapted to frost than the tropical trees and lianes which gave rise to it, but it is unlikely that frost played any significant part in the evolution of the habit.

Literature on geoxylic suffrutices is sparse and scattered. Only Burt Davy (1922) has attempted a general review.

Growth Forms

There are many kinds of suffrutex and the term is often loosely or erroneously applied. The stems of a suffrutex are woody at the base and persist for several years, giving rise to less persistent shoots, which die back after a relatively short time, sometimes each year, sometimes after a longer interval. The suffrutices dealt with here are unusual, in that, at least under present-day conditions, their stems are burnt back almost to ground-level nearly every year. Suffrutices are clearly adapted to this condition. Shortly after burning and well before the onset of the rainy season they send out new shoots, which often produce flowers precociously at the base of the shoot before it is fully developed. The associated grasses and other herbs, which when fully grown may completely conceal the suffrutices, do not begin their vegetative development until after the rains break, by which time the suffrutices have finished flowering.

The suffrutices dealt with here are very sensitive to fire. Even if their shoots are only lightly singed, they die back to the base. A severe fire might kill all the subaerial parts, in which case renewal is from subterranean stems and the plant behaves as a geophyte. Normally, however, the basal parts of the subaerial stems remain and the plant behaves as a chamaephyte.

Different species of suffrutex, and sometimes different populations within species, behave differently when they are protected from fire. In some species there is a considerable die-back every year almost to the base. In other species there is a limited amount of upward growth which may continue for a few years. In obligate suffrutices, however, upward growth is severely restricted and ultimately the subaerial parts become moribund. Few flowers are produced and there is progressive die-back towards the base. In *Parinari capensis* all herbarium specimens from the northern Transvaal are less than 15 cm. tall. Burt Davy transplanted *P. capensis* "to more favourable conditions of temperature and soil moisture" but it "did not show any change of habit after several years". North of the Limpopo, when individuals escape fire, they are capable of attaining a height of 40 cm. but no more. At the extreme south-eastern limits of its range in southern Moçambique and northern Natal it can grow up to a height of 2 m.

All the suffrutices dealt with here have massive woody underground parts and the term 'geoxylic', used by Du Rietz (1921) in a somewhat different context, is appropriate. In the majority, several axes radiate just beneath the surface of the soil from the main vertical subterranean axis, which, except in young plants, is relatively poorly developed. Sometimes they extend for a distance of several metres. In some species these axes can reach a diameter of 10 cm. or more. They are usually very hard and consist mostly of secondary xylem, the total amount of which is probably no less than that of a medium-sized woodland tree growing in the same general region. These radiating axes are usually referred to as 'rhizomes'. Their true nature, however, requires careful investigation since the arboreal relatives of some suffrutices are said to sucker freely from their extensive superficial roots. The suffruticose *Parinari capensis*, for instance, looks very similar to a suckering clump of the tree species *P. curatellifolia* Planch. ex Benth. though their proportions are different.

Some species, e.g. *Erythrina baumii* Harms, have specialised water-storing tissue (Duvigneaud, 1954), but this does not seem to be a general feature.

Some species are not rhizomatous or only slightly so and the underground part consists of a large vertical axis which may be greatly expanded at ground level where many annual shoots arise. Rawitscher & Rachid (1946) describe these for *Cochlospermum insigne* St. Hil. and a palm, of the genus *Acanthococos*. They call them 'xylopodia' and say they are stems. This type seems to be rare in Africa.

This account is confined to suffrutices which not only are closely related to large trees or lianes and have presumably evolved from large trees or lianes, but occur in genera which except for their suffruticose members consist exclusively of large woody plants. Suffrutices of similar habit, though usually with smaller underground parts, which belong to otherwise shrubby groups are excluded from consideration. Similarly the suffruticose species of genera which include true herbs and trees, e.g. *Cassia* and *Phyllanthus* are omitted.

Fig. 1 illustrates *Euclea crispa* a typical "rhizomatous" geoxylic suffrutex. In this polytypic species some subspecies, like the one illustrated are obligate suffrutices, whereas others are always trees. The latter sometimes occur as single-stemmed individuals, but sometimes form thickets of trees which arise from suckers from the superficial 'roots'.



Fig. 1. *Euclea crispa* (Thunb.)
Gürke. A typical rhizomatous,
geoxylic suffrutex. Note the charred
remains of last-year's stems.

Distribution and Ecology

General distribution

Geoxylic suffrutices are a conspicuous feature of the *campos cerrados* of the Planalto of Central Brazil, and are recorded in the classical literature (Schimper, 1898: 376; Warming, 1892). No general review has been published but information can be gleaned from a scattered literature — *Andira inermis* Mart. and *Anacardium pumilum* St. Hil. (Rawitscher *et al*, 1963) *Jacaranda decurrens* Cham., *Cochlospermum insigne* St. Hil. and *Acanthococos* sp. (Rawitscher & Rachid, 1946), *Byrsonima verbascifolia* Rich. ex Juss. (Aubréville, 1961), *Chrysophyllum soboliferum* Rizzini (Mangenot, 1969), *Licania dealbata* Hook. f. and *Parinari obtusifolia* Hook. f. (Prance, 1972), and *Caryocar brasiliense* Cambess. subsp. *intermedium* (Wittmack) Prance & Freitas da Silva (Prance & Freitas da Silva, 1973).

