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# 2 Opportunistic Growth and Desiccation Tolerance: The Ecological Success of Poikilohydrous Autotrophs

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## POIKILOHYDROUS WAY OF LIFE

Poikilohydry, or the lack of control of water relations, has typically been a subject studied by lichenologists and bryologists. For many years, much was unknown about poikilohydrous vascular plants, and evidence for their abilities was mostly anecdotal. A small number of these plants were studied by a few physiologists and ecologists who were fascinated by the capability of these “resurrection plants” to quickly switch from an anabiotic to a biotic state and vice versa (Pessin 1924, Heil 1925, Walter 1931, Oppenheimer and Halevy 1962, Kappen 1966, Vieweg and Ziegler 1969). Recently, a practical demand has released an unprecedented interest in poikilohydrous plants. The increasing importance of developing and improving technologies for preserving living material in the dry state for breeding and medical purposes has induced tremendous research activity aimed at uncovering the molecular and biochemical basis of desiccation tolerance. Poikilohydrous plants have proven to be very suitable for exploring the basis of this tolerance with the target of genetic engineering (Stewart 1989, Oliver and Bewley 1997, Yang et al. 2003, Bernacchia and Furini 2004, Alpert 2006). Consequently, much of the current literature discusses poikilohydrous plants mainly as a means of explaining basic mechanisms of desiccation tolerance (Hartung et al. 1998, Scott 2000, Bartels and Salamini 2001, Rascio and Rocca 2005) instead of exploring their origin, life history, and ecology (Raven 1999, Porembski and Barthlott 2000, Belnap and Lange 2001, Ibisch et al. 2001, Proctor and Tuba 2002, Heilmeier et al. 2005).

Many new resurrection plants have been discovered during the last 25 years, especially in the Tropics and the Southern Hemisphere (Gaff 1989, Kubitzki 1998, Proctor and Tuba 2002). This has provided new insights into the biology of these organisms. In this chapter, structural and physiological features of poikilohydrous autotrophs and the different strategies in different ecological situations are discussed. As desiccation tolerance itself is the most—but not only—striking feature, our goal is to assess in addition the life style and the ecological success of poikilohydrous autotrophs. We give attention to the productivity of poikilohydrous autotrophs, how they manage to live in extreme environments, the advantage of their opportunistic growth, and what happens to structure and physiology during desiccation and resurrection.

### POIKILOHYDROUS CONSTITUTION VERSUS POIKILOHYDROUS PERFORMANCE: TOWARD A DEFINITION OF POIKILOHYDRY

According to Walter (1931), poikilohydry in plants can be understood as analogous to poikilothermy in animals. The latter show variations of their body temperature as a function of ambient temperature, whereas poikilohydrous autotrophs (chlorophyll-containing organisms) exhibit variations of their hydration levels as a function of ambient water status (Walter and Kreeb 1970). The term autotroph is used here to comprise an extensive and heterogeneous list of autotrophic unicellular and multicellular organisms (cyanobacteria, algae, bryophytes, and vascular plants), including the lichen symbiosis. Poikilohydrous performance (from the Greek words *poikilos*, changing or varying, and *hydor*, water) is applied to organisms that passively change their water content in response to water availability (“hydrolabil”; Stalfelt 1939), eventually reaching a hydric equilibrium with the environment. This fact does not necessarily imply that the organism tolerates complete desiccation (Table 2.1). There is no general consensus on the definition of poikilohydrous autotrophs. The Greek word *poikilos* also means malicious, which, figuratively speaking, may apply to the difficulty of comprising the outstanding structural and functional heterogeneity of this group of organisms.

It is difficult to be precise about the vast number of poikilohydrous nonvascular taxa, comprising 2000 Cyanophyta, *c.*23,000 Phycophyta, *c.*16,000 Lichenes, and *c.*25,000 Bryophyta. The number of poikilohydrous vascular plant species could be almost 1500 if the

## Opportunistic Growth and Desiccation Tolerance

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**TABLE 2.1**  
**Desiccation Tolerance of Isolated Chloroplasts and of Poikilohydrous Autotrophs<sup>a</sup>**

Species	Degree of Desiccation Survived	Time of Drought Survived	Reference
Isolated chloroplasts ( <i>Beta</i> )	15% RWC	Until equilibrium	Santarius 1967
<i>Nostoc</i> and <i>Chlorococcum</i>	Air-dry	73 years	Shields and Durrell 1964
Lichens	2%–9% d.wt.	38–78 week air-dry	Lange 1953
Lichens (50 species)	45%–65% rh	24–56 week P <sub>2</sub> O <sub>5</sub>	Green et al. 1991
<i>Pseudocypbellaria dissimilis</i>		8–10 h until equilibrium	
Bryophytes			
<i>Ctenidium molluscum</i>	Varying between <10% rh and >60% rh	40 h	Dircksen 1964
<i>D. scoparium</i>	<10% rh in winter, >50% in summer	40 h	Dircksen 1964
Epiphytic mosses (14 species)	0%–30% rh	Until equilibrium	Hosokawa and Kubota 1957
<i>Fissidens cristatus</i>	Varying between <10% rh and >60% rh	40 h	Dircksen 1964
<i>Mnium punctatum</i>	<25% rh in winter and >80% rh in summer	40 h	Dircksen 1964
<i>Racomitrium lanuginosum</i>	32% rh	239 days	Dilks and Proctor 1974
<i>Sphagnum</i> sp.	Air-dry	<5 days	Wagner and Titus 1984
<i>E. holstii</i>	Air-dry	8 months	Dinter 1921 (S. Hellwege et al. 1994)
<i>Riccia canescens</i> (bulbils)	Air-dry	7 year	Jovet-Ast 1969
Pteridophytes			
<i>S. lepidophylla</i>	Air-dry	About 1 year	Eickmeier 1979
<i>Isoetes australis</i>	0% rh	Until equilibrium	Gaff and Latz 1978
<i>Asplenium ruta-muraria</i>	5%–10% RWC	1–3 days H <sub>2</sub> SO <sub>4</sub> (winter)	Kappen 1964
<i>Asplenium septentrionale</i>	7%–20% RWC	1–3 days H <sub>2</sub> SO <sub>4</sub> (winter)	Kappen 1964
<i>Asplenium trichomanes</i>	7%–15% RWC	1–3 d H <sub>2</sub> SO <sub>4</sub> (winter)	Kappen 1964
<i>C. rhizophyllum</i> (gametophyte)		H <sub>2</sub> SO <sub>4</sub>	Pickett 1914
<i>Cheilanthes</i> (8 species)	2%–20% rh	Until equilibrium	Gaff and Latz 1978
<i>H. tunbridgensis</i>	43%	15 days	Proctor 2003
<i>Hymenophyllum wilsonii</i>	20%	30 days	Proctor 2003
<i>Notholaena maranthae</i>	6% RWC		Ijijn 1931
<i>Paraceterach</i> sp.	15% rh	Until equilibrium	Gaff and Latz 1978
<i>Pellea</i> (2 species)	2%–30% rh	Until equilibrium	Gaff and Latz 1978
<i>Pleurosorus rutifolius</i>	2% rh	Until equilibrium	Gaff and Latz 1978
<i>P. polypodioides</i>	3% RWC	50 h	Stuart 1968
<i>P. vulgare</i>	3%–10% RWC	10 D P <sub>2</sub> O <sub>5</sub> (winter)	Kappen 1964
<i>Polystichum lobatum</i>	7%–10% RWC	24 h (air) winter	Kappen 1964
Gametophytes of ferns (5 species)	20–65 rh	36 h	Kappen 1965

(continued)

**TABLE 2.1 (continued)**  
**Desiccation Tolerance of Isolated Chloroplasts and of Poikilohydrous Autotrophs<sup>a</sup>**

Species	Degree of Desiccation Survived	Time of Drought Survived	Reference
Angiosperms			
Dicotyledons			
<i>R. serbica</i>	Air-dry	6–12 months	Markowska et al. 1994
<i>R. myconi</i>	2% RWC	2 days	Kappen 1966
<i>Haberlea rhodopensis</i>	Air dry	6–12 months	Markowska et al. 1994
<i>Boea hygrosco피아</i>	0% rh	Until equilibrium	Gaff and Latz 1978
<i>C. intrepidus</i>	Dry desert soil	10 months	Heil 1925
<i>C. intrepidus</i> , floating leaves	96% rh	Until equilibrium	Gaff 1971
<i>C. intrepidus</i> , submersed leaves	5% rh	4.5 months	Gaff 1971
<i>Craterostigma</i> (2 species)	0%–15% rh	Until equilibrium	Gaff 1971
<i>Limosella grandiflora</i> (corms)	5% rh	4.5 months (but both species decayed at 100% rh)	Gaff and Gress 1986
<i>M. flabellifolius</i>	Air-dry, 0%	Leaves (several year)	Ziegler and Vieweg 1969, Gaff 1971
<i>B. litiputana</i>	18% of initial weight	33 months	Barthlott and Porembski 1996
Monocotyledons			
Poaceae from India (10 species)	0–2 (11%) rh	3 months	Gaff and Boile 1986
Southern African Poaceae (11 species)	0%–5% rh	2–7 months	Gaff and Ellis 1974
Poaceae from Africa and Kenya (5 species)	0%–15% rh	Until equilibrium	Gaff and Latz 1978
<i>Trilepis pilosa</i> (African Inselberg)	8% RWC	Up to 1 year	Hambler 1961
<i>Coleochloa setifera</i>	Air-dry	5 years	Gaff 1977
<i>Oropetium</i> sp.	0%–15% rh	Until equilibrium	Gaff 1971
Australian Poaceae (6 species)	0%–15% rh	Until equilibrium	Gaff and Latz 1978
Australian Cyperaceae (4 species)	0%–2% rh	Until equilibrium	Gaff and Latz 1978
Southern African Cyperaceae (4 species)	0%–5% rh	27 months	Gaff and Ellis 1975
Cyperaceae from Africa and Kenya (3 species)	Tissues: 0%–5% rh		Gaff 1986a
Australian Liliaceae (2 species)	0%–5% rh	Until equilibrium	Gaff and Latz 1978
<i>B. nitida</i>	Air dry	>4 year	Gaff and Churchill 1976
<i>Xerophyta squarrosa</i>	Air-dry	5 year	Gaff 1971
<i>X. scabrada</i>	Air-dry	5 year	Csintalan et al. 1996
Xerophyta (5 species)	0%–15% rh	Until equilibrium	Gaff 1971
Velloziaceae from Africa and Kenya (2 species)	Mature leaf tissues: 5%–30% rh		Gaff 1986a

*Abbreviation:* RWC, relative water content; d.wt., dry weight; rh, relative humidity; until equilibrium, until equilibrium between moisture content and ambient air relative humidity.

<sup>a</sup> The list in this table is not exhaustive.

hydrophytes (c.940 spp.) are included. Among the land plants, we know nearly 90 species of pteridophytes and approximately 350 of the angiosperms (Gaff 1989, Proctor and Tuba 2002). Within the angiosperms only 10 families have to be taken into account, the Myrothamnaceae, Cactaceae, Acanthaceae, Gesneriaceae, Scrophulariaceae, and Lamiaceae (contributing in total only 35 dicotyledonous species), and the Cyperaceae, Boryaceae (*sensu* Lazerides 1992), Poaceae, and Velloziaceae (together 300 monocotyledonous species). Solely the latter, old and isolated family comprises 8 genera with nearly 260 species (Kubitzki 1998), all most likely desiccation tolerant, and more Velloziaceae species may be discovered in the future (Ibisch et al. 2001). Gaff (1989) suggests an early specialization of the poikilohydrous taxa within their small and often isolated genera.

Nonvascular autotrophs (cyanobacteria, algae, bryophytes, and lichens) are considered constitutively poikilohydrous because they lack the means of controlling water relations (Stocker and Holtheide 1938, Biebl 1962, Walter and Kreeb 1970). This is in contrast with vascular plants, which in general have constitutively homoiohydrous “sporophytes,” and keep their hydration state within certain limits by such means of roots, conducting tissues, epidermis, cuticles, and stomata. The poikilohydrous performance of vascular plants is to be taken as an acquired (“secondary”: Raven 1999) trait and is realized in phylogenetically unrelated plant species, genera, or families (Oliver et al. 2000). Because poikilohydry is constitutional in nonvascular autotrophs and rare among vascular plants, it is tempting to consider it a primitive property and to suggest that evolutionarily early terrestrial, photosynthetic organisms based their survival on tolerance (Raven 1999) instead of avoidance mechanisms. However, poikilohydry is not an indicator of an early evolutionary stage among vascular plants. Although several recent pteridophytes are poikilohydrous, there is no known poikilohydrous recent gymnosperm, and poikilohydry is frequent only in highly derived angiosperm families (Oliver and Bewley 1997, Oliver et al. 2000). Therefore, poikilohydrous performance by vascular plants can be interpreted evolutionarily as an adaptive response to climates and habitats with infrequent moist periods (see also Proctor and Tuba 2002).

The term *resurrection* has been commonly used for some species and, in general, matches the capability of poikilohydrous plants to quickly reactivate after falling into a period of anabiosis caused by dehydration. It is very appropriate for spikemosses (*Selaginella*) and certain bryophytes and lichens that curl strongly with water loss and unfold conspicuously on rehydration. Similar performance can be observed in the dead remnants of plants in deserts and steppes. In addition, in fact, the annual homoiohydrous species *Anastatica hierochuntica* was called a resurrection plant by some investigators (Wellburn and Wellburn 1976) because of the dramatic change between a curled and shriveled stage in the dry season and the spreading of the dead branches in the rainy season to release the seeds. Consequently, *resurrection*, in a broad, intuitive sense, could also be applied to certain homoiohydrous desert perennials (e.g., *Aloe*, Mesembryanthemaceae, and certain cacti). On the other hand, the shape and appearance of some constitutively poikilohydrous autotrophs, such as terrestrial unicellular algae and crustose lichens, do not visibly change. To add to the confusion, water loss can be dramatic in some homoiohydrous desert plants, whereas it can be minor in constitutively poikilohydrous plants such as *Hymenophyllum tunbridgense* or bryophytes and lichens from moist environments. Therefore, the resurrection phenomenon (visible changes in shape and aspect with hydration) is only part of the poikilohydrous performance and it is not exhibited to the same extent by all poikilohydrous autotrophs.

Ferns are dual because they produce constitutively poikilohydrous gametophytes and a cormophytic sporophyte with the full anatomy of a homoiohydrous plant. Knowledge about gametophytes is scant. They are usually found in humid, sheltered habitats where hygic and mesic bryophytes also grow. Previous literature reports on extremely desiccation-tolerant prothallia of the North American *Camptosorus rhizophyllus*, and of *Asplenium platyneuron* and *Ceterach officinarum* (= *Asplenium ceterach*) (Walter and Kreeb 1970). The desiccation

tolerance of prothallia of some European fern species varied with species and season (Kappen 1965). They usually overwinter, and their ability to survive low temperatures and freezing is based on increased desiccation tolerance. Prothallia of rock-colonizing species (*Asplenium* species, *Polypodium vulgare*) could withstand 36 h drying in 40% relative humidity; some species were partly damaged but could regenerate from surviving tissue. Prothallia of other ferns from European forests were more sensitive to desiccation (Table 2.1).

The poikilohydrous nature of a terrestrial vascular plant is frequently defined by the combination of a passive response to ambient water relations and a tolerance to desiccation (Gaff 1989), but the emphasis on the different functional aspects involved and the actual limits of poikilohydry are matters of debate. Some poikilohydric species cannot even tolerate a water loss greater than 80% of their maximal water content (Gaff and Loveys 1984), and others can be shown to gain their tolerance only by a preconditioning procedure. Boundaries between poikilohydrous and homoiohydrous plants can be rather blurry, especially if we include examples of xerophytes that can survive extremely low water potentials (Kappen et al. 1972). Surviving at very low relative humidities is not a useful indicator because a limit of 0%–10% relative humidity excludes many nonvascular plants that are undoubtedly poikilohydrous. Considering the photosynthetic performance and low tolerance to desiccation of certain forest lichens (Green et al. 1991) and the fact that, in particular, endohydric bryophytes depend on moist environments, Green and Lange (1994) concluded that the passive response to ambient moisture conditions of poikilohydrous autotrophs varies in a species- and environment-specific manner.

The conflict between ecologically based and physiologically or morphologically based criteria cannot be easily solved. However, a compromise can be reached by distinguishing between stenopoikilohydrous (narrow range of water contents) and eurypoikilohydrous (broad range of water content) autotrophs. This distinction is especially useful for nonvascular, that is, for constitutively poikilohydrous autotrophs. For instance, microfungi that spend all their active lifetime within a narrow range of air humidity are stenopoikilohydrous. As xeric species they grow in equilibrium with relative humidities as low as 60% (Pitt and Christian 1968, Zimmermann and Butin 1973). Aquatic algae and cyanobacteria are also typically stenopoikilohydrous. The so-called hygric and mesic bryophytes and filmy ferns that are not able to survive drying to less than 60% water content or less than 95% relative humidity also belong to the stenopoikilohydrous type. The same is the case with some wet forest lichens that have low desiccation tolerance (Green et al. 1991). A stenopoikilohydrous performance is also apparent in those ephemeral bryophytes that germinate after heavy rain and then quickly develop gametophytes and sporogons. Some examples with this drought evasion strategy are the genera *Riella*, *Riccia*, and species of Sphaerocarpaceae, Pottiaceae, and Bryobatrachiaceae. These annual shuttle species are characteristic of seepage areas and pond margins where the soil remains wet for a few weeks (Volk 1984). The many vascular plant species growing permanently submersed in water have also a stenopoikilohydrous life style (see Raven 1999).

All nonvascular and vascular species that are extremely tolerant to desiccation and typically perform as resurrection plants (Gaff 1972, 1977, Proctor 1990) belong to the eurypoikilohydrous group. Because many of these species grow in dry or desert environments, poikilohydry was often associated with xerophytism (Hickel 1967, Patterson 1964, Gaff 1977). However, seasonal changes in the tolerance to desiccation can confound this distinction between stenopoikilohydrous and eurypoikilohydrous organisms. These changes have been found in bryophytes (Dilks and Proctor 1976b) and ferns (Kappen 1964) and are very likely to occur in angiosperms. As suggested by Kappen (1964), such plants may be considered as temporarily poikilohydrous. Hence, the number of eurypoikilohydrous bryophyte species cannot be fixed until temporal changes of desiccation tolerance are better studied in mesic species (Proctor 1990, Davey 1997, Proctor and Tuba 2002). Most of the available

information and, consequently, most of what follows, involves eurypoikilohydrous autotrophs. The different groups of poikilohydrous autotrophs that can be identified according to the range of water contents experienced in nature or tolerated are summarized later.

