Chapter 8
Evolution, Diversity, and Habitats of Poikilohydrous Vascular Plants

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8.1 Introduction

Only a few species of vascular plants are able to cope with extreme temporal variations of water availability. Most higher plants are homoiohydrous, i.e., their water content varies very little. Very exceptionally the water content of vascular plants follows fluctuations of humidity in their environment. Walter (1931) called plants whose water content closely follows fluctuations of humidity in their environment poikilohydrous. Desiccation tolerant vascular plants are able to survive cycles of dehydration and rehydration without losing viability. In the desiccated state they survive the loss of up to 95% of their cellular water. Detailed overviews of the ecological and physiological adaptations of resurrection plants were provided by Gaff (1981, 1989), Bewley (1995), Hartung et al. (1998), Tuba et al. (1998), Kluge and Brulfert (2000), Walters et al. (2002) and Kappen and Valladares (2007). A survey of the anatomy of desiccation tolerant vascular plants was given by Fahn and Cutler (1992). Recently, the molecular genetics of desiccation tolerance became objects of research (for surveys see Ingram and Bartels 1996; Phillips et al. 2002, see also Chaps. 13–17).

Desiccation tolerance is widespread among cryptogams but is very rare among higher plants. Early reports of desiccation tolerant angiosperms were provided by e.g., Dinter (1918) and Heil (1924). Knowledge about their natural growth sites became more detailed through the studies of e.g., Hambler (1961) and Gaff (1977) which already emphasized the role of rock outcrops as habitats for desiccation tolerant vascular plants. Since almost two decades own studies are devoted to plant ecological investigations on granitic and gneissic outcrops (inselbergs) and ferricretes over a broad geographic spectrum. Inselbergs are characterized by harsh microclimatic and edaphic conditions, and desiccation-tolerant vascular plants dominate in certain plant communities (e.g., monocotyledonous mats). Based on extensive fieldwork and laboratory experiments, the existing knowledge on the systematic position and the ecology of desiccation tolerant vascular plants was summarized by Porembski and Barthlott (2000). It was demonstrated clearly that rock outcrops such as inselbergs form centres of diversity for poikilohydrous vascular plants. Rather neglected hitherto was the fact that the canopy of forests

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(mostly tropical) harbours numerous desiccation tolerant ferns which outnumber poikilohydrous rock outcrop dwellers. Over the last decade, more information on the number and ecology of desiccation tolerant plants have accumulated and will here be reported in an updated survey in the following.

8.2 Systematic Distribution and Evolutionary Aspects

Among higher plants desiccation tolerant species occur within ferns and fern allies and angiosperms and are completely lacking within gymnosperms. The absence of poikilohydrous species among the mostly phanerophytic gymnosperms can be explained by the fact that certain ecophysiological constraints exclude trees from being desiccation tolerant.

Preceding surveys have estimated the number of desiccation tolerant vascular plants on rock outcrops to be around c. 300 species (Porembski and Barthlott 2000). No such account has been given on the number of desiccation tolerant epiphytic vascular species. Based on own calculations their number can be estimated to comprise between 700 and 1,000 species (almost exclusively ferns). This number contains a considerable percentage of the mainly epiphytic filmy ferns (Hymenophyllaceae) that are probably mainly desiccation tolerant. Consequently the number of desiccation tolerant vascular plant species could reach c. 1,300 if all members of the Hymenophyllaceae are desiccation tolerant which seems to be rather likely (Kornás 1977; Nitta 2006). A list of desiccation tolerant genera is given in Table 8.1.

8.2.1 “Ferns” and “Fern Allies”

Within the paraphyletic group of “ferns and fern allies” both lycophytes and monilophytes (ferns sensu Pryer et al. 2004) contain desiccation tolerant species. A considerable number of both terrestrial and epiphytic ferns and fern allies are notable for colonizing xeric habitats such as inselbergs and forest canopies. For many clades, however, only anecdotic evidence is available with regard to the number of desiccation tolerant species.

