



Dedicated to Prof. Dr Karl Eduard Linsenmair (Universität Würzburg) on the occasion of his 60th birthday.

## Granitic and gneissic outcrops (inselbergs) as centers of diversity for desiccation-tolerant vascular plants

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**Key words:** *Afrotrilepis*, *Borya*, Desiccation tolerance, Granitic outcrops, *Myrothamnus*, Poikilohydry, Resurrection plants, Velloziaceae, Water stress

### Abstract

Although desiccation tolerance is common in non-vascular plants, this adaptive trait is very rare in vascular plants. Desiccation-tolerant vascular plants occur particularly on rock outcrops in the tropics and to a lesser extent in temperate zones. They are found from sea level up to 2800 m. The diversity of desiccation-tolerant species as measured by number of species is highest in East Africa, Madagascar and Brazil, where granitic and gneissic outcrops, or inselbergs, are their main habitat. Inselbergs frequently occur as isolated monoliths characterized by extreme environmental conditions (i.e., edaphic dryness, high degrees of insolation). On tropical inselbergs, desiccation-tolerant monocotyledons (i.e., Cyperaceae and Velloziaceae) dominate in mat-like communities which cover even steep slopes. Mat-forming desiccation-tolerant species may attain considerable age (hundreds of years) and size (several m in height, for pseudostemmed species). Both homoiochlorophyllous and poikilochlorophyllous species occur. In their natural habitats, both groups survive dry periods of several months and regain their photosynthetic activity within a few days after rainfall. Other desiccation-tolerant species colonize shallow depressions, crevices and even temporarily water-filled rock pools on inselbergs. Desiccation-tolerant vascular plants occur in 13 families and are best represented within the monocotyledons and ferns. Only a few desiccation-tolerant dicots exist, in the Gesneriaceae, Myrothamnaceae and Scrophulariaceae. In total, about 330 species of vascular desiccation-tolerant plants are known, of which nearly 90% occur on inselbergs. With regard to morphological adaptations, the mat-forming monocotyledons are particularly remarkable due to the possession of roots with a velamen radicum, which is reported here in the genus *Borya* for the first time.

### Introduction

Harsh environmental conditions have led to the convergent development of specific plant traits that allow for the survival of hostile environmental conditions. Remarkable and well-known in this respect are, for example, plants that cope with extreme nutrient deficiency via carnivory or that store water in different plant organs (i.e., succulents) as an adaptation to life in arid habitats. The distinctive characters of these highly specialized plant life-forms were noticed rel-

atively early and still continue to attract considerable scientific interest.

Among the life-forms that possess particular adaptations to extreme environmental conditions, desiccation-tolerant vascular plants (often called 'resurrection plants') are one of the least-known, especially with regard to ecology. This neglect may be due to the fact that most desiccation-tolerant plants occur outside the temperate zone and colonize disjunct habitats (i.e., mainly rock outcrops) that are not easy to travel to. Walter (1931) called plants whose water content closely follows fluctuations of

humidity in their environments 'poikilohydrous' in contrast to 'homoiohydrous' plants, in which water content varies relatively little. According to Hartung et al. (1998), desiccation-tolerant vascular plants are characterized by their ability to survive cycles of dehydration and rehydration without losing viability. In the desiccated state they can survive the loss of up to 80–95% of their cell water. For detailed descriptions of the physiological consequences of the nearly complete desiccation of tissues of resurrection plants the reader is referred to Gaff (1981, 1989), Bewley (1995), Hartung et al. (1998), Tuba et al. (1998) and Kluge & Brulfert (2000). Desiccation tolerance is widespread among cryptogams but is very rare among higher plants, particularly in the angiosperms. Early descriptions of desiccation-tolerant angiosperms were made by, e.g., Dinter (1918) and Heil (1924). Fahn & Cutler (1992) provided a survey of the anatomy of desiccation-tolerant vascular plants, and a number of studies have recently been conducted on their physiology (e.g., Schiller 1998; Sherwin et al. 1998; Sherwin & Farrant 1996; Tuba et al. 1998). In the last decade, desiccation-tolerant vascular plants became objects of genetic approaches aimed at identifying the molecular basis of desiccation tolerance (Bartels & Nelson 1994; Ingram & Bartels 1996), which might have considerable economic importance for future agriculture. Despite the growing interest in studying desiccation-tolerant plants, only sparse information is available on the habitat preferences and other ecological aspects of this life-form. The purpose of this contribution is to provide an overview of the main habitat preferences and the diversity of desiccation-tolerant vascular plants, and some additional information about their morphology, anatomy and biogeography.