## ECOLOGY AND DISTRIBUTION OF POIKILOHYDROUS AUTOTROPHS

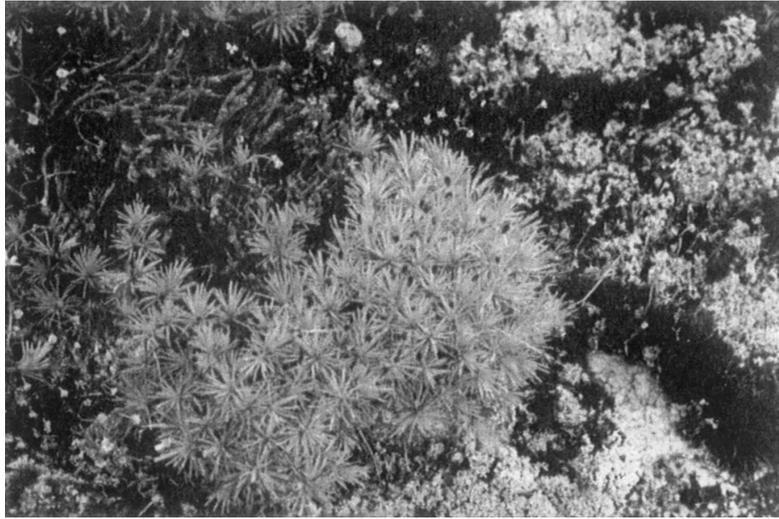
Nowhere else in the world are poikilohydrous autotrophs more conspicuous than in arid and climatically extreme regions (e.g., Namib desert, Antarctica). It is somewhat paradoxical that precisely in habitats with extreme water deficits the dominant organisms are the least protected against water loss. Additionally, the poikilohydrous angiosperms show in general no typical features against water loss, but they can compete well with extremely specialized taxa of homoiohydrous plants. However, again the distinction between stenopoikilohydrous and eurypoikilohydrous plants becomes important, because stenopoikilohydrous autotrophs can be very abundant in moist habitats (e.g., cloud forests: Gradstein 2006). In the moist and misty climate of San Miguel, Azores, even *Sphagnum* species are able to grow as epiphytes on small trees. However, eurypoikilohydrous autotrophs, which are capable of enduring prolonged drought and extreme temperatures, represent the most interesting group because they have more specifically exploited the ecological advantages of their opportunistic strategy. The remainder of this chapter presents examples of poikilohydrous autotrophs living under very limiting ecological conditions in many different regions of the earth.

In temperate climates, poikilohydrous autotrophs are mainly represented by aerophytic algae, bryophytes, and lichens. Depending on their habitat, bryophytes can be eurypoikilohydrous or stenopoikilohydrous. Among the temperate vascular plants, poikilohydrous performance is realized in some mainly rock-colonizing fern genera such as *Asplenium*, *Ceterach*, *Cheilanthes*, *Hymenophyllum*, *Notholaena*, and *Polypodium* and the phanerogamous genera *Haberlea* and *Ramonda*.

From the arctic region, no poikilohydrous vascular plants are known, and most parts of Antarctica are inhabited solely by algae, bryophytes, lichens, and fungi, which are mainly eurypoikilohydrous. In the polar regions and in hot, extremely arid deserts, nonvascular autotrophs may be restricted to clefts and rock fissures or even grow inside the rock as endolithic organisms or hypolithic on the underside of more or less translucent rock particles and stones (Friedmann and Galun 1974, Scott 1982, Danin 1983, Kappen 1988, 1993b, Nienow and Friedmann 1993).

In subtropical regions bryophytes, algae, and lichens are well known as crust-forming elements on open soils (Belnap and Lange 2001). The coastal Namib desert, with extremely scattered rainfall, consists of wide areas where no vascular plants can be found, but a large cover of mainly lichens forms a prominent vegetation. In rocky places of the Near East, southern Africa, arid northwest North America, coastal southwest North America, and the South American westcoast, lichens and bryophytes coexist with xeromorphic or succulent plants. They also occupy rock surfaces and places where vascular plants do not find enough soil, or they grow as epiphytes on shrubs and cacti. Under such extreme conditions, lichens and bryophytes share the habitat with poikilohydrous vascular plants as for instance *Borya nitida* on temporarily wet granitic outcrops (Figure 2.1) with shallow soil cover in southern and western Australia (Gaff and Churchill 1976).

In Africa, subfruticose poikilohydrous plants such as *Lindernia crassifolia* and *Lindernia acicularis* grow in sheltered rock niches (Fischer 1992). The same is true for the fruticose poikilohydrous species, *Myrothamnus flabellifolius*, occurring in southern Africa and Madagascar from Namibia (Child 1960, Puff 1978, Sherwin et al. 1998), which is frequently associated with other resurrection plants (e.g., *Pellaea viridis*, *Pellaea calomelanos*). In the wet season, these plants benefit from run off water that floods the shallow ground (Child 1960). Particularly remarkable are poikilohydrous aquatic *Lindernia* species (*L. linearifolia*,



**FIGURE 2.1** Two very different examples of poikilohydrous autotrophs co-occurring on a shallow depression of a granite outcrop near Armadale, western Australia: the monocotyledonous plant *B. nitida* (left), mosses, and the whitish fruticose lichen *Siphula* sp. (Photograph from Kappen, L., *Physiological Plants Ecology, Vol. I. Responses to the Physical Environment*, O.L. Lange, P.S. Nobel, C.B. Osmond, and H. Ziegler, eds, Sprigner-Verlag, Berlin-Heidelberg, 1981.)

*L. monrio*, *L. conferta*) and *Chamaegigas (Lindernia) intrepidus* (Heil 1925, Hickel 1967, Gaff and Giess 1986, Heilmeier et al. 2005), which grow in small temporarily water-filled basins of granitic outcrops in Africa (Angola, Zaire, Zimbabwe, South Africa, Namibia). Many of the poikilohydrous grass species (less than 20 cm high) and sedges (30–50 cm high) are pioneering perennial plants colonizing shallow soil pans in southern Africa (Gaff and Ellis 1974). In Kenya and West Africa, the resurrection grasses, sedges, and Velloziaceae (in Africa 30 species, Ibisch et al. 2001) are confined to rocky areas, except *Sporobolus fimbriatus* and *Sporobolus pellucidatus*. *Eragrostis invalida* is the tallest poikilohydrous grass species known with a foliage up to 60 cm (Gaff 1986). *Vellozia schnitzleinia* is a primary mat former following algae and lichens on shallow soils of African inselbergs, persisting during the dry season with brown, purple-tinged rolled leaves that turn green in the wet season (Owoseye and Sandford 1972).

The resurrection flora of North America is represented mainly by pteridophytes. Most of the poikilohydrous fern species so far known are preferentially found in rock cervices, gullies, or sheltered in shady rocky habitats (Nobel 1978, Gildner and Larson 1992). By contrast, the most famous resurrection plant *Selaginella lepidophylla* colonizes open plains in Texas (Eickmeier 1979, 1983). In Middle and South America, 220 species of the Velloziaceae form the dominant part of the poikilohydrous flora. They grow in various habitats and even in alpine regions. The endemic *Vellozia andina* seems to be an opportunistic species as it takes benefit from degraded formerly forested sites (Ibisch et al. 2001). Fire resistance is typical of many Velloziaceae species (Kubitzki 1998). Gaff (1987) has enumerated 12 fern species for South America. *Pleopeltis mexicana* and *Trichomanes bucinatum* may also be candidates (Hietz and Briones 1998). One of the most remarkable poikilohydrous vascular plants could be *Blossfeldia liliputana*, a tiny cactus that grows in shaded rock crevices of the eastern Andean chain (Bolivia to northern Argentina) at altitudes between 1200 and 2000 m (Barthlott and Porembski 1996). This plant is unable to maintain growth and shape during periods of drought, and it persists in the dry state

(18% of initial weight) for 12–14 months, looking like a piece of paper. When water is again available, it can rehydrate and resume CO<sub>2</sub> assimilation within 2 weeks; it is the only known example of a succulent poikilohydrous plant.

From a plant–geographical perspective, inselberg regions in Africa, Madagascar, tropical South America, and Western Australia have the largest diversity of poikilohydrous vascular plants in the World. Porembski and Barthlott (2000) state that 90% of the known vascular poikilohydrous plant species occur on tropical inselbergs. The presence of almost all known genera with poikilohydrous plants could be recorded from such sites. Despite the existence of similar potential habitats for poikilohydrous vascular plants in Australia, species are less numerous there than in southern Africa. Lazarides (1992) suggested that this biogeographical difference between Australia and southern Africa is due to the fact that the Australian arid flora has been exposed to alternating arid and pluvial cycles for a shorter geological period of time than the arid flora of southern Africa. The former has experienced these alternations since the Tertiary, whereas the latter has been exposed to dry–wet cycles since the Cretaceous. Ferns, represented by a relatively large number of species [14], and most of the poikilohydrous grasses found in Australia [10] grow in xeric rocky sites (Lazarides 1992). We have very few records about poikilohydrous vascular plants from Asia, although such a type of plant must exist there as well. Gaff and Bole (1986) recorded 10 poikilohydrous Poaceae (genera *Eragrostidella*, *Oropetium*, *Tripogon*) for India. The Gesneriaceae *Boea hygrometrica*, closely related to the Australian *Boea hygroskopica*, is a poikilohydrous representative in China (see Yang et al. 2003).

Most of the resurrection plants are confined to lowland and up to 2000 m a. s. l. However, a few Velloziaceae species such as *Xerophyta splendens* reach altitudes of 2800 m in Malawi (Porembski 1996) and *Barbaceniopsis boliviensis* reach 2900 m in the Andes (Ibisch et al. 2001), the latter staying in anabiosis with reddish-brown leaves for half a year. In such high altitudes, they are exposed to frost periods.

### DOES POIKILOHYDRY RELY ON SPECIFIC MORPHOLOGICAL FEATURES?

Poikilohydrous performance cannot be typified by any one given set of morphological and anatomical features because of the heterogeneity of this functional group of photosynthetic organisms. Poikilohydry can be found in autotrophs ranging from those with the most primitive unicellular or thallose organization to those with the most highly derived vascular anatomy. In angiosperms, desiccation tolerance is, in general, inversely related to anatomical complexity. It seems that plants can operate either by avoidance or tolerance mechanisms at all levels of organization if they are adapted to temporarily dry habitats. Gaff (1977) called resurrection plants “true xerophytic” just because they live in xeric environments. However, poikilohydrous angiosperms do not necessarily have xeromorphic traits. Xeromorphic features such as small and leathery leaves are typical for *Myrothamnus*; xeromorphic narrow or needle-like leaves for many Velloziaceae, Cyperaceae, and the genus *Borya* (see Figure 2.1); and massive sclerenchymatic elements, for example, several Velloziaceae and *Borya* (Gaff and Churchill 1976, Lazarides 1992, Kubitzki 1998). Hairs on leaves (e.g., Velloziaceae, Gesneriaceae) are mostly small, and scales (e.g., *Ceterach*) or succulence (*Blossfeldia*) are the exception rather than the rule in poikilohydrous vascular plants. Xeromorphic structures would also counteract the potential of rehydration during the wet period. However, curling and uncurling of leaves, frequently enabled by contraction mechanism, is a widespread phenomenon in poikilohydrous vascular plants.

Poikilohydrous vascular plants are mainly perennials represented by various types of hemicryptophyte and chamaephyte life forms but no trees. Lignification of stems is not rare, and the two existing *Myrothamnus* species are true shrubs reaching approximately 1.5 m height. Within the monocotyledons, a tree-like habit is achieved either by an enhanced

primary growth of the main axis or by secondary thickening, and trunks may reach up to 4 m length. Such pseudostems are realized in the genus *Borya* (secondary growth) and by some Cyperaceae and Velloziaceae (Gaff 1997, Kubitzki 1998, Porembski and Barthlott 2000). For instance, a sample of *Vellozia kolbekii* was looking with its stem (covered by roots and leaf sheaths) like a tree fern, was 3 m tall, and was estimated to be 500 years old (Alves 1994).

As most of the phanerogamous resurrection plants do not show peculiar or uniform anatomical features, it is hard to decide whether a particular plant is poikilohydrous just from herbarium material or from short-term observations in the field (Gaff and Latz 1978). It is still uncertain, for instance, whether more members of the Lindernieae can be identified as poikilohydrous in studies such as that by Fischer (1992) and Proctor (2003). Many species that grow in shady habitats or that colonize temporarily inundated habitats exhibit a hygromorphic tendency (Volk 1984, Fischer 1992, Markowska et al. 1994). For instance, *C. intrepidus* has, like other aquatic plants, aerenchyma and two types of leaves, floating and submerged. *B. liliputana*, the only known poikilohydrous Cactaceae, combines a succulent habit with a typically hygromorphic anatomy: very thin cuticle, no thickened outer cell walls, absence of hypodermal layers, and extremely low stomatal density (Barthlott and Porembski 1996). Poikilohydrous vascular plants exhibit, in general, very low stomatal control of transpiration (Gebauer 1986, Sherwin et al. 1998, Proctor 2003). The leaves of *Satureja gilliesii* even have protruding stomata on the underside (Montenegro et al. 1979).

The secondarily poikilohydrous nature of aquatic vascular plants has rarely been acknowledged (Raven 1999). Most of them have reduced xylem structure and no sustaining function. Roots merely act to fix to the substratum, and nutrients are taken up by the leaves. Cuticles are thin and stomata are scattered and frequently nonfunctional (*Isoetes*, *Litorea*, *Elodea*, *Vallisneria*, Potamogetonaceae, etc). Living in streams and underwater rapids in the Tropics, the Podostemaceae are very remarkable examples with a drastic reduction of their homoiohydrous architecture. With their thallus-like shoots they resemble foliose liverworts.

Small size is recognized frequently as typical of the shape of the poikilohydrous autotrophs. Indeed, only a few vascular species are fruticose and reach more than 50 cm height. Alpert (2006) discusses whether there is a trade-off between low growth and desiccation tolerance in the sense of a disadvantage, because the plant has to invest in protection mechanisms instead of extension growth as most of the homoiohydrous plants do. Proctor and Tuba (2002) on the other hand, refer to poikilohydry as an advantage particularly for living in temporarily dry environments. High desiccation tolerance is the ultimate drought-evading mechanism. The resurrection strategy is ecologically as successful as that of homoiohydrous plants with CAM or the adaptation to live on heavy-metal soils or in raised bogs. In addition, the slow growth and small size of poikilohydrous plants is not only a function of changing water status but also of nutrient deficiency, which is obvious from most of their natural habitats. *C. intrepidus*, for instance, has to use urea as nitrogen source by means of free urease in the sediments of rock pools (Heilmeier et al. 2000) and free amino acids (Schiller 1998).

Living under water, the nonvascular autotrophs are able to develop a size (*Macrocystis* spp.: 60 m) comparable to that of tall trees, and the vascular plant species *Elodea canadensis* may produce up to 6 m long shoots (see Raven 1999). Endohydrous mosses such as the Dawsoniaceae and Polytrichaceae may reach a height of 1 m in the damp atmosphere of rain forests. This demonstrates that the small size of eurypoikilohydrous plants is an adaptive trait to respond flexibly to drought events rather than remaining principally handicapped with respect to growth and productivity.

## EXPLOITING AN ERRATIC RESOURCE

Water is evasive in many terrestrial habitats, and plants in general have to deal with the changing availability of this crucial resource. This is especially true for poikilohydrous

autotrophs, which have successfully explored many different strategies within their general tolerance to water scarcity. However, some of the features that make tolerance to desiccation possible are irreconcilable with those that enhance water use. Poikilohydrous autotrophs, therefore, have had to trade-off between surviving desiccation against uptake, transport, and storage of water. Some adaptive conflicts appear, for instance, when a particular feature retards water loss. The important functional problems that arise when the plant has to resume water transport after desiccation might have limited the range of growth forms and plant sizes compatible with poikilohydry.

### DIFFERENT MODES OF WATER UPTAKE AND TRANSPORT

Plants must be efficient in acquiring water, particularly in arid regions where rainfall is scarce and sometimes the only available water comes from dew, mist, or fog. Poikilohydrous plants can outcompete their homoiohydric counterparts in dry habitats if they can rehydrate efficiently. The following section describes the different possibilities for water capture exhibited by poikilohydrous autotrophs, with emphasis on the role of the growth form and of the morphology and anatomy of the structures involved.

Aerophytic algae and lichens with green-algal photobionts can take up enough water from humid atmospheres to become metabolically active (Lange 1969b, Blum 1973, Lange and Kilian 1985, Lange et al. 1990a, Bertsch 1996a,b). Rehydration in lichens from humid atmospheres may take 1–4 days until equilibrium, whereas mist and dewfall yield water saturation within hours (Kappen et al. 1979, Lange and Redon 1983, Lange et al. 1991). Even water vapor over ice and snow serves as an effective water source for the activation of lichens in polar regions (Kappen 2000, Pannowitz et al. 2006; see Chapter 14). As a consequence, lichens in deserts can survive well with sporadic or even no rainfall (Kappen 1988, Lange et al. 1990c, 1991). Anatomical structures such as long cilia, rhizines, branching, or a reticulate thallus structure are characteristic of lichens from fog deserts (e.g., *Ramalina melanothrix*, *Teloschistes capensis*, *Ramalina menziesii*), suggesting that these structures are means for increased water absorption (Rundel 1982a). In lichens, liquid water is absorbed by the entire body (thallus), usually within a few minutes (Blum 1973, Rundel 1982a, 1988). The thallus swells and can unfold lobes or branches. However, there is little evidence of a water transport system in these organisms (Green and Lange 1994). Nevertheless, not all lichens have the same capacity for exploiting the various forms of water from the environment. For example, lichens with cyanobacteria as photobiont cannot exist without liquid water (Lange et al. 1988). For the Australian erratic green-algal *Chondropsis semiviridis*, rainwater is necessary to allow photosynthetic production because the curled lobes must be unfolded (Rogers and Lange 1971, Lange et al. 1990a).

The kinetics of water uptake seems to be similar in lichens and mosses, and the larger the surface area to weight ratio, the more rapid the water uptake (Larson 1981). Rundel (1982a) suggested that thin cortical layers of coastal Roccellaceae in desert regions may be a morphological adaptation to increase rates of water uptake. However, textural features of the upper cortex seem to be more important for water uptake than just thickness (Larson 1984, Valladares 1994a). Valladares (1994a) found that species of Umbilicariaceae that possess the most porous and hygroscopic upper cortex (equal to filter paper) are adapted to live mainly from water vapor (aero-hygrophytic), whereas species that have an almost impervious cortex were more frequently exploiting liquid water from the substratum (substrate-hygrophytic; Sancho and Kappen 1989).

Most bryophytes need a humid environment or externally adhered water to keep a level of hydration high enough for metabolic functions. Many species form cushions, turfs, or mats that aid to keep capillary water around the single shoots (Gimingham and Smith 1971, Giordano et al. 1993). At full saturation, the water content of mosses (excluding external

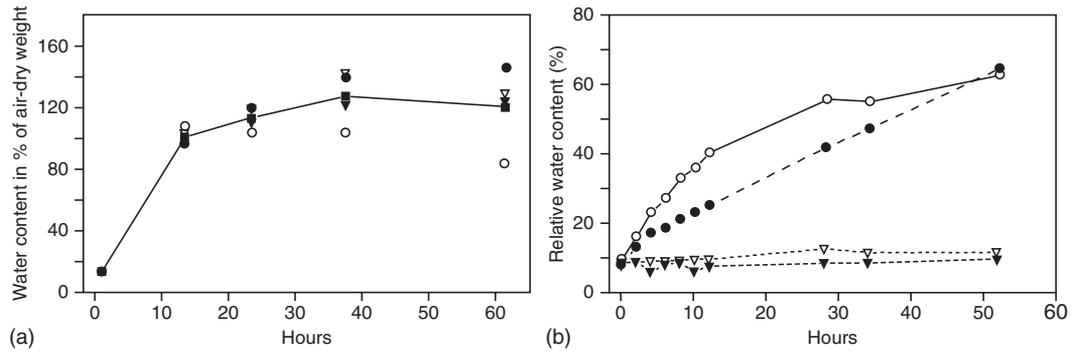
water) can vary between 140% and 250% dry weight (d.wt.) (Dilks and Proctor 1979), which is similar to that of macrolichens. Thallose hygrophytic liverworts require higher levels of hydration, and their maximal water content can be more than 800% d.wt. In shaded or sheltered habitats, hygric and some mesic bryophytes are able to keep their water content relatively constant throughout the year, which is characteristic for a stenopoikilohydrous lifestyle (Green and Lange 1994). In more open and exposed sites, the fluctuations in water content are very large (Dilks and Proctor 1979).