Selaginellaceae form an ancient group of lycopods and date back to the Carboniferous Period (330–350 million years ago). The genus *Selaginella* (Fig. 8.1) comprises desiccation tolerant species in the subgenera *Tetragonostachys* (moss-like species with small leaves that possess thick cuticles, distributed throughout the tropics) and *Stachygynandrum* (rosette forming species such as the “Rose of Jericho” *Selaginella lepidophylla*, distributed throughout the tropics) as well as in a clade that is still unnamed (Korall and Kenrick 2002). According to the latter authors, desiccation-tolerant species evolved at least three times in different clades of *Selaginella*. Based on own observations and on available literature it can be

Table 8.1 Genera of vascular plants containing desiccation tolerant taxa (see also Table 9.1)

Genus	Family	Distribution	Growth sites
*Acanthochlamys**	Velloziaceae	SW China	Rock outcrops
Actiniopteris	Pteridaceae	Paleotropics	Rock outcrops
Afrotrilepis	Cyperaceae	W. Africa	Rock outcrops
Anemia	Schizaeaceae	S. America	Rock outcrops
*Aponogeton**	Aponogetonaceae	Paleotropics	Rock outcrops
Asplenium	Aspleniaceae	Subcosmop.	Rock outcrops
Barbacenia	Velloziaceae	S. America	Rock outcrops
Barbaceniopsis	Velloziaceae	S. America	Rock outcrops
Boea	Gesneriaceae	Paleotropics	Rock outcrops
Borya	Boryaceae	Australia	Rock outcrops
Bulbostylis	Cyperaceae	S. America	Rock outcrops
Burlemarxia	Velloziaceae	S. America (only Brazil)	Rock outcrops
Cheilanthes	Pteridaceae	Subcosmop.	Rock outcrops
Coleochloa	Cyperaceae	W./E. Africa, Mad.	Rock outcrops Rarely epiphytic
*Corallodiscus**	Gesneriaceae	Trop. Asia	Rock outcrops
Craterostigma	Linderniaceae	W./E. Africa	Rock outcrops
Doryopteris	Pteridaceae	S. America	Rock outcrops
Drynaria	Polypodiaceae	Subcosmop.	Canopy
Eragrostiella	Poaceae	Australia	Rock outcrops
Eragrostis	Poaceae	E./S. Africa	Rock outcrops
Fimbristylis	Cyperaceae	Trop. Africa, Australia	Rock outcrops
*Guzmania**	Bromeliaceae	Neotropics	Canopy
Haberlea	Gesneriaceae	S. Europe	Rock outcrops
Hemionitis	Pteridaceae	S. America	Rock outcrops
*Henckelia**	Gesneriaceae	Trop. Asia	Rock outcrops
Hymenophyllum	Hymenophyllaceae	Subcosmop.	Canopy
Jancaea	Gesneriaceae	Greece	Rock outcrops
Limosella	Plantaginaceae	S. Africa	Rock outcrops
Lindernia	Linderniaceae	Trop. Africa	Rock outcrops
Micrairia	Poaceae	Australia	Rock outcrops
Microchloa	Poaceae	Mostly Paleotropics	Rock outcrops
Microdracoides	Cyperaceae	W. Africa	Rock outcrops
Myrothamnus	Myrothamnaceae	E./S. Africa, Mad.	Rock outcrops
Nanuza	Velloziaceae	Brazil	Rock outcrops
Notholaena	Pteridaceae	N./S. America	Rock outcrops
Oropetium	Poaceae	Paleotropics	Rock outcrops
*Paraboea**	Gesneriaceae	Trop. Asia	Rock outcrops
Pellaea	Pteridaceae	Trop. Africa	Rock outcrops
Phymatosorus	Polypodiaceae	Paleotropics	Canopy Rock outcrops
Platycerium	Polypodiaceae	Mainly Paleotropics	Canopy Rock outcrops
Pleopeltis	Polypodiaceae	Subcosmop.	Canopy
Pleurostima	Velloziaceae	Brazil	Rock outcrops
Polypodium	Polypodiaceae	Subcosmop.	Rock outcrops Canopy
Ramonda	Gesneriaceae	S. Europe	Rock outcrops
Satureja	Lamiaceae	S. America	Rock outcrops
Schizaea	Schizaeaceae	E. Africa, Seychelles	Rock outcrops
Selaginella	Selaginellaceae	Pantrop., N. America	Rock outcrops