Desiccation-tolerant vascular plants became our research subjects during plant ecological studies on granitic and gneissic outcrops ('inselbergs'). Inselbergs are monolithic rock outcrops which are only sparsely covered with soil (Figure 1). Due to harsh edaphic and microclimatic conditions, their vegetation is clearly distinct from that of their surroundings. According to Barthlott et al. (1993), a number of typical habitat types can be distinguished (e.g., monocotyledonous-mats, ephemeral flush vegetation, shallow soil-filled depressions). Since the vegetation cover of higher plants is usually relatively sparse, most of the precipitation is lost as run off. Inselbergs are widespread on old crystalline continental shields and are particularly frequent in the tropics. In most regions their vegetation is influenced by a markedly seasonal



Figure 1. Granitic and gneissic inselbergs are characterized by extreme environmental conditions and bear a vegetation that differs markedly from that of the surroundings. Throughout the tropics they form centres of diversity for desiccation-tolerant vascular plants. In the foreground is a carpet-like mat formed by a desiccation-tolerant Cyperaceae, *Afrotrilepis pilosa*, which occurs throughout West Africa.

climate; many short-lived species develop only during the rainy season. The importance of inselbergs as habitats for desiccation-tolerant vascular plants has already been emphasized (e.g., Hamblen 1961; Gaff & Churchill 1976; Gaff 1977; Meirelles et al. 1997). However, a broad survey covering this theme is still not available.

## Methods

The results presented here are based on extensive fieldwork conducted over more than a decade on hundreds of inselbergs in both temperate and tropical regions. In the Palaeotropics, the main study areas were mainland Africa (e.g., Bénin, Côte d'Ivoire, Guinea, Malawi, Zimbabwe) and Madagascar. In the New World, desiccation-tolerant species were studied with particular intensity in Brazil (including the states of Rio de Janeiro, Espírito Santo, Minas Gerais, Bahia and Pernambuco) and in the southeastern parts of the USA. Additionally, inselbergs in western Australia were studied. Data on desiccation tolerance were extracted from the literature and examinations were conducted in the field. Detailed visual examinations of plants in natural habitats in both the rainy and the dry season as well as of plants under cultivation were used to characterize species as desiccation-tolerant. Phytosociological analyses of inselberg plant communities were undertaken (for methodological details see Porembski et al. 1996, 1998) in order to detect

the habitat affinities of desiccation-tolerant vascular plants. For morphological and anatomical studies, living material of desiccation-tolerant ferns, Cyperaceae, Myrothamnaceae, Scrophulariaceae and Velloziaceae was collected in the field and cultivated in the Botanical Garden of the University of Bonn. Material fixed in FAA was examined by light- and scanning electron microscopy.

