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Poikilohydry and homoihydry: antithesis or spectrum of possibilities?

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Summary

Key words: desiccation tolerance, bryophytes, pteridophytes, resurrection plants, ectohydry and endohydry, water stress, poikilochlorophylly, adaptive strategies.

Plants have followed two principal (and contrasting) strategies of adaptation to the irregular supply of water on land, which are closely bound up with scale. Vascular plants evolved internal transport from the soil to the leafy canopy (but their 'homoihydry' is far from absolute, and some are desiccation tolerant (DT)). Bryophytes depended on desiccation tolerance, suspending metabolism when water was not available; their cells are generally either fully turgid or desiccated. Desiccation tolerance requires preservation intact through drying–re-wetting cycles of essential cell components and their functional relationships, and controlled cessation and restarting of metabolism. In many bryophytes and some vascular plants tolerance is essentially constitutive. In other vascular plants (particularly poikilochlorophyllous species) and some bryophytes tolerance is induced by water stress. Desiccation tolerance is adaptively optimal on hard substrates impenetrable to roots, and on poor dry soils in seasonally dry climates. DT vascular plants are commonest in warm semiarid climates; DT mosses and lichens occur from tropical to polar regions. DT plants vary widely in their inertia to changing water content. Some mosses and lichens dry out and recover within an hour or less; vascular species typically respond on a time scale of one to a few days.

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I. Introduction

1. Plant life on land: aims of this review

Plants emerging onto land faced quite different constraints from their evolutionary precursors in water. For photosynthetic organisms in water the environment is essentially uniform; although individual nutrients (e.g. P, Si, Fe) may be limiting in particular instances, the major fundamental limitation is availability of light. Solid surfaces may be important for support, but mineral nutrients can be absorbed and gas exchange can take place over the whole surface of the organism from the water that surrounds it. Plants on land face an essentially discontinuous environment. Water and mineral nutrients may be continuously available below ground, but there is light only above the ground surface, where the supply of water is often intermittent and uncertain. Raven (1977, 1984) has emphasised the essential role played by the development of supracellular transport systems as a prerequisite for the evolution of a land flora. These are exemplified particularly by the xylem and phloem of the vascular plants that dominate present-day vegetation, with their ventilated photosynthetic tissues, impermeable cuticles and stomatal regulation of water loss. It is easy to regard this as *the* solution to the problem of plant life on land. But some major groups of plants depend on the alternative solution of carrying on their photosynthesis and growth when water is available – and when it is not, suspending metabolism until favourable conditions return. These alternative adaptive strategies may be contrasted as ‘homoihydry’ and ‘poikilohydry’.

In what follows we argue three propositions. First, poikilohydry is not merely the primitive starting point of plants that failed to achieve homoihydry, but a highly evolved strategy of adaptation in its own right, optimal in some situations and at least a viable alternative in some others. Second, these two strategies are not as sharply bounded as appears at first sight. Third, they are intimately confounded with physical considerations of scale. It is implicit in much of our argument that traditional vascular-plant preconceptions are not universally true, and can be obstacles to understanding – even sometimes of vascular plants.

We begin with some basic environmental physiology to provide background and context. We then outline the taxonomic distribution and some characteristics of poikilohydric, desiccation-tolerant (DT) land plants. We conclude by examining in more detail some specific aspects of the physiology of DT plants, and considering their adaptive relationships in a broad ecophysiological context. The present review may be read in the context of, and is complementary to, recent reviews by Hartung *et al.* (1998), Kappen & Valladares (1999), Scott (2000), and the book edited by Black & Pritchard (2002).

2. The vascular-plant strategy

We take for granted the basic physiology of water movement in the vascular-plant. Water is absorbed by roots from the soil at relatively high water potential. The xylem then provides a low-resistance pathway to the photosynthetic tissue of the leaves. The leaves (and other subaerial plant parts) are covered with a more-or-less waterproof cuticle, and loss of water vapour is regulated by the variable diffusion resistance of the stomata. Indisputably effective (and the basis of most plant biomass on the planet), this vascular-plant pattern of adaptation has limitations. It depends critically on the more-or-less continuous availability of a reservoir of water in the soil. If this fails, or if there is no soil or equivalent substrate in which a root system can develop, the habitat is untenable to plant growth. Stomatal regulation of water loss itself has limitations. Uptake of CO₂ for photosynthesis necessarily carries with it the possibility of water loss. Transpiration is linked not only to water balance but also with the heat balance of the plant, and in some situations evaporative cooling may be an inescapable price of survival. These limitations, and adaptations that circumvent or minimise them, are further considered below.

3. The poikilohydric strategy

The poikilohydric alternative is exemplified by many bryophytes and lichens, such as the various saxicolous and desert lichens studied by Ried (1960a,b) and by Lange and colleagues (Lange & Bertsch, 1965; Lange *et al.*, 1968, 1970; Lange, 1969, 1988; Lange & Evenari, 1971; Kappen *et al.*, 1979), the much-studied moss *Tortula* (*Syntrichia*) *ruralis* (Willis, 1964; Schonbeck & Bewley, 1981a,b; Tuba, 1985; Oliver, 1991; Oliver *et al.*, 1993; Tuba *et al.*, 1996), and various other mosses and liverworts (Abel, 1956; Clausen, 1952; Hosokawa & Kubota, 1957; Hinshiri & Proctor, 1971; Dilks & Proctor, 1974, 1976). In general, these plants can gain and lose water rapidly, and there is no control over water loss comparable to that in vascular plants. Water conduction is typically external and diffuse. The plants can survive drying to a point where no liquid phase remains in the cells and the water content may be no more than 5–10% d. wt (equivalent to an equilibrium water potential of –100 MPa or less). On remoistening, essentially normal metabolism returns within minutes or hours. The capillary space associated with the plant often provides a substantial reservoir of water external to the photosynthesising cells while still permitting relatively free gas exchange (Dilks & Proctor, 1979; Proctor & Smith, 1995; Zotz *et al.*, 2000), which is probably essential to the functioning of most if not all of these plants. Most of this external water can be lost without affecting cell water status. The response of photosynthesis to *cell* water content appears to be substantially the same as in vascular plants (Dilks & Proctor, 1979; Tuba *et al.*, 1996; Proctor, 2000).

