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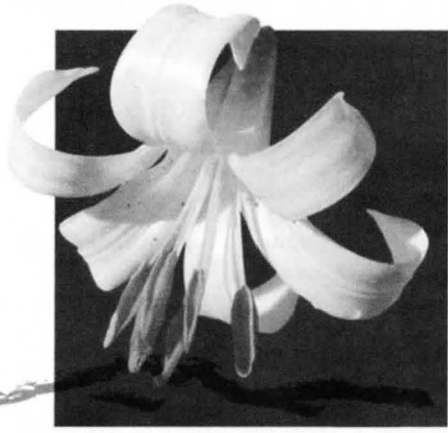
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**MONOCOTS**  
Comparative Biology and Evolution  
Excluding Poales

Morphology

## VEGETATIVE ARCHITECTURE OF DESICCATION-TOLERANT ARBORESCENT MONOCOTYLEDONS

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### ABSTRACT

Within the monocotyledons the acquisition of the tree habit is enhanced by either primary growth of the axis or a distinctive mode of secondary growth. However, a few arborescent monocotyledons deviate from this pattern in developing trunks up to four meters high that resemble those of tree ferns, i.e., their “woody-fibrous” stems consist mainly of persistent leaf bases and adventitious roots. This type of arborescent monocotyledon occurs in both tropical and temperate regions and is found within Boryaceae (*Borya*), Cyperaceae (*Afrotrilepis*, *Bulbostylis*, *Coleochloa*, *Microdracoides*), and Velloziaceae (e.g., *Vellozia*, *Xerophyta*). They have developed in geographically widely separated regions with most of them occurring in the tropics and only *Borya* being a temperate zone outlier. These mostly miniature “lily trees” frequently occur in edaphically and climatologically extreme habitats (e.g., rock outcrops, white sand savannas). Characterized by a high degree of desiccation tolerance and a certain amount of fire-resistance, these plants are xerophytes that among vascular plants possess a unique combination of ecophysiological and morphoanatomical adaptations (e.g., poikilohydry, roots with velamen radicum). Moreover, most “lily trees” tend to form clonal populations of considerable age by means of stolons or by basal branching, which provides substantial advantages for the rapid and long lasting occupation of suitable sites. A summary is given of the major vegetative traits that obviously evolved independently within Boryaceae, Cyperaceae, and Velloziaceae.

Key words: *Borya*, Cyperaceae, desiccation, rock outcrops, velamen radicum, Velloziaceae.

### INTRODUCTION

Due to the lack of a cambium in most monocotyledons the growth of their shoot systems is limited (Holttum 1955). Consequently, trees possessing woody stems are relatively rare among the monocotyledons. Within the monocotyledons the acquisition of the tree habit via true stems is either by enhanced primary growth of the axis (e.g., palms) or by a distinctive mode of anomalous secondary growth (e.g., *Aloe* L., *Cordyline* Comm. ex R. Br., *Dracaena* L., *Xanthorrhoea* Smith). Certain monocotyledons such as *Musa* L. acquire a treelike habit by developing pseudostems that consist of embracing sheaths of foliage leaves. An alternative mode of attaining a treelike habit has been achieved by a few arborescent monocotyledons in developing trunks up to four meters high that resemble those of tree ferns, i.e., their “woody-fibrous” stems consist mainly of persistent leaf bases and adventitious roots (Fig. 1–4). Within this particular group of arborescent monocotyledons the majority of species is desiccation-tolerant, i.e., survives the reversible drying out of living tissues over prolonged periods. Early reports on desiccation-tolerant arborescent monocotyledons (DAM) were provided by Hua (1906), Engler and Krause (1911), and Chevalier (1933). Subsequently, in particular Weber (1954, 1964), Ayensu (1973), and Mora-Osejo (1989) published detailed accounts on the morphology of selected DAM. However, due to the lack of ecological knowledge of DAM in their natural habitats (mainly because of the inaccessibility of their growth sites) a comprehensive treatment of this highly specialized habit was hitherto lacking. In studying a broad spectrum of DAM both in the field and under greenhouse

conditions the author has attempted to synthesize the present knowledge about DAM.

### RESULTS

#### *Desiccation-Tolerant Arborescent Monocotyledons*

In the following, basic information on the systematics, morphology/anatomy, and ecology of desiccation-tolerant arborescent monocotyledons is provided. The data given are mainly based on personal fieldwork, greenhouse observations, and laboratory analyses. When appropriate, other sources used are mentioned.