## Results

### *Geographical distribution*

Most resurrection plants occur in southern and southeastern Africa, eastern South America and western Australia (Gaff 1977, 1987). The vast majority of desiccation-tolerant vascular plants show a strong affinity for rock outcrops as natural growth sites; inselbergs are of particular importance. Desiccation-tolerant vascular plants are widely distributed on inselbergs throughout the world. However, there is a gradient of species richness from temperate regions towards the tropics, where most of the species occur (Table 1). In the tropics, seasonally wet regions are richer in desiccation-tolerant vascular plants than constantly wet or arid regions. In the Palaeotropics, eastern and southern Africa and Madagascar form centers of diversity for desiccation-tolerant vascular plants. Scrophulariaceae and Velloziaceae dominate the desiccation-tolerant vascular flora here, but Poaceae and Cyperaceae also have many species. The desiccation-tolerant Myrothamnaceae (comprising two species) is an endemic family present in Africa and Madagascar (Figure 2). Less rich in desiccation-tolerant species but still characteristic of the vegetation on outcrops in this region are ferns and the genus *Streptocarpus* (Gesneriaceae). Remarkably, the latter family is represented by a few desiccation-tolerant lithophytes in southern Europe (e.g., *Ramonda pyrenaica*). Among the ferns and fern allies, the genera *Selaginella*, *Asplenium* and *Pellaea* are dominant.

The Velloziaceae form a phytogeographical link between East African and Malagasy inselbergs and South American ones (Figure 3). Within the Neotropics this family and other desiccation-tolerant vascular plants have a center of diversity on disjunct sites in southeastern Brazil; species number rapidly declines towards other areas. Desiccation-tolerant ferns and fern allies are prominent on Brazilian inselbergs, where the genera *Anemia*, *Doryopteris* and *Selaginella*



Figure 2. On East African and Malagasy inselbergs, the desiccation-tolerant Cyperaceae *Coleochloa setifera* is the dominant mat-forming species. The mats offer growth sites for the desiccation-tolerant shrub *Myrothamnus flabellifolia* (Myrothamnaceae).



Figure 3. Miniature desiccation-tolerant 'trees' in the Velloziaceae form typical elements of the mat-vegetation of rock outcrops in South America, Africa, Madagascar and the Arabian Peninsula. At the edge of the mat of *Vellozia*, the poikilohydrous fern *Selaginella sellowii* forms dense cushions.

are most important. Ferns clearly dominate among the desiccation-tolerant vascular plants on North American inselbergs.

India and Sri Lanka are well-known for the widespread occurrence of inselbergs, but there are no detailed accounts of their vegetation. Gaff & Bole (1986) report desiccation-tolerant grasses (e.g., *Tripsogon*) from shallow soils in rocky areas in India. On Australian inselbergs, the genus *Borya* (Boryaceae) is represented by a number of desiccation-tolerant species. Most occur in the western part of the continent. The Poaceae are also well-represented among Australian resurrection plants; *Micraira* is the most species-rich genus. According to Gaff (1981), the Australian resurrection plants are less desiccation-

Table 1. Important desiccation-tolerant vascular plant genera on inselbergs. Data on geographic distribution and habitat are mainly based on personal observation. Indications of geographical region and habitat type refer to desiccation-tolerant species. An asterisk (\*) indicates original observations by the authors and their collaborators.