It appears that geoxylic suffrutices are fewer in species in South America than in tropical Africa, and that taxonomically isolated, obligate suffrutices are proportionally less well represented.

In Asia it appears that there are very few geoxylic suffrutices. From Australia they seem to be absent, though many multiple-stemmed, tall-shrubby species of *Eucalyptus* have large woody underground parts (*mallee*).

It is in tropical Africa that this growth form is found in its greatest diversity. Here there are no less than 109 species belonging to 56 genera occurring in 31 families. These are listed systematically in an appendix.

Distribution in Africa

In Africa geoxylic suffrutices are almost confined to the two great savanna regions — the Zambezan and Sudanian. Only a few species occur in the transitional region to the south of the Zambezan Region, the prevalent vegetation of which is grassland and wooded grassland. There are also a few others in the southern part of the Indian Ocean coastal belt, the Tongaland-Pondoland Region, which is a mosaic of savanna-like and forest formations (Fig. 2). Since very few species are confined to the Tongaland-Pondoland Region it is not considered further.

The Sudanian Region occurs as a wide band north of the equator between the rainforests of the Guineo-Congolian Region and arid and semi-arid regions to the north. The Zambezan Region occupies a comparable position south of the equator. In area these two regions are comparable. Their vegetation which consists mainly of woodland, wooded grassland and various types of edaphic and secondary grassland, is broadly similar, as is their climate. The mean annual rainfall varies from 500 to 1500 mm, and the dry season lasts from 5 — 7 months. The Zambezan Region, however, is somewhat more diverse in its physiography and climate. In both regions dry season fires are an annual occurrence over extensive areas. Neither region can be said to be more fire-prone than the other.

The representation of geoxylic suffrutices in the two great savanna regions is very uneven. Only 7 species belonging to 2 genera in 2 families are known from the Sudanian Region, whereas 102 species in 55 genera in 30 families occur in the Zambezan Region. Of the 7 Sudanian suffrutex species, 6 belong to the genus *Combretum* and 5 of them are closely related. 4 species are of very restricted distribution and are confined to upland areas such as Fouta Djallon and the Jos Plateau. Another species, *C. sericeum* G. Don f., is of uncertain taxonomic status and is connected by intermediates to a climbing species, *C. paniculatum* Vent.

The Sudanian and Zambezan Regions are so different in their suffruticose floras that an explanation must be sought, either in their unequal opportunities for the evolution of suffruticose species or in those for the survival of a suffruticose flora which was formerly common to both.

It is well known that the flora of the Sudanian Region is, in general, much poorer than that of the Zambezan Region. In two analyses of the larger woody plants occurring in the two regions, White (1962, 1965) has shown that the flora of the Zambezan Region is probably between two and four times as rich as that of the Sudanian Region. He suggests (1962) that this may, at least in part, be due to differential extinction during the Pleistocene. A region as physiographically diverse as the Zambezan offers better opportunities for migration and survival than does a region of low general relief such as the Sudanian. There is much phytogeographical evidence to support this idea. Several species which are widespread in the Zambezan Region, e.g. *Ochna schweinfurthiana* F. Hoffm., *Protea*