(*continued*)

Table 8.1 (continued)

Genus	Family	Distribution	Growth sites
Sporobolus	Poaceae	Paleo-/Neotropics	Rock outcrops
Streptocarpus	Gesneriaceae	E. Africa/Mad.	Rock outcrops
Talbotia	Velloziaceae	S. Africa	Rock outcrops
Trichomanes	Hymenophyllaceae	Subcosmop.	Canopy
Trilepis	Poaceae	S. America	Rock outcrops
Tripogon	Poaceae	Subcosmop.	Rock outcrops
*Trisepalum**	Gesneriaceae	Trop. Asia	Rock outcrops
Vellozia	Velloziaceae	S. America (mainly Brazil)	Rock outcrops
Xerophyta	Velloziaceae	Trop. Africa, Mad.	Rock outcrops

Information on geographic distribution and growth sites is based on literature sources and own personal observations. For genera marked with * direct proof of desiccation tolerance is still lacking. Indications on growth sites refer to desiccation tolerant taxa within the respective genus

Fig. 8.1 Dry season aspect of *Selaginella* spec. on inselberg in southern India (Karnataka). Throughout the tropics species of the genus *Selaginella* are common on rock outcrops

estimated that more than 50 species of this genus are desiccation tolerant with the vast majority living on rock outcrops both in temperate and tropical regions.

Within the monilophytes desiccation tolerant species have evolved independently several times. Among orders that contain resurrection plants are Hymenophyllales, Polypodiales, and Schizaeales. On the family level desiccation tolerant species occur in Anemiaceae (*Anemia*), Aspleniaceae (*Asplenium* s.l.), Hymenophyllaceae (*Hymenophyllum* s.l., *Trichomanes* s.l., Fig. 8.2), Polypodiaceae (e.g., *Drynaria*, *Phymatosorus*, *Platycerium*, *Polypodium*, Fig. 8.3), Pteridaceae (e.g., *Actiniopteris*, *Cheilanthes*, *Doryopteris*, *Hemionitis*, *Notholaena*, *Pellaea*, Fig. 8.4), and Schizaeaceae (*Schizaea*). It has to be emphasized, however, that more experimental tests are needed in order to conclusively decide about the desiccation tolerance of a large number of ferns (e.g., within Hymenophyllaceae). Bearing in mind the lack of robust data it can only be speculated that the number of

Fig. 8.2 Despite their delicate appearance filmy ferns such as *Trichomanes reniforme* (New Zealand) are able to survive long dry spells in a desiccated state

Fig. 8.3 The staghorn fern *Platycerium stemaria* grows epiphytically and epilithcally in wetter parts of tropical Africa

desiccation tolerant ferns ranges between 200 and 1,200 species with the higher number being more probable.

8.2.2 Angiosperms

Among angiosperms, the desiccation tolerant monocotyledons outnumber the dicotyledons. Otherwise it is difficult to identify clear patterns in the systematic distribution of desiccation tolerant angiosperms. However, it is obvious that the basal lineages of angiosperms do not contain any resurrection plants. Desiccation

Fig. 8.4 Typical elements of rock outcrop vegetation in the Paleotropics are species of the fern genus *Actiniopteris*