II. The soil–plant–atmosphere continuum

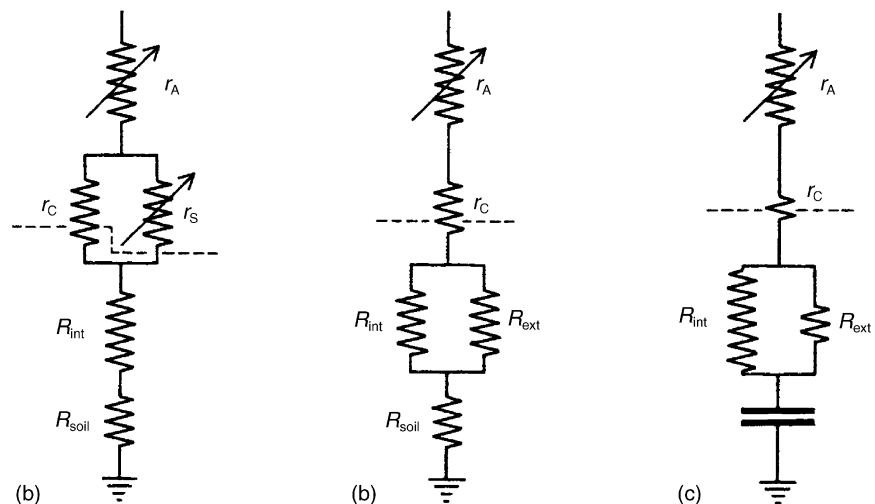
1. Generalities: internal and external water conduction

In general, water must move from the soil into the roots, through the conducting system to the aerial parts of the plant, and finally be lost to the atmosphere, down a gradient of progressively falling water potential. Conceptually the pathway is analogous to an electrical circuit, in which a current passes from earth, through a network of resistances, to a terminal at a negative potential (Van den Honert, 1948; Jones, 1992; Tyree, 1997). In principle, the potential at any point in the system can be calculated from Ohm's law if the current and resistances are known. In fact, in the soil–plant–atmosphere continuum the system falls into two parts. In the liquid phase from the soil to the evaporating surface of the leaf, rate of flow depends on pressure difference (directly related to water potential), and a hydraulic resistance which depends on the dimensions of the channels carrying the transpiration stream and the viscosity of the moving liquid (relatively insensitive to temperature). In the gas phase from the evaporating surface to the free atmosphere, water potential dictates the direction of flow, but the rate is determined by (a) the difference in water-vapour concentration between the saturated air at the evaporating surface and the surrounding atmosphere (which typically changes steeply with temperature), and (b) the diffusion resistance of the laminar boundary layer plus whatever other impediments to free diffusion the plant surface may impose (Jones, 1992).

Resistance diagrams for the soil–plant–atmosphere continuum are most often drawn for vascular plants, on the lines of Fig. 1(a), which envisages a series of hydraulic resistances, in the soil immediately surrounding the roots, in the root parenchyma, in the xylem between root and leaf, and between the finest tracheids and the evaporating surfaces of the mesophyll. From the mesophyll to the atmosphere there are two parallel

pathways, one via the variable resistance of the stomata (of low resistance when the stomata are open), the second (of relatively high and constant resistance) through the cuticle. Similar diagrams can be drawn for other plants. Figure 1(b) is for a small ground-dwelling moss (e.g. *Barbula convoluta*), which can maintain turgor for a period after rain as long as the ground surface remains moist and evaporation is not too rapid; some mosses of continuously wet habitats are striking instances of this type of adaptation (e.g. *Dicranella palustris*, *Pohlia albicans*). Water conduction can take place internally in the free space of the cell walls, and externally through capillary spaces on the wettable exterior of the shoots. Typically, some development of water-repellent cuticular material on the surface of the younger cells keeps them free of superincumbent water which would interfere with gas exchange (Kershaw, 1972, 1985; Dilks & Proctor, 1979; Proctor, 1979b; Nash, 1996; Tuba *et al.*, 1996; Zotz *et al.*, 2000). The diffusion resistance of the laminar boundary layer accounts for the whole of the gas-phase resistance to water loss. Figure 1(c) represents a mat or cushion-forming moss on an impermeable substrate (e.g. *Hypnum cupressiforme* on a tree branch, *Grimmia pulvinata* on a wall top). These plants function on water stored after rain; the low-resistance path to 'earth' of the electrical analogy in Fig. 1(a,b) is replaced by a capacitor or rechargeable battery, charged by rain and then drained over a period of time by evaporation. Water conduction is external, with very low hydraulic resistance to water movement in the capillary spaces around the shoots. As long as water remains in these spaces, the water potential of the cells must remain high. When it is exhausted, water potential rapidly falls to levels at which all metabolism stops. Intermediates between these three types occur widely. Some large ground mosses (e.g. Polytrichaceae, Mniaceae) have well-developed internal water-conduction strands of 'hydroids' (Mägdefrau, 1935; Héban, 1977); mosses and leafy liverworts provide a complete range of intermediates between the types of Fig. 1(b,c).

Fig. 1 Resistance to water flow in (a) a vascular plant (b) an endohydric bryophyte on a moist porous substrate, and (c) an ectohydric bryophyte dependent on stored water, represented as analogous electrical circuits. Capital letters represent hydraulic resistances (R_{int} , internal; R_{ext} , external), small letters (r) gaseous diffusion resistances. Cuticular resistance (r_c) may be regarded as substantially constant, but stomatal resistance (R_s) varies with stomatal opening, and boundary-layer resistance (r_A) with windspeed; these are the most important resistances in controlling water loss. The external hydraulic resistance varies with water content, but will generally be low. Redrawn from Proctor (1982, 1990).



2. What are the possibilities (and limitations) for regulation of plant water content?

This may at first sight appear a trivial question, because it is so easy to see the answer simply in terms of stomata. Consideration of the potential limits of regulation shows that the question is far from trivial; indeed we all know that stomata are not the answer to all the plant's problems of water acquisition and loss (Jarvis & McNaughton, 1986). If water is freely available from the soil, even with negligible stomatal resistance, the rate of water loss is limited by physical considerations (boundary-layer resistance, supply of latent heat of evaporation) whose effect can be calculated from the Penman-Monteith equation (Monteith & Unsworth, 1990), and under all but extreme conditions the plant typically remains turgid. If the soil dries (or its solute content increases) to the point where its water potential equals that of the mesophyll, water cannot flow from root to leaf and turgor cannot be maintained, even with fully closed stomata and zero transpiration. But zero water loss will generally entail zero CO₂ uptake; a positive carbon balance is generally inseparable from some loss of water. Even with a substantial water-potential difference between soil and mesophyll, loss of cell water and wilting may still occur if this is exceeded by the potential difference needed to drive the transpiration stream through the xylem. Vascular plants only achieve homoiohydry within certain limits.

Absorbed solar radiation must be balanced by heat loss, principally through a combination of radiation, convective heat transfer to the air, and the latent heat of evaporation of transpired water (Campbell, 1977; Gates, 1980; Monteith & Unsworth, 1990; Jones, 1992). If irradiance and resistance to convective heat loss are both high, as in many situations close to the ground, convective and radiative heat loss alone are often inadequate to keep the surface temperature below lethal levels on a clear sunny day. Evaporative cooling is then vital to survival. Low-growing plants of open sunny habitats typically transpire rapidly even under apparently dry conditions. If water is limiting they progressively senesce leaf area, or die (usually having first set seed). Perennial plants of semiarid habitats typically have a plant and leaf form offering minimal resistance to convective heat transfer, and little or no leaf close to the ground in the dry season. Trees and shrubs with small or narrow leaves are closely coupled to the temperature of the air, and can close their stomata to minimise water loss – but at the price of limiting significant carbon gain and growth to periods when water is more freely available. A plant cover in which heat exchange is concentrated within the boundary layer close to soil level is very much at the mercy of water availability and its radiation environment, regardless of stomatal regulation.