The more complex and differentiated morphology and anatomy of bryophytes, in comparison with lichens, allow for more varied modes of water uptake (Proctor 1982, 1990, Rundel 1982b). Bryophytes can take up water vapor to limited extent and reach only low (less than 30% of maximum water content) relative values (Rundel and Lange 1980, Dhindsa 1985, Lange et al. 1986). Dew uptake was recorded for *Tortula ruralis* (Tuba et al. 1996a) and for 10 sand-dune mosses (Scott 1982). Leaves of certain desert mosses (e.g., Pottiaceae) act as focus for condensation of water vapor and mist by means of their recurved margins, papillose surfaces, and hair points (Scott 1982). However, the presence of lamellae, filaments, and other outcrops on the adaxial surface of the leaves, which is common in arid zone mosses, may act more as sun shelter rather than as means to enhance water uptake. The role of scales and hyaline structures on the midrib of desert liverworts (e.g., *Riccia*, *Exormotheca*, and *Grimaldia*), which is inverted and exposed to the open when the thallus is dry, is not clear, but they start absorbing rainwater and swelling to turn down rapidly and may help in storing water (Rundel and Lange 1980). Mosses of the family Polytrichaceae have so-called rhizomes or root-like structures, which are not very efficient for water uptake (Hebant 1977). In general, water uptake of mosses from the soil is poor and needs to be supplemented by external water absorption.

Two main groups of bryophytes have been described according to the mode of water transport. Ectohydrous species resemble lichens because they take up water over all or most of their thallus surface and have no internal water transport system, whereas endohydrous species have various water-proofed surfaces (cuticles), often well developed near to the gas exchange pores (stomata on the sporophytes), and have a significant water-transport pathway (Proctor 1984, Green and Lange 1994). These properties of the latter are similar to those of homoiohydrous plants (Hebant 1977). However, they differ from vascular plants in that their conductive structures are not lignified, and all these properties are functional only in moist environments. Therefore desert mosses are typically ectohydrous (Longton 1988a), and the water transport in eurypoikilohydrous bryophytes growing in dry environments is predominantly external. However, some eurypoikilohydrous mosses (Fabroniaceae, Orthotrichaceae) have large masses of stereom tissue (usually a supporting tissue), that is considered to be an alternative route for the conduction of water (Zamski and Trachtenberg 1976).

Proctor (1982) summarized four different pathways or modes by which water moves in a bryophyte: (1) inside elongated conductive cells (hydroids), forming a central strand in the stems of mosses and some liverworts; (2) by the cell walls, which are frequently thickened (in fact, bryophyte cell walls have higher water conductivity than those of vascular plants); (3) through intervening walls and membranes; and (4) by extracellular capillary spaces. The highest internal conduction for water in Polytrichaceae at 70% relative humidity was 67% of the total conduction (Hebant 1977).

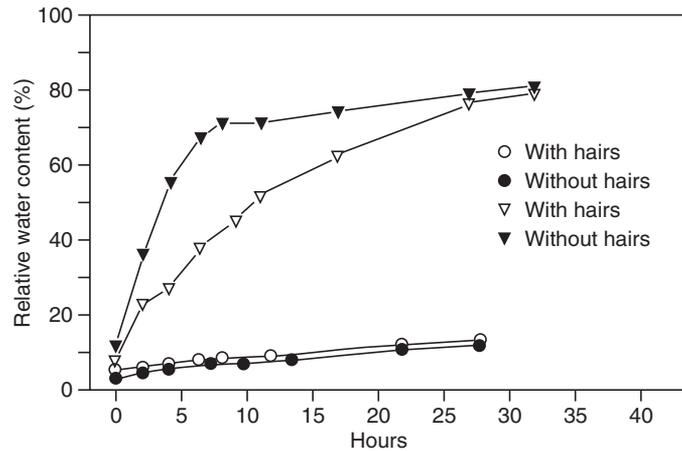
Water uptake in poikilohydrous vascular plants can be very complex because of interactions between different organs. For instance, in the fern *Cheilanthes fragrans*, water uptake through the leaf surface from a water vapor-saturated atmosphere allows it to reach 80% of its maximal water content within 50 h (Figure 2.2a). Petiolar water uptake was also efficient, but only if the leaves were in high air humidity (Figure 2.2b). Stuart (1968) found that the fern *Polypodium polypodioides* was not able to rehydrate by soil moistening if the air was dry, and the leaves reached only 50% of their maximal water content within 2–3 days, even in a water



**FIGURE 2.2** (a) Water-vapor uptake of leaves of the fern *Cheilanthes fragrans* with sealed petioles in a moist chamber. The different symbols stand for four replicates (L. Kappen, unpublished results). (b) Water uptake of leaves of *C. fragrans* placed on filter paper in a moist chamber (open circles); with petiole in a vessel with water and standing in a moist chamber (closed circles), and (open and closed triangles) with petiole in water in a room (approximately 60% rh) (L. Kappen, unpublished results).

vapor-saturated atmosphere (Stuart 1968, confirming the results of Pessin 1924). Fronds of the highly desiccation-tolerant *Polypodium virginianum* were, however, not able to absorb water from air as was shown with Deuterium-labeled water (Matthes-Sears et al. 1993). Thus, the capacity of the leaves to take up water vapor varies significantly among species and seems not to be associated with the tolerance to desiccation. In contrast, liquid-water uptake by leaves has been shown to be a common feature in poikilohydrous vascular plants. Detached leaves of *P. polypodioides* regained full saturation within 20–30 min if submerged in liquid water (Stuart 1968). However, leaves attached to the rhizome needed 10 times longer for saturation than detached leaves. Stuart explained this by alluding to anaerobic conditions that impede rapid water uptake. Rapid water uptake by leaves was also shown in *S. lepidophylla* (Eickmeier 1979). It seems that, in pteridophytes, water uptake through leaves is an important mechanism for reestablishing water relations of the whole plant and for resuming xylem function. Similarly, rehydration of the whole plant solely by watering the soil in dry air is also incomplete in poikilohydrous angiosperms (Gaff 1977).

Water uptake from mist or from saturated atmospheres is insignificant in poikilohydrous angiosperms (Vieweg and Ziegler 1969), as has been shown for isolated leaves of *Ramonda myconi* (Gebauer et al. 1987). In addition, exposure to dewfall could only raise the relative water content to less than 13% in *Craterostigma wilmsii* (Gaff 1977). Foliar water uptake by desert plants has been investigated, particularly with respect to dew uptake (Barthlott and Capesius 1974), but it seems to be insignificant in homoiohydrous plants except in the genus *Tillandsia* (Rundel 1982b). In contrast, foliar water uptake from rain by poikilohydrous vascular plants may be important to resume functioning of the hydraulic system, as Gaff (1977) found that leaves of resurrection plants in contact with liquid water can rehydrate within 1–14 h, depending on the species. The quickest uptake was measured in *C. intrepidus* (Hickel 1967). The cuticle of vascular plants is generally considered an efficient protection against water loss. However, the cuticle of poikilohydrous vascular plants may also enhance water uptake by leaves (e.g., *Borya*; Gaff 1977). The permeability of the cuticle to water was assumed for *C. intrepidus* (Hickel 1967). Barthlott and Capesius (1974) suggested that the cuticle of some of these plants seems to be more permeable to water from outside than from inside the leaf. However, this is not clear as some studies attribute permeability to the state of the cuticular layer rather than to the cuticle itself (Schönherr 1982). According to Kerstiens (1996), water uptake through the cuticle is most likely, but evidence needs to be shown.



**FIGURE 2.3** Water uptake of leaves of *R. myconi* (Gesneriaceae) with sealed petioles. Leaves with hairs (open triangles) and after removing the hairs (closed triangles) soaking from sprayed water; and leaves with hairs (open circles) and without hairs (closed circles) in a moist chamber. (From Gebauer, R., Löscher, R., and Kappen, L., *Verh. Ges. Ökologie.*, XVI, 231, 1987.)

Hairs and scales can function as auxiliary structures for water uptake because they absorb water more easily than the leaf epidermis. The lower surface of the curled and folded leaflets of ferns like *Ceterach officinarum*, densely covered with scales and trichomes, should enhance water capture (Oppenheimer and Halevy 1962). The so-called hydathodes on the leaves of *Myrothamnus* may actually function as water-absorbing trichomes (Rundel 1982b). However, Sherwin and Farrant (1996) do not believe in any water uptake by leaves of this species. In addition, scales of *P. polypodioides* did not facilitate water uptake, but allowed the water to spread homogeneously on the leaf surface (Pessin 1924, Stuart 1968), and the scales on the leaves of several species of *Ceterach* and *Cheilanthes* retarded water uptake for several hours because of the air that was trapped between the scales (Oppenheimer and Halevy 1962, Gaff 1977, Gebauer 1986). The hairs of the leaves of *R. myconi* (and of other *Ramonda* species) had the same effect (Figure 2.3). Spraying of the detached hairy leaves resulted in less water uptake than immersion in water or spraying hairless leaves. The retarding effect of scales and hairs suggests that a very rapid water uptake after desiccation could be injurious to the leaf cells.

#### PROBLEMS OF RESUMING WATER TRANSPORT

Poikilohydrous plants that possess an internal system for water transport (endohydrous bryophytes and vascular plants) are exposed to cavitation (break down of a vessel by air bubbles) during desiccation, which compromise the functioning of the conducting tissues on rehydration. This was particularly investigated in trees (Sperry and Tyree 1988, Tyree and Sperry 1988, Hargrave et al. 1994, Lewis et al. 1994, Kolb et al. 1996, Tyree, Chapter 6, this volume). Emboli in a fraction of the conductive elements confines water transport into a diminished number of vessels, which requires an increased tension and further increased the risk of embolism. Embolized conduits can become functional again through bubble dissolution or expulsion, which requires a positive pressurization (Zimmermann and Milburn 1982). Poikilohydrous plants face the dilemma of restoring water transport through their old, embolized tissues or investing in new conducting tissues, which reduces the resources available to be allocated elsewhere in the plant. The fact that most of the poikilohydrous

vascular plants are herbaceous and smaller than 50 cm might be explained by the difficulties of restoration of conductivity of the xylem. The same mechanical difficulties of resuming water conductivity of embolized tissues might also be behind the remarkable lack of poikilohydrous species among the gymnosperms, which consist only of trees and shrubs. The low flexibility due to the xylem anatomy of gymnosperms was demonstrated by Ingrouille (1995).

Poikilohydrous vascular plants that would be able to resume water transport only if their shoot tissues have been hydrated by external water uptake perform like the endohydrous bryophytes, where water conduction in the hydroids is supported by lateral and apoplastic water transport. The imbibition of the cell walls of leaf and stem tissues generates the necessary pressure to induce dissolution of emboli in the tracheary tissues. Capillary forces in poikilohydrous plants at 40% relative humidity and under laboratory conditions could move water to a height of 2–12 cm (Galace 1974, cited in Gaff 1977). These forces are sufficient to rehydrate many of the small herbaceous poikilohydrous species. Other mechanisms to eliminate emboli are temperature-associated osmosis at the plant apex (Pickard 1989) and generation of a root pressure that is able to dissolve gas bubbles in the conduits of small herbs and grasses (Zimmermann and Milburn 1982). The latter was shown to be able to restore full liquid continuity and was assumed to be important in larger poikilohydrous species like *Xerophyta eglandulosa* (Gaff 1977). Reversal of almost complete embolism in stems of the homoiohydrous *Salvia multiflora* was related to the presence of narrow vessels and tracheids, which were better to refill than wider conduits (Hargrave et al. 1994). Very narrow vessels (approximately 14  $\mu\text{m}$ ) are also true for *M. flabellifolius*. In addition, it has reticular perforation plates and knob-like protuberances on the outer walls of the vessels and tracheids, obviously to provide stability when the tissues swell and shrink. The hydraulic conductivity is, however, low and the shrub needs approximately 70 h to regain turgor (Sherwin et al. 1998). Water rise in the axes is substantially aided by root pressure (which develops 3–4 h after watering the plants and ceases after 4–5 days) and additionally, mechanisms that disintegrate lipid films on the lumen walls of the xylem elements, such as radial water flow along the xylem parenchyma, the phloem, and cortical cells (Schneider et al. 2000). This demonstrates that a woody poikilohydrous plant has to take great efforts for its rehydration. As soon as a leaf is reached by the water front, it is unfolded and hydrated to 65% RWC within 2 h and soon photosynthetically functional (Sherwin and Farrant 1996).

The slow recovery on rehydration of whole plants when compared with detached leaves (Stuart 1968, Gebauer 1986) might be because of the time required to form new roots. This topic has been better explored in homoiohydrous plants from arid environments. For instance, the hydraulic conductivity of roots of *Agave deserti* and *Agave acanthodes*, which decreased dramatically after several days of drought, rapidly recovered when water was again available, not by formation of new roots but by refilling the extant tissues, which were made up of flexible and un lignified vessels (North and Nobel 1991, Ewers et al. 1992). In fact, a flexible structure in the conductive system was identified in the poikilohydrous *B. liliputana* (Barthlott Porembski 1996). Contractive tracheids evidently enable the dry, contracted, and submersed leaves of *C. intrepidus* to swell by 800%–900% in water (Schiller et al. 1999). Another means of rapid water uptake is provided in this poikilohydrous species (Heilmeyer et al. 2000) and in the genus *Borya*, Cyperaceae, and *Xerophyta pinifolia* (Porembski and Barthlott 1995, 2000) by a *Velamen radicum*, which is otherwise typical for epiphytic orchids. Earlier literature has recorded the formation of new adventitious roots in poikilohydrous plants subsequent to rehydration (Walter and Kreeb 1970). This was confirmed recently for Velloziaceae (e.g., *Xerophyta scabrida*), *Borya sphaerocephala*, and *Craterostigma plantagineum*, where such roots appeared after the regreening of the plant, replacing the drought-killed original roots (Tuba et al. 1993a, Porembski and Barthlott 2000, Norwood et al. 2003).

## RETARDING WATER LOSS

Poikilohydrous autotrophs can maintain their water content at a constant level only to a limited extent, but they can extend hydration into the dry period by certain, mostly structural, mechanisms. By retarding water loss, such organisms can enhance their exploitation of the transient periods of water availability. Retarding water loss could, however, counteract some advantageous aspects of the poikilohydrous strategy. For instance, extending hydration sometimes reduces water capture. Poikilohydry also provides a remarkable tolerance for desiccated autotrophs to other stresses that usually occur with drought, such as heat and excessive light (see Section "Preventing Damage and Tolerating Stresses"). Thus, if metabolic activity is extended into these harmful periods, it could not only reduce overall productivity but also compromise survival.

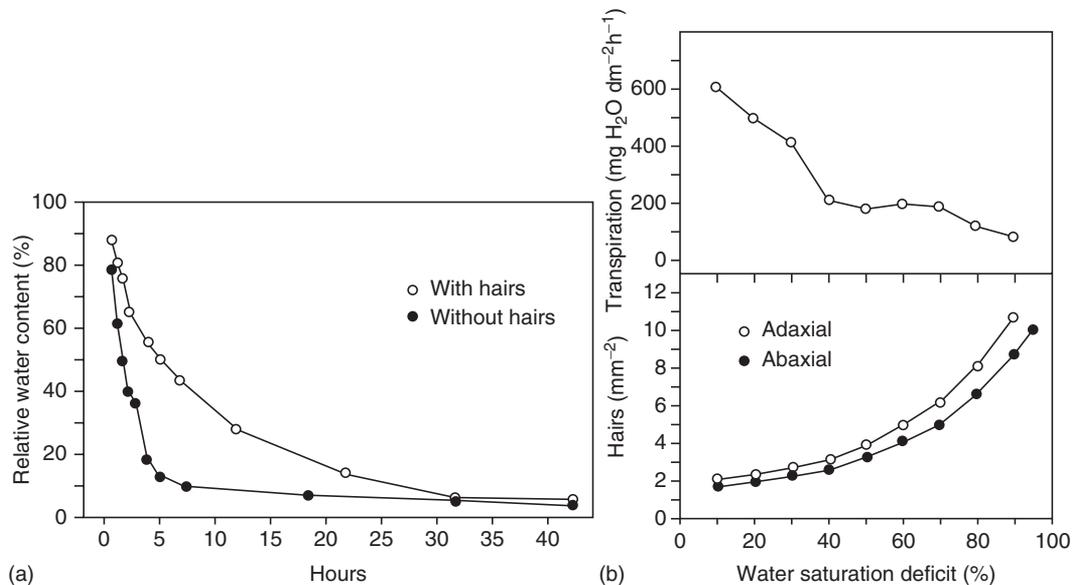
One way of retarding water loss in lichens is by increasing the water that can be stored within the plectenchyma (Valladares 1994b, Valladares et al. 1998). Anatomical characteristics, such as porous and thick medulla layers and rhizinae, have been suggested as means of increasing water storage in lichens (Snelgar and Green 1981, Valladares et al. 1993, Valladares and Sancho 1995). However, because water and CO<sub>2</sub> share the pathway in lichens, enhanced water storage can hamper CO<sub>2</sub> diffusion and consequently reduce photosynthetic carbon uptake (Green et al. 1985, Lange et al. 1996, Maguas et al. 1997). Thus, again, these plants must reach a compromise between two opposing situations. Large foliose lichens can possibly separate photosynthesis and water storage in space somewhat, as young, growing zones of the thallus optimize gas diffusion, whereas old, thick regions act primarily as water reservoirs, sacrificing gas diffusion and carbon gain (Green et al. 1985, Valladares et al. 1994). This trade-off between gas diffusion and water storage seems to be flexible, and lichens have been shown to exhibit a remarkable phenotypic plasticity in their water storage and retention capacities in response to habitat conditions (Larson 1979, 1981, Pintado et al. 1997). Dry habitats induce increased water storage (Tretiach and Brown 1995), but there are complex interactions with light availability for photosynthesis. In shaded sites without access to liquid water, the Antarctic lichen *Catillaria corymbosa* enhanced both water storage and photosynthesis via increased light harvesting by chlorophylls (Sojo et al. 1997), whereas in exposed sites (dry and receiving high irradiance), the lichen *Ramalina capitata* enhanced photosynthetic utilization of brief periods of activity via improved gas diffusion at the expense of reducing water storage capacity (Pintado et al. 1997). These problems are not faced by bryophytes because most of them have rather complex photosynthetic tissues, where the CO<sub>2</sub> exchange surface is separated from water storage volumes (Green and Lange 1994). The capacity of bryophytes to keep high rates of photosynthesis at high water contents is a very likely explanation for the dominance of these organisms in wet habitats (Green and Lange 1994). Zotz et al. (2000) demonstrated experimentally with *Grimmia pulvinata* a positive relationship between cushion size and water retention capacity and also an increasing CO<sub>2</sub> gain up to an optimum water content. However, despite mechanistic differences between mosses and lichens, in certain cases overall performance can be similar.