Fig. 8.5 Velloziaceae are the largest family of desiccation tolerant angiosperms. *Nanuza plicata* frequently occurs on inselbergs in the Brazilian Mata Atlantica-region

tolerance evolved several times independently within angiosperms and mostly within rather herbaceous lineages. Within the monocotyledons, resurrection plants have evolved independently within Alismatales (Aponogetonaceae, *Aponogeton desertorum* from Namibia seems to be poikilohydric), Asparagales (Boryaceae), Pandanales (Velloziaceae), and Poales (Cyperaceae, Poaceae and possibly Bromeliaceae). Among the monocotyledons Velloziaceae comprise most desiccation tolerant species (more than 200, Fig. 8.5) whereas Poaceae (e.g., within the genera *Microchloa*, *Tripogon*), Cyperaceae (e.g., *Afrotrilepis*, *Coleochloa*, *Microdracoides*, Fig. 8.6), and Boryaceae (*Borya*, Fig. 8.7) are by far less speciose. In addition, there are hints that Bromeliaceae too contain desiccation tolerant species.

Fig. 8.6 The stem-forming Cyperaceae *Microdracoides squamosus* is endemic on rock outcrops in West Africa

Fig. 8.7 In particular on rock outcrops in Western Australia several desiccation tolerant species of *Borya* occur

According to Zotz and Andrade (1998), the epiphytic *Guzmania monostachya* can lose more than 90% of the water present in full turgor and shows a typical response of desiccation tolerant plants. Moreover, the genus *Tillandsia* might include desiccation tolerant epiphytic and lithophytic representatives but detailed data are not available yet. Remarkable is the acquisition of the tree habit by desiccation tolerant arborescent monocotyledons (within Boryaceae, Cyperaceae, Velloziaceae, see Porembski 2006). These have mostly developed in the tropics with *Borya* being a temperate outlier.

Fig. 8.8 *Lindernia welwitschii* is a typical element of shallow depressions on rock outcrops in southern Africa

Among the dicotyledons, desiccation tolerant representatives occur within Gunnerales (Myrothamnaceae) and Lamiales (Gesneriaceae, Linderniaceae, Plantaginaceae: *Limosella*). Here Linderniaceae (*Craterostigma*, *Lindernia*, incl. *Chamaegigas*), Fig. 8.8) and Gesneriaceae (e.g., *Boea*, *Streptocarpus*, possibly also *Corallodiscus*, *Henckelia*, *Paraboea*, *Trisepalum*, see Weber 2004) each contain more than a dozen species whereas Myrothamnaceae comprise only two species (*Myrothamnus flabellifolius* in tropical Africa, *Myrothamnus moschatus* in Madagascar, Fig. 8.9).

In total c. 300 desiccation tolerant species occur within angiosperms but it should be emphasized again that more information is needed about the behaviour of certain taxa (e.g., *Tillandsia*) that might include resurrection plants too.

8.3 Habitats and Geographic Distribution

In contrast to poikilohydrous cryptogams that are conspicuous in arid ecosystems throughout the world (incl. hot deserts and Antarctica), poikilohydrous vascular plants are not centred in arid and semi-arid regions. The majority of desiccation tolerant vascular plants occur on zonal growth sites, which are characterized by very harsh environmental conditions (for details see Szarzyinski 2000) but where precipitation is higher than in deserts. It is only under these conditions that resurrection plants are not outcompeted by homoiohydrous plants and they are thus usually not found in zonal ecosystems. A further hitherto rather neglected hotspot of diversity for vascular resurrection plants is the canopy of tropical and temperate forests where poikilohydrous epiphytes (almost exclusively ferns) can occur in great profusion.

Fig. 8.9 The shrub *Myrothamnus moschatus* is endemic to Malagasy rock outcrops

Most prominent terrestrial habitats are rock outcrops such as inselbergs. The latter form centres of diversity for resurrection plants where mat-forming monocotyledons can form extensive stands. Monocotyledonous mat-formers prefer freely exposed rocky slopes, ferns rather occur in shaded places and Linderniaceae (e.g., *Craterostigma*) show a preference for shallow depressions and rock pools. Among fern allies, several species of *Selaginella* grow sun-exposed on rock outcrops in temperate and tropical regions.