Genus	Family	Distribution	Habitat on inselbergs
<i>Actiniopteris</i>	Actiniopteridaceae	E. Africa	crevices, mats
<i>Afrotrilepis</i>	Cyperaceae	W. Africa	mats
<i>Anemia</i>	Schizaeaceae	S. America	crevices, mats
<i>Asplenium</i>	Aspleniaceae	Tropical Africa, Madagascar	crevices, mats
<i>Barbacenia</i>	Velloziaceae	S. America	mats
<i>Borya</i>	Boryaceae	Australia	shallow depressions, mats
<i>Chamaegigas</i>	Scrophulariaceae	Namibia	rock pools
<i>Cheilanthes</i>	Sinopteridaceae	E. Africa, S. America, Australia	crevices
<i>Coleochloa</i>	Cyperaceae	E. Africa, Madagascar	mats
<i>Craterostigma</i>	Scrophulariaceae	E. Africa	shallow depressions
<i>Doryopteris</i>	Pteridaceae	S.E. Brazil	crevices, mats
<i>Eragrostiella</i>	Poaceae	Australia	shallow depressions
<i>Eragrostis</i>	Poaceae	E., S. Africa	shallow depressions
<i>Fimbristylis</i>	Cyperaceae	Tropical Africa, Australia	crevices, shallow depressions
<i>Hemionitis*</i>	Pteridaceae	S. America	crevices, mats
<i>Limosella</i>	Scrophulariaceae	S. Africa	rock pools
<i>Lindernia</i>	Scrophulariaceae	Tropical Africa	shallow depressions, rock pools
<i>Micraira</i>	Poaceae	Australia	shallow depressions
<i>Microchloa</i>	Poaceae	Tropical Africa, S. America	shallow depressions
<i>Microdracoides*</i>	Cyperaceae	W. Africa	mats
<i>Myrothamnus</i>	Myrothamnaceae	E. Africa, Madagascar	crevices, mats
<i>Nanuzia</i>	Velloziaceae	Brazil	mats
<i>Notholaena</i>	Sinopteridaceae	N., S. America	crevices
<i>Oropetium</i>	Poaceae	S. Africa, India	shallow depressions
<i>Pellaea</i>	Sinopteridaceae	N., S. America, Africa	crevices, mats
<i>Pleurostima</i>	Velloziaceae	S. America	mats
<i>Schizaea*</i>	Schizaeaceae	E. Africa, Seychelles	crevices, mats
<i>Selaginella</i>	Selaginellaceae	Pantropical, N. America	mats
<i>Sporobolus</i>	Poaceae	Tropical Africa	shallow depressions
<i>Streptocarpus</i>	Gesneriaceae	E. Africa, Madagascar	crevices
<i>Talbotia</i>	Velloziaceae	S. Africa	mats
<i>Trilepis*</i>	Cyperaceae	S. America	mats, crevices
<i>Tripogon</i>	Poaceae	Tropical Africa, S. America, Australia	shallow depressions
<i>Vellozia</i>	Velloziaceae	S. America (mainly Brazil)	mats, shallow depressions
<i>Xerophyta</i>	Velloziaceae	Tropical Africa, Madagascar	mats, shallow depressions

tolerant than their southern African counterparts. This might indicate a shorter time period for adaptation within the genera of desiccation-tolerant species in Australia.

Desiccation-tolerant plants vary greatly in the sizes of their geographical ranges. Some species are narrow endemics and some (in particular Cyperaceae and Poaceae) are fairly widely distributed. For example, the West African species *Afrotrilepis pilosa* occurs from Senegal southeast to Gabon, a distance of more than 3500 km. Within this region, *Afrotrilepis pilosa* is present on nearly all inselbergs, absent only from those below a certain minimum size. Over its geographical range, *Afrotrilepis pilosa* shows a remarkable degree of morphological variation. For example, the main growth form in different populations ranges from plants with strictly creeping rhizomes to plants with tall, upright pseudostems. Similar morphological variation occurs in species in the Velloziaceae; many species of *Vellozia* and *Xerophyta* are taxonomic nightmares.

Most desiccation-tolerant vascular plants occur at low to moderate elevations (i.e., below 2000 m). *Xerophyta splendens* (Velloziaceae) reaches 2800 m above sea level at Mt. Mulanje in Malawi, where freezing temperatures regularly occur. This is the highest elevation at which any desiccation-tolerant plant is known to grow (Porembski 1996). Certain species show a broad range in elevation. In Brazil, *Nanuza plicata* (Velloziaceae) colonizes rocky substrates from the sea-border up to more than 1500 m a.s.l.

#### *Functional morphology and anatomy*

Most desiccation-tolerant vascular plants are monocotyledons, and these are typical elements of mat communities on inselbergs. Of particular interest are the pseudostemmed desiccation-tolerant species within the Boryaceae, Cyperaceae and Velloziaceae, which have received little previous attention. The number of studies devoted to their morphology and anatomy is small: Engler & Krause (1911), Weber (1963), Bonardi (1966), Menezes (1971), Ayensu (1974), Mora-Osejo (1989) and Porembski & Barthlott (1995). In the following text, a concise description of the major morphological and anatomical characters of these remarkable species is given. In addition, there are herbaceous resurrection plants within the Poaceae (e.g., *Tripogon minimus*) and Cyperaceae (e.g., *Kyllinga alata*). Information about their morphology and anatomy is given by Gaff (1986, 1987).