Discussing the role of morphological properties for lichens, Rundel (1982a) concluded that evaporative water loss can be reduced by a decrease in surface/volume ratio, but such a decrease reduces uptake of water vapor similarly. This seems not to be the case for liquid water, since structures on the lower side of the thallus such as the rhizinomorphs of the lichen family Umbilicariaceae enhance capture and storage of water from run-offs without significantly increasing water loss by evaporation (Larson 1981, Valladares 1994b, Valladares et al. 1998). Reduction of evaporative water loss by structural traits such as a tomentum on the upper surface (Snelgar and Green 1981), a thick cortex (Larson 1979, Büdel 1990), or a decreased surface/volume ratio is very limited in open habitats, but can be significant in sheltered or humid places or in areas with frequently overcast skies (Kappen 1988) or under

the influence of drip water from trees or from antennae on roofs. Bryophytes can also retard water loss by an increased boundary layer resistance and due to growth forms of low surface-to-volume ratios (Gimingham and Smith 1971, Proctor 1982, Giordano et al. 1993).

Comparing water retention of a terricolous moss and a terricolous lichen, Klepper (1968) found that both remained hydrated for the same period of time after the rainfall although the moss stored initially more water. Then, regardless of the initial water content, they dried out quickly when the ambient water vanished and the atmosphere became dry. Measurements on desert lichens have clearly shown that the thalli start drying as soon as the sun is rising and their period of hydration depends solely on evaporative conditions (Kappen et al. 1979, Kappen 1988).

As has been repeatedly demonstrated, the water content of vascular resurrection plants varies with the soil moisture and, like their nonvascular counterparts, they dehydrate within a few hours or days after soil water supply has declined (Gaff and Churchill 1976, Gaff 1977). In their shaded habitats some resurrection plants, especially the ferns, take profit from less evaporative stress than in the open. Water-storing tissues of the succulent *B. liliputana* and those within the leaves of some Velloziaceae (e.g., *V. tubiflora*, *V. luteola*, *Barbacenia reflexa*; Kubitzki 1998) may retard water loss. Since stomatal conductance of resurrection vascular plants is, in general, rather high (Tuba et al. 1994), water loss must be retarded by structural features such as scales, as was shown for leaves of *C. officinarum* (Oppenheimer and Halevy 1962). However, scales were almost ineffective in *Cheilanthes maranthae* (Gebauer 1986, Schwab et al. 1989). A retarding effect of hairs in leaves of *Ramonda* (Figure 2.4a) has long been known (Bewley and Krochko 1982) and the efficiency of leaf pubescence in retarding water loss is increased when the leaves shrink (Gebauer et al. 1987, Figure 2.4b).



**FIGURE 2.4** (a) Water loss from leaves of *R. myconi* in air (approximately 50% rh) with hairs and after hairs were removed before the experiment. (After Gebauer, R., Löscher, R., and Kappen, L., *Verh Ges Ökologie*, XVI, 231, 1987.) (b) Transpiration rates of leaves of *R. myconi* with increasing water saturation deficit. Hair density on the upper (adaxial) and the lower (abaxial) axial leaf surface increases as the leaf shrinks with increasing water loss. At approximately 40% saturation deficit, stomatal closure becomes effective. (After Gebauer, R., *Wasserabgabe und Wasseraufnahme poikilohydrer höherer Pflanzen im Hinblick auf ihre physiologische Aktivität*. Diploma thesis, Universität zu Kiel., 97 pp., 1986.)

The effect of hair density in reducing the transpiration rate strongly increased when the leaf water-saturation deficit went beyond 40%. Reduction of the exposed surface is also a typical mechanism to reduce transpiration. This is the case with poikilohydrous ferns (Pessin 1924); with *S. lepidophylla*, which curls the whole shoot rosette (Lebkuecher und Eickmeier 1993); with *M. flabellifolius*, which regularly pleats its fan-like leaves (Vieweg and Ziegler 1969, Puff 1978); and with Velloziaceae, which fold or curl their leaves; and with other xeromorphous structures in *Sporobolus stapfianus* (Gaff 1977, Kubitzki 1998, Vecchia et al. 1998). Leaves of *C. plantagineum* can reduce surface area to 15% (Sherwin and Farrant 1998) and those of *X. scabrada* to 30% (Tuba et al. 1997b) of the original size. Leaf or shoot movements of most of these plants are due to differential imbibition of the tissues involved, rather than to osmotic phenomena, because they still operate in dead plants. Slow drying over periods of several days may typically occur in monocotyledonous plants such as *X. scabrada* (Tuba et al. 1997b). Its ecological significance for hardening and conditioning is discussed later.

## PREVENTING DAMAGE AND TOLERATING STRESSES

### DESICCATION TOLERANCE

Recent literature focuses on the phenomenal desiccation tolerance (although this is only relevant for the eurypoikilohydrous organisms) and wonders whether it is a primitive strategy (Oliver et al. 2005) or how it can be genetically traced down (Illing et al. 2005) or whether it constrains growth and competitiveness (Alpert 2006). Today, 74 pteridophyte and 145 angiosperm poikilohydrous species have been investigated with respect to desiccation tolerance (see Proctor and Pence 2002).

The first, but not the only, stress during desiccation is the lack of water itself, which imposes dramatic structural and physiological changes on the tissues of poikilohydrous organisms. Some poikilohydrous plants exhibit a remarkable tolerance to intense desiccation. The moss *T. ruralis* survived a water content as low as 0.008%, which is equivalent to –6000 bars (Schonbeck and Bewley 1981a). Desiccation tolerance of eurypoikilohydrous autotrophs can be defined as the capacity to withstand equilibrium with a relative humidity less than 20% (Lange 1953, Biebl 1962, Bertsch 1966b, Gaff 1986). The lowest relative water contents tolerated by vascular plants were reported to be between 1.4% and 8.4%, which is equivalent to 4% and 15% of their dry weight (Kaiser et al. 1985) (see Table 2.1 for a detailed list). Detached leaves of resurrection plants proved to be much less tolerant to severe water loss (Gaff 1980). Table 2.1 also shows tolerance to extended periods of anabiosis. *Nostoc* may tolerate 5 years of desiccation, but other cyanobacteria do not survive desiccation at all (Biebl 1962, Scherer et al. 1986). Most lichens, bryophytes (Lange 1953, Biebl 1962, Proctor 1982), and poikilohydrous vascular plants (Hallam and Gaff 1978, Lazarides 1992) survive dry periods that last for a few months. Although Marchantiales were reported to be exposed to 6–8 months of drought in their habitat in Namibia (Volk 1979), such extremely long periods of desiccation are usually rare for this kind of bryophyte. Several vascular resurrection plants have been shown to tolerate air-dry periods of 2–5 years (Hickel 1967, Gaff and Ellis 1974, Gaff 1977), and some lichens can become photosynthetically active again after a period of 10 years frozen in the dry state (Larson 1988).

Bryophytes comprise taxa that have an intrinsic capacity of desiccation tolerance, as well as taxa that need acclimation (Proctor and Tuba 2002). Although the so-called xerophytic moss species such as *Syntrichia ruralis*, *Rhacomitrium canescens*, *Neckera crispa*, and others always immediately survive extreme desiccation, mesophytic and even hygrophytic species such as *Bryum caespitium*, *Plagiothecium platyphyllum*, *Pohlia elongata*, or *Mnium seligeri* become extremely desiccation tolerant only if they were pretreated at a relative humidity of

96% for 24 h (Abel 1956, Biebl 1962). Most remarkable is that the water moss *Fontinalis squamosa* is as tolerant as a xerophytic moss, whereas *Fontinalis antipyretica* is drought-sensitive even when pretreated at 96% relative humidity. The intrinsic desiccation tolerance of eurypoikilohydrous bryophytes can be modified by the rapidity of desiccation processes (Gaff 1980). Desiccation tolerance was observed to vary seasonally in many bryophytes (Dirksen 1964, Dilks and Proctor 1976a,b), in ferns (Kappen 1964), and also in *B. nitida* (Gaff 1980) as they can acclimate to frost desiccation in winter or to summer drought. Several bryophytes (*Dicranum scoparium* and *Mnium punctatum*) and ferns (*Asplenium spp.* and *P. vulgare*) gained an extremely high desiccation tolerance in winter (Dirksen 1964, Kappen 1964). Like seeds, air-dry lichens (Lange 1953), bryophytes (Hosokawa and Kubota 1957, Gaff 1980, Proctor 1990), and vascular resurrection plants can persist longer if stored at humidities lower than 30% relative humidity (Leopold 1990). This was explained by the fact that intermediate-to-low water contents allow some enzyme activity and lead to respiratory carbon loss, destructive processes, and infections (Gaff and Churchill 1976 [*B. nitida*], Proctor 1982). Most of our current knowledge of the effects of environmental conditions before and during desiccation on the tolerance to desiccation and related stresses comes from experiments under controlled conditions.

More important for eurypoikilohydrous autotrophs is their capacity to withstand repeated changes between dry and moist states. Lichens in deserts and the Mediterranean regions, for instance, oscillate regularly between periods of a few hours of activity and anabiosis for the rest of the day (Kappen et al. 1979, Redon and Lange 1983, Kappen 1988, Lange et al. 1991, Sancho et al. 1997). Similarly, it is typical of several poikilohydrous phanerogams such as *C. intrepidus* living in ephemeral rock pools (Woitke et al. 2004) and changing repeatedly between hydrated and dried state within one season. The capacity to tolerate several changes between dry and wet states was tested experimentally for different moss species by Dilks and Proctor (1976a, 1979). *T. ruralis*, as an eurypoikilohydrous species, performed well during up to 63 changes within a period of 18 months, whereas *Rhytidiadelphus loreus* was killed when continually dry for 18 months or when the oscillation phase was 1 day wet/1 day dry, but it retained 50% of its normal net photosynthetic rate if the wet periods were longer (6 or 7 days) or the dry period was shorter. Mosses such as *T. ruralis* and the angiosperm *B. nitida* (Schonbeck and Bewley 1981b) were actually able to increase their desiccation tolerance if drying and rehydration were repeated. However, cultivation under moist conditions for 2 weeks can decrease the desiccation tolerance of most eurypoikilohydrous autotrophs (algae and lichens: Kappen 1973, Farrar 1976b; bryophytes: Schonbeck and Bewley 1981b, Hellwege et al. 1994; vascular plants: Gaff 1977, 1980). In contrast, continuous hydration over several days decreased the tolerance to desiccation in *T. ruralis* (Schonbeck and Bewley 1981b), a result also found for some lichens (Ahmadjian 1973). Apparently, in the absence of contrasting oscillations of moisture content, the algal partner of lichens grows excessively, altering its symbiotic relation with the mycobiont (Farrar 1976b). Repeated drying seems to be essential for the internal metabolic balance of lichens (McFarlane and Kershaw 1982), and also in poikilohydrous vascular plants, as indicated by the fact that cultivation of *M. flabellifolius* is only successful if the plants dry occasionally (Puff 1978). For several desert cyanobacteria, hydration is a very rare event. Pleurococcoid green algae (e.g., *Apatococcus lobatus*) and many epilithic lichens are water-repellent (Bertsch 1966a). Species of the genera *Chrysothrix*, *Lepraria*, and *Psilolechia* growing under overhanging rocks never receive liquid water during their lifetime (Wirth 1987).

#### CELLULAR AND PHYSIOLOGICAL CHANGES DURING DESICCATION

Great attention has been given in the last 25 years to the investigation of the ultrastructural changes and the biochemical processes that take place during dehydration and rehydration of

poikilohydrous autotrophs. Rather than providing a detailed account here, we refer the interested reader to some reviews (Gaff 1980, 1989, Bewley and Krochko 1982, Stewart 1989, Leopold 1990, Proctor 1990, Bewley and Oliver 1992, Ingram and Bartels 1996, Hartung et al. 1998, Bartels 2005, Rascio and Rocca 2005). Two main mechanisms are involved, one that downregulates the processes and structures, leading to desiccation tolerance, and another that contributes to full metabolic and structural recovery (Bernacchia et al. 1996).

Nonvascular autotrophs are desiccation tolerant if they can retain cellular integrity and limit cellular damage during drying. To accomplish this with *bryophytes* we summarize some salient facts from reviews by Bewley and Oliver (1992), Oliver and Bewley (1997), and Oliver et al. (2000, 2005). The capability of xeric bryophytes like *T. ruralis* to recover quickly even from extremely rapid desiccation indicates that their desiccation tolerance is intrinsic. Membrane structure does not suffer from drying, however, protein synthesis ceases rapidly during drying (Bewley and Krochko 1982). Specific protective substances or mechanisms are not apparent (Bewley and Oliver 1992, Oliver and Bewley 1997), as sugar content does not change significantly, and no membrane protective mechanism is detectable. On rehydration a transient leakage indicates membrane phase transitions, and cells regain normal shape and structure within 24 h. During the first 2 h of rehydration an extensive alteration in gene expression indicates synthesis of proteins, the *rehydrins*. The rehydrins are late embryo abundant (LEA) or LEA-like proteins (see III.C), which may stabilize membranes lipids or help to enable quick lipid transport for reconstitution of eventually damaged membranes (Oliver 2005). They may be more important for the mesic, less-tolerant mosses and liverworts, where according to Bewley (1979) changes in membranes and metabolism during dehydration were observed. However, mesic bryophytes may increase tolerance by previous drying treatment or by addition of ABA. The presence of ABA was found in moss (e.g., *Funaria hygrometrica*: Werner et al. 1991) and in hepatic species (e.g., the europaikilohydric *Exormothea holstii*: Hellwege et al. 1994, Hartung personal communication). Accumulation of ABA during drying and disappearance in wet culture and the capacity of inducing hardiness when applied to dehardened gametophytes reveal its role in the drought hardening process, except in *T. ruralis* where ABA was not detected (Reynolds and Bewley 1993a).

The mechanism of lichens for dealing with desiccation remains broadly unknown but is strongly related to their high content of polyols (Farrar 1976a). Membrane leakage in lichens as a consequence of repeated drying and wetting (Farrar 1976a) is harmless. The role of ABA, recently detected in lichens, is unclear, as this hormone is produced by the fungal biont and, as opposed to its activity in plants, increases as a response to water uptake (Dietz and Hartung 1998).

Pteridophytes have a performance, intermediate between bryophytes and angiosperms. For instance, as was shown with *P. virginianum* (Oliver et al. 2000), they carry out synthesis of proteins on dehydration (dydrins) as well as subsequent to rehydration (rehydrins). Interestingly, the proteins synthesized during drying disappear rapidly on rehydration, but later (after 24 h) some of these proteins increase again. In addition, immediately after rehydration novel polypeptides are synthesized, which are not exclusively related to the desiccation regime, and another set of new proteins is produced after 24 h. ABA is present in *Polypodium* but notably decreases during drying. Nonetheless, ABA application can induce synthesis of proteins similar to dehydrins and survival of otherwise lethal-rapid desiccation (Reynolds and Bewley 1993a,b). From dehydrated microphylls of *S. lepidophylla*, an expressed gene sequence tag (EST) database was generated and compared with that of other, not poikilohydrous *Selaginella* species. The percentage of functional categories, which were disease/defense-related comprising induction of secondary metabolism, molecular chaperons, and LEA proteins, was significantly higher in the poikilohydrous *Selaginella* species (Iturriaga et al. 2006).

In *S. lepidophylla*, 74% of the activity of 9 enzymes of the carbohydrate metabolism was conserved during drying. The conservation of photosynthetic enzymes was lower than that for respiratory enzymes (Eickmeier 1986).

Based on the fact that most monocotyledonous poikilohydrous species show a dramatic color change when desiccated and most dicots do not, we can distinguish between poikilochlorophyllous and homoiochlorophyllous angiosperms. Comparative, mainly electron-microscopical studies illustrate these differences (Sherwin and Farrant 1996, 1998, Farrant 2000).

In the poikilochlorophyllous species, structural changes are considerable (see Gaff 1980, Hetherington and Smillie 1982, Tuba et al. 1996b, 1997), except in the nucleus (Barthley and Hallam 1979), containing a dense mass of chromatin (Hetherington and Smillie 1982). Ultrastructural changes in poikilochlorophyllous plants may be even greater than in desiccation-sensitive homoiohydrous species at a comparable dehydration level (Gaff 1989). Investigations with *Xerophyta villosa* and *X. scabrida* show the following: The polysome content rises significantly with water loss (*X. villosa*; Gaff 1989). Virtually all thylacoids and most of the carotenoids content are lost. Obviously, the destruction of the chlorophyll is structured, as grana are retained (Bartley and Hallam 1979). However, as most of the chlorophyll can be preserved in *X. scabrida*, if it is desiccated in darkness, Tuba et al. (1997) suggest that under natural conditions chlorophyll loss is due to photooxidation rather than metabolic destruction. Although most of their cristae disappear, mitochondria remain functional (see Hallam and Capicchiano 1974). A continuation of respiration still measurable below  $-3.2$  MPa (Tuba et al. 1996b) in desiccated plants of *X. scabrida* suggests that energy is required for dismantling the thylacoids and the formation of the so-called desiccoplasts. Thus, rather than being deleterious, these organelle changes involve an organized remobilization of cell resources in these resurrection plants.

Structural changes by desiccation are usually small in the homoiochlorophyllous species, and thylacoid membranes and associated chlorophyll complexes apparently remain widely preserved (Owoseye and Sandford 1972, Hallam and Cappicchiano 1974, Gaff and McGregor 1979, Gaff 1989). However, changes in the chloroplast structure and loss of chlorophyll by 20% in *M. flabellifolius* (Wellburn and Wellburn 1976, Farrant 2000) and by 40%–50% in *C. wilmsii* (Sherwin and Farrant 1998) were observed, which recovered within 24–45 h subsequent to rehydration. Kaiser and Heber (1981) and Schwab and Heber (1984) state that the lens shape of the chloroplasts permits dehydration without greater surface area reduction, and in vivo rupture of chloroplasts during desiccation is rarely observed. In dry *Talbotia elegans*, the mitochondria are reduced to membrane-bound sacks (Hallam and Gaff 1978). Transient membrane leakage has been reported for several species. Vacuoles, fragmented into numerous vesicles, become filled with a nonaqueous substance, obviously generating a backpressure for the desiccating cell (Farrant 2000) and lysosomes seem to be maintained intact (Gaff 1980, 1989, Hartung et al. 1998). As a consequence, repair processes may last for 2 days in small herbaceous species (*Ramonda* and *Haberlea* species: Gaff 1989, Markowska et al. 1995), and the extended time for recovery of the large fruticose *M. flabellifolius* is due to the restoration of its hydraulic system.

As a rule, the processes of desiccation and recovery take more time in the poikilochlorophyllous than in the homoiochlorophyllous species. Tuba et al. (1997) state that under field conditions *X. scabrida* may take more than 2 weeks until the plants are dry and inactive. Correspondingly, also repair processes are extended over periods of several days (*X. viscosa* 92–120 h: Sherwin and Farrant 1996, 1998). Poikilochlorophyllous performance is obviously a highly derived adaptation. It allows avoidance of stress from free radicals. In ecological terms, such species are adapted to sites where drought periods are extended over weeks or months, whereas homoiochlorophyllous species easily manage in sites with frequent oscillations between dry and wet stages in shorter periods of time.