The most extensive stands globally of desiccation tolerant vascular plants are found in the mountain range of the Western Ghats that in the western parts of India runs for more than 1,500 km in north–south direction. Here nearly vertical rocky slopes are characteristic where desiccation tolerant grasses (*Tripogon* spp.) cover large parts of the rocky surface (Fig. 8.10).

Moreover, lateritic plateaus (e.g., ferricretes) that are characterized by sharp contrasts between flooding in the rainy season and drought in the dry season form growth sites for desiccation tolerant plants (Fig. 8.11) in seasonal parts of the tropics. Here, Poaceae are most important with the genera *Microchloa* and *Oropetium* being prominent in the Paleotropics. In addition, ferns (e.g., *Actiniopteris* spp., *Polypodium* spp.) and Velloziaceae (in the Neotropics) are common on these flat outcrops.

Ferns represent the largest number of desiccation tolerant epiphytes with Hymenophyllaceae (only a minority of filmy ferns grows terrestrially) being particularly prominent. Based on observations by Kornás (1977) and Nitta (2006) who

Fig. 8.10 Steep rocky cliffs of the Indian Western Ghats are colonized by resurrection plants, such as grasses (*Tripogon* spp.)

Fig. 8.11 In many parts of the tropics lateritic plateaus occur with desiccation tolerant Poaceae (e.g., *Oropetium* spp., *Tripogon* spp.) being particularly important

confirmed desiccation tolerance for a considerable number of filmy fern species it could be assumed that Hymenophyllaceae (comprising c. 700 spp.) are the largest family of vascular resurrection plants. Likewise members of the Polypodiaceae (e.g., *Phymatodes*, *Platycerium*, *Polypodium*) occur with desiccation tolerant epiphytic species in tropical but also in temperate regions. Very rarely desiccation tolerant Poaceae (*Tripogon* spp., in India) and Cyperaceae (*Coleochloa* spp., tropical Africa) can be found growing epiphytically.

Reports on desiccation tolerant epiphytic angiosperms are rare with *G. monostachya* being the only example (Zotz and Andrade 1998) hitherto known. A closer examination

Fig. 8.12 The fern *Asplenium ceterach* is a common colonizer of walls in southern and maritime Europe

of other epiphytic bromeliads (particularly within *Tillandsia*) might reveal that their number is higher than hitherto expected.

A small number of resurrection plants have managed to colonize appropriate growth sites in human settlements. In Europe different species of *Asplenium* (e.g., *A. ceterach*, *A. trichomanes*, Fig. 8.12) can be found in crevices of buildings. Here they are characteristic elements of clearly circumscribed plant communities (e.g., *Asplenietea trichomanis*) that are characterized by prolonged droughts. In wetter parts of tropical Africa the staghorn fern *Platycerium stemaria* is common on roofs and walls of buildings where it can withstand periods of desiccation.

The vast majority of resurrection plants occur as epiphytes or lithophytes in the tropics. Both the tropical parts of Africa and South America are rich in desiccation tolerant monocotyledons in contrast to tropical Asia where this group is less species rich. However, our knowledge about resurrection plants from tropical Asia is comparatively poor and thus species numbers might increase for this region depending on future explorations. It can, however, be stated that southern Asia forms a centre of diversity for desiccation tolerant Gesneriaceae (e.g., *Boea*, *Corallodiscus*, *Paraboea*) where some representatives occur in altitudes above 4,500 m (*Corallodiscus kingianus*, experimental proof of desiccation tolerance is still missing). In this context it would be interesting to get more information about the desiccation tolerance of *Acanthochlamys bracteata* (high altitude areas in SW China) which is the only Asiatic representative of the largely poikilohydrous Velloziaceae.