Nonvascular plants without stomatal regulation may thus be less disadvantaged than appears at first sight. Their 'disadvantage' is lack (or limitation) of water supply from the soil,

rather than lack of regulation of water loss. External rather than internal water conduction is a viable adaptive possibility for a plant which for other reasons operates only when water is freely available in its immediate surroundings.

3. What happens when stomatal regulation fails?

For many vascular mesophytes, regulation of water loss may be no problem. If soil water is adequate, the highest resistance to water loss is in the gas phase, and we see the common pattern of stomata open during the day, and closed during the night – and most of the time serving no more than a minor trimming function in relation to water loss. This may seem to belittle the significance of stomata. But it should also alert us against taking too-facile a view of the leaf with its ventilated mesophyll, epidermis and stomata, as simply a set of adaptations for regulation of water loss. Arguably the primary functional significance of ventilated photosynthetic tissues is in increasing the effective area for CO₂ uptake (driven by a small concentration gradient, with the main resistance in the liquid phase within the mesophyll cells), without increasing the area for water loss (driven by a large concentration gradient, with the resistance mainly in the much longer gas-phase diffusion path outside the cells) (Von Caemmerer, 2000). Stomatal closure at night may relate mainly to conserving respired CO₂, so enhancing early morning photosynthesis (Martin, 1996). In this scenario, regulation of water loss by stomata could be secondary!

Accepting that regulation of water loss by stomata is often important, what are the fall-back options when stomatal regulation fails? A common vascular-plant solution to predictable seasonal drought is to set seed and die – the 'therophyte' strategy, which of course involves a desiccation-tolerant phase in the life-cycle, the seed. Another solution is to senesce the above-ground parts of the plant and to withdraw underground for the dry season into a bulb, tuber or rhizome – the 'geophyte' strategy. Both of these are well-known Raunkiaer life forms (Raunkiaer, 1934; Whittaker, 1975), common in seasonally dry habitats.

Maintaining a continued living presence above ground is another matter. As already indicated, some perennial plants of dry grasslands respond by progressively senescing older leaves, so reducing demand on the root system, but this is merely a survival expedient differing from the geophyte strategy only in degree. Species of semiarid or saline habitats have evolved adaptations allowing more or less normal cell function at lowered water potentials, often by segregating high concentrations of ions in the vacuole, balanced by the production of compatible solutes in the cytoplasm. In effect the water potential of the whole soil–plant–atmosphere continuum is shifted downwards.

A different category of adaptations still depend on stomatal regulation but increase water-use efficiency. These are devices minimising the water loss concomitant with growth rather

than a fall-back when regulation fails. The carbon-concentrating mechanism of C₄ photosynthesis gives a CO₂ compensation point an order of magnitude lower than the simple C₃ pathway, allowing tighter regulation of water loss. C₄ plants are commonly well coupled to the atmosphere so have minimal need of transpirational cooling; they typically have high optimum temperatures for photosynthesis, and rather high lethal temperatures. Crassulacean acid metabolism (CAM) largely evades the problems of water loss by temporal separation of (daytime) photosynthesis and (night-time) CO₂ uptake. CAM plants typically have compact plant bodies which present a limited target to solar radiation and, with their succulence, form a substantial heat sink – the big columnar cacti and succulent euphorbias are the ultimate expression of this morphology. As a group, CAM succulents can generally survive higher temperatures than typical C₃ plants (Larcher, 1995a,b).

A final possibility is evolution of true desiccation tolerance. This is very widespread (Crowe *et al.*, 1992), occurring, for instance, in nematodes, tardigrades, crustacea (brine shrimps, etc.), lichens, bryophytes, and vascular plants (spores, pollen, seeds, and mature plants from taxonomically diverse groups), as well as in numerous microorganisms. Desiccation tolerance is, in a real sense, the ultimate drought-evading mechanism. The plant continues to occupy its physical space in the habitat, fully developed and ready to resume active metabolism and growth when favourable conditions return, while escaping the need to maintain normal cell function under unfavourable conditions of water stress. But this undoubtedly imposes its own morphological limitations, and carries its own physiological price. Desiccation tolerance cuts across other functional categories. It occurs in heterotrophs and autotrophs, in unicellular and multicellular organisms, and in plants with and without vascular systems and functional stomata. This paper is primarily concerned with the more highly organised green land plants, bryophytes, pteridophytes and flowering plants, but there are relevant insights to be drawn from other organisms too.

III. Desiccation-tolerant plants: taxonomic distribution and functional characteristics

1. Bryophytes

Desiccation tolerance is very common amongst bryophytes, but varies greatly between species. The greatest degree of tolerance is seen in mosses of dry, sun-exposed rock surfaces and comparable habitats experiencing extreme desiccation. *Andreaea rothii*, which grows as small blackish cushions on hard, acidic mountain rocks, can recover and photosynthesise apparently normally after 12 months desiccation at 32% rh and 20°C. *Grimmia pulvinata*, a common small cushion moss of dry wall tops, and *Racomitrium lanuginosum* and *Tortula ruralis*, abundant and characteristic species, respectively, of mountain and subarctic fellfields and dry sand-dune and

steppe grasslands, are scarcely less tolerant. These and comparable mosses typically have small or narrow cells, with apparently rather dense contents and small vacuoles, and have readily wetted surfaces, the leaves expanding within a couple of minutes from the dried state to their normal moist appearance on addition of water. Liverworts as a group tend to favour rather moister habitats than the mosses, but many are at least moderately desiccation tolerant, some markedly so (Clausen, 1952). *Porella platyphylla* (which grows in dry, but usually somewhat shaded situations) showed apparently complete recovery after 60 days desiccation at 50% rh (Hinshiri & Proctor, 1971); *Frullania dilatata*, *Gymnomitrium* spp. and other leafy liverworts which commonly grow on sun-exposed rocks are likely to be at least as tolerant as this. *P. platyphylla* has moderate-sized cells, with a large vacuole (Marschall *et al.*, 1998). All of these desiccation-tolerant bryophytes are 'ectohydric' in the sense of Buch (1945, 1947). Many bryophytes that are at least in some degree desiccation tolerant show no obvious concession to intermittent drying in the form and structure of their cells and leaves, and once dry, remoisten comparatively slowly. This is the case, for instance, in *Funaria hygrometrica* and some common *Bryum* species, and in the big Polytrichaceae and Mniaceae. Buch characterised such bryophytes as 'endohydric' or 'mixohydric'. A broad (but not sharp) division can be drawn between desiccation-tolerant species that withstand long drying better at low than at higher water contents (usually surviving best in the range *c.* –100 to –300 MPa), and those that can tolerate light desiccation but are progressively more damaged as water content falls (Fig. 2). The first category, for example *Racomitrium lanuginosum* (Dilks & Proctor, 1974) and *Tortula ruralis* (Schonbeck & Bewley, 1981a), match the usual situation encountered with seeds in storage. The second category, for example *Plagiothecium undulatum* (Dilks & Proctor, 1974) and the species of Fig. 2(a–c), have their counterpart in so-called 'recalcitrant' seeds (Farrant *et al.*, 1993) which will not withstand drying to low water content. They grade continuously into desiccation-sensitive species (e.g. many Hookeriales amongst mosses, many liverworts of moist habitats), which are damaged by even moderate drying.