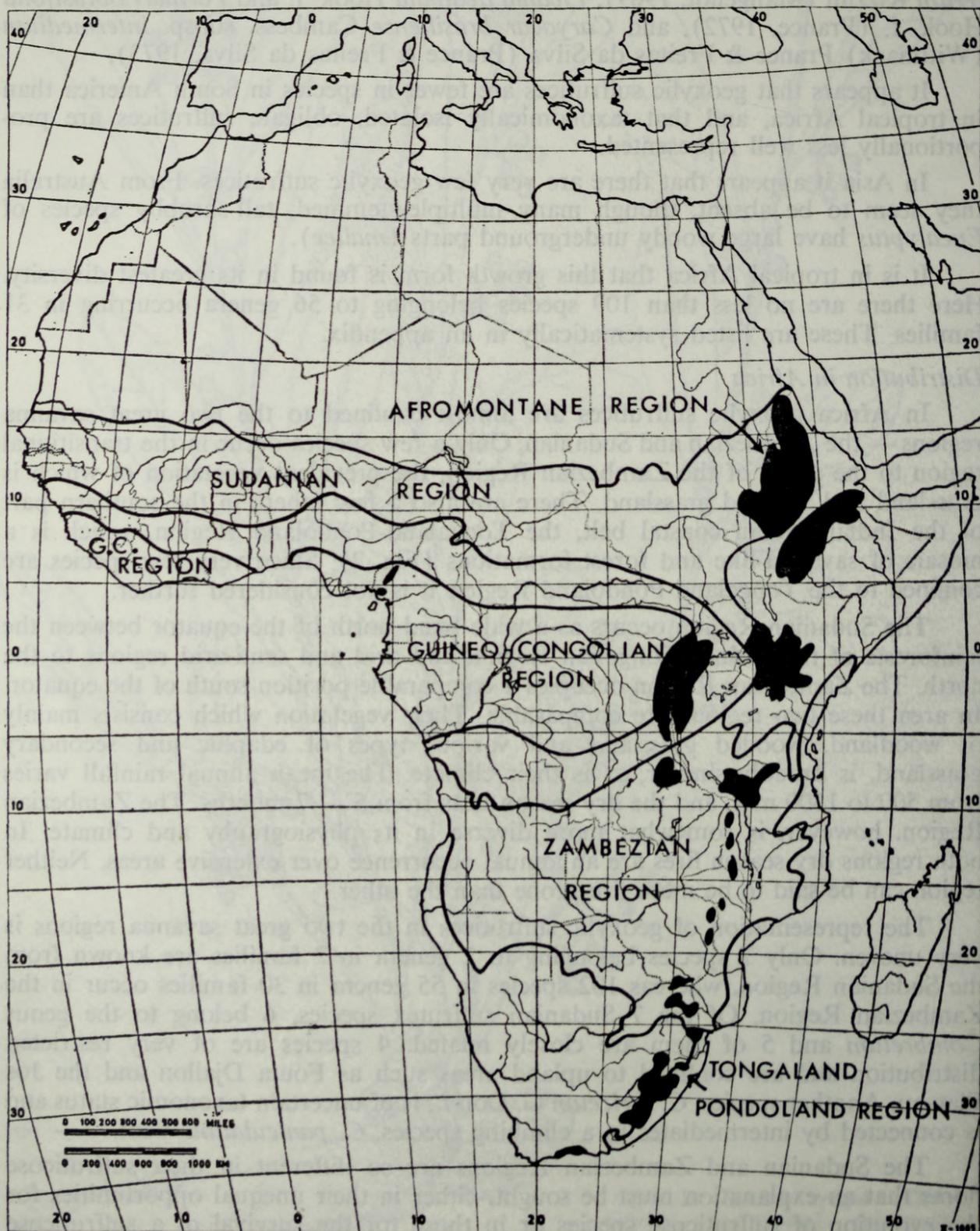


Fig. 2. Map of Africa showing chorological regions referred to in the text.

madiensis Oliv., *Terminalia mollis* Laws., are very sporadic in the Sudanian Region. Their distributions suggest that in the Sudanian Region they have only just avoided extinction due to climatic change. If they have only just managed to persist, is it not likely that some of their former associates have perished? Similar considerations might apply to the suffrutices, but here the discrepancy between the two regions is so much greater — the Zambezian suffruticose flora is 15 times as rich as the Sudanian and, at the generic level, 22 times as diversified — that the explanation must surely be sought in differential opportunity for speciation. This leads us to a consideration of the ecology of geoxylic suffrutices.

Ecology in Africa

The most characteristic habitat of the geoxylic suffrutex in the Zambezian Region is seasonally anaerobic grassland, mostly on sandy, extremely oligotrophic soils, which are waterlogged and badly aerated for part of the year and dry out at least in their upper layers during the dry season. Such conditions are inimical to the growth of trees. Even the growth of the grasses, which share dominance with Cyperaceae, is sparse and wiry.

The best-known occurrences of this habitat are at the edges of *dambos*, the seasonally waterlogged grassy depressions which are such a characteristic feature of the unrejuvenated plateau surface representing the African cycle of erosion (King, 1951) which occupies a large part of the Zambezian Region.

By far the most extensive occurrences, however, are on the Kalahari Sands which occupy the Upper Zambezi basin and its periphery, and extend northwards as a narrow belt far into the Guineo-Congolian Region (fig. 3.). The relief of this region is so gentle that waterlogged soils occur very extensively in the Zambezi basin on the virtually flat interfluves between the lower reaches of the tributary rivers of the Zambezi, and, locally, on watersheds of higher elevation which in general are better drained.

This type of anaerobic grassland with suffrutices is the most widespread vegetation type in the upper Zambezi basin (White, in press). Apart from the *dambos* mentioned above, it does not occur anywhere else in Africa, except very locally. There are small areas associated with impeded drainage in places near the coast in the Tongaland-Pondoland Region, which is contiguous with the Zambezian Region, and a few suffrutices occur there.

In the Sudanian Region anaerobic grasslands on sandy oligotrophic soils comparable to those of Zambezia are fragmentary in the extreme, because the land surface has reached a different stage in the cycle of erosion. Apart from a few small patches scattered along the coast they are confined to small areas, each only a few acres in extent, on the flat tops of mesa-like hills where the drainage is impeded by the occurrence of hardpan near the surface (J. B. Hall, *in litt.*). Under these circumstances it is difficult to see how a suffruticose flora could have evolved.