In tropical Africa the Sudano-Zambezian Region and Madagascar form centres of diversity for poikilohydrous vascular plants. Particularly rich in species are Linderniaceae (*Craterostigma*, *Lindernia*) and Velloziaceae (*Xerophyta*) whereas

Cyperaceae (*Afrotrilepis*, *Coleochloa*, *Microdracoides*) and Poaceae (*Microchloa*, *Oropetium*, *Tripogon*) are less speciose but can become dominant on e.g., inselbergs. Some poikilohydrous members of *Lindernia* are colonizers of seasonally water-filled rock pools (e.g., the famous *L. intrepidus*, endemic to Namibia, see Heil 1924, Hartung et al. 1998; Chap. 12). Most important mat-forming taxa are *Afrotrilepis pilosa* (West Africa, see Porembski et al. 1996), *Coleochloa setifera* (East Africa, Madagascar), *Microdracoides squamosus* (West Africa), and *Xerophyta* spp. (mainly in the Zambezian Region). Endemic to tropical Africa and Madagascar are the shrubby Myrothamnaceae *M. flabellifolia* (Zambezian Region) and *M. moschatus* (Madagascar) that typically occur in monocot-mats and crevices. In the same region *Streptocarpus* spp. (Gesneriaceae) can be found on rock outcrops. Among ferns and fern allies, both lithophytes (e.g., *Asplenium*, *Pellaea*, *Selaginella*) and epiphytes (e.g., *Hymenophyllum*, *Platycerium*) occur widespread in tropical Africa and Madagascar.

In North and Central America resurrection plants are exclusively represented by mostly rock-colonizing ferns and grasses (*Sporobolus atrovirens*) that can be found from the warm temperate to the arctic regions. Most typical is the genus *Selaginella* with *Cheilanthes*, *Notholaena*, *Pellaea*, and *Polypodium* (with the lithophytic/epiphytic *P. polypodioides* and *Polypodium virginianum*) being less important (cf. Iturriaga et al. 2000). Of particular interest is the so-called Rose of Jericho *S. lepidophylla*, a characteristic colonizer of open sites in the Chihuahuan desert.

In South America rock outcrops in Brazil form centres of diversity for resurrection plants with both inselbergs and quartzitic outcrops harbouring many species (Porembski et al. 1998). The so-called campo rupestre vegetation (widespread in Minas Gerais and Bahia) is also rich in resurrection plants. Of particular importance are Velloziaceae which can be found from inselbergs at sea level up to the high altitude zone of the Itatiaia Mts. (above 2,200 m). The shrubby to tree-like Velloziaceae have their centre of diversity in the quartzitic Serra do Espinhaço where numerous local endemics (mostly *Vellozia* spp.) occur. Nearly all species grow on sun-exposed rocks and form mat-like communities or grow in crevices. Ferns and fern allies (e.g., *Doryopteris*, *Selaginella*) are the second largest taxonomic group whereas Cyperaceae (*Bulbostylis*, *Trilepis*) are of less importance and desiccation tolerant dicotyledons are almost absent. The only exception is the tiny Cactaceae *Blossfeldia liliputana* (northern Argentina, southern Bolivia). Informations on poikilohydrous epiphytic ferns in the Neotropics are sparse but it can be assumed that species of *Pleopeltis* and *Trichomanes* belong to this group (cf. Hietz and Briones 1998). Moreover, it should be tested of whether certain lithophytic and epiphytic Bromeliaceae are poikilohydrous.

In Europe ferns dominate among resurrection plants with mainly limestone colonizing species of e.g., *Asplenium*, *Cheilanthes*, *Hymenophyllum* and *Polypodium* being most prominent. These genera link tropical and temperate zones where they occur with numerous desiccation tolerant species. Only a few desiccation tolerant angiosperms occur in temperate regions such as the relictual gesneriads *Haberlea*, *Jancaea*, and *Ramonda* (Fig. 8.13) that are endemic in certain mountain areas (e.g., the Balkans) around the Mediterranean Sea.