#### *Systematic Occurrence*

Within the monocotyledons, DAM have evolved independently within Asparagales (Boryaceae), Pandanales (Velloziaceae), and Poales (Cyperaceae). The genus *Borya* Labill. is restricted to Australia and contains both homoiohydrous and DAM taxa. Velloziaceae contain more desiccation-tolerant species than any other family, with over 200 species in about eight genera that are distributed in South America, tropical Africa, Madagascar, and on the southern tip of the Arabian Peninsula (Kubitzki 1998). Within Cyperaceae, DAM occur in the genera *Afrotrilepis* (Gilly) Raynal, *Bulbostylis* Kunth, *Coleochloa* Gilly, and *Microdracoides* Hua. In contrast to *Bulbostylis*, which comprises DAM in the neotropics, the other three genera with DAM occur in tropical Africa and (*Coleochloa*) Madagascar. DAM occur in different subfamilies (Cyperoideae and Scleroideae) of Cyperaceae and might have evolved independently (Goetghebeur 1998). Based on published information (e.g., Mora-Osejo



Fig. 1-4.—Representatives of desiccation-tolerant arborescent monocotyledons.—1. *Borya* species (Boryaceae), Australia, 20 cm high.—2. *Microdracoides squamosus* (Cyperaceae), up to 1.5 m tall.—3. *Xerophyta splendens* (Velloziaceae), 2200 m elev. on Mt. Mulanje, Malawi, 2 to 6 m tall.—4. *Afrotrilepis pilosa* (Cyperaceae), near Boundiali, Côte d'Ivoire, 50 cm high.

1989), other genera in Cyperaceae might also encompass DAM. In particular, genera such as *Cephalocarpus* Nees and *Everardia* Ridley ex Thurn (both occurring in northern South America, often on bare rocks), which belong to Cryptangieae contain caudex-forming dwarf shrubs that morphologically closely resemble the habit of DAM. However, there is no information available with regard to their desiccation-tolerance.

#### *Selected Morphological and Anatomical Characters*

A key morphological character of DAM is their treelike habit. They usually possess upright trunks up to four meters in height that mainly consist of persistent leaf bases and dead adventitious roots. The trunks are simple to highly branched, bear their leaves apically, and have a fibrous consistency. It has already been remarked by Engler and Krause (1911) and Chermeson (1933), for example, that the true stem itself is relatively thin and attains only a few millimeters in diameter. In both Cyperaceae and Velloziaceae, the living portions of the trunk consist of only a short apical portion. These DAM thus literally grow like epiphytes upon the dead parts of their own trunks, as has already been remarked by Chevalier (1933). *Borya* deviates from the other DAM by possessing a living stem that extends throughout the whole trunk.

The apically crowded leaves of DAM are xeromorphic (e.g., possessing considerable amounts of sclerenchyma accompanying the vascular bundles), and the stomata are mostly confined to longitudinal furrows (Ayensu 1968, 1969). The positioning of stomata in furrows allows inrolling or outrolling of the blades depending on the water status. Trichomes are frequently present on leaves, but usually no dense indumentum is formed.

The adventitious roots of DAM can grow back down along the entire length of the stem until they reach the substrate (Holm 1895). Remarkably the roots of most DAM possess a velamen radicum (Fig. 5, 6) that is otherwise mainly known to occur within epiphytic orchids (Porembski and Barthlott 1988). In DAM the velamen radicum is uni- to multiseriate (in Velloziaceae, 4–12 layered) and consists of dead cells that occasionally show circular pores in their walls, as is the case of *Microdracoides squamosus* Hua (Porembski and Barthlott 1995). In older roots the velamen radicum disintegrates due to mechanical stress, leaving a frequently multiseriate exodermis with thickened cell walls as the outermost layer. In general, the exodermis of old roots of DAM is free of passage cells.