Desiccation tolerance is not an absolute and constant characteristic of a bryophyte species. Some degree of drought hardening can take place in many if not all (Höfler, 1946; Abel, 1956; Proctor, 1972; Dilks & Proctor, 1976; Schonbeck & Bewley, 1981a), and there is evidence of hormonally mediated changes of desiccation tolerance in several species (Schwabe & Nachmony-Bascomb, 1963 (lunularic acid/*Lunularia cruciata*); Hellwege *et al.*, 1994 (abscisic acid/*Exormotheca*); Bopp & Werner, 1993 (abscisic acid/*Funaria hygrometrica*)), as in some (perhaps most) vascular 'resurrection plants' (see Section 6 below). Desiccation-tolerant bryophytes will survive much higher temperatures dry than moist, but survival time is steeply related to temperature (Lange,

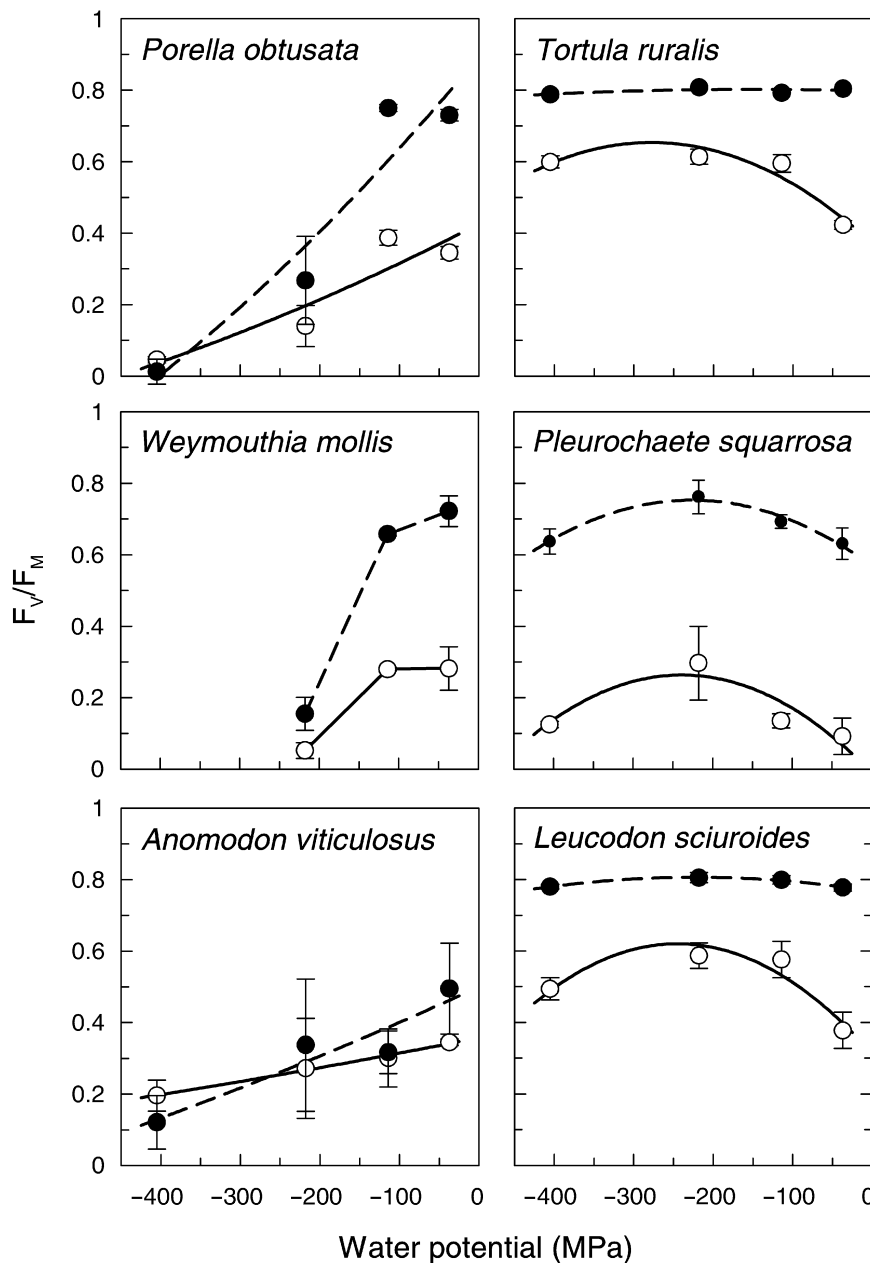


Fig. 2 Relation of desiccation tolerance to desiccation intensity: values of the chlorophyll-fluorescence parameter F_v/F_m 20 min (open circles) and 24 h (closed circles) after re-wetting in (a) *Porella obtusata*, East Prawle, Devon, UK (b) *Weymouthia mollis*, Otway Range, Vic., Australia (c) *Anomodon viticulosus*, Chudleigh, Devon, UK (d) *Tortula* (*Syntrichia*) *ruralis*, Felsötárkány, Hungary (e) *Pleurochaete squarrosa*, Chudleigh, Devon, UK (f) *Leucodon sciuroides*, Tejada, Gran Canaria; (a) (d) and (e) after 60 d desiccation, (b) (c) and (f) after 30–31 d.

1955; Nörr, 1974; Hearnshaw & Proctor, 1982; Meyer & Santarius, 1998).

2. Vascular plants

In vascular plants desiccation tolerance of the vegetative tissues has been demonstrated in only some 350 species, making up less than 0.2% of the total flora. Lists of the higher taxa including DT species are given by Bewley & Krochko (1982) and Porembski & Barthlott (2000), and a more detailed list by Proctor & Pence (2002), but the tally is constantly being extended. Genera with DT species include (number of currently known DT members in parentheses):

Pteridophytes. Lycopsidea. *Isoetes* (corms only, at least 1 terrestrial sp.), *Selaginella* (13). Pteropsida. *Actiniopteris* (2), *Adiantum* (1), *Anemia* (1), *Arthropteris* (1), *Asplenium* (8), *Ceterach* (2), *Cheilanthes* (27), *Ctenopteris* (1), *Doryopteris* (3), *Hymenophyllum* (3), *Mobria* (1), *Notholaena* (3), *Paraceterach* (1), *Pellaea* (13), *Platynerium* (1), *Pleurosorus* (1), *Polypodium* (4), *Schizaea* (1), *Woodsia* (1).

Angiosperms. Monocotyledons. Cyperaceae. *Afrotrilepis* (1), *Carex* (1), *Coleochloa* (2), *Cyperus* (1), *Fimbristylis* (2), *Kyllingia* (1), *Mariscus* (1), *Microdracoides* (1), *Trilepis* (1). Liliaceae (Anthericaceae). *Borya* (3). Poaceae. *Brachyachne* (1), *Eragrostiella* (3), *Eragrostis* (4), *Micrainera* (5), *Microchloa* (3), *Oropetium* (3), *Poa* (1), *Sporobolus* (7), *Tripogon* (10).