Within the monocotyledons, a tree-like habit is achieved either by enhanced primary growth of the main axis or by a distinctive mode of secondary thickening. However, a few arborescent monocotyledons deviate from this pattern. They develop trunks up to 4 m high which resemble those of tree ferns, with fibrous stems consisting mainly of persistent leaf bases and adventitious roots. This type of pseudostemmed monocotyledon occurs mainly on tropical and temperate rock outcrops and is found in the Boryaceae (*Borya*), Cyperaceae (e.g., *Afrotrilepis*, *Bulbostylis*, *Coleochloa*, *Microdracoides*) and Velloziaceae (e.g., *Vellozia*, *Xerophyta*). The parallel acquisition of desiccation tolerance and of this particular habit within these families indicates a functional link between these two characters and repeated evolutionary convergence. The architecture of these plants is probably a key adaptive trait for coping with highly variable moisture conditions.

The fibrous, simple to highly-branched pseudostems of these monocotyledons bear apical leaf rosettes and adventitious roots. In the Velloziaceae, root production shows an annual pattern. By extrapolating annual growth rates and measuring the height of individuals in the field, Alves (1994) calculated an age of 551 years for a *Vellozia kolbekii* specimen 3 m tall. Many desiccation-tolerant monocotyledons that form miniature 'lily trees' frequently tend to form clonal populations of considerable age by means of stolons or by basal branching. In Cyperaceae and Velloziaceae, the stem is completely surrounded by roots, and its living part consists of only a short apical portion. These plants thus grow like epiphytes upon the dead parts of their own pseudostems. The genus *Borya* differs in having stems with secondary growth similar to the type reported for *Thysanotus* and *Herreria* by Rudall (1995).

The leaves of the pseudostemmed Cyperaceae, Velloziaceae and species of *Borya* are xeromorphic; the stomata are confined to longitudinal furrows that permit inrolling or outrolling of the blades in response to water status. Curling and uncurling of leaves and stems occurs in many desiccation-tolerant ferns and fern allies (e.g., *Selaginella*, Lebkuecher & Eickmeier 1993), monocotyledons and dicotyledons. Curling and shrinkage during desiccation serves to protect the plants from damage due to high irradiance and high temperature. Intense shrinkage of leaves of resurrection plants without tissue damage is provided by cytorrhysis, i.e., the contraction of whole cells with tight connections between plasma membrane and cell wall.