## SYNTHESIS OF PROTEINS AND PROTECTIVE SUBSTANCES

Obviously, a network of genes with presumably different functions is activated by water stress. Hartung et al. (1998) estimated that 800–3000 genes could be involved in the response of plants to desiccation. Poikilohydrous plants exhibit a great variety of down- and upregulation of cellular processes, which can be retained at very low water potentials (Leopold 1990). Particularly, genes that code for enzymes relevant to photosynthesis, both in vascular plants and in mosses (Ingram and Bartels 1996, Bernacchia et al. 1996, Oliver and Bewley 1997) were downregulated. In general, the decline of total protein is smaller than in drought-sensitive plants. Loss of water-insoluble proteins is common in resurrection plants, especially in the poikilochlorophyllous species, probably because of degradation of the lipoproteins of the membrane (Gaff 1980). The preservation of polysomes and of RNA may enable protein synthesis after drought (Bewley 1973). Many novel proteins (*dehydrins*) are synthesized during desiccation, most of which were considered specific to extremely desiccation-tolerant plants (Hallam and Luff 1980, Eickmeier 1988, Bartels et al. 1990, Piatkowski et al. 1990, Bartels et al. 1993, Kuang et al. 1995). Nevertheless, certain polypeptides, such as those found in desiccated *P. virginianum*, are not exclusive to the desiccation regime (Reynolds and Bewley 1993b). The majority of the dehydrins belongs to LEA proteins, they are hydrophilic and resistant to denaturation, and typical of orthodox seeds. They are believed to protect desiccation-sensitive enzymes and to stabilize membranes during dehydration (Schneider et al. 1993, Bernacchia et al. 1996, Ingram and Bartels 1996, Bartels 2005). Proteins are necessary also during the rehydration phase. They can be gained by translation of already existing transcripts, as was shown for poikilohydrous species (Dace et al. 1998). Bartels and Salamini (2001) suggest that desiccation tolerance (of *C. plantagineum*) is in most cases not due to structural genes, unique to resurrection plants and could be present as well in desiccation-sensitive homoiohydrous plants. However, the latter may have less amounts of LEA proteins and the expression pattern may be different. Only one, a LEA-6 protein, was identified as typical exclusively for *Xerophyta humilis* and seeds (Illing et al. 2005).

In most resurrection plants, including the aquatic species *Chamaegigas intrepidus*, abscisic acid (ABA) is strongly accumulated and is involved in attaining desiccation tolerance and in stimulating the synthesis of dehydrins (Gaff 1980, 1989, Gaff and Loveys 1984, Reynolds and Bewley 1993a, Hellwege et al. 1994, Schiller et al. 1997). As was hypothesized by Bartels et al. (1990), Nelson et al. (1994), and Oliver and Bewley (1997), there is evidence now in vascular plants that ABA is necessary to induce the genes for desiccation tolerance. With experiments of mutants of *C. plantagineum*, the so-called CDT-1/2 gene family was shown to function by ABA signal transduction (Smith-Espinoza et al. 2005). Leaves of *M. flabellifolius* and *B. nitida* did not survive dehydration if they were dried so rapidly that ABA could not be accumulated (Gaff and Loveys 1984). Abscisic acid accumulation obviously can occur only in leaves attached to the whole plant (Hartung et al. 1998).

A common phenomenon in drought stress is the accumulation of organic compatible solutes because they stabilize proteins and membranes (Levitt 1980, Crowe and Crowe 1992). Lichens are permanently rich in sugar alcohols, which are assumed to be the basis of their remarkable desiccation tolerance (Kappen 1988). Cowan et al. (1979) have demonstrated that the synthesis of amino acids and sugar alcohols was active in lichens in equilibrium with humidities as low as 50%. In contrast, desiccation-tolerant bryophytes contain a low amount of sugars, mainly sucrose, and show no or very little increase in sugar content during drying (Bewley and Pacey 1978, Santarius 1994). Strong sugar accumulation, mainly sucrose, during desiccation has been demonstrated in seeds and many resurrection grasses, species of *Ramonda*, *Haberlea*, and *Boea*, and *X. villosa* (Kaiser et al. 1985, Scott 2000, Zirkovic et al. 2005). Other resurrection plants for example, of the genera *Ceterach* and *Craterostigma* already contain comparatively high amounts of sugar in the leaves when turgid

(Schwab and Gaff 1986). In these and other species (e.g., *M. flabellifolius*), sugar composition was observed to be changed during dehydration (Bianchi et al. 1991, Hartung et al. 1998). Unusual sugars such as stachyose that appear in the turgid leaves and roots are storage products, but they are converted into sucrose during the drying process (Bianchi et al. 1991, 1993, Albini et al. 1994, Heilmeier and Hartung 2001, Norwood et al. 2003). For instance, 2-octulose is typical for hydrated leaves of *C. plantagineum* and is converted into sucrose on dehydration (Bartels and Salamini 2001). Thus, sucrose accumulation during desiccation is generally recruited from metabolizing storage carbohydrates rather than directly from photosynthesis.

Inositol, present in *Xerophyta viscosa*, may be an effective osmoprotectant (Mayee et al. 2005). Proline concentration in many plant species associated with water stress was comparatively high in *Ceterach* and *Craterostigma*, but did not significantly increase during dehydration (Schwab and Heber 1984). Application of proline had no effect on detached leaves of *B. nitida* and *M. flabellifolius* (Gaff 1980). In the latter species, polyphenols have been identified (Moore et al. 2005) that might be relevant to desiccation tolerance, as provenances from Namibia subjected to greater drought stress were genetically different from those in South Africa and contained more and different polyphenols (e.g., 3,4,5-tri-*O*-galloquinic acid).

One of the internal hazards of desiccation is the increase in oxidative processes, which occurs in plants exposed to a wide range of environmental stresses (Smirnov 1995). An increase in or a high level of defense enzymes of the ascorbate/glutathione cycle was associated with the protection of the membrane lipids in *S. stapfianus* during drying (Sgherri et al. 1994a). Oxidized glutathione was much lower in slowly dried (unimpaired) samples than in rapidly (injured) dried samples of *Boea hygroskopica* (Sgherri et al. 1994b), and glutathione was shown to play the primary role in maintaining the sulfhydryl groups of thylacoid proteins in reduced state during desiccation (Navarri-Izzo et al. 1997). The reversible decrease in phenolic acids far below the level in the hydrated state, which is joined by a decrease in the enzyme ascorbate peroxidase (AP) while antioxidants were accumulated, indicates that *Ramonda serbica* leaves are able to keep up an antioxidative status when subjected to desiccation (Sgherri et al. 2004). Kranner and Grill (1997) postulate that glutathione reductase (GR) and glucose-6-phosphate dehydrogenase are needed for the reduction of desiccation-induced oxidized glutathione. It is suggested that this pathway provides the NADPH during the critical rehydration phase when photosynthesis is still inactive. Accordingly, when photosynthesis is recovered a decrease in antioxidants and production of reactive oxygen species was observed in a lichen species (Weissman et al. 2005). Antioxidants such as AP, GR, and SOD (superoxide dismutase) were increased but to various extents in subsequent phases of water loss in *C. wilmsii*, *M. flabellifolius* (mainly GR), and *X. viscosa* (Sherwin and Farrant 1998) and went down to normal level when the tissues were rehydrated. Anthocyanins recognized as antioxidants (Smirnov 1993) were observed to increase in drying leaves of poikilochlorophyllous species such as *Eragrostis nindensis* (Van der Willigen et al. 2001) and particularly in *Xerophyta humilis* (Farrant 2000). In *C. plantagineum*, lipoxygenase, which catalyzes lipid peroxidation at membranes, becomes increasingly inhibited during drying (Smirnov 1993). Similar processes may also operate in desiccation-tolerant bryophytes (Dhindsa and Matowe 1981, Seel et al. 1992a) in which lipid peroxidation during drought is low. Oxidative processes can take place both in the presence and the absence of light, and light can exacerbate oxidation. This situation—oxidative stress caused or accentuated by light—is discussed in the following section.

#### PHOTOPROTECTION OF THE PHOTOSYNTHETIC UNITS

If plants absorb more light than required during photosynthesis, they are exposed to the risk of photooxidative destruction of their photosynthetic apparatus (Long et al. 1994).

Photooxidative stress can therefore be an important limiting factor for poikilohydrous autotrophs. Bryophytes and algae that are restricted to shady habitats were shown to have limited photoprotective capacities (Öquist and Fork 1982b). Negative effects of strong light were observed in hydrated lichens in the tropical, temperate (Coxson 1987a,b), and Mediterranean region (Manrique et al. 1993, Valladares et al. 1995). Nevertheless, tolerance to strong light can be enhanced by acclimation. Cyanobacterial mats taken from exposed habitats proved to be highly tolerant to high irradiance, whereas cyanobacteria from shaded sites were very sensitive (Lüttge et al. 1995). Field studies have revealed, for instance, that the cyanobacterial lichen *Peltigera rufescens* was at least photoinhibited under certain conditions in winter (Leisner et al. 1996). On the other hand, cryptogam species in Antarctica such as *Umbilicaria aprina*, *Leptogium puberulum*, *Xanthoria mawsonii*, and *Hennediella heimii* were very resistant to the combination of low temperatures and high irradiance while the thallus was photosynthetically active (Schlensog et al. 1997, Kappen et al. 1998a, Pannowitz et al. 2003, 2006).

In hydrated autotrophs, photosynthetic productivity is maintained because only that part of the light energy that is in excess to that used for energy conservation is thermally dissipated by a mechanism that requires zeaxanthin, a carotenoid of the xanthophyll cycle, and the protonation of a special thylacoid protein (Niyogi 1999, Heber et al. 2006). Thermal energy dissipation should be in equilibrium in hydrated autotrophs with ongoing photosynthesis. This means that energy dissipation is in equilibrium with energy conservation based on charge separation, the production of a strong oxidant and a reductant in the reaction centers of PS II. If energy dissipation caused is faster (photostress), it would inhibit photosynthesis (Wiltens et al. 1978, Öquist and Fork 1982a, Demmig-Adams et al. 1990b). Downregulation of photosynthetic processes and the so-called dynamic or recoverable photoinhibition (i.e., inhibition of photosynthesis by light, but no damage) has been observed in a number of poikilohydrous plants, bryophytes, and lichens (e.g., Seel et al. 1992, Leisner et al. 1996, Ekmekci et al. 2005), and as a result, avoidance of photooxidation (Eickmeier et al. 1993, Valladares et al. 1995, Calatayud et al. 1997, Heber et al. 2000, 2001, Bukhov et al. 2001).

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A prevention of photooxidative damage by drying may be apparent from the fact that isolated *Trebouxia* as well as green-algal lichens resisted photostress in the field by quick desiccation under high irradiances (Öquist and Fork 1982b, Leisner et al. 1996). This would resemble in effect the strategy of poikilochlorophyllous plants that radically destruct the photosynthetic apparatus during desiccation (Smirnoff 1993). It was hypothesized that the photosynthetic apparatus of homoiochlorophyllous autotrophs cannot be affected by strong irradiance because it undergoes a functional dissociation between light harvesting complexes and photosystem II during desiccation (Bilger et al. 1989, Smirnoff 1993). However, water content has been proved to influence both dynamic and chronic photoinhibition of lichens (Valladares et al. 1995, Calatayud et al. 1997). Some air-dried lichens typical of shady habitats exhibited even damage after exposure to high light (Valladares et al. 1995, Gauslaa and Solhaug 1996, 1999, 2000, Gauslaa et al. 2001). In addition, stenopoikilohydrous mosses were more damaged by drying at high irradiance than at low irradiance (Seel et al. 1992a).

According to recent findings since Shuvalov and Heber (2003), it has become apparent that reaction centers are capable of charge separation even in the absence of water (Heber et al. 2006a). Thus, functional reaction centers would cause damaging oxidative reactions. A revised and more comprehensive approach to understanding photoprotection in desiccated autotrophs has recently come from Heber and coauthors (Heber et al. 2000, 2001, Heber and Shuvalov 2005, Kopecky et al. 2005, Heber et al. 2006a,b) who have demonstrated that more than one photoprotective mechanism of energy dissipation is active in lichens and bryophytes. Available evidence suggests that zeaxanthin-dependent energy dissipation remains active on desiccation (Eickmeier et al. 1993, Kopecky et al. 2005, Georgieva et al. 2005), but it is not clear whether the zeaxanthin-dependent energy dissipation is fast enough to prevent charge separation in functional reaction centers particularly in lichens and xeric bryophytes.

A second protective mechanism was evident from the finding that functions of the reaction center of PS II can change on desiccation (Heber et al. 2006a,b). In desiccated samples of the moss *Rhytidiadelphus squarrosus*, energy dissipation has been shown to occur in PS II reaction centers. In this case, a photoreaction is responsible for the formation of a quencher of fluorescence in the reaction center (Heber et al. 2006b). A third protective mechanism was apparent from the observation that light was not even necessary for the formation of a quencher during desiccation. After lichen thalli were carefully predarkened to avoid light activation of the mechanism of energy dissipation, fluorescence was quenched after desiccation took place in darkness. This reveals the activation of the third mechanism of thermal energy dissipation (Heber et al. 2006b, Heber personal communication). The latter two protective mechanisms were operating only under desiccation and ceased by rehydration. Lichens with cyanobacteria as photobionts lack the zeaxanthin-dependent thermal energy dissipation mechanism; however, other carotenoids may play a role at least in the hydrated state (Demmig-Adams et al. 1990b, Leisner et al. 1994, Lange et al. 1999). In the desiccated state, the desiccation-induced thermal energy dissipation mechanism (mechanism 3) may be operating (Heber, personal communication). As soon as water becomes available to the chloroplasts of homoiochlorophyllous autotrophs, photosynthetic water oxidation is resumed (Kopecky et al. 2005, Heber et al. 2006a).

In vascular plants, only the zeaxanthin-dependent dissipation mechanism is known to be protective also in the desiccated state. It also operates in homoiohydrous xerophytic plants (e.g., *Nerium oleander*: Demmig et al. 1988; *Clusia* spp. with CAM: Winter and Königer 1989). In resurrection plants, it was shown with *S. lepidophylla* (Casper et al. 1993, Eickmeier et al. 1993). Accumulation of zeaxanthin on drying was reported for the poikilohydrous species *C. plantagineum* (Amalillo and Bartels 2001) and *B. hygrometrica* (see Yang et al. 2003). In *R. serbica*, the photoprotection appeared to be achieved, when dry, by the zeaxanthin-dependent dissipation as well as by ascorbate and glutathione (Augusti et al. 2001). In the poikilochlorophyllous *X. scabrida*, 22% of the carotenoids were still preserved in the dry leaves when the photosynthetic apparatus was dismantled, but the carotenoids seemed to be protective or essential when the chloroplasts reorganized during rehydration (Tuba et al. 1993b).

Poikilohydrous autotrophs exhibit various photoprotective mechanisms in addition to the thermal energy dissipation via carotenoids. In the case of lichens, filtering or screening effects of the upper cortex formed by the mycobiont and of certain secondary compounds such as parietin have been shown to be potentially important in reducing the risk of photodamage of the photosynthetic units (Büdel 1987, Solhaug and Gauslaa 1996, Kappen et al. 1998a, Gauslaa and Ustvedt 2003, Gauslaa and McEvoy 2005). Anthocyanins, which reflect photosynthetically active light, may prevent excessive light–chlorophyll interaction. An accumulation of anthocyanins was observed in sun-exposed leaves of several resurrection plants, mainly on the abaxial leaf face, which is everted when the leaves are curled or folded (Farrant 2000). Leaf and shoot curling during drought, despite not effective in certain bryophytes (Seel et al. 1992a), can confer photoprotection simply by shadowing. For instance, leaf curling by everting the reflectant abaxial leaf surface was effective in *P. polypodioides*, a species sensitive to strong light under water stress (Muslin and Homann 1992, Helseth and Fischer 2005). Additionally, photorespiration and light-activated photosynthetic enzyme activity were not affected by intense radiation in *S. lepidophylla* due to leaf curling (Lebkuecher and Eickmeier 1991, 1993). The protective role of curling is important for plants growing in open and exposed habitats and, although not yet thoroughly explored, it may be relevant also for lichens such as *Parmelia convoluta* and *C. semiviridis*, or for thallose desert liverworts all everting a whitish underside when dry (Lange et al. 1990a).

Another radiative stressor is UV B, particularly in polar and alpine regions; however, experiments proved that it never harmed lichens and mosses in open habitats (Lud et al. 2003,

Nybakken et al. 2004). Moreover, UV B (280–320 nm) was shown to be an essential requisite for the synthesis of sun-screening pigments (parietin, melanin) in lichens (Solhaug et al. 2003).

### DESICCATION TOLERANCE: AN OLD HERITAGE

Taking desiccation as a fundamental heritage, geneticists and molecular biologists were challenged to trace down this capability of plants to the beginning of plant evolution and to ask whether this is unique to poikilohydrous organisms and why it is absent in the vegetative parts of the majority of vascular plants and certain bryophytes, and, whether it is mono- or polyphyletically evolved, and, on which genes desiccation tolerance is located.

According to Oliver et al. (2000) recent synthetic phylogenetic studies confirm the idea that vegetative desiccation tolerance is primitively present in the bryophytes but was then lost in the evolution of vascular plants. It is hypothesized that desiccation tolerance was crucial for ancestral fresh-water autotrophs to live on land. The tolerance might have been lost on the way of a more complex (homoiohydrous) organization of the vascular plants, and independent evolution or re-evolution of desiccation tolerance has happened in the Selaginellales, leptosporangiate ferns, and the 10 families of angiosperms. Evolutionary progress may be evident from the fact that pteridophytes, in common with bryophytes, are able to synthesize rehydrins but can also synthesize dehydrins, the only capability of angiosperms. Tracing possible pathways by identifying possible gene orthologs of LEA-like proteins that are synthesized on dehydration provided a network of land plant phylogeny. Oliver et al. (2005) proved his earlier theory and extended it by discussing the fact that several genera of bryophytes (*Haplomitrium*, *Sphagnum*, *Takakia*, *Tetraphis*) lack the particular genes and are not desiccation tolerant either constitutively or due to loss of phenotype, which involves the possibility that precursors of these bryophytes also did not realize desiccation tolerance in the vegetative state. There was also negative evidence that ancestors of the hornworts and of all vascular plants were desiccation tolerant. Keeping up the idea that desiccation tolerance of spores may elucidate the problem, Illing et al. (2005) demonstrated by molecular responses a crucial role of orthodox seeds as the carriers of genes for desiccation tolerance, which may, or not, be expressed in the vegetative part of vascular plants. Analyzing sequences of genes of *Arabidopsis* seeds and a set of vegetative homoio- and poikilohydrous plant species with respect to certain LEA proteins, RNA transcripts for antioxidants that are expressed during desiccation, and in addition, sugar accumulation revealed the following results: Among the antioxidant activities only that with l-cys peroxidase appeared to be a mechanism specific to desiccation tolerance of resurrection plants and seeds. Most of the antioxidants are activated also as a response to various other abiotic stresses. However, genes belonging to the LEA six superfamily are uniquely associated with dehydration stress in resurrection plants and in seeds. Moreover, sucrose accumulation on drying seems to be a desiccation-tolerance specific mechanism of resurrection plants and orthodox seeds, albeit it was also observed in some recalcitrant seeds (Kermode and Finch-Savage 2002). As a general result, desiccation tolerance is not considered the result of parallel origins, and the loss of desiccation tolerance can be interpreted as the result of suppression of latent genes in the vegetative state of the plant. However, single gene loss in certain instances (Dickie and Pritchard 2002) cannot be excluded.