Velloziaceae. *Aylthonia* (1), *Barbacenia* (4), *Barbaceniopsis* (2), *Nanuza* (1), *Pleurostima* (1), *Vellozia* (c. 124), *Xerophyta* (c. 28). Dicotyledons. Myrothamnaceae. *Myrothamnus* (2). Cactaceae. *Blossfeldia* (1) (Barthlott & Porembski, 1996). Acanthaceae. *Talbotia* (1), Gesneriaceae. *Boea* (1), *Haberlea* (1), *Ramonda* (3). Scrophulariaceae. *Chamaegigas* (1), *Craterostigma* (3), *Ilysanthes* (1), *Limosella* (1), *Lindernia* (> 15). Lamiaceae. *Micromeria* (1), *Satureja* (1).

Desiccation tolerance is thus widely, but thinly and unevenly, scattered amongst vascular plants. Virtually all vascular plants have DT spores (including pollen) or seeds, so the potentiality for desiccation tolerance is probably universal. However, its expression in vegetative tissues is rare, and must have re-evolved independently in *Selaginella*, in ferns, and at least eight times in angiosperms (Oliver *et al.* 2000a). In bryophytes it is a reasonable assumption that vegetative desiccation tolerance is primitive. In vascular plants it is clearly a derived condition, and DT vascular plants have often evidently evolved from precursors adapted in other ways to cope with drought. Thus DT angiosperms include species showing some indication of CAM activity or with close CAM relatives, and DT and drought tolerant C4 species can be found within the same genus (e.g. in *Eragrostis* and *Sporobolus*), though DT plants are in general C3. For many DT vascular plants, their tolerance can be seen as a fall-back option when 'homoihydry' fails.

Because of their larger size and greater complexity, DT vascular plants tend to dry out and rehydrate more slowly than bryophytes or lichens. In most cases they have a fully functional vascular system which can support the needs of the photosynthetic tissues as long as water is reasonably plentiful. Recovery entails refilling of the xylem to re-establish water conduction as well as return to normal cell metabolism. This is no great problem for a small plant, in which (given time) xylem embolisms can be repaired by root pressure or from neighbouring tissues when water is freely available. However, a DT tree is hardly conceivable, and the recorded limit for a DT angiosperm is c. 3–4 m (monocotyledonous pseudo-shrubs; Porembski & Barthlott, 2000).

IV. Anatomical and physiological requirements and implications of desiccation tolerance

1. Morphological adaptation, changes of volume, tissue protection

Morphological adaptations are important to DT plants both mechanically, and in protection against the deleterious effects of excessive irradiance (Demmig-Adams & Adams, 1992; Björkman & Demmig-Adams, 1995). DT bryophytes mostly have rather thick cell walls and often look remarkably different wet and dry, exposing much less leaf area in the dry state (Fig. 3c–d). The dry leaves often show regular patterns of folding and shrinkage (Proctor, 1979a). Leaves of vascular

resurrection plants typically roll rather than becoming flaccid in response to water loss, protecting the more delicate desiccated cell walls and giving the plants mechanical strength; the surface exposed in the dry state is often heavily pigmented, hairy or scaly (e.g. *Ceterach*, Fig. 3a–b). The lack of obvious wilting is due to the even shrinking of the mesophyll cells and intercellular spaces, compared with the collapse of mesophyll cells and enlargement of intercellular spaces that occurs in sensitive species (Lebkuecher & Eickmeier, 1991). Leaf area can decrease by as much as 85% in *Craterostigma* as the leaves contract and curl during desiccation. The leaf cells shrink, preserving the contact between plasmalemma and cell wall during desiccation, with accordion-like folding of the cell walls (Sherwin & Farrant, 1996; Hartung *et al.*, 1998). Leaf folding can occur along or perpendicularly to the leaf axis. Ferns and some DT grasses curl rather than folding. These movements are caused by differential imbibition, rather than by osmotic effects (Gaff, 1989). The remarkable longitudinal zigzag folding of *Nanuza plicata* (Velloziaceae) leaves is a result of the alternating reinforced and nonreinforced bands in the epidermis (Rosetto & Dolder, 1996). The similar contraction of mesophyll between parallel veins of *Xerophyta scabrida* (Velloziaceae) during dehydration results in a decreasing specific leaf area, which in turn minimizes water loss (Tuba *et al.*, 1996). *Borya nitida* has small, needle-like leaves with cutinised outer epidermal walls and stomata confined to longitudinal grooves (Gaff & Churchill, 1976). Similar morphology is often seen in plants tolerant of drought but not of desiccation. Other features traditionally seen as xeromorphic, like leathery or pubescent leaves, sclerenchyma, hairs and scales, also occur among DT 'resurrection' plants, but not consistently. They should be interpreted with the same caution as the 'xeromorphic' features of peat-bog Ericaceae, which a century ago were explained as adaptations to 'physiological drought'. It is not possible to be sure from its anatomy whether a plant is desiccation tolerant or not.

2. Questions of scale

Appropriate adaptation depends greatly on scale (Niklas, 1994). Area increases as the square, and volume (and mass) as the cube, of linear dimensions. Surface tension operates on linear liquid–surface contacts and is therefore most effective and important at small scales. It is a trivial force for large vertebrates but life-or-death for insects; it plays little part in the rise of water up tall trees but is vitally important for lichens and bryophytes. Conversely, effects of gravity are trivial at small scales, but paramount at the scale of large animals or trees. Fluid boundary-layer thickness varies as the square root of the linear dimensions of an obstruction in the flow. To a first approximation the thickness of the atmospheric boundary layer may be thought of as an invariant part of the environment as perceived by an individual plant.

Scale thus has profound effects on mechanical and physiological constraints and adaptation in plants. The small size of bryophytes gives them larger cross-section to mass ratios, reducing the need for specialised supporting and conductive tissues; a bryophyte is similar in scale to an individual leaf or root of a vascular plant. Small vascular plants seldom show much secondary thickening; wood is a structural material evoked by the mechanical needs of trees. Large size both permits and demands a specialised internal conducting system. It is among the largest erect-growing mosses (e.g. Polytrichaceae, Dawsoniaceae, Mniaceae) that the nearest approach to a seed-plant vascular system and seed-plant rigidity are seen. The small size of bryophytes means that surface tension is a powerful force determining the distribution of water around their shoots, and that the shoots and leaves tend to lie within the laminar atmospheric boundary layer. Mass-transfer rates in their immediate vicinity are therefore dominated by (slow) molecular diffusion rather than (fast) turbulent mixing. Consequently, bryophytes do not in general need to package their photosynthetic systems within a ventilated epidermis, although Polytrichaceae, Dawsoniaceae and Marchantiales demonstrate that they have the evolutionary potential to produce functional equivalents of vascular-plant leaves. Individual bryophyte leaves are not comparable physiologically with vascular-plant leaves. A typical bryophyte colony is a photosynthetic system on a scale intermediate between a vascular-plant leafy canopy and a vascular-plant mesophyll. At low windspeeds, a higher-plant leaf as a gas-exchange system may be compared with the surface of a smooth bryophyte mat or cushion, in which the surfaces of the individual leaves are functionally a scaled-up mesophyll. Leaf canopies of bryophytes tend to have very high 'LAIs' by vascular-plant standards; a few estimates by one of us gave figures of 6 in *Tortula (Syntrichia) intermedia*, 18 in *Mnium hornum* and 20–25 in *Scleropodium (Pseudoscleropodium) purum*. The higher of these figures are in the same range as mesophyll/leaf-area quotients of vascular plants (Nobel, 1974, 1977). At higher windspeeds the bryophyte colony has no close analogue in terms of familiar vascular-plant physiology, but is readily comprehensible in terms of the physics of boundary layers, gaseous diffusion and heat balance. Evolution of much of the detailed morphology of bryophyte shoot systems has probably been driven by selection pressures balancing movement and storage of water against free gas exchange to the leaf surfaces (Dilks & Proctor, 1979; Proctor, 1979a). Carbon isotope discrimination measurements of bryophytes (Rundel *et al.*, 1979; Teeri, 1981; Proctor *et al.*, 1992) generally give $\delta^{13}\text{C}$ figures in the same range as C3 vascular plants, which suggests that the relation between diffusive and 'carboxylation' resistances is similar in the two groups. This is consistent with the finding of Martin & Adamson (2001) that on a per-chlorophyll basis photosynthetic rates of bryophytes and vascular plants are similar.