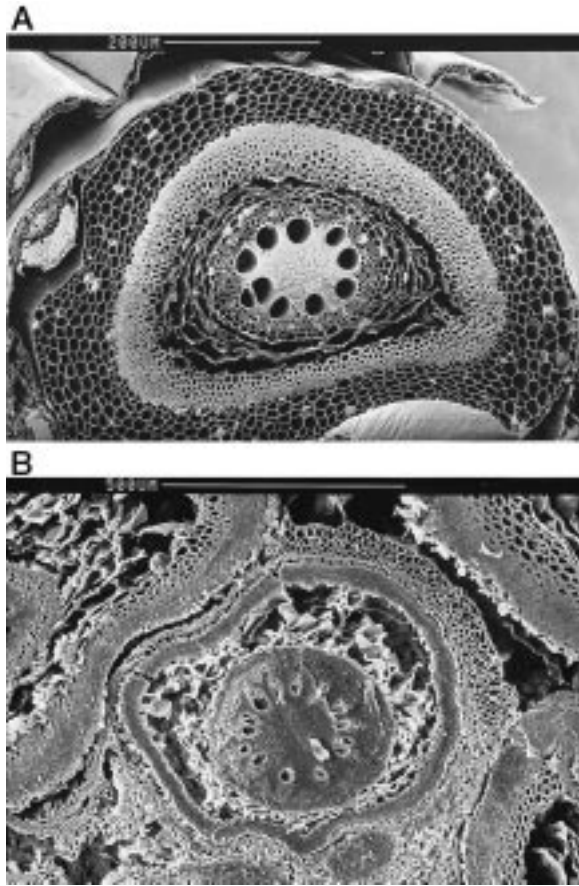


Figure 4. SEM micrographs of transverse sections through an adventitious root of: (a) *Xerophyta pinifolia* (Velloziaceae; the multilayered velamen radicum is clearly visible) and (b) *Borya sphaerocephala* (Boryaceae).

This property is lacking in drought-sensitive plants where tissues are severely damaged after dehydration (Hartung et al. 1998).

The adventitious roots of many of these outcrop-inhabiting, pseudostemmed monocotyledons possess an unusual, uni- to multiseriate velamen radicum (Figure 4a), which is here reported for the first time in the genus *Borya* (Figure 4b). Possession of a velamen is widespread within epiphytic Orchidaceae (Porembski & Barthlott 1988), where its function is related to water absorption (Barthlott & Capesius 1975). It has already been suggested (Porembski & Barthlott 1995) that desiccation-tolerant monocotyledons might also use the velamen for the rapid uptake of water. Moreover, the dense cover of roots and leaf sheaths protects the pseudostems from fire. In many species of *Vellozia*, the leaf sheaths are densely packed and glued together

by resin, keeping out oxygen and preventing burning (Alves 1994).

The fibrous pseudostems of Cyperaceae and Velloziaceae provide growth sites for a number of highly specialized epiphytic orchids. In tropical Africa and South America, certain Orchidaceae (e.g., *Polystachya microbambusa* on *Afrotrilepis pilosa*, *Polystachya johnstonii* on *Xerophyta splendens*, *Pseudolaelia amabilis* and *Constantia cipoensis* on *Vellozia* spp.) occur naturally only on desiccation-tolerant Cyperaceae and Velloziaceae and are very difficult to cultivate on other substrata. Details about the nature of this relationship are still not known.

Among dicotyledonous families, the Scrophulariaceae contains the highest number of desiccation-tolerant species. Most belong to the genera *Craterostigma* and *Lindernia* and are relatively small rosette plants. These have a centre of diversity on rock outcrops in tropical Africa. The Scrophulariaceae even includes an aquatic resurrection plant, *Chamaeigigas intrepidus*, which is endemic to Namibia and occurs in seasonally water-filled rock pools (Hickel 1967). This species has desiccation-tolerant submerged leaves which are contractile and develops desiccation-sensitive floating leaves after rainfall (Heil 1924). According to Schiller et al. (1999) the submerged leaves shrink by 75–80%, mainly due to contraction of xylem vessels characterized by extremely densely packed helical thickenings. *Chamaeigigas intrepidus* accumulates large amounts of abscisic acid during desiccation (Schiller et al. 1997).

Among the desiccation-tolerant plants the genus *Myrothamnus* (Myrothamnaceae, with two species on rock outcrops in Africa and Madagascar) is unique in possessing true woody stems. The sympodially branched shrubs may attain a height of ca. 1.5 m and bear decussate leaves which shrink and fold longitudinally during dehydration. The wood anatomy and ecophysiology of the African species *M. flabellifolia* have been studied in detail (Carlquist 1976; Sherwin et al. 1998). The species survives dehydration of roots and stems, which is accompanied by embolism in all xylem vessels. Sherwin et al. (1998) suggest that xylem refilling is due to root pressure. Gaff (1977) proposes that rehydration through the leaves is equally important; this was denied by Sherwin & Farrant (1996).