Fig. 8.13 The gesneriad *Ramonda serbica* occurs as a paleoendemic in the Balkans

Endemic to Australia is the genus *Borya* that is common on rock outcrops where it is particularly typical in the temperate parts of this continent. In addition, ferns (e.g., *Cheilanthes*), grasses (*Micrairia* spp.), and the gesneriad *Boea hygroscopica* are present (Gaff and Latz 1978).

8.4 Adaptive Traits

Within certain groups of poikilohydrous vascular plants specific key adaptive traits occur which obviously have been evolved several times independently in close connection with their particular way of life. In the following, a concise survey is given about their most important adaptive traits from a morphological–anatomical viewpoint.

There are differences in the ability to survive periods of drought between individual desiccation tolerant species. It is conceivable that factors such as speed of tissue desiccation, duration of desiccation, and temperature influence the desiccation tolerance of poikilohydrous plants. However, the data hitherto available are still too fragmentary, and it is thus not possible to draw conclusions on the relationships between the degree of desiccation tolerance and taxonomic or ecological characteristics. Nevertheless one can possibly outline some tendencies. Based on own observations it can be stated that both in temperate and tropical regions certain species of *Selaginella* seem to be among the most desiccation tolerant colonizers of rock outcrops. According to Gaff (1981) the most hardy resurrection plants (e.g., *Borya nitida*) survive the loss of over 94% of their water content at full turgor. Dehydration of leaves of poikilohydrous species is often accompanied by a change in leaf colour. With regard to this aspect, one can distinguish between poikilochlorophyllous (i.e., losing most or all of their chlorophyll) and homoiochlorophyllous (i.e., species that preserve their chlorophyll content) plants. Most poikilohydrous monocotyledons are poikilochlorophyllous whereas most desiccation tolerant dicots and ferns are homoiochlorophyllous. The latter are usually more rapid in recovering their water content and photosynthetic activity.

As far as their reproductive traits are concerned, vascular resurrection plants have not developed unique strategies. Among desiccation tolerant angiosperms, both pollination by wind (Cyperaceae, Myrothamnaceae, Poaceae) and animals (Gesneriaceae, Linderniaceae, Velloziaceae) can be found. Among the latter, entomophily seems to dominate but for certain Velloziaceae pollination by bats and birds has been reported too (e.g., Sazima and Sazima 1990). Dispersal of diaspores over larger distances seems to be almost exclusively by wind but on a smaller scale water dispersal could play a role too. Moreover, accidental transport of diaspores by birds cannot be ruled out. The lack of fleshy fruits is probably a consequence of the vagaries of water availability that makes the production of berries or drupes for desiccation tolerant plants too risky. Most poikilohydrous angiosperms have hermaphrodite flowers but dioecy (*Microdracoides*, *Myrothamnus*) and monoecy (Cyperaceae) are likewise present.

Leaf size of poikilohydrous vascular plants varies widely from tiny leaflets (e.g., *Selaginella*) up to the large fronds (e.g., *P. stemaria*) of certain ferns. With regard to leaf shape it can be stated that all poikilohydrous angiosperms possess undivided leaves whereas other types of leaves are completely lacking. This is in contrast to ferns and fern allies where both undivided and divided leaves occur. Very common in all groups of vascular resurrection plants is the curling of leaves during the process of desiccation what appears to be a mechanism for avoiding photoinhibitory damage.

Desiccation tolerant arborescent monocotyledons form a remarkable example of convergent evolution. This type of arborescent monocotyledons 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 possess a number of ecophysiological and morphoanatomical adaptations (e.g., roots with velamen radicum, Porembski and Barthlott 1995) that render them perfectly adapted for the colonization of rock outcrops. Besides their treelike habit, their ability to form clonal populations of considerable age (i.e., hundreds of years) by means of stolons or by basal branching allows for the long lasting occupation of suitable sites (for details see Porembski 2006). The trunks of arborescent Cyperaceae and Velloziaceae are regularly colonized by vascular epiphytes with certain orchids (e.g., *Polystachya* spp. in tropical Africa, *Pseudolaelia vellozicola* in Brazil) showing a remarkably high degree of phorophyte specificity (Porembski 2005).