Raven (1999) has emphasised that there is a lower size limit for homoihydric vascular plants. In fact, the vascular pattern of adaptation probably ceases to be optimal at a considerably larger scale than the limit he suggests, because the vascular pattern of adaptation only becomes seriously competitive for a plant large enough to tap reserves of water at significant depth in the soil, and tall enough to create its own individual boundary layer above ground.

3. Water-content components, water storage and water movement in vascular and nonvascular plants

The water associated with a plant may be divided into several components. Water inside the plasmalemma is symplast water. Water in the cell walls and intercellular spaces is often referred to as apoplast water, but this is less satisfactorily defined, and various components may be excluded from it. In vascular plants it is physically continuous with the xylem sap, which often may be better considered separately. Again, for some purposes, intercellular water may be recognised as a separate component, distinct from (and much more mobile than) the water in the cell walls (Beckett, 1995, 1997). Bryophytes generally lack intercellular spaces, but often carry large amounts of (physiologically important) external capillary water (Buch, 1945, 1947; Dilks & Proctor, 1979; Proctor *et al.*, 1998). Water may be stored in various parts of the soil-plant system, buffering the plant against rapid changes in availability of water in the environment. Vascular plants typically rely almost entirely on the store of water in the soil. Halophytes and CAM succulents store large amounts of water in the symplast, and symplastic water storage is important in underground storage organs of geophytes, sometimes providing most or all of the water for development of inflorescences during the dry season. The structure of many bryophytes favours short-term storage of large quantities of external capillary water. Many algae and cyanobacteria have thick gelatinous cell walls or mucilaginous envelopes. Lichen thalli can store substantial amounts of water, generally in intercellular or apoplast locations (including the thick mucilaginous cell walls of *Collema* and other lichens with *Nostoc* as photobiont). In all of these nonvascular plants, much or most of the extracellular water can be lost before water potential falls sufficiently to affect metabolism. Although conventionally regarded as 'poikilohydric', when they are hydrated they probably experience less variation in cell water content or water potential than most 'homoihydric' vascular plants.

Water movement in a plant may take place entirely through the symplast, passing from cell to cell through the plasmodesmata, or water may pass through the plasmalemma of one cell, across the intervening cell wall, and enter through the plasmalemma of the other. These have generally been taken to be relatively high-resistance pathways. The apoplast pathway through the 'free space' of the cell walls and intercellular

spaces commonly shows a lower resistance to water movement, and is generally assumed to be the main pathway within the root cortex and the mesophyll of vascular-plant leaves, though this assumption has been questioned recently (Steudle & Peterson, 1998). The xylem of vascular plants provides a pathway of very much lower resistance than either. Although 'intracellular' in origin, the lumina of the mature xylem vessels and tracheids are in effect a major extension of the apoplast pathway with which they are in contact. The hydroids of some large mosses (e.g. Polytrichaceae, Dawsoniaceae, Mniaceae) (Héban, 1977) are in effect a parallel evolutionary development of different ontogeny serving a similar function (Ligrone *et al.*, 2000). But typically, water movement in bryophytes is mostly external (Mägdefrau, 1935; Buch, 1945, 1947), and many species show elegant external capillary conducting structures (Dilks & Proctor, 1979; Proctor, 1979a). External capillary water movement is also important in the monocotyledon *Xerophyta* and other Velloziaceae, especially during the initial stages of remoistening.

In general, the internal symplastic and apoplastic pathways can support substantial differences in water potential. Despite recent controversy (Zimmerman *et al.*, 1993; Canny, 1995; Milburn, 1996; Tyree, 1997), there can be little doubt that the internal xylem pathway of vascular plants, sealed from the exterior by the surrounding tissues, can also support substantial negative water potentials – though the water relations of trees are probably less simple, and local negative tensions in the xylem may not be as large, as has been commonly envisaged. The external conducting systems of bryophytes (and *Xerophyta*) are dependent on the maintenance of high water potentials (> *c.* –0.05 MPa) in their immediate surroundings – which must include the cells with which they are in contact.

4. What are the fundamental requirements for desiccation tolerance? Why are some species more tolerant than others?

The minimum requirements for survival of desiccation must include preservation intact of the genetic material, the mechanism for protein synthesis, and some essential spatial relationships of structures within the cell. Considerations of energetics and synthesis capacity in relation to observed rates of recovery suggest that retention intact of the major structural proteins and enzyme systems should be added to that minimal list.

The adaptations involved in desiccation tolerance are of two kinds, those essential to tolerance (without which tolerance would not be conceivable), and those that are consequences or corollaries of it. In the first group are factors that preserve the integrity of membranes and macromolecules in the dry state, and maintain essential spatial relationships within the cytoplasm; this must include ability of cell walls to shrink or fold without strain as the cytoplasm loses volume on drying. Control must also be maintained over the relative

rates and integration of metabolic processes during drying and remoistening; vitrification of the cell contents as water is lost may be important in achieving all of these needs (Crowe *et al.*, 1998; Buitink, 2000; Buitink *et al.*, 2002). The second group includes larger-scale structural adaptations, and, for example, metabolic protection against oxidative damage (Smirnov, 1993; Foyer *et al.*, 1994; Alscher *et al.*, 1997) – important to all plants, but a hazard often assumed as likely to bear more heavily on DT plants during drying and recovery.