Geoxylic suffrutices are normally absent from secondary grassland following the destruction of forest or woodland. They are only plentiful on soils which are so impoverished that they can only support sparse secondary grassland which in composition and luxuriance is similar to edaphic suffruticose grassland. This occurs chiefly in montane areas and on Kalahari Sand.

Chapman & White (1970) present evidence which indicates that during the last 1000 years extensive areas of montane forest in Malawi have been destroyed by fire and replaced by grassland which owing to soil erosion has become progressively shorter and less luxuriant. The ultimate stage is a sparse grassland in which suffrutices such as species of *Protea* and *Parinari capensis* are often conspicuous. According to Fanshawe (1969: 45) sparse grassland with abundant suffrutices, which has spread from the waterlogged interfluves and depressions, may represent the last stage of degradation of Kalahari forest and woodland following clearing and persistent burning.

Kalahari Sand formerly covered a much larger area than it does today as is shown by the many residual patches which still survive.

The great majority of geoxylic suffrutices occurring in the Zambezi Region are either confined to the main occurrence of Kalahari Sand centred on Barotse-land, e.g. *Trichilia quadrivalvis* C. Dc. (fig. 3), or have their centre of distribution there, or occur within the range of the former distribution of Kalahari Sands.

The most abundant species on Kalahari Sand is *Parinari capensis*, which is also the most widespread Zambezi geoxylic suffrutex (fig. 3). It occurs beyond the former limits of Kalahari Sand on other types of sandy soil, not only the sandy

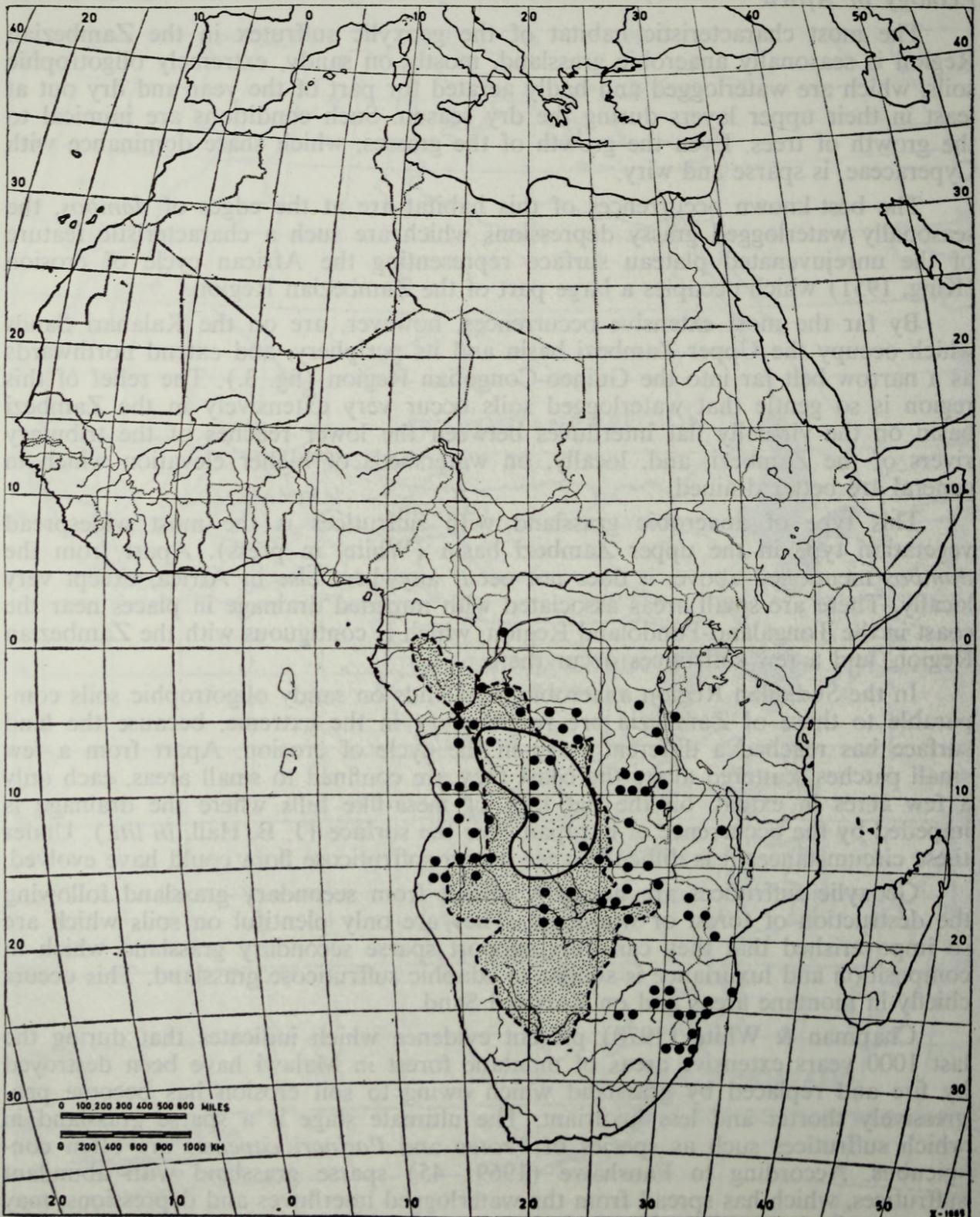


Fig. 3. Map of Africa showing distribution of (a) Kalahari Sand (broken line); (b) *Trichilia quadrivalvis* C. DC. (continuous line); (c) *Parinari capensis* Harv. (solid circles).

edges of *dambos* but also on shallow sandy soils surrounding granite inselbergs in the Transvaal and on maritime sands of the Tongaland coastal plain. Most Zambe- zian geoxylic suffrutices have distributions intermediate between those of *Trichilia quadrivalvis* and *Parinari capensis*.