Morphological characters of certain DAM show tremendous variation over short geographical distances. For example, variability of growth forms in the West African member of Cyperaceae, *Afrotrilepis pilosa* (Boeck.) J. Raynal, ranges from populations growing with more or less creeping stems to plants with tall, upright trunks. Moreover, this species shows large variations in leaf width and indumentum over short geographic distances. These morphological peculiarities are retained under cultivation in a greenhouse over extended periods of time (more than a decade, pers. obs.). Similar observations have been made for certain Velloziaceae, with species of *Vellozia* Vand. and *Xerophyta* Juss. especially notorious for being subject to taxonomic problems

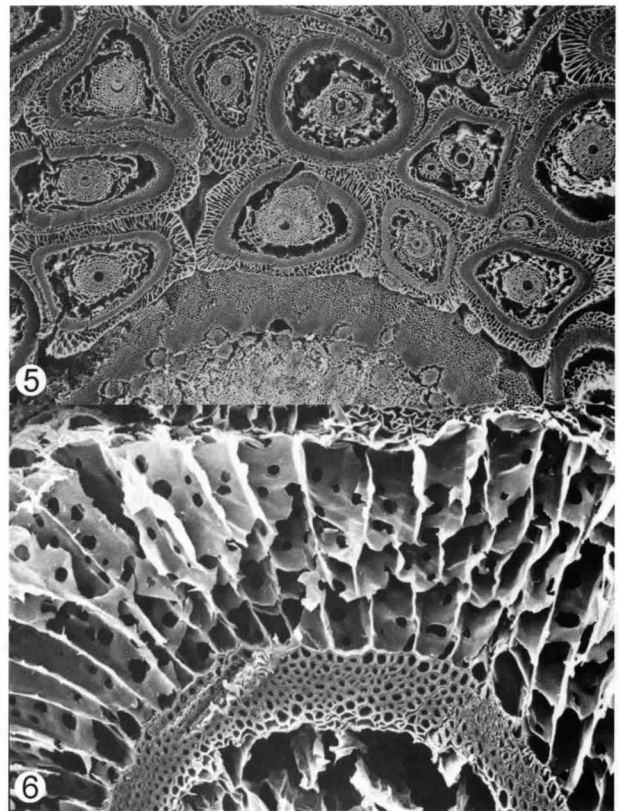


Fig. 5–6.—*Microdracoides squamosus*. The stems of desiccation-tolerant arborescent monocotyledons largely consist of adventitious roots.—5. SEM of adventitious roots and stem.—6. SEM of velamen radicum.

because of the variability of both reproductive and vegetative features.

The size spectrum of DAM comprises trunks ranging in height from ca. 20 cm (*Borya* spp.) to up to 4 m (e.g., *Xerophyta splendens* L. B. Smith and Ayensu, from Mt. Mulanje, Malawi). In the latter species, the stem diameter reaches more than 20 cm at the base. The stems usually have a grayish to blackish coloration and their surface is rather uneven due to protruding remains of leaves and adventitious roots.

#### *Ecological Aspects*

Desiccation tolerance is uncommon in vascular plants. It has been estimated that about 330 species of vascular plants are desiccation tolerant. They are dispersed over 13 families and are best represented within the monocotyledons and ferns (Gaff 1971, 1986; Porembski and Barthlott 2000). DAM are largely restricted in their habitat preferences to azonal localities. Prominent among the latter are rock outcrops, such as granitic and gneissic inselbergs and white sand savannas, which are characterized by extreme environmental conditions (e.g., high temperatures, shortage of water). Most DAM are restricted to tropical rock outcrops and occur far less frequently in temperate zones (i.e., *Borya* in Australia). On rock outcrops, DAM colonize microsites where most homoiohydrous species are not able to grow due to harsh environmental conditions. Under these adverse con-

ditions DAM (Cyperaceae and Velloziaceae) frequently dominate in matlike communities that cover even precipitous rocky slopes (Porembski et al. 1998). These mats are firmly attached to the underlying rock by a dense root system. The roots are literally glued to the rock, and no crevices or fissures are needed for their firm attachment. Mat-forming DAM may attain a considerable age of hundreds of years (Bonardi 1966; Alves 1994) and thus form relatively stable communities. Often short-lived herbaceous species become established in these mats that accumulate a considerable amount of organic material. All mat-forming DAM are poikilochlorophyllous, i.e., they lose most or all of their chlorophyll during desiccation. Dehydration of the leaves of DAM is accompanied by a change in leaf color from green to grayish between the wet and the dry state, as has already been noted by Hambler (1961) for *Afrotrilepis pilosa*. At their natural growth sites, most DAM survive in the dry state for several consecutive months (e.g., *Afrotrilepis pilosa* for six to seven months in the West African savanna zone). However, even during the rainy season, DAM are adapted to survive drought periods that occur unpredictably and thus go through several desiccation-rehydration cycles within relatively short time periods. Despite being perfectly adapted to the stressful water conditions on rock outcrops, DAM are poor competitors when compared to most homoiohydrous plants. This is mainly due to their comparatively slow growth rate that is presumably a consequence of the costs of recovery (i.e., reinitiation of cell function) after desiccation (for a survey, see Proctor and Pence 2002).