A further remarkable example of a highly specialized resurrection plant is provided by *Lindernia* (*Chamaegigas*) *intrepidus* (Chap. 12) which is endemic to Namibia where it occurs in seasonally water-filled rock pools (Heil 1924; Heilmeier et al. 2005). This species has desiccation tolerant submerged leaves which are contractile and develops desiccation sensitive floating leaves after rainfall. The submerged leaves shrink by 75–80%, mainly due to contraction of xylem vessels that are characterized by extremely densely packed helical thickenings (Schiller et al. 1999).

8.5 Economic Importance

Resurrection plants have become important experimental models for understanding the physiological and molecular aspects of desiccation tolerance. In the future this knowledge might be of interest for the development of drought tolerant crop species (Vicré et al. 2004).

Whereas the vast majority of resurrection plants are currently not yet used economically a limited number of them is of economic relevance. One of the best known examples is the "Rose of Jericho" (*S. lepidophylla*, a Chihuahuan element, USA and Mexico) which is globally sold for ornamental purposes. Apart from this example, resurrection plants are rarely used as ornamentals. This is the case with *M. squamosus* in the surroundings of the Cameroonian capital Yaoundé. Here individuals of this showy species are collected on inselbergs and sold in markets. A further case of commercial use of poikilohydrous plants is the sale of the epiphytic fern *P. stemaria* as ornamental in West Africa (Porembski and Biedinger 2001).

An additional case is the "wonder bush" (*M. flabellifolia*) which is marketed in large amounts in parts of southern Africa. The species is commonly used as a medicinal plant (for its antimicrobial attributes see van Vuuren 2008) throughout its distributional range where local collecting activities sometimes take a heavy toll on local populations on inselbergs (own observations in Angola). Certain leaf ingredients provide components of skin moisturizing creams which are sold globally as is the case with individual twigs of this species that are marketed under the name "wonder bush". Own recent observation have shown that the Malagasy inselberg endemic *M. moschatus* too is used as a medicinal plant which is sold in local markets.

Alves (1994) reports on the sale of c. 50 cm long stem segments of *Vellozia* species in Brazil (Bahia) which are used as fire starters that burn even in torrential rains.

8.6 Conservation

Up to now almost no vascular resurrection plants are protected by law in their countries of origin. This is mainly due to the fact that most of them occur in rather inaccessible habitats and thus have escaped the attention of conservationists. However, there are numerous dangers to these species with the destruction of their habitats being the most relevant factor for the decrease in population numbers. The list of the driving forces behind the destruction of their habitats (forest canopies, rock outcrops) includes the conversion of forest in farmland, quarrying, human-lit fires, grazing, and off-road driving. In addition, the introduction of invasive weeds can also impose serious threats on desiccation tolerant plants. For example, this has been the case on certain inselbergs in the West African rainforest zone where introduced pineapples (*Ananas comosus*) have occasionally outcompeted *A. pilosa*. All over the world the most serious threats to the habitats of desiccation

Fig. 8.14 Burnt stems of *Microdracoides squamosus* due to human lit fires on an inselberg in Cameroon

tolerant rock outcrop colonizing plants are both quarrying and fire. Due to the ever increasing demand for rocks for e.g., construction works the quarrying of inselbergs has regionally reached dramatic extents as can be seen around Bangalore (southern India) where numerous inselbergs have completely disappeared during the last decades. Human lit fires are particularly widespread nowadays on inselbergs where mat communities made up by desiccation tolerant Cyperaceae and Velloziaceae are heavily influenced (Fig. 8.14). Whereas old specimens are relatively well protected against fire by their insulating sheaths of adventitious roots and old leaves, recruitment by juveniles becomes extremely limited.

Certain resurrection plants are endangered by the collection of huge amounts of individuals for ornamental purposes (s. above). One of the best known examples is *S. lepidophylla* that is currently imported in large numbers into the European Community as to warrant monitoring.

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