Evolution

The significance of fire

In the absence of fire, some, perhaps most, suffrutices are capable of a limited amount of upward growth, but eventually the shoots become moribund and die back. Fire destroys this slowly dying, not very floriferous, material, and stimulates the production of numerous precociously-flowering shoots. This response to fire is clearly adaptive. Flowering takes place some weeks or months before the associated grasses, which eventually conceal the suffrutices, begin their growth. Their flowers are visible and accessible to pollinating insects and much of the season's growth is completed before competition for light becomes a serious factor.

It is difficult, however, to see how the suffruticose habit *arose* in response to fire. Chorological and ecological evidence are both against it.

We have seen that in Africa geoxylic suffrutices have a very uneven distribu- tion. The great majority are concentrated in part of the Zambe- zian Region. The Sudanian Region, with various qualifications mentioned elsewhere, is comparable in size, climate and flora to the Zambe- zian. The incidence of fire is the same in both, or, if anything, greater in the Sudanian, and yet the latter is almost bereft of suffrutices.

Because of the climatic vicissitudes of the Pleistocene, the Sudanian Region has suffered more extinction than the Zambe- zian, but the disparity between the two suffruticose floras, compared with that of some other growth forms, is so great, that differential extinction from a former common suffruticose flora provides an unlikely explanation.

Within the Zambe- zian Region geoxylic suffrutices show a very uneven distribution in relation to the intensity of burning. Their most characteristic habitat is edaphic grassland. This is a fire-sensitive community and is frequently burnt. But it does not burn fiercely, in contrast to most types of secondary grassland occurring in the same general area. Suffrutices are conspicuously absent from the latter. It has been demonstrated experimentally (Trapnell, 1959, White, unpublished) that when Zambe- zian woodland is subjected to annual fires at the end of the dry season, when the burn is more intense, the trees are progressively eliminated, and the grass becomes more luxuriant. Suffrutices are not normally found under these conditions. Whether fire or competition with the coarse grasses is the primary cause is uncertain. The trees may be eliminated as trees, but they are not always killed outright. The underground parts survive, and, each year, after the fire, produce an annual crop of *non-flowering* coppice shoots. Even after 40 years of yearly late burning, the rootstocks survive and, were the fires to cease, could give rise to trees again. Burning as prolonged and intense as this far exceeds the destructive effects of natural fires, or fires started in connection with land clearance and farming. Lawton (1972) has shown that under the latter conditions many tree species, even some which are relatively fire-sensitive, can become established from seed in secondary grassland which is subjected to fierce, though not necessarily annual, fires. The inescapable fact is that the woodland trees of the Zambe- zian Region are well-adapted to withstand fire — even to withstand a fire-regime far fiercer than anything they have experienced in their whole evolutionary history. They have no need to evade a menace which does not exist. In some cases the tree which is adapted to fierce fires and the related suffrutex which evades them are so similar in everything other than pattern of growth and habit that identification is difficult

when the habit is unknown. Examples of such pairs of sibling species are *Parinari curatellifolia* Planch. ex Benth. (tree) and *P. capensis*, and *Diospyros batocana* Hiern (tree) and *D. chamaethamnus* Dinter ex Mildbr. It is perhaps significant that *Parinari curatellifolia* is as common in the Sudanian Region as it is in the Zambezi, but has not given rise to a suffrutex there.

The significance of frost

Burt Davy's early account (1922) was concerned with the Highveld in the Transvaal. Here the prevalent vegetation is grassland "bare of trees except in the shelter of rocky kopjes and even there only a few scattered individuals are met with". A few suffrutices, which also occur on Kalahari Sand, e.g. *Dichapetalum cymosum*, *Elephantorrhiza elephantina* and *Parinari capensis* extend into the Highveld grassland. A few other suffrutices, e.g. *Elephantorrhiza obliqua*, *Erythrina zeyheri* and *Eugenia pusilla*, are more or less confined to it. The winters on the Highveld are cold with considerable extremes. Frosts are a regular feature. Killing frosts fall as early as March and as late as October. Burt Davy suggests that in the Transvaal the suffruticose habit has evolved in response to frost. This could very well be so for the endemic species, but probably less than 10% of the suffrutex flora of South Central Africa occur mainly in frosty regions and many species occur in or are confined to frost free regions. Other chorological and ecological evidence points in another direction.