Vegetative propagation by means of stolons or basal branching is common in Cyperaceae and Velloziaceae. Many rock outcrop dwelling Cyperaceae and Velloziaceae form clonal colonies by extensive vegetative propagation. In this case clonal growth provides several advantages:

- (1) Large populations can be rapidly built up after the establishment of a single individual.
- (2) Clonal populations promote the long-term persistence (i.e., hundreds of years) at individual localities. In this case, extensive vegetative propagation, in combination with the considerable age of individual DAM, enables the long-lasting occupancy of rock outcrop habitats independent of reproductive success.
- (3) Vegetative reproduction reduces the risk of local extinction under harsh environmental conditions.

Among the ca. 330 species of desiccation-tolerant vascular plants there are no species that grow more than 6 m tall. Obviously there is an ecophysiological and possibly biomechanical limitation to the height of desiccation-tolerant plants. Most importantly, the embolism of xylem components during the process of desiccation is irreversible in large trees since repair mechanisms only work over relatively short distances (e.g., Sherwin et al. 1998). To circumvent this problem, tall DAM with trunks several meters high thus could only be developed by the restriction of living tissues to the uppermost apical stem portions, as present in certain monocots but completely lacking in dicots.

The fibrous trunks of arborescent Cyperaceae and Velloziaceae are regularly colonized by vascular epiphytes, with certain orchids showing a remarkable degree of phorophyte specificity. In tropical Africa, several species of *Polystachya*

Hook. seem to be almost exclusively restricted to mats and stems of Cyperaceae (e.g., *P. microbambusa* Kraenzl. on *Afrotrilepis pilosa*) and Velloziaceae (e.g., *P. johnstonii* Rolfe on *Xerophyta splendens*). In Brazil, certain orchids (e.g., *Constantia cipoensis* Porto & Brade, *Pseudolaelia vellozicola* (Hoehne) Porto & Brade) are largely restricted to the stems of Velloziaceae growing on rock outcrops (de Souza Werneck and Marcos do Espirito-Santo 2002). The reasons for the extraordinarily high degree of phorophyte specificity of these orchids are not known. Like tree ferns, the fibrous stems of DAM have considerable water-holding capacity that promotes the establishment of vascular epiphytes. These epiphytes, however, have to cope with extreme environmental conditions on rock outcrops, which prevent the establishment of a more profuse epiphyte flora on DAM. The remarkable water-holding capacity of the trunks of DAM is to a large extent due to the presence of roots possessing a velamen radicum, which is well known for its ability to absorb water rapidly.

#### DISCUSSION

Within the vascular plants, DAM form a unique life-form that has developed from "normal" homoiohydrous herbaceous progenitors under the constraints of harsh environmental conditions on azonal growth sites such as rock outcrops. Despite comprising only a relatively small number of species, DAM are derived from multiple evolutionary origins within the monocotyledons and have developed in different clades. The most prominent common adaptive traits of DAM are desiccation tolerance and the presence of a velamen radicum. The latter tissue acts like a sponge and enables DAM to rapidly absorb water that is only available during, or shortly after, rainfall on rock outcrops. Within the monocotyledons, a velamen radicum has mainly evolved independently within clades that comprise species that mainly rely on the atmospheric uptake of water (e.g., epiphytes, DAM).

It is conceivable that within both Velloziaceae and in the genus *Borya* (including also several homoiohydrous species), the acquisition of desiccation tolerance and a tree-like habit has occurred only once. This assumption is supported by the fact that DAM are present in all genera of Velloziaceae and occur both in the Old and New World tropics. It would be difficult to accept the idea that DAM have developed independently both in paleotropical and neotropical Velloziaceae. Rather, they had ancestral representatives that already had acquired desiccation tolerance in response to their widespread occurrence in azonal habitats before diverging geographically throughout the remnants of Gondwana. Velloziaceae are ubiquitous on azonal sites throughout their distributional area but are almost completely absent from West African rock outcrops. Possibly the presence of DAM belonging to Cyperaceae, such as *Afrotrilepis pilosa*, has prevented the successful establishment of Velloziaceae in this region. In the genus *Borya*, too, DAM are scattered throughout Australia and a multiple, independent origin of this life-form seems to be rather improbable. In contrast, DAM are certainly of multiple origin within Cyperaceae. Within this largely herbaceous family, DAM have independently arisen in the paleotropics (in the genera *Afrotrilepis*,

*Coleochloa*, and *Microdracoides*) and neotropics (in the genus *Bulbostylis*). *Microdracoides squamosus* is remarkable for its disjunct distribution in West Africa with occurrences in Guinea/Sierra Leone and, at a distance of more than 2500 km, in Nigeria/Cameroon. Further, stem-forming Cyperaceae that preferably occur on rock outcrops may qualify as DAM (e.g., the South American *Cephalocarpus dracaenula* Nees), but no details are available concerning their desiccation tolerance.