High concentrations of disaccharide sugars are a common characteristic of DT organisms. Trehalose fills this role in organisms ranging from bacteria and fungi to nematodes, brine shrimps and the clubmoss *Selaginella lepidophylla* Adams *et al.* (1990). Yeast (*Saccharomyces cerevisiae*) produces little trehalose during rapid growth and is then relatively intolerant of drying, but trehalose accumulates and dehydration tolerance increases in the stationary phase, or following heat shock. In plants, sucrose is generally the dominant disaccharide that accumulates in DT cells. Disaccharides stabilise phospholipid bilayers by hydrogen bonding to the polar head groups, maintaining the spacing between them and preventing damaging phase transitions. Trehalose has also been shown to be effective in stabilising labile proteins during drying (Crowe *et al.*, 1992), and sucrose has similar effects (Schwab & Gaff, 1990; Bustos & Romo, 1996; Suzuki *et al.*, 1997). By contrast with the protective effects of the disaccharides, reducing sugars show a browning reaction with dry proteins, which leads to denaturation (Wettlaufer & Leopold, 1991). The possible stabilising role of linear polyols (Crowe *et al.*, 1998; Buitink *et al.*, 2002), which occur widely in DT (and non DT) liverworts, algae and lichens needs further investigation.

Sucrose levels show marked increases in the course of dehydration in most DT vascular plants (Albini *et al.*, 1994; Bianchi *et al.*, 1991, 1993; Müller *et al.*, 1997; Ghasempour *et al.*, 1998). With occasional exceptions, reducing sugars decrease or remain at low levels on drying (Koster & Leopold, 1988; Bianchi *et al.*, 1991, 1993). Trehalose occurs widely in DT plants, but usually at low concentrations, and Ghasempour *et al.* (1998) found no consistent pattern with drying; trehalose seems to be completely absent from such DT species as *Boea hygroskopica* and *Xerophyta villosa* (Bianchi *et al.*, 1991; Ghasempour *et al.*, 1998). The carbon source for sucrose synthesis probably varies from species to species. In *Craterostigma plantagineum* the main source is 2-octulose stored in the leaves (Bianchi *et al.*, 1991; Norwood *et al.*, 2000). Possible sources in other species include starch (or other carbohydrate) in the leaves or other parts of the plant, or photosynthesis during the drying period, but few critical measurements have been made (Scott, 2000). In bryophytes, the available evidence indicates that sucrose concentrations remain constantly high, with no increase on drying, but reducing sugars remain at (or decline to) very low levels as the plant dries (Smirnov, 1992).

It is generally agreed that disaccharides (and other sugars) have an essential role in desiccation tolerance, but that other

factors must be important too. The most discussed of these is the part played by proteins and protein synthesis. Two questions may be asked. Are particular protein molecules an essential part of the equipment of desiccation-tolerant cells?; and, where and when is protein synthesis important in reinstating or repairing cell components damaged or inactivated during dehydration and re-wetting (Osborne *et al.*, 2002; Walters *et al.*, 2002)?

At least a partial answer to the first question may be drawn from analogy with seeds, where late-embryogenesis abundant (LEA) proteins play a major part in establishing the desiccation tolerance of the mature embryo. LEA proteins (including dehydrins (Close, 1996)) are hydrophilic and resistant to denaturation, and fulfil a role in membrane and protein protection parallel with that of the disaccharides. They are also important along with the sugars in maintaining vitrification of the cell contents; indeed the physical properties of intracellular glasses appear to be determined primarily by their protein rather than their sugar component (Buitink *et al.*, 2000, 2002).

In answer to the second question, it is evident that a wide range of response exists between poikilochlorophyllous DT vascular plants such as *Xerophyta humilis* in which recovery entails extensive protein synthesis (mostly translation of existing transcripts) for reinstatement of the photosynthetic system (Dace *et al.*, 1998), and DT bryophytes of exposed sites such as *Racomitrium lanuginosum* or *Tortula (Syntrichia) ruralis* in which recovery is essentially complete within an hour or two, even in the presence of protein-synthesis inhibitors (Proctor & Smirnov, 2000; Proctor, 2000, 2001). Some (probably many) vascular DT plants fall between these extremes. Thus *Craterostigma wilmsii* requires protein synthesis for full recovery of photosynthetic function if dried fast (< 24 h), but not if it dries slowly over several days (Cooper, 2001). In all DT plants there is of course likely to be an ongoing need for some protein synthesis to balance protein degradation when partially hydrated (Gaff, 1989). Characteristic changes in gene expression during desiccation and rehydration have been reported from vascular resurrection plants including the fern *Polypodium virginianum* (Reynolds & Bewley, 1993a), the dicotyledon *Craterostigma plantagineum* (Ingram & Bartels, 1996), the monocotyledon (grass) *Sporobolus stapfianus* (Gaff *et al.*, 1997; Blomstedt *et al.*, 1998), and in the DT moss *Tortula (Syntrichia) ruralis* (Oliver, 1996; Oliver & Bewley, 1997; Oliver *et al.*, 1998; Wood *et al.*, 1999; Oliver *et al.*, 2000a). It has been possible to point to a few homologies with proteins of known function in other organisms (e.g. genes in *Craterostigma* and *Tortula* which appear homologous with LEA proteins of seeds, and various metabolic enzymes), but the function of most of these genes is unknown and relating them to processes involved in desiccation tolerance remains a research challenge for the future.

It is widely considered that cell damage and metabolic disruption during drying and rehydration must exacerbate

release of active oxygen species, and that high antioxidant activity to deal with it should be an essential part of the adaptation of DT plants (Stewart, 1990; Smirnov, 1993; Navari-Izzo *et al.*, 1997). Protection against active oxygen species produced during normal metabolism is essential to all plants (Foyer *et al.*, 1994; Alscher *et al.*, 1997), and up-regulation of active oxygen-scavenging enzymes in response to drought is well documented in nonDT plants. However, when responses to desiccation are compared, both DT and sensitive species show stimulation of antioxidant activity at one or another point in the drying–rehydration cycle but it generally appears that oxidative damage in the DT species is well controlled whereas the sensitive species show clear signs of oxidative damage (Dhindsa & Matowe, 1981; Seel *et al.*, 1992a,b). Dhindsa & Matowe found activities of both superoxide dismutase (SOD) and catalase higher in the DT moss *Tortula ruralis* than in the sensitive *Cratoneuron filicinum* by a factor of around four. Seel *et al.* (1992b) found SOD and catalase activity substantially higher in (DT) *Tortula ruraliformis* than in (sensitive) *Dicranella palustris*, but activities of peroxidase and ascorbate peroxidase (AP) were somewhat greater in the sensitive than in the DT species; they suggested that the role of active oxygen-processing enzymes may be less important than that of antioxidants (tocopherols and glutathione) in determining desiccation tolerance. Sgherri *et al.* (1994a) found the activity of glutathione reductase (GR) and dehydroascorbate reductase (DHAR) approximately doubled, and that of AP halved, in dried leaves of the DT grass *Sporobolus stapfianus*, with a return towards normal levels after 24 h rehydration. The proportion of oxidized ascorbate roughly doubled on drying, and doubled again on rehydration, but there was little change in the ratio of oxidized to reduced glutathione. In the dicotyledon *Boea hygroskopica* (Sgherri *et al.*, 1994b) they found total ascorbate doubled and glutathione increased 50-fold on drying; activity of GR and DHAR fell markedly on drying but AP was little changed. All the variables returned to normal levels after 24 h rehydration, in both slowly dried plants which recovered, and rapidly dried plants which did not. In *Craterostigma wilmsii*, *Myrothamnus flabellifolia* and *Xerophyta viscosa* Sherwin & Farrant (1998) and Farrant (2000) found activity of all three enzymes, AP GR and SOD increased during at least some phase of the drying–rehydration cycle, but the detailed pattern of response varied greatly between species. Thus there is plenty of evidence of responses of antioxidants and antioxidant enzyme systems to drying and rehydration, but it is hard to discern any consistent general pattern. Lebkuecher & Eickmeier (1991, 1993) and Muslin & Homann (1992) showed that leaf curling in dry *Selaginella lepidophylla* and *Polypodium polypodioides* brings clear benefits in limiting photodamage during rehydration in bright light, but their results do not suggest any fundamental differences from nonDT plants. Over all, the evidence suggests that DT plants generally deal with the potential hazards of oxidative damage during the drying–re-wetting cycle by