Edaphic control

We have seen that in Africa the great majority of geoxylic suffrutices occur on the mantle of Kalahari Sand centred on Barotseland, or within the region of its former extent. They are mostly found on sandy soils on very gently sloping or almost flat surfaces. The sands, some of which have been redistributed by water, are extremely poor in nutrients. Because of the low relief and seasonal climate, the sandy soils are seasonally waterlogged and seasonally dry. The fluctuating water-table causes the formation of impervious horizons near the surface. This accentuates the seasonal differences in soil-water content and restricts the rooting environment and hence the nutrient supply of woody plants. In general, seasonally waterlogged soils in the same general region favour the growth of grasses *vis à vis* woody plants, but the Kalahari Sands are sometimes so deficient in nutrients that, even in the absence of competition from woody plants, the grass growth is sparse.

The trees of the Zambezi Region cannot withstand seasonal waterlogging followed by seasonal drying out of the soil. Under such conditions on the Kalahari Sand, and at the sandy edges of *dambos* on the Central African plateau, trees are replaced by suffrutices. Where flooding is prolonged, woody plants are completely excluded.

Except when the suffrutices are flowering, the communities they occur in have the appearance of grassland and are usually described as such. The phytomass of the suffrutices however greatly exceeds that of the grasses.

The correlation between the edaphic conditions just described and the distribution of geoxylic suffrutices is so great, and the correlation between the incidence of fire and the incidence of frost and the occurrence of suffrutices so weak, that we must postulate a causal connection for the former. We must also look for confirmatory evidence.

Although edaphic grassland with suffrutices is the most extensive vegetation type in the upper Zambezi basin, dry forest (now largely destroyed) occurs on the deeper well-drained sands, and is separated from the edaphic grassland by an ecotone of woodland and wooded grassland.

Within the upper Zambezi basin there is a complex mosaic of different edaphic conditions largely dependent on effective depth of soil and its water-relations. It is under circumstances such as these, especially where soil fertility is at a critical low level, that one would expect to find intermediate stages in the evolution of the suffruticose habit. The best example is provided by *Baikiaea plurijuga* Harms.

Baikiaea is a small genus of trees which is confined to the Guineo-Congolian Region, except for *B. plurijuga* which dominates dry semi-deciduous forest on deep well-drained Kalahari Sand in the lower half of the upper Zambezi basin. The northernmost occurrences of *B. plurijuga* are separated from the Guineo-Congolian Region by an interval of 600 km. *B. plurijuga* is normally a tree 20 m. or more in height. There are no suffruticose species of *Baikiaea*, but *B. plurijuga* has recently (Fanshawe & Savory, 1964) been found to occur on sites which appear to be intermediate between typical forest sites and typical suffruticose grassland. Here *Baikiaea* forms dwarf forests less than 2 m. tall. "If the root is excavated a candelabra effect is exposed". Just below the soil surface the original tap root gives off a number of comparatively short twisted branches from the ends of which tufted shoots arise. The latter apparently persist for no more than 4 years. This life-form of *Baikiaea* is very similar to that of a rhizomatous geoxylic suffrutex. Fanshawe and Savory suggest that the curious growth-form of *Baikiaea* might be due to a peculiarity of nutrient status but is more likely to be due to impeded drainage. A more detailed study of the edaphic conditions would be most instructive.

A change in growth-form as drastic as that between a forest tree and a geoxylic suffrutex could not be caused by the tree invading a new and very different habitat under a stable environment, followed by its descendants gradually adapting to the different conditions by mutation and selection. The original invader would be eliminated by selection from the start. Such a change is much more likely to happen if the environment of a population undergoes a gradual change to which the population gradually adapts. In a region of such low relief and imperfect drainage as Barotseland, relatively little change, either climatic or physiographic, would be necessary to bring this about. Indeed, in another publication, Fanshawe (1969b) discusses evidence which suggests that in one part of Barotseland the water-table is at present rising and causing the deaths of trees over a large area.

It is currently fashionable to interpret most patterns of plant distribution in Africa and some patterns of taxonomic relationship, especially where closely related species are involved, in terms of climatic events of the Pleistocene, very often in terms of the most recent phases, involving a period of no more than 20,000 years. Much, doubtless, can be interpreted in this way, but much cannot. It is likely that edaphic conditions favourable for the evolution of suffrutices were greatly extended in Barotseland during the pluvial periods of the Pleistocene, but this does not mean that the suffrutices originated then. Quite small physiographic events such as minor warping of the earth's crust or the capture of major tributary rivers could produce, over quite extensive areas, the kind of edaphic change required for transformation in growth form. This could have happened repeatedly over a very long period of geological time. The genus *Parinari*, which has figured so prominently in this discussion, is well represented in tropical America, Africa and Asia, and occurs in Madagascar. In its leaves, flowers and fruits it is remarkably uniform, and has diversified little since the breakup of Gondwanaland. Is it necessary to postulate that its speciation occurred in the Pleistocene? Is it not more likely that the tumultuous events of that period have merely sharpened the edges of taxa which began their differentiation a very long time before?