Obviously, DAM have developed in widely separated geographical regions as an adaptation in response to common environmental stress factors. Most DAM occur in the tropics, with only *Borya* being a temperate zone outlier. Possibly, low temperatures prevent the widespread presence of DAM on rock outcrops in regions with cold winters. Most DAM occur on rock outcrops that are located on old crystalline continental shields and thus frequently are of a considerable age. Open slopes on tropical rock outcrops are dominated by cryptogamic crusts that consist of cyanobacteria and lichens, and where vascular plants are comparatively rare. The occupation of steep rocky slopes by vascular plants only became possible after the development of species that were able to cope with extreme environmental conditions, such as prolonged periods of drought, and to firmly attach themselves to the underlying rock. Today, DAM are the dominant group of vascular plants (in terms of the number of individuals and biomass) on bare rocky outcrops in many parts of the tropics. Remarkably, within the dicotyledons, not a single species has developed the same adaptive traits nor can it occupy the same niche on rock outcrops as do DAM. Apart from DAM, certain lithophytic bromeliads (e.g., *Encholirium* Mart. ex Schult. & Schult. f., *Tillandsia* L., and *Vriesea* Lindl.), orchids (*Brassavola* R. Br., *Epidendrum* L.), and a few other taxa (e.g., *Anthurium* Schott), possessing external or internal water reservoirs, have become colonizers of the precipitous flanks of tropical rock outcrops. No explanation is available yet for the complete absence of DAM from tropical Asia despite the widespread distribution of rock outcrops there. Extraordinarily rich in DAM species are the southeastern Brazil rock outcrops and to a lesser degree in East Africa and Madagascar, with a consequent rich representation of Velloziaceae. Conceivably DAM have evolved in these regions, which are characterized by a vast number of azonal growth sites that offer particular speciation opportunities due to their isolated patchy distribution and considerable age.

No information is available as yet on the evolutionary age of DAM. The vast majority of DAM belongs to Velloziaceae, a strongly isolated family with affinities that are still disputed (Kubitzki 1998), and that almost completely consist of desiccation-tolerant species. Moreover, the family has a wide distribution with a focus on old continental shields. Throughout its range, Velloziaceae are rich in local endemics that occur in isolated mountain ranges. This can be interpreted as indicative of the considerable age of Velloziaceae, which probably evolved in close association with isolated azonal localities. DAM belonging to Cyperaceae occasionally have a wide distribution, such as *Afrotrolepis pilosa* that occurs as the dominant mat-forming species in West Africa, ranging from Senegal southward to Gabon. In contrast to Velloziaceae, however, cyperaceous DAM do not comprise



Fig. 7.—*Afrotrolepis pilosa* (Cyperaceae) growing on inselbergs in the vicinity of a village in the rainforest zone of Côte d'Ivoire. Regular burning by humans has caused a complete change in growth form.

a large number of local endemics. For certain taxa, such as *Afrotrolepis pilosa*, however, a considerable number of synonyms are available, demonstrating considerable morphological variation that possibly resulted from geographic isolation.

In their natural habitat, DAM suffer increasingly from human burning practices. In their dry state, stems of DAM catch fire easily and are frequently burned down to their bases. High instance of fires can lead to dramatic changes in the growth form of DAM, as is illustrated by *Afrotrolepis pilosa* (Fig. 7). Moreover, recruitment of juveniles of DAM is strongly impeded by recurrent fires (pers. obs.). In addition, the destruction of rock outcrops by human activities, such as quarrying and tourism, has severe consequences for their DAM vegetation. Slow-growing DAM are in serious danger of being replaced by short-lived or perennial exotics that become established preferentially after detrimental human impacts. For example, the bromeliad *Ananas comosus* (L.) Merr. has become established on inselbergs in humid parts of West Africa. *Ananas comosus* is a strong competitor to the indigenous DAM *Afrotrolepis pilosa* and at certain localities the bromeliad is now the dominant mat-forming species (Porembski 2000).

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