anticipating the problem at source rather than by invoking extravagantly high activity of antioxidant enzymes or antioxidants after the event. Protective mechanisms include leaf and stem curling, heavy anthocyanin pigmentation (Sherwin & Farrant, 1998; Farrant, 2000), progressive reduction of molecular mobility and controlled down-regulation of metabolism on drying (Hoekstra *et al.*, 2001), and high levels of zeaxanthin-mediated photo-protection (Demmig-Adams & Adams, 1992; Eickmeier *et al.*, 1993; Björkman & Demmig-Adams, 1995) manifested in chlorophyll-fluorescence measurements as high levels of (quickly relaxing) NPQ (Csintalan *et al.*, 1999; Marschall & Proctor, 1999; M.C.F. Proctor, unpublished). A fuller discussion of active oxygen and antioxidant systems in relation to desiccation tolerance is given by Smirnoff (1993), and further references will be found in Walters *et al.* (2002).

5. Homoichlorophylly and poikilochlorophylly

Vascular DT plants fall into two groups depending on the degree to which they retain their chlorophyll when dry. Homoichlorophyllous (HDT) species retain their photosynthetic apparatus and chlorophylls in a readily recoverable form. Poikilochlorophyllous (PDT) species dismantle their photosynthetic apparatus and lose all of their chlorophyll during drying; these must be resynthesised following rehydration (Tuba *et al.*, 1994; Sherwin & Farrant, 1996; Tuba *et al.*, 1998). The phenomenon of loss of chlorophyll during desiccation was first described by Vassiljev (1931) in *Carex physoides* from central Asia; the concept was reintroduced and the terms homoichlorophylly and poikilochlorophylly coined by Hamblen (1961), and it was regarded as a special case in certain DT monocotyledonous plants (Hamblen, 1961; Gaff & Hallam, 1974; Gaff, 1977, 1989; Bewley, 1979; Hetherington & Smillie, 1982a,b).

The HDT strategy is based on the preservation of the integrity of the photosynthetic apparatus by protective mechanisms considered in earlier sections of this review. The PDT strategy evolved in plants which are anatomically complex and which include the biggest in size of all DT species, and it can be seen as the evolutionarily youngest strategy. It is based on the dismantling of internal chloroplast structure by an ordered deconstruction process during drying, and its resynthesis upon rehydration by an ordered reconstruction process. These processes can thus be thought of as not only being superimposed on an existing cellular protection mechanism of vegetative desiccation tolerance (Oliver *et al.*, 2000) but as a distinct new DT strategy (Tuba *et al.*, 1994; Tuba *et al.*, 1998). The selective advantage of poikilochlorophylly, in minimising photo-oxidative damage and not having to maintain an intact photosynthetic system through long inactive periods of desiccation, presumably outweighs the disadvantage of slow recovery and the energy costs of reconstruction.

Taxonomically the PDT plants appear to be restricted to the monocots (Gaff, 1977, 1989; Bewley & Krochko, 1982).

Poikilochlorophylly is currently known in eight genera of four families (Cyperaceae, Liliaceae (Anthericaceae), Poaceae and Velloziaceae). Most occupy the almost soil-less rocky outcrops known as inselbergs, in strongly seasonal subtropical climates (Porembski & Barthlott, 2000); the best studied physiologically are the African *Xerophyta scabrida*, *X. viscosa* and *X. humilis* and the Australian *Borya nitida* (Gaff & Churchill, 1976; Hetherington & Smillie, 1982a,b; Hetherington *et al.*, 1982a,b; Gaff & Loveys, 1984; Tuba *et al.*, 1993a,b, 1994, 1996; Sherwin & Farrant, 1996; Dace *et al.*, 1998; Farrant, 2000; Cooper, 2001).

HDT plants preserve much or all of their chlorophyll through a drying–re-wetting cycle. The fern *Pellaea calomelanos* retains chlorophyll and chloroplasts with discernible grana when dry (Gaff & Hallam, 1974). DT dicotyledons, although all retaining chlorophyll, vary in the details of their behaviour. In the southeast-European HDT Gesneriaceae *Haberlea rhodopensis* and *Ramonda serbica*, Markovska *et al.* (1994) found no significant changes in chlorophyll content on drying and re-wetting, but Drazic *et al.* (1999) found that *Ramonda nathaliae* lost 20% of its chlorophyll when desiccated in the glasshouse and 70% in natural habitats; *Myrothamnus flabellifolia* preserves its thylakoids but loses half its chlorophyll on drying (Farrant *et al.*, 1999). The extent of chlorophyll loss in dicotyledons thus varies from species to species, and may be influenced by environmental factors. By contrast, *Xerophyta scabrida*, a characteristic PDT plant, loses all its chlorophylls and dismantles apparently all of the internal structures of the chloroplast during desiccation (Tuba *et al.*, 1993a,b).

Desiccation-induced breakdown of the photosynthetic apparatus in PDT plants is different from the processes involved in leaf senescence. Indeed Gaff (1986) found that senescence reduced desiccation tolerance. The dismantling of the photosynthetic apparatus can be seen as a strictly organized protective mechanism, rather than ‘damage’ to be repaired after rehydration. If the PDT *Borya nitida* is desiccated rapidly, it does not have the time to break down chlorophyll and loses viability (Gaff & Churchill, 1976) and the same is true of *Xerophyta humilis* (Cooper, 2001). Chlorophyll breakdown in *Borya nitida* does not appear to be controlled by abscisic acid (ABA) (Gaff & Loveys, 1984), and *Xerophyta scabrida* preserves most of its chlorophyll when desiccated in the dark, so most of the loss seems to be a result of photooxidation under natural circumstances (Tuba *et al.*, 1997). This suggests that PDT plants in general probably do not decompose their chlorophyll enzymatically, but rather do not invest in preserving it through the dry state. However, dismantling of the thylakoid membranes is strictly organized and leads to the formation of nearly isodiametric ‘desiccoplasts’, which, unlike chromoplasts, are able to regreen and photosynthesise after rehydration (Tuba *et al.*, 1993b). Desiccoplasts contain granular stroma, a couple of translucent plastoglobuli possibly containing lipoquinones and neutral lipids. The thylakoid

material is not arranged in plastoglobuli but can be found as osmiophilic lipid material stretched in the place of the former thylakoids (Tuba *et al.*, 1993b). In *X. villosa* not only chloroplast internal membranes but even most of