Desiccation-tolerant vascular plants differ in the length and degree of desiccation that they can survive (Gaff 1981). The most hardy resurrection plants (e.g., *Borya nitida*) survive the loss of over 94% of

their water content at full turgor, whereas the least tolerant species withstand losses of only 87% of their water content. Dehydration of the leaves of resurrection plants is usually paralleled by a change in leaf colour. In particular, the cyperaceous resurrection plants on inselbergs are remarkable for their change in leaf colour from green to greyish between the wet and the dry state. This phenomenon was noted long ago, but it was not until Hambler's (1961) work that a detailed description of a desiccation-tolerant and poikilochlorophyllous species (i.e., *Afrotrilepis pilosa*) was given. Plants which lose most or all of their chlorophyll and thylakoids are referred to as poikilochlorophyllous, in contrast to homoiochlorophyllous species, which preserve their chlorophyll content and photosynthetic apparatus during desiccation (Bewley 1979; Tuba et al. 1993). Most desiccation-tolerant monocotyledons are poikilochlorophyllous, whereas most desiccation-tolerant dicotyledonous species and ferns keep most of their photosynthetic apparatus during dehydration. Since homoiochlorophyllous species retain most of their photosynthetic apparatus, their recovery of water content and photosynthetic activity is generally more rapid than in poikilochlorophyllous plants. Rehydration after complete desiccation took 92 h for the poikilochlorophyllous *Xerophyta viscosa*, whereas leaves of the homoiochlorophyllous *Craterostigma wilmsii* were fully hydrated after 48 h (Sherwin & Farrant 1996). Detailed accounts on changes of, e.g., chloroplast structure during dehydration and rehydration were given by, e.g., Hetherington et al. (1982), Tuba et al. (1993) and Sherwin & Farrant (1996). Up to now it is not clear which of these two types is better adapted to the harsh environmental conditions encountered on rock outcrops. The African genus *Craterostigma* includes the most thoroughly studied desiccation-tolerant vascular plant species. *Craterostigma plantagineum*, an African representative of this family, has been used as an experimental model in which to elucidate the metabolic pathways leading to desiccation tolerance (Bartels et al. 1996; Ingram and Bartels 1996).

#### *Ecological aspects*

Desiccation tolerance is the most spectacular adaptation in vascular plants to the stressful water conditions on inselbergs. Observations by Ayo-Owoseye & Sanford (1972) and Gaff (1977, 1987) indicate that these species survive in the desiccated state for months or

even years and can withstand losses of their water content of more than 90%.

On rock outcrops, desiccation-tolerant vascular plants colonize microsites where environmental conditions prevent the establishment of most homoiohydrous species. In certain regions, however, resurrection plants have to compete with xerophytic desiccation-intolerant species. Monocotyledonous mats on Brazilian inselbergs usually consist of both desiccation-tolerant and desiccation-intolerant species. The mats are sometimes fairly large, in which case the latter group of species frequently dominates the central portions, whereas desiccation-tolerant species mainly occur at the periphery.

#### *Systematic distribution*

It can be stated with certainty that rock outcrops (in particular inselbergs) form a centre of diversity for desiccation-tolerant vascular plants (see Table 1 for an overview of the most important taxa) and that outcrops have played a decisive role for the convergent evolution of this life-form within non-related clades. Altogether between 250 and 300 species of desiccation-tolerant vascular plants out of 13 families are found on inselbergs, probably representing more than 90% of all resurrection plants. Among the desiccation-tolerant vascular plants, the monocotyledons (4 families) and ferns clearly outnumber the dicotyledons, and desiccation-tolerant gymnosperms are not known at all (cf., Fahn & Cutler 1992). The Velloziaceae contains more desiccation-tolerant species than any other family, with over 200 species in about 8 genera (Kubitzki 1998). These species occur mainly on rock outcrops, and almost all of them seem to be desiccation-tolerant. The number of resurrection species is far smaller in the Cyperaceae (with desiccation-tolerant species in 6 genera) and Poaceae (7 genera). However, some, in particular certain Cyperaceae, are dominants in inselberg plant communities. Three families of dicotyledons contain resurrection plants. The Myrothamnaceae and Gesneriaceae each contain only a few species. The Scrophulariaceae contains four genera with a total of more than 20 desiccation-tolerant species. It is difficult to identify any overall patterns in the systematic distribution of desiccation-tolerant angiosperms. However, it is obvious that groups that mainly contain trees have relatively few desiccation-tolerant species. The only exception is *Myrothamnaceae*, whose systematic status is disputed. It seems likely that all

other resurrection plants evolved from herbaceous ancestors and that the development of slow growing, pseudostemmed desiccation-tolerant monocotyledons is a highly derived condition.