APPENDIX

Systematic List of Obligate and Facultative Geoxylic Suffrutices occurring in Africa.

S — occurring in Sudanian Region. T-P — occurring in Tongaland-Pondoland Region.
Z — occurring in Zambezian Region.

ANACARDIACEAE

- Z. *Heeria nitida* Engl. & v. Brehm. and
c. 8 other species
Z. *Lannea edulis* (Sond.) Engl.
Z. *L. gossweileri* Exell & Mendonça
Z. *L. katangensis* Van der Veken
Z. *L. virgata* R & A. Fernandes
Z. *Rhus kirkii* Oliv. and c. 4 other
species

ANNONACEAE

- Z. *Annona stenophylla* Engl. & Diels

APOCYNACEAE

- Z. *Chamaecлитandra henriquesiana* (K.
Schum. ex Warb.) Pichon
Z. *Landolphia gossweileri* (Stapf) Pichon
— facultative; liane
Z. *Rauvolfia nana* E. A. Bruce
Z. *Strophanthus angusii* F. White

ARALIACEAE

- Z. *Cussonia corbisieri* De Wild.

CELASTRACEAE

- Z. *Salacia bussei* Loes. — facultative;
shrub
Z. *S. luebbertii* Loes.
T-P, *S. kraussii* — (Harv.) Harv. — facul-
tative; shrub

CHRYSOBALANACEAE

- Z. *Magnistipula sapinii* De Wild.
Z. *Parinari capensis* Harv.

COCHLOSPERMACEAE

- S. *Cochlospermum tinctorium* A. Rich.

COMBRETACEAE

- Z. *Combretum argyrotichum* Welw. ex
Laws.
S. *C. brassiciforme* Exell
S. *C. harmsianum* Diels
S. *C. lineare* Keay
Z. *C. platypetalum* Welw. ex Laws.
S. *C. relictum* Hutch & Dalz.
S. *C. sericeum* G. Don f.
Z. *C. viscosum* Exell

DICHAPETALACEAE

- Z. *Dichapetalum bullockii* Hauman
Z. *D. cymosum* (Hook.) Engl.
Z. *D. rhodesicum* Sprague & Hutch.

DILLENIACEAE

- Z. *Tetracera masuiana* De Wild. & Th.
Dur.

EBENACEAE

- Z. *Diospyros chamaethamnus* Dinter ex
Mildbr.
Z, T-P. *D. galpinii* Hiern
Z, T-P. *D. lycioides* Desf. — facul-
tative; shrub, small tree
Z. *D. virgata* (Gürke) Brenan
Z. *Euclea crispa* (Thunb.) Gürke —
facultative; shrub, small tree

FLACOURTIACEAE

- Z. *Caloncoba suffruticosa* (Milne-Redh.)
Exell & Sleumer

GUTTIFERAE

- Z. *Garcinia buchneri* Engl.
Z. *Psorospermum mechowii* Engl.

IXONANTHACEAE

- Z. *Ochthocosmus candidus* (Engl. &
Gilg) Hall. f.

LECYTHIDACEAE

- Z. *Napoleona gossweileri* Baker f.

LEGUMINOSAE: CAESALPINIOIDEAE

- Z. *Brachystegia russelliae* Johnston
Z. *Cryptosepalum exfoliatum* De Wild.
— facultative, small tree
Z. *C. maraviense* Oliv.

LEGUMINOSAE: MIMOSOIDEAE

- Z, T-P *Elephantorrhiza elephantina*
(Burch.) Skeels
Z. *E. obliqua* Burt Davy
T-P *E. woodii* Phillips
Z. *Entada dolichorrhachis* Brenan
Z. *E. nana* Harms

LEGUMINOSAE: PAPILIONOIDEAE

- Z. *Erythrina baumii* Harms
Z. *E. zeyheri* Harv.

LINACEAE

- Z. *Hugonia gossweileri* Bak. f. & Exell
ex De Wild.

LOGANIACEAE

- Z. *Strychnos gossweileri* Exell — facul-
tative; liane

MALPIGHIACEAE

- Z. *Sphedamnocarpus angolensis* (A.
Juss.) Planch. ex Oliv.

MELIACEAE

- Z. *Ekebergia pumila* I. M. Johnston
Z. *Trichilia quadrivalvis* C. DC.