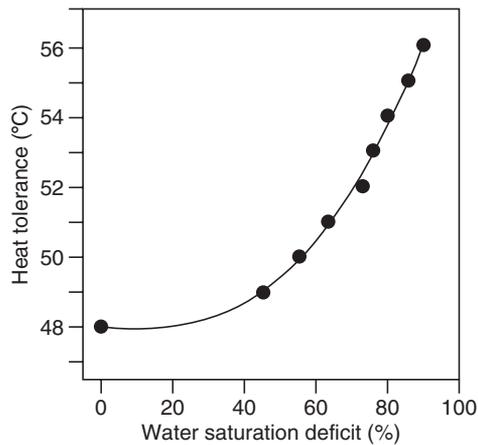
Generally speaking of desiccation tolerance suggests that it relates to a fundamental uniform mechanism; however, a differentiated view is obvious now. On the one hand, it has to be realized that the most primitive autotrophs, such as Cyanobacteria, are extremely desiccation tolerant, whether they live in water or in the porous space of rock. This indicates that desiccation tolerance is a very early trait in evolution. Moreover, the fact that organelles such as chloroplasts of spinach (Table 2.1) are desiccation tolerant and that vegetative tissues can be lyophilized without harm suggests that it is the way of withdrawing water that can be damaging but not the dehydration itself. Thus, it can be

concluded that the capability of surviving dehydration must be basic and ubiquitous. On the other hand, phenotypic tolerance must have been acquired at various advanced stages of organismic complexity by evolving metabolic or structural protective mechanisms. These must be very specific, either because of a distinct combination or quantitatively selected ubiquitous “house-keeping” mechanisms (Illing et al. 2005), or because of inventing genetic structures that act species-specific, as most likely the CDT-1 gene in *C. plantagineum* (Furini et al. 1997, Bartels and Salamini 2001). So far it is reasonable to consider desiccation tolerance of vascular plants (and highly derived bryophytes) as modified (see Oliver and Bewley 1997) or secondary (Raven 1999).

#### TOLERANCE TO EXTREME TEMPERATURES: A PROPERTY LINKED TO POIKILOHYDRY

Plants capable of surviving desiccation may be tolerant also to other environmental stresses such as extreme temperatures. Some lichen species, for example, are extremely resistant to freezing both in hydrated and dehydrated states. The freezing tolerance of hydrated lichens can exceed by far the temperature stresses that occur in winter or in polar environments (Kappen 1973). Bryophytes are less freezing-tolerant, but many species are well adapted to live and persist in cold environments (Richardson 1981, Proctor 1982, Longton 1988b). Fern gametophytes and vascular resurrection plants from the temperate zone have a moderate ( $-9^{\circ}\text{C}$  to  $-18^{\circ}\text{C}$ ) freezing tolerance in winter (Kappen 1964, 1965). Most poikilohydrous vascular plants come from subtropical climates and are sensitive to freezing. For example, *B. nitida* can only survive temperatures between  $-1^{\circ}\text{C}$  and  $-2^{\circ}\text{C}$  in winter (Gaff and Churchill 1976), and poikilohydrous grass species do not survive temperatures below  $0^{\circ}\text{C}$  (Lazarides 1992). However, desiccated leaves, fronds, or other vegetative parts become highly tolerant to cold depending on the remaining water content. For instance, experiments with *R. myconi*, *P. vulgare*, *M. flabellifolius*, and gametophytes of several fern species revealed that the tissues resisted  $-196^{\circ}\text{C}$  if they were desiccated to a relative water content of, for example, 6% (Kappen 1966, Vieweg and Ziegler 1969, Pence 2000). Thus, the tolerance of these vascular poikilohydrous plants to low temperatures was not different from that of dry algae, lichens, and bryophytes (Levitt 1980), which also indicates water content as a crucial factor in the freezing tolerance of organisms in general.

Heat tolerance of plants can also be increased if they are desiccated (Kappen 1981). This fact becomes ecologically relevant if we consider that dry plants can easily heat up to over  $50^{\circ}\text{C}$  in their natural habitats. Thallus temperatures in dry moss turfs and dry lichens can reach  $60^{\circ}\text{C}$ – $70^{\circ}\text{C}$  under field conditions (Lange 1953, 1955, Richardson 1981, Proctor 1982, Kershaw 1985). A similarly high temperature was reported for desert soil around *S. lepidophylla* (Eickmeier 1986). The temperature in the rock pools where *C. intrepidus* lives can reach  $41^{\circ}\text{C}$  (Gaff and Giess 1986). Although some lichens such as *Peltigera praetextata* and *Cladonia rangiferina* did not survive temperatures higher than  $35^{\circ}\text{C}$ , even in the desiccated state (Tegler and Kershaw 1981, Gauslaa and Solhaug 1999, 2001), tolerance to  $70^{\circ}\text{C}$  and even to  $115^{\circ}\text{C}$  was recorded for many other dry lichen and bryophyte species (Lange 1953, 1955, Proctor 1982, Meyer and Santarius 1998). Heat tolerance of bryophytes and vascular plant species varies with season. The maximal temperature tolerated in the turgescence state by the temporarily poikilohydrous fern *P. vulgare* and by *R. myconi* was highest in winter (approximately  $48^{\circ}\text{C}$ ), and by decreasing water content, the heat tolerance could be increased to approximately  $55^{\circ}\text{C}$  (Kappen 1966, Figure 2.5). *C. intrepidus* was able to thrive at  $60^{\circ}\text{C}$  temperatures (Heil 1925), and dry leaves of *M. flabellifolius* were reported to have resisted at  $80^{\circ}\text{C}$  (Vieweg and Ziegler 1969). Eickmeier (1986) could demonstrate an increase in photosynthetic repair capacity of *S. lepidophylla* if dry plants were subjected to  $45^{\circ}\text{C}$  and  $65^{\circ}\text{C}$ , but he found also that desiccation tolerance decreased with increasing temperatures ( $25^{\circ}\text{C}$ ,  $45^{\circ}\text{C}$ ,  $65^{\circ}\text{C}$ ). However, since the water content of these dry plants was not defined,



**FIGURE 2.5** Shift of heat tolerance limit with increasing water saturation deficit in leaves of *R. myconi*. (After Kappen, L., Schroeter, B., Hestmark, G., and Winkler, J.B., *Flora*, 156, 427, 1966.)

it still remains unclear whether metabolic disturbance at the higher temperature was weakening the plants.

### LIMITS AND SUCCESS OF POIKILOHYDRY

Poikilohydrous land plants are typically small and slow growing like many other ecological specialists, obviously as a response to environmental constraints. The carbon economy of poikilohydrous autotrophs is influenced by the frequency and duration of the periods of metabolic activity and by repair and other processes that delay maximal net photosynthesis once the plant enters the biotic state by rehydration. In fact, poikilohydrous species exhibit significant differences in their speed of recovery from dehydration and in their photosynthetic performance while they are active.

### PHOTOSYNTHESIS

While cyanobacteria, algae, lichens, and bryophytes can reach maximal photosynthetic rates within 10–30 min after rehydration, poikilohydrous vascular plants usually require much longer (Table 2.2). Generally, the threshold for respiratory activity is lower than that for net photosynthesis (Lange and Redon 1983). The capacity of chloroplasts and mitochondria to function at low water potentials is remarkable in aerophytic green algae and green-algal lichens (–50 and –38 MPa, respectively; Nash et al. 1990, Bertsch 1996a) and also in homoiohydrous vascular plants (–19 MPa in the mesophyll of *Valerianella locusta*, Bertsch 1967; beet chloroplasts, Santarius 1967). However, each particular poikilohydrous organism has a suite of morphological and functional traits that exert specific influences on photosynthetic yield and overall performance during periods of water availability. These organisms are covered in the following sections.

### Lichens and Bryophytes

Lichens can be photosynthetically active at water contents as low as 20% d.wt. (Lange 1969b, Lange et al. 1990b), under high saline stress (Nash et al. 1990), and at temperatures as low as –20°C (Kappen 1989, 1993a, Schroeter et al. 1994; see also Chapter 14). Schroeter and Scheidegger (1995) demonstrated that net photosynthesis was still positive when the algal

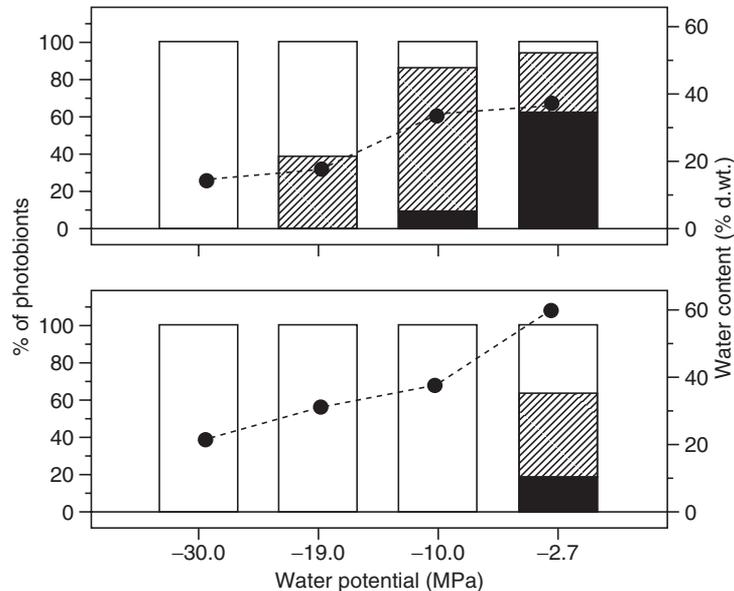
**TABLE 2.2**  
**Time Required by Different Poikilohydrous Autotrophs to Resume Photosynthetic Activity (Net Photosynthesis) after Rehydration with Water Vapor (>90% Relative Humidity) or with Liquid Water**

Species	Water Source	Time	Reference
<i>Parmelia hypoleucina</i>	Water vapor	<1 h	Lange and Kilian 1985
<i>Cladonia portentosa</i>	Water vapor	6 h	Lange and Kilian 1985
<i>Caloplaca regalis</i>	Water vapor	24 h	Lange and Kilian 1985
<i>L. pulmonaria</i>	Liquid	<30 s <sup>a</sup>	Scheidegger et al. 1997
<i>H. cupressiforme</i>	Water vapor	12 h	Lange 1969
<i>T. ruralis</i>	Liquid	90 min	Scott and Oliver 1994
<i>E. holstii</i>	Liquid	2 h <sup>a</sup>	Hellwege et al. 1994
<i>P. virginianum</i>	Liquid	6 h <sup>b</sup>	Reynolds and Bewley 1993
<i>C. plantagineum</i>	Liquid	15 h <sup>b</sup>	Bernachia et al. 1969
<i>S. lepidophylla</i>	Liquid	24 h <sup>b</sup>	Eickmeier 1979
<i>R. serbica</i>	Liquid	24 h	Markowska et al. 1997
<i>M. flabellifolius</i>	Liquid	c. 40 h	Sherwin and Farrar 1996
<i>X. scabrada</i>	Liquid	72 h	Tuba et al. 1993b

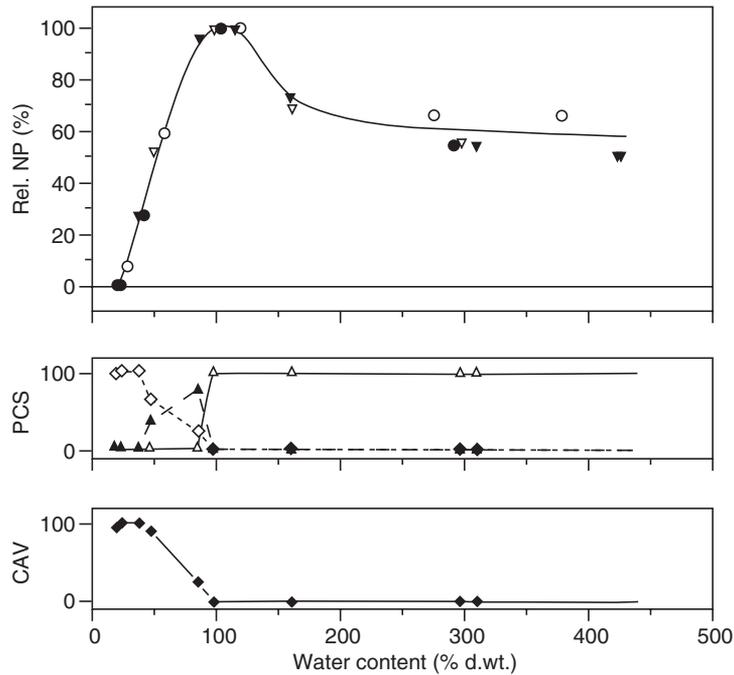
<sup>a</sup> Chlorophyll a fluorescence positive.

<sup>b</sup> Chloroplasts reconstituted.

cells were shriveled and the fungal hyphae cavitated because of the low water content of the thallus. At a given low water potential, different lichen species exhibited different fractions of collapsed photobiont cells and different photosynthetic rates (Figure 2.6). It has therefore



**FIGURE 2.6** Amount of photobionts (open bars, heavily collapsed; hatched bars, partially folded; solid bars, globular) and water content (solid circles, % dry weight) of thalli of the lichens *R. maciformis* (top) and *Pseudevernia furfuracea* (bottom) at an equilibrium with water potentials between  $-30$  and  $-2.7$  MPa. (After Scheidegger, C., Schroeter, B., and Frey, B., *Planta*, 197, 399, 1995.)

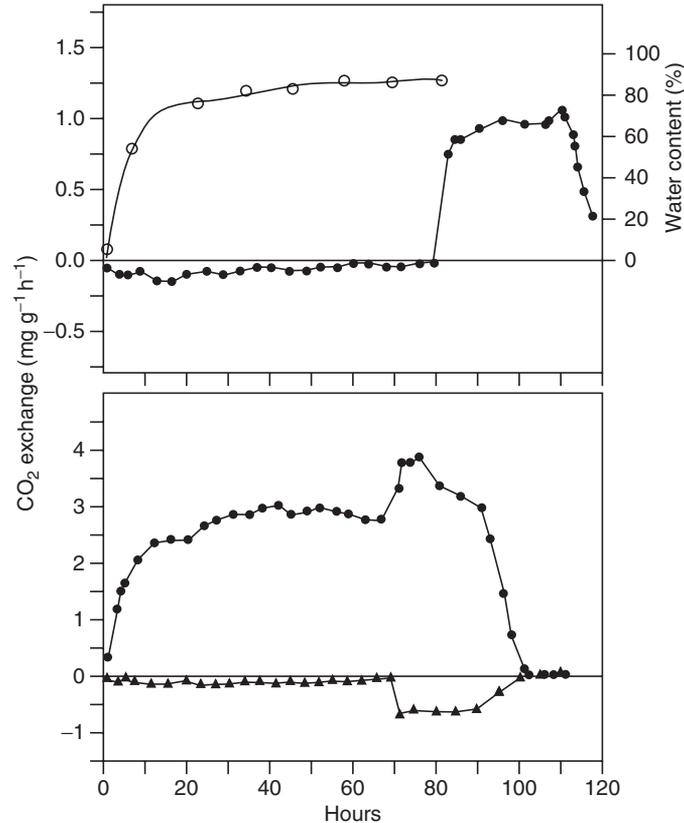


**FIGURE 2.7** Relative net photosynthetic rates (rel. NP as % of the maximum rate) in the lichen *Lobaria pulmonaria*, changes of photobiont cell shape (PCS) given as percentage of globular ( $\Delta$ ), slightly indented ( $\blacktriangle$ ), and heavily collapsed cells ( $\blacksquare$ ), and percentage of cavitated hyphae (CAV) in the upper cortex in relation to water content (% dry weight). (After Scheidegger, C., Schroeter, B., and Frey, B., *Planta*, 197, 399, 1995.)

been suggested that an increase in net photosynthesis is, in general, proportional to an increase in the amount of functional photobiont cells (Figure 2.7). However, the levels of hydration at which algal cells reach maximal and minimal photosynthetic rates are unknown. The fungal part of the lichens proved to be totally impotent in aiding the algal cells to absorb water vapor, as was shown by comparing lichens and isolated photobionts (Lange et al. 1990b, Kappen 1994). Most importantly, these lichens are able to start photosynthesis by water-vapor uptake at low water potentials, as was observed in the laboratory (Lange and Bertsch 1965, Lange and Kilian 1985, Scheidegger et al. 1995) as well as in the field (Kappen 1993a, Schroeter et al. 1994).

Lichens with cyanobacteria as photobionts need liquid water for activation of their photobionts (Figure 2.8). Their water content for starting photosynthesis (85%–100% d.wt.) is 3–6 times higher than that of green-algal lichens (15%–30% d.wt.; Lange et al. 1988). The deficiency of cyanobacteria to become photosynthetically activated by water vapor cannot be compensated by the symbiosis with the fungus (Kappen 1994) nor in photosymbiodeme lichens, where only the green-algae fraction of the thallus becomes activated (Green et al. 2002). The explanation for this inability to resume turgidity by water-vapor uptake remains unclear, but the possibility that diffusion resistance by the gelatinose sheath of cyanobacteria could impede water vapor absorption has been excluded (Büdel and Lange 1991).

Quick recovery of  $\text{CO}_2$  exchange during the daily wetting and drying cycles has been demonstrated in lichens from various habitats (Kappen et al. 1979, Lange and Redon 1983, Lange et al. 1990c, 1991, Bruns-Streng and Lange 1991). However, in some cases,  $\text{CO}_2$  exchange of lichens and bryophytes revealed only respiratory  $\text{CO}_2$  release, frequently at high rates (lichens 1–3 times of normal), during periods of 15 min up to 7 h (lichens) after soaking



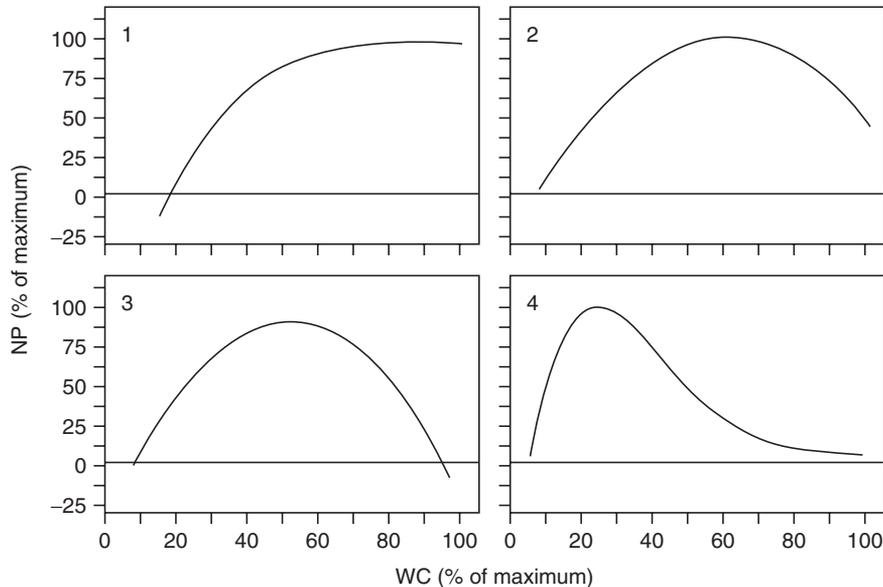
**FIGURE 2.8** Water content (open circles) and net photosynthetic rates (closed circles) following water-vapor and then liquid-water uptake of the lichen species *Nephroma resupinatum* with cyanobacterial photobionts (top) and *Ramalina menziesii* with green-algal photobionts (bottom). In *N. resupinatum*, water-vapor uptake (open circles) resulted in maximum thallus water content of 85% d.wt. but induced only a weak respiratory response in light, whereas spraying activated photosynthetic CO<sub>2</sub> uptake. In *R. menziesii*, both dark respiration (closed triangles) and net photosynthesis (closed circles) were activated within the first 30 min of water-vapor uptake. (After Lange, O.L., Kilian, E., and Ziegler, H., *Oecologia*, 71, 104, 1986.)

with water. This resaturation respiration indicates recovery processes (Ried 1960, Hinshiri and Proctor 1971, Smith and Molesworth 1973, Dilks and Proctor 1974, 1976a, Farrar 1976b, Sundberg et al. 1999), which cause a significant carbon loss (Lechowicz 1992). Slow recovery was shown by species of moist habitats (stenopoikilohydrous species), whereas quick recovery was found in species subjected to frequent and severe drying (eurypoikilohydrous species).