## Conclusions

The development of desiccation tolerance among vascular plants was a key adaptive step which allowed the colonization of habitats that otherwise would only be occupied by cyanobacteria, lichens and mosses. Desiccation-tolerant vascular plants mainly occur in the tropics where they show a close affinity for rock outcrops as growth sites. Apart from the woody genus *Myrothamnus*, desiccation tolerance evolved among the angiosperms only within primarily herbaceous lineages. This is probably due to the fact that dehydration of woody stems leads to extensive xylem cavitation that is difficult to reverse after rehydration. Detailed insights into the evolution of desiccation tolerance within the angiosperms are still lacking. It seems likely that the ancestors of today's desiccation-tolerant species already occurred in seasonally dry habitats, such as inselbergs, in tropical and subtropical regions. These outcrops are not only present centres of diversity for desiccation-tolerant plants but also centers of origin for this relatively derived adaptive strategy.

Despite being less productive than non-desiccation-tolerant species, desiccation-tolerant vascular plants dominate the vegetation under certain environmental conditions. Habitats that are characterized by rapid fluctuations of water availability, like more or less soil-free rocky slopes, form highly suitable growth sites for desiccation-tolerant species. They are completely absent from vegetation types where they are outcompeted by desiccation-intolerant species. In combination with morphological (pseudostems) and anatomical adaptations (velamen radicum), desiccation tolerance allows vascular plants to establish in extreme habitats. Other life-forms that are adapted to xeric conditions, such as annuals, rely on a continuous water supply to complete their life cycle and usually cannot withstand prolonged drought while they are growing. In certain regions such as Brazil and Madagascar, the slopes of rock outcrops are covered by monocotyledonous mats which consist of desiccation-tolerant and desiccation-intolerant xeromorphic species. So far, it is still not completely clear under which circumstances desiccation-tolerant species outcompete desiccation-intolerant mat-formers and *vice versa*.



Figure 5. The blackened 'trunks' of *Afrotrilepis pilosa* are indicative of frequent fires lit by humans. Old individuals are relatively resistant to fire, but juvenile plants are not.

The desiccation-tolerant mat-formers are also threatened in many regions today by human interference. Fire frequency has increased dramatically on rock outcrops near human settlements, causing considerable damage to their vegetation on the outcrops. Most mat-formers are relatively resistant to fires. However, the habit of older individuals is seriously changed (Figure 5), and establishment from seedlings is largely inhibited. Conservation efforts to protect the unique flora and vegetation of rock outcrops should therefore focus on these ecologically highly unique desiccation-tolerant vascular plants.

## Acknowledgements

Financial support of our inselberg studies by the Deutsche Forschungsgemeinschaft is gratefully acknowledged. The authors wish to express their thanks to L. Ake Assi (Abidjan), N. Biedinger (Rostock), K. Dixon (Perth), P. Goetghebeur (Gent), A. Gröger (München), S.D. Hopper (Perth), J. Lejoly (Bruxelles), K. E. Linsenmair (Würzburg), G. Martinelli (Rio de Janeiro), M. Sales (Recife), R. Seine (Bonn), B. Sinsin (Cotonou), R. Wyatt (Athens, Georgia) and in particular to D. F. Gaff (Clayton) for valuable discussions, remarks and support during fieldwork. Moreover, we thank P. Alpert (Amherst) and Z. Tuba (Gödöllő) for their efforts to bring together all who share a common interest in desiccation-tolerant plants at the occasion of the XVI International Botanical Congress (1999) held at St. Louis, USA.



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