MORACEAE

- Z. *Ficus pygmaea* Welw. ex Hiern
 Z. *F. verruculosa* Warb. — facultative;
 small tree

MYRTACEAE

- Z. *Eugenia angolensis* Engl.
 T-P *E. capensis* (Eckl. & Zeyh.) Sond.
 — facultative; tree
 Z. *E. pusilla* N. E. Br.
 Z. *Syzygium guineense* (Willd.) DC.
 subsp. *huillense* (Hiern) F. White

OCHNACEAE

- Z. *Brackenridgea arenaria* (De Wild. &
 Dur.) N. Robson — facultative;
 shrub.
 Z. *Ochna confusa* Burt Davy & Green-
 way
 Z. *O. katangensis* De Wild.
 Z. *O. leptoclada* Oliv.
 Z. *O. macrocalyx* Oliv. — facultative;
 shrub
 Z. *O. manikensis* De Wild.
 Z. *Ochna mossambicensis* Klotzsch —
 facultative; shrub
 Z. *O. pygmaea* Hiern
 Z. *O. richardsiae* N. Robson

PASSIFLORACEAE

- Z. *Paropsia brazzeana* Baill. — faculta-
 tive; shrub

PROTEACEAE

- Z. *Protea angolensis* Welw.
 Z. *P. heckmanniana* Engl.
 Z. *P. paludosa* Welw.
 Z. *P. trichophylla* Engl. & Gilg

RHAMNACEAE

- Z. *Ziziphus zeyherana* Sond.

RHIZOPHORACEAE

- Z. *Anisophyllea quangensis* Engl. ex
 Henriques

RUBIACEAE

- Z. *Ancylanthus rubiginosus* Desf.
 Z. *Gardenia subacaulis* Stapf & Hutch.
 Z. *Leptactina benguelensis* (Welw. ex
 Benth. & Hook. f.) R. Good
 Z. *Morinda angolensis* (R. Good) F.
 White
 Z. *Pachystigma pygmaeum* (Schlecht.)
 Robyns
 Z. *Pavetta pygmaea* Brem.
 Z. *Psychotria* spp.
 Z. **Pygmaeothamnus conrescens*
 Bullock
 Z. *P. zeyheri* (Sond.) Robyns
 Z. *Tapiphyllum* spp.
 Z. *Tricalysia cacondensis* Hiern
 Z. *T. suffruticosa* Hutch.

SAPINDACEAE

- Z. *Deinbollia fanshawei* Exell

TILIACEAE

- Z. *Grewia decemovulata* Merxm. —
 facultative; shrub
 Z. *G. falcistipula* K. Schum. — faculta-
 tive; shrub
 Z. *G. herbacea* Welw. ex Hiern

VERBENACEAE

- Z. *Clerodendrum buchneri* Gürke
 Z. *C. lanceolatum* Gürke
 Z. *C. milne-redheadii* Moldenke
 Z. *C. pusillum* Gürke
 Z. *C. triplinerve* Rolfe

* This genus only has suffruticose members. It is however very closely related to the
 arborescent *Canthium*.

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... by Richards (1952, pp. 91-102) and by White (1971, pp. 118-123). The present notes are an attempt to expand the subject a little further, by recording some observations on the growth patterns of dicotyledonous herbs and comparing the contrasts both with monocotyledons and with temperate forest vegetation. At present the relations between structural features of the leaves and the photosynthetic function is, in general, rather uncertain, and this is not the field for a taxonomist to enter. Nevertheless I have ventured a few speculations, if only as a stimulus of the questions a field-botanist wants to ask. These notes are obviously limited by my personal experience, which wholly excludes the New World and is derived largely from collecting trips in Sarawak.

The importance of the massive tropical palms (*Palmeae*) and other palms (*Pandanales*) in attaining a balanced superposition of monocotyledons as a group is now widely recognized. But even at the level of rain-forest herbs a comparison between monocotyledons and dicotyledons illuminates some fundamental differences more brightly than a similar study in temperate forests. When areas are brought into the picture, it is immediately apparent that under the canopy of a strongly seasonal climate, the contrast between monocotyledons and dicotyledons has been lessened.

First let us look at growth habits, particularly at the underground parts. In temperate forests straggles or suckers with some stems are frequent, both amongst dicotyledons and monocotyledons. For instance, *Asteraceae* (Shrub *Senecio* — see Muller, 1966) or *Zostera* (*Characeae* — see K. S. Singh, Looe & Schaffer, 1961) in Europe, *Podophyllum* (*Berberidaceae* — see Smith, 1971) or *Melicope* (*Umbelliferae* — see Bell, 1974) in North America, among a rather many to be multiplied.

In the herbs of tropical rain-forest (Richards (1952, p. 76) says "... plants with underground rhizomes are frequent, but the rhizomes are adapted for mainly photosynthetic and vegetative rather than generative" — see also Richards, 1961, p. 123). The present study is equipped with underground persisting organs such as rhizomes and tubers. For these serve not as storage organs for reserves but as a means of vegetative reproduction. These rhizomes and tubers are *stolons*. They might seem to imply, as does White (1962, p. 71), that the rhizomes of temperate forest herbs do not serve for spread or vegetative reproduction of clones, but clearly do so. Secondly, in my experience, rhizomes may be common in tropical rain-forest but they are certainly very characteristic of dicotyledons in temperate rain-forest. In the two groups rhizomes are distinguished.

It may be as well to remind the reader "stolon" and "rhizome" is not when a seasonal dormancy is accompanied by complete or lack of aerial shoots. Thus the situation found in many temperate rain-forest herbs with underground rhizomes may be described as the superposition of two rhizomes. The importance of this may not be underlined in the monocotyledons. The rhizomes of some



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