Most bryophytes require liquid water for activation of photosynthesis, although some species (e.g., *Hypnum cupressiforme*) are able to activate photosynthesis by uptake of water vapor (Lange 1969a). Thalli of the desert moss *Barbula aurea* showed high respiration rates in a water-saturated atmosphere, but could achieve an almost negligible net photosynthetic rate when irradiated (Rundel and Lange 1980). In bryophytes as well as in lichens, net photosynthetic rate can become maximal within 15–30 min subsequent to moistening with liquid water (see Proctor and Tuba 2002). Photosynthetic rates of mosses decreased with increasing length of the drought period before hydration. Repeated dry–wet cycles caused a greater decrease in net photosynthesis in mesic stenopoikilohydrous mosses than in xeric species (Davey 1997).

As mentioned in the Section “Exploiting an Erratic Resource,” photosynthetic  $\text{CO}_2$  uptake can be severely impeded by excessive water contents. This has been intensively studied in lichens (Lange 1980, Lange and Tenhunen 1981, Lange et al. 1993, Green et al. 1994), where the major resistance to  $\text{CO}_2$  diffusion seems to result from the soaking of the cortex (Cowan et al. 1992), but the effect is specific to species and can also be absent. According to Lange et al. (1993), four different types of net photosynthetic response to water content can be discerned in lichens (Figure 2.9): (1) net photosynthesis follows a saturation curve and does not decrease at high water content; (2) photosynthesis is maximal over a wider range of water contents but decreases slightly at high water content; (3) similar to (2) but net photosynthesis becomes zero or even negative at high water contents; and (4) the range of water content for high rates of net photosynthesis is narrow, with a clear optimum followed by a sharp decrease at high water contents where a low but positive net photosynthesis occurs. Surprisingly, these different photosynthetic responses to hydration could not be related with the environmental conditions under which each species was found, but species from xeric habitats have their maximal photosynthetic rates at relatively low water contents (60%–120% d.wt.) (Lange 1980, Lange and Matthes 1981, Kappen 1983).

In bryophytes (mainly endohydrous species; Green and Lange 1994), a similar effect can be identified (Dilks and Proctor 1979, Rundel and Lange 1980, Tuba et al. 1996a). However, the effect of diffusion resistance is diminished in ectohydrous bryophyte species as their growth form and anatomy allow a separation of the water-storing sites from the photosynthetic tissues and as they have ventilated structures (Proctor 1990, Green and Lange 1994). It is remarkable that photosynthetic response curves of intertidal algae show also a depression at high water contents (Quadir et al. 1979, Bewley and Krochko 1982). This indicates that increased  $\text{CO}_2$  resistance with hydration is not only due to free water blocking gaseous pathways within the thallus, but also due to tissue swelling, which seems to be a widespread phenomenon among nonvascular plants.



**FIGURE 2.9** The four types (see text) of response of net photosynthesis (NP) to thallus water content (WC). Schematic curves based on measurements on 11 different lichen species from forests in New Zealand. (After Green, T.G.A., Lange, O.L., and Cowan, I.R., *Crypt. Bot.*, 4, 166, 1994.)

Maximal net photosynthetic rates of lichens are generally low, although there are rare exceptions (Table 2.3). The most productive lichens are epiphytes from shady forests (Green and Lange 1994). The photobionts of lichens from open habitats are frequently screened by a pigmented or thick upper cortex (Büdel 1987, Kappen et al. 1998a). Thus, although the chlorophyll content of lichens is usually enough to harvest more than 80% of the incident light (Valladares et al. 1996), the photosynthetic units of lichens experience light limitations even in high-light environments (Büdel and Lange 1994). This fact, together with some additional structural and physiological features (thylakoid structure, low-light compensation point, and large amounts of light-harvesting protein complexes), has led to the suggestion that lichens generally resemble shade plants (Green and Lange 1994).

### Vascular Plants

Although C<sub>3</sub> photosynthesis is by far the most common photosynthetic pathway among poikilohydrous vascular plants, all of the other pathways have also been found in these plants. In many resurrection grasses of the genera *Eragrostidella*, *Sporobolus*, and *Tripogon* from Australia, Kranz-type anatomy indicated that they were C<sub>4</sub> plants (Lazarides 1992). Certain poikilohydrous vascular plants such as *R. serbica* and *Haberlea rhodopensis*, with slightly succulent leaves when soaked, exhibited a crassulacean acid metabolism (CAM) under water stress (Kimenov et al. 1989, Markowska et al. 1994, 1997, Markowska 1999). This was confirmed by the diel CO<sub>2</sub> exchange pattern and by phosphoenol pyruvate (PEP) carboxylase activity. CAM activity was interpreted as a mechanism to delay periods of metabolic inactivity and to recycle CO<sub>2</sub>. As this enhances reductive capacity, photo- and drought-induced oxidative processes can be ameliorated. The only known truly succulent resurrection plant, *B. liliputana*, is a CAM plant according to its carbon isotopic and carbon discrimination values (Barthlott and Porembski 1996). The presence of CAM activity in poikilohydrous plants demonstrates that water conservation mechanisms can be combined with a desiccation–resurrection strategy.

Resurrection plants strictly depend on liquid water to recover their photosynthetic activity after desiccation, and they need longer periods of time than nonvascular autotrophs to regain full activity (Table 2.2). Ferns and allies require 4.5–48 h to gain full or reduced photosynthetic rates (Oppenheimer and Halevy 1962, Stuart 1968, Proctor and Tuba 2002), whereas in other cases, up to 4 days of hydration are necessary to recover net photosynthesis (Hoffmann 1968, Vieweg and Ziegler 1969). *C. plantagineum* recovered chlorophyll-a-fluorescence totally after 18 h of rehydration and *M. flabellifolius* after 60 h, and full photosynthetic capacity of *C. wilmsii* was even reached before the chlorophyll content was fully recovered (Sherwin and Farrant 1996). The compensation point of net photosynthesis can be surpassed at 40%–50% RWC (Farrant 2000). In contrast, dark respiration of most poikilohydrous plants is active still at lower RWC (>10%: *C. wilmsii*, *M. flabellifolius*: Farrant 2000), and therefore can be long lasting if desiccation and rehydration phases are extended. The deleterious role of extended respiration is most likely the reason why *H. wilsonii* dies when subjected to 74% rh over 15 days (Proctor 2003). Plants of *S. lepidophylla* that were dry during a whole year recovered full photosynthetic capacity within 20 h whether the plants were rehydrated in light or in darkness (Eickmeier 1979). During the first 6 h, the plants exhibited only respiration, and the photosynthetic recovery was linked to the regaining of ribulose bis-phosphate carboxylase activity, which was conserved by 60% during the long abiotic period (Eickmeier 1979). *Selaginella* species differed in the rapidity of recovering photosynthesis and the length of the initial period of respiration (Eickmeier 1980).

Long periods of drought, too-frequent cycles of drying and wetting, and too-rapid drying can decrease the productivity of poikilohydrous plants by affecting the maximal rates of net photosynthesis. In *Selaginella*, rates of net photosynthesis after hydration decreased with increasing length of the period of desiccation (Eickmeier 1979). In *R. myconi*,

**TABLE 2.3**  
**Maximal Rate of Net Photosynthesis, Photosynthetic Light Compensation, and Saturation Points, and Minimum Water Content Allowing Photosynthetic Activity in Different Poikilohydrous Autotrophs**

Organism	Maximum Rate of Net Photosynthesis (Different Units)	Light Compensation Point ( $\mu\text{mol Photons m}^{-2} \text{ s}^{-1}$ )	Light Saturation Point ( $\mu\text{mol Photons m}^{-2} \text{ s}^{-1}$ )	Minimum Water Content for Net Photosynthesis	Source
<i>Fucus distichus</i> (high intertidal zone)	6.3 mg $\text{CO}_2 \text{ g}^{-1} \text{ h}^{-1}$			80% desiccation	Quadir et al. 1979
Lichens (in general)	0.2–5.0 mg $\text{CO}_2 \text{ g d.wt.}^{-1} \text{ h}^{-1}$				Kallio and Kärenlampi 1975, Green et al. 1984
<i>L. crystallina</i>	7.0 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$				Lange et al. 1998
<i>B. aurea</i>	5.9 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$	28–43		0.13 mg $\text{m}^{-2}$	Lange et al. 1994
<i>T. ruralis</i>	1.4 mg $\text{CO}_2 \text{ g d.wt.}^{-1} \text{ h}^{-1}$	20	200	23% d.wt.	Rundel and Lange 1983
<i>P. virginianum</i>	4.8 mg $\text{CO}_2 \text{ g d.wt.}^{-1} \text{ h}^{-1}$			10% d.wt.	Tuba 1987
<i>C. maranthae</i>	3.5 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$	20–30	100–200		Gildner and Larson 1992
<i>C. maderensis</i>	3.48 mg $\text{CO}_2 \text{ g d.wt.}^{-1} \text{ h}^{-1}$	5–50	500–750		Gebauer 1986
<i>N. parryi</i>	4.04 mg $\text{CO}_2 \text{ g d.wt.}^{-1} \text{ h}^{-1}$	5–25	100–500		Gebauer 1986
<i>S. lepidophylla</i>	5.5 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$		150		Nobel 1978
<i>R. myconi</i>	2.44 mg $\text{CO}_2 \text{ g d.wt.}^{-1} \text{ h}^{-1}$	30	>2000		Eickmeier 1979
<i>X. scabrada</i>	2.39 mg $\text{CO}_2 \text{ g d.wt.}^{-1} \text{ h}^{-1}$		400–500	20% RWC	Gebauer 1986
Homiohydrous sclerophylls of dry regions	4.0 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$				Tuba et al. 1994
Homiohydrous sun plants	7.9–23.8 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$				Larcher 1980
	10–20 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$				Lüttge et al. 1988

Abbreviation: d.wt., dry weight; RWC, relative water content.

net photosynthesis decreased to one-third after the fifth cycle of drying and wetting (Gebauer 1986). In *S. lepidophylla*, intermediate drying speeds (52–94 h until complete curling of the plant was reached) led to maximal recovery, whereas either rapid (5.5 h) or very slow (175 h) drying was associated with significantly reduced photosynthetic rates (Eickmeier 1983). Rapid drying implied increased membrane dysfunction, whereas slow drying caused retarded de novo protein synthesis.

Poikilochlorophyllous plants typically undergo a long hiatus in photosynthetic activity during the periods of drying and rehydration because of the destruction of the photosynthetic apparatus and resynthesis of the desiccoplasts. Under natural conditions, the desiccation process may take several days or weeks (Hetherington and Smillie 1982, Tuba et al. 1997). In slowly drying leaves of *X. scabrida*, net photosynthesis became negative after 3 days when leaf RWC was 54%, and respiration ceased after 15 days at 8% leaf RWC. A similar value limiting respiratory activity (less than 10%) was reported for *X. humilis* and also the homoiohydrous *C. wilmsii* and *M. flabellifolius* (Farrant 2000). Accordingly, respiration of *X. scabrida* was activated within 20 min of rehydration and reached full rates within 6 h, even before turgor was restored in the cells (Tuba et al. 1994). However, chlorophyll resynthesis started only after 12 h of rehydration and was not complete until 36 h had elapsed. The time required to fully restore photosynthetic capacity on rehydration was not different whether the plants were exposed to air with 350 or 700 ppm of CO<sub>2</sub>, but downregulation of photosynthetic rates was found at 700 ppm (Tuba et al. 1996b). During regreening on rehydration, photosystem I activity appeared to recover faster than that of photosystem II (Gaff and Hallam 1974, Hetherington and Smillie 1982).

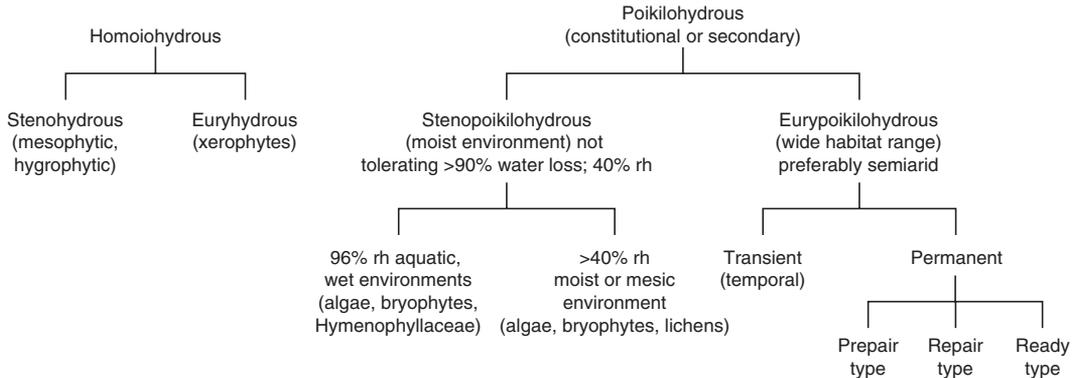
Available studies on poikilohydrous plants have mainly focused on the cellular and molecular mechanisms underlying inactivation and reactivation of photosynthesis and respiration. With a few exceptions, seemingly relevant aspects of the recovery of plant CO<sub>2</sub> exchange such as stomatal responses (Lichtenthaler and Rinderle 1988, Schwab et al. 1989, Tuba et al. 1994), leaf performance (Stuart 1968, Matthes-Sears et al. 1993), and whole plant behavior (Eickmeier et al. 1992) have been widely neglected. Field studies of the CO<sub>2</sub> exchange during the dehydration/rehydration cycles, such as those conducted with lichens (see Section “Opportunistic Metabolic Activity In Situ”), are necessary to reach a better ecological understanding of the carbon economy of poikilohydrous plants. AQ5

## DIFFERENT STRATEGIES

Poikilohydrous life style does not obligatively mean that the organism is a perennial, as several of the constitutively poikilohydrous bryophytes and a few lichen taxa are ephemeral (Longton 1988a). Compared with the strategy of homoiohydrous plants, it can be characterized by the hydration range and rapidity with which the poikilohydrous plant enters into the anabiotic state during desiccation and with which it recovers normal activity during rehydration (Figure 2.10). According to the features discussed throughout this chapter, we can discern four kinds of strategies among the eurypoikilohydrous organisms.

The *Ready type* is exhibited by constitutively poikilohydrous nonvascular species (cyanobacteria, algae, lichens, and some bryophytes), which can easily lose and absorb water, switching their metabolism on and off very quickly. Their cellular structures are highly strengthened and do not need extensive, time-consuming repair processes, which allows them to oscillate frequently (daily or even within a few hours) between anabiosis and active state.

Certain bryophytes and vascular plants need variable periods of time (hours in the case of the former, days in the case of the latter) to recover completely from desiccation and therefore represent a *Repair type*. Preventing rapid water uptake may protect from deleterious effects during rehydration. The most drastic example of this strategy is poikilochlorophyllous plants. The partial destruction of organelles and photosynthetic pigments during desiccation seems



**FIGURE 2.10** Water status-related plant performance.

to be disadvantageous, since it reduces the period of activity and limits photosynthetic carbon gain. However, this response type prevents oxidative membrane deterioration, particularly in plants that grow in open-exposed habitats. Such plants need rather long and continuous periods of activity and oscillate between dry and wet states only once or a few times per year (Gaff and Gies 1986). Homoiochlorophyllous plants manage better with repeated changes in hydration.

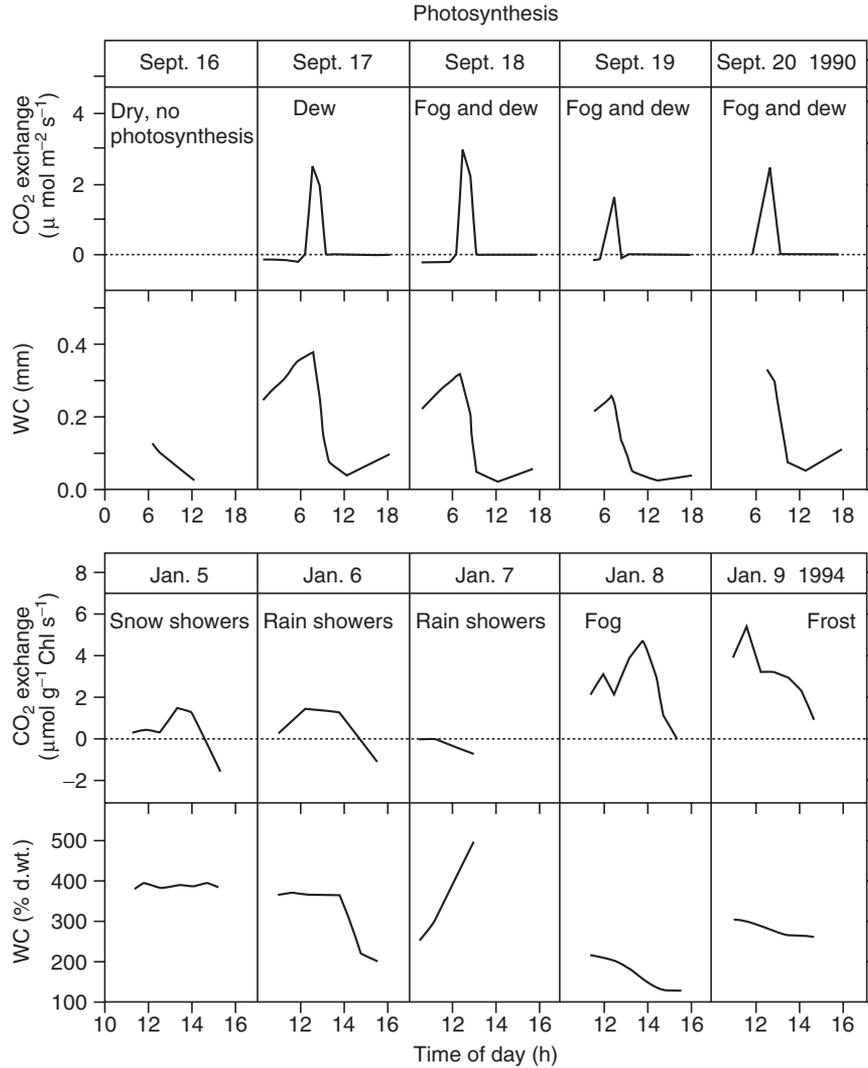
Certain bryophytes and vascular plants are not capable of tolerating extreme desiccation without a previous acclimation or preconditioning and are therefore typical of the *Prepare type*. Tolerance to desiccation is increased if they are exposed to a slow water loss, or if water loss occurs under a low vapor pressure deficit (e.g., *Bryum caespitium* and *Pohlia elongata*). Such plants either make use of structural features that retard water loss or grow in sheltered habitats where the evaporative potential is low (rock colonizing ferns, *B. nitida*, some Velloziaceae).

The *Transient type* includes certain bryophytes and ferns that acquire a eurypoikilohydrous character only temporarily by hardening as their fronds become extremely desiccation-tolerant during the winter or the dry season (mesic bryophytes, *P. vulgare*, *Asplenium* species).

A type with *mixed strategy* is realized with plants that act poikilohydrously only with a major part of the individual. By shifting between functioning with larger “dolichoblasts” in the rainy season and small, extremely desiccation-tolerant “brachyblasts” in the dry season, the small shrub *Satureja gillesii* can reduce its transpiring leaf surface (Montenegro et al. 1979). Brachyblasts have a mesophytic anatomy and are covered by filamentous trichomes. Among the plants that live in ephemeral rock pools, those species (*Aponogetum desertorum* and *Limosella* species) that are preserved by desiccation-tolerant rhizomes or corms (Gaff and Gies 1986) may also reveal a mixed strategy type. However, the heterophyllous *C. intrepidus* typically does. It survives with dry rhizome and contracted conic basal leaves most of the year. On flooding the pool the basal submersed leaves do expand (it is not clear whether they carry out significant photosynthesis). The floating leaves can be produced within a few days and are the productive part of the plant. They perform according to the repair-type, as they can pass periods of desiccation repeatedly (up to 20 times) during one season and are able to regain full photosynthetic capacity within 18 h (Woitke et al. 2004).

#### OPPORTUNISTIC METABOLIC ACTIVITY IN SITU

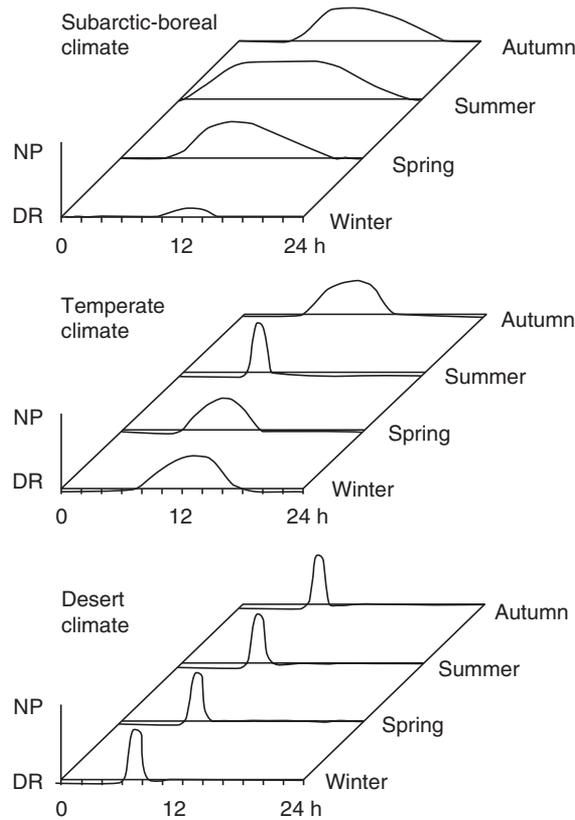
The photosynthetic activity of lichens has been monitored in situ in various climatic regions (Kappen 1988). Figure 2.11 depicts diurnal courses for lichens in two xeric habitats, the



**FIGURE 2.11** Series of diurnal courses of lichen water content (WC) and CO<sub>2</sub> exchange of *Lecidella crystallina* (on an area basis) from southern Africa in spring (September 16–20, 1990) and of *Umbilicaria spodochoea* (on chlorophyll basis) from Norway in winter (January 5–9, 1994). (After Lange, O.L., Meyer, A., Zellner, H., and Heber, U., *Funct. Ecol.*, 8, 253, 1994; Kappen, L., Schroeter, B., Hestmark, G., and Winkler, J.B., *Botanica Acta*, 109, 292, 1996.)

Namib desert in spring (Lange et al. 1990c, 1994) and south-exposed rocks of southern Norway in winter (Kappen et al. 1996). It may be noted here that frozen water is able to maintain CO<sub>2</sub> exchange in winter if irradiance is sufficient.

Different types of diurnal courses of gas exchange of lichens result from the existence of several possible sources of moisture (dew, fog, and rainfall, each one alone or in combination). Löscher et al. (1997) have proposed a simplified scheme for the seasonal variation of the periods of photosynthetic activity of nonvascular autotrophs with regard to the climatic conditions. In subpolar and polar regions, the most productive and extended periods of activity occur in spring, summer, and fall. In temperate regions, the periods of activity are regular but rather short and occur during all seasons, although they are somewhat limited in



**FIGURE 2.12** Schematic description of typical diurnal photosynthetic activity in the seasonal course for bryophytes and lichens in different climatic regions. NP, net photosynthesis; DR, dark respiration. (After Lösch, R., Pause, R., and Mies, B., *Bibl. Lichenol.*, 67, 145, 1997.)

summer. In hot arid regions, the periods of activity are brief but frequent, since they potentially occur throughout the year or every day during the wet season, depending on the regions (Figure 2.12). Examples of field studies in different environments are those by Hahn et al. (1989, 1993), Bruns-Strenge and Lange (1991), Sancho et al. (1997), and in the Antarctic (see Chapter 14 of this volume). The daily periods of moistening may last from midnight to up to 3 h in sunlight if dewfall is involved. In arid regions, the length of the period of lichen hydration is directly influenced by the exposure and compass direction of the site. In warm and temperate climates, shaded habitats allow the longest periods of hydration, but in frigid climates, hydration is combined with insolation of the habitat (Kappen et al. 1980, Kappen 1982, 1988, 1998b, Nash and Moser 1982, Pintado et al. 1997).

A long-term investigation of the lichen *Ramalina maciformis* in the Negev desert revealed that thalli were active most days of the year: Dewfall caused 306 days of metabolic activity (of which carbon balance was positive on 218 days and negative on 88 days), whereas rainfall produced activity on only 29 days per year (Kappen et al. 1979). In high mountains and polar regions, melting snow can extend the productive period of lichens and bryophytes over several days or weeks (Kappen et al. 1995, 1998b). In Antarctica, the lichen *Usnea aurantiaco-atra* was active for a total of 3359 h within 268 days of 1 year in the wet maritime region (Schroeter et al. 1997), whereas the period of activity was reduced to one-fifth of this value within 120 days in the Antarctic dry valleys for cryptoendolithic microorganisms (see Table 2.4)

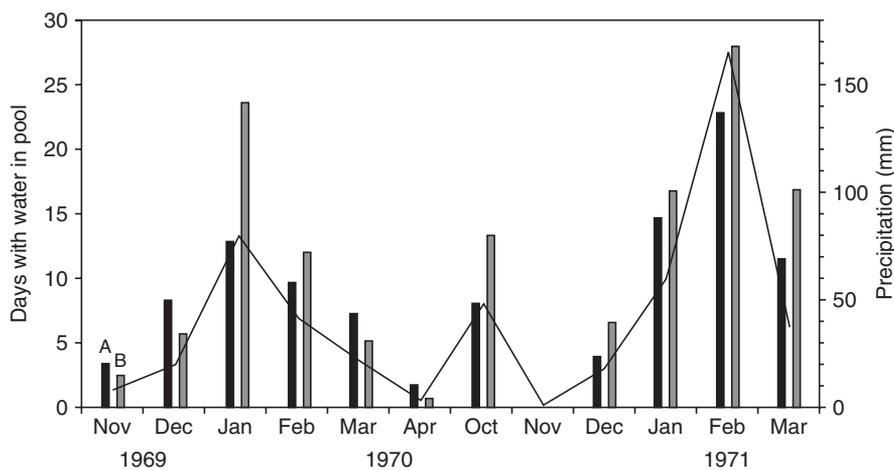
**TABLE 2.4**  
**Number of Days with Metabolic Activity within 1 Year in Various Regions**

	Active	Positive CO <sub>2</sub> Balance	Negative CO <sub>2</sub> Balance	Source
Negev 1971/1972, <i>R. maciformis</i>	306	218	88	Kappen et al. 1979
Maritime Antarctic 1992/1993, <i>U. aurantiaco-atra</i>	268	150	118	Schroeter et al. 1997
Continental Antarctic 1985/1988, <i>Cryptoendolithic</i> lichen community	120	120(?)	0(?)	Friedmann et al. 1993 <span style="border: 1px solid black; padding: 0 2px;">AQ6</span>

(Friedmann et al. 1993, Nienow and Friedmann 1993). The latter agrees with the findings on lichens in Botany Bay, continental Antarctica, where the productive period of the lichens was restricted to only the melt period in spring and some moist summer days since it was too dark and too cold under the snow cover in the cold season and frequently too dry in the warm season (Pannewitz et al. 2003).

Diurnal cycles of field-measured photosynthetic activity of bryophytes have been recorded for temperate (Lösch et al. 1997), subarctic, and polar habitats (Hicklenton and Oechel 1977, Oechel and Sveinbjörnson 1978), demonstrating the dependency of the periods of activity on weather conditions and habitat factors, as shown in lichens. In polar regions and high mountains, the photosynthetic activity of typically shade-adapted bryophytes may be depressed by temporarily high insolation combined with snow melt (Kappen et al. 1989, Valanne 1994).

For poikilohydrous vascular plants, we can only refer to one diurnal course measured in *Notholaena parryi* of the western Colorado desert, showing full light-driven CO<sub>2</sub> exchange (Nobel 1978), and two studies on *C. intrepidus* (Gaff and Gies 1986, Woitke et al. 2004). In one case the authors found 11 events of activity, each lasting for 2–23 days over a period of 1.5 years (Figure 2.13), and in the other 20 events per year were counted.



**FIGURE 2.13** Amount of rainfall (line) and periods of filling two rockpools (columns) in Fritz Gaerdes Reserve, Okahandja, Namibia, where *C. intrepidus* (Scrophulariaceae) grows. (After Gaff, D.F. and Giess, W., *Dinteria*, 18, 17, 1986.)

## PLACE IN PLANT COMMUNITIES

Their remarkable tolerance to climatically extreme conditions, their capacity to colonize both the exterior and the interior of rocks, and their relative success as epiphytes allow many poikilohydrous nonvascular autotrophs to survive and grow in the absence of strong competition by homoiohydrous plants. This is evident with the numerous lichen and bryophyte communities formed in polar regions, high mountains, and on rock outcrops, everywhere where vascular plants fail to grow. In real desert lands (Shields et al. 1957, Scott 1982), and also the Mediterranean and steppe regions, deserted land in southern Australia (Rogers and Lange 1971) and on dunes, bryophytes, lichens, and soil algae cover the soil as crusts with characteristic community structure such as for instance of many others like the famous *Fulgensietum fulgentis* in Europe or the *Crossidio crassinervis-Tortuletum obtusatae* in the Irano-Turanian territory (Galun and Garty 2001). These types of vegetation, especially the crusts, are ecologically crucial because they reduce erosion and contribute to the preservation of hydric, chemical, and physical properties of the soil (Danin and Garty 1983, Belnap and Lange 2001).

A particular phenomenon in semiarid regions is the occurrence of erratic (vagrant) lichens (Kappen 1988, Rosentreter 1993, Perez 1997) and bryophytes (Scott 1982). With their curled lobes or shoots, they are blown by the wind to shallow depressions and await a flush of water or just a bit of rain to unfold their thalli and to become productive. Without roots and not dependent on any soil formation, lichens and bryophytes typically form pioneer communities on young volcanic material or areas around receding glaciers as long as these sites are prepared for the establishment of homoiohydrous plants (Kappen 1988). In many habitats, mosaics are formed between vascular plant and cryptogam communities like in the boreal region, or lichens and bryophytes together with poikilohydrous vascular plants form communities in temporarily moist habitats with shallow soil cover (Gaff 1977, Volk 1984, Müller 1985, Lazarides 1992, Belnap and Lange 2001).

Communities with dominant poikilohydrous angiosperms were recognized since Lebrun (1947) who described a *Craterostigmatum nanolanceolati*, comprising *C. lanceolatum*, *C. plantagineum*, *C. hirsutum*, *Lindernia philcoxii* together with *Riccia* and Cyperaceae on lateritic crusts in Zaire. Typical are communities between resurrection plants and bryophytes and elsewhere lichens that have exploited temporal ponds or run-offs on Inselbergs in subtropical and tropical regions, such as the *Xerophytetum humilis* in Namibia (Volk 1984) where *Xerophyta* (= *Barbacenia humilis*) is associated with *Riccia*, *Bryum*, and cyanobacteria and locally with *C. plantagineum*, some succulents, and grasses. Similar communities with dominating poikilohydrous Scrophulariaceae were described for the African savannah region (Fischer 1992). Volk (1984) observed that communities of the *Nanocyperion teneriffae* are typical of pioneering vegetation that combines the strategies of therophytes and resurrection plants. In these places, the resurrection plants can outcompete therophytes, as they are able to defend their place against invasion of seeds and seedlings. Forming stable herds, turfs, or mats, their dominant position on inselbergs was demonstrated by Porembski and Barthlott (1997).

A transition from dominance to exclusion of poikilohydrous vascular plants was found in southern Africa as a function of soil depth (Gaff 1977). Initial stages are characteristic with poikilohydrous water plants (*C. intrepidus* in Namibia or *Craterostigma monroi* in Zimbabwe) and lead to grass-herb communities over several steps to, finally, a pluvio-therophytic grass vegetation or associations between *Xerophyta* species and perennial succulent life forms. Although they grow slowly, they are also very successful in cracks and rock ledges with changing water supply once they are established. Species-rich communities of nonvascular autotrophs are frequently formed on tree trunks, branches, and even leaves in wet forests, particularly on mountain slopes.

Algae, lichens, and bryophytes grow potentially everywhere because of their small and easily transportable vegetative and generative propagules (Kappen 1995). The evolution of a great variety of asexual means of reproduction has made nonvascular plants extremely successful in the colonization of remote and difficult sites. We have only limited knowledge about the reproductive strategies and success of poikilohydrous vascular plants. *M. flabellifolius* forms perianthless inconspicuous monoecic flowers, which are most likely anemogamous (Puff 1978, Child 1960). According to Puff (1978), pollen tetrads may increase the fertility on a receptaculum (success of mating) in this species. The seeds are extremely small and can be dispersed over long distances by the wind, but we have no records about periods and conditions of flowering. The flowers of poikilohydrous Scrophulariaceae do not differ much from those of the homoiohydrous members of the family (Heil 1925, Hickel 1967, Smook 1969, Gaff 1977). However, the rapidity of producing flowers is remarkable in species such as *C. intrepidus*, as flower buds appeared simultaneously with the floating levels. As expected, the reproductive phase occurred predominantly during the wet season, and a general requirement was a period of photosynthetic activity before reproduction, as was shown for *Vellozia schnitzleinia* (Nigeria: Owoseye at Sandford 1972) and poikilohydrous grass species in Australia (Lazarides 1972). Nevertheless, a few grass species can reproduce during the dry period. *C. intrepidus* has a high genetic variability within and between populations on one site. Although gene flow over long distances is low, there is no evidence of genetic isolation of populations by distance (Heilmeier et al. 2005). Describing the reproductive biology and ecology of the Velloziaceae (Kubitzki 1998, Ibisch et al. 2001) helps to interpret the ecological strategy of poikilohydrous plants and to compare their relative success with that of homoiohydrous co-occurring species.

#### PRIMARY PRODUCTION OF POIKILOHYDROUS AUTOTROPHS

A measure of the success of a given plant is its rate of biomass production and its primary production integrated throughout a growth period. As previously discussed, photosynthetic and growth rates of poikilohydrous plants are low in comparison with homoiohydrous species (Table 2.3). Thus, the time period during which the plant is hydrated becomes a crucial factor for the primary production of poikilohydrous plants in relation to that of the potentially more productive homoiohydrous plants. To our knowledge, no data are available regarding the primary production of poikilohydrous vascular plants. Studies with lichens and bryophytes have revealed the existence of different diel cycles of activity depending on the season, the habitat, and the weather (Figure 2.12), each combination resulting in very different carbon balance. In the Namib desert, fog resulted in an annual carbon gain of 20% of the standing carbon mass for the lichens studied (Lange et al. 1990c). Annual carbon gain was 20%–30% in the maritime Antarctic and northern Europe (Schroeter et al. 1995, Kallio and Kärenlampi 1975) and went up to 79% in a coastal habitat with high precipitation in northern Germany (Bruns-Strengé and Lange 1992). In contrast, the estimated annual carbon gain was only 3.8% in the harsh conditions of the continental Antarctic (Kappen 1985).

The biomass of lichens can be surprisingly high in tundra ecosystems, especially when compared with that of vascular plants. For instance, in the Alaskan tundra (Atkasook), lichen biomass was 76 g dry matter m<sup>-2</sup>, which represented 26% of the total aboveground biomass of the system, and it reached 1372 g m<sup>-2</sup> near Anatumuk Pass in the Brooks Range (Lechowicz 1981). In Scotland, the annual increase in dry biomass of the lichen *Cladonia portentosa* alone was 47 g m<sup>-2</sup> (Prince, quoted by Bruns-Strengé and Lange 1992). Lichen primary production is also surprising in deserts, where they locally exhibit values similar to or higher than those of homoiohydrous vascular plants. A field study of the desert lichen *R. maciformis* found an annual carbon gain of 60–195 mg CO<sub>2</sub> g<sup>-1</sup> d.wt., which is equivalent to a net carbon gain of 4.5%–15.0% (Kappen et al. 1980). On the poor soils of the Namib desert, the lichen

*Teloschistes capensis* forms dense turfs of a biomass of 250 g m<sup>-2</sup> (Kappen 1988). Similar values were found in the Negev desert, where the lichen biomass was within the range of that of the vascular plant vegetation (145–323 g m<sup>-2</sup>; Kappen et al. 1980). The annual carbon production of soil crusts with dominating lichens can be comparatively high with 12–37 g C m<sup>-2</sup> year<sup>-1</sup> in Arizona and Utah and in the Namib fog desert approximately 32 g C m<sup>-2</sup> year<sup>-1</sup> (Evans and Lange 2001).

Bryophytes are frequent in deserts, but they are not very productive in these arid environments. They rarely surpass a 0.3%–8% cover and a biomass of 2 g m<sup>-2</sup> (Nash et al. 1977). However, in tundra ecosystems they can be as productive and abundant as lichens and vascular plants. For example, in the Alaskan Arctic, bryophytes exhibit an average cover of almost 60%, and they contribute 36% of the net aboveground production of the ecosystem (Webber 1978). In certain areas of the maritime Antarctic, where cryptogamic phytomass reaches values of 1900 g m<sup>-2</sup>, bryophytes are dominant (Kappen 1993b). However, most of them are stenopoikilohydrous moss species that, in warmer and moist habitats, form up to 4750 g m<sup>-2</sup> measured in the uppermost 10 cm of the profile (Longton 1988b). *Sphagnum* species, for instance, may cover 1%, and lichens were estimated to dominate in total approximately 8% of the land surface of the Globe (Clymo 1970, Larson 1987, Ahmadjian 1995).

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## Author Queries

- AQ1: The year of publication has been changed as per the list for Jovet-Ast. Is this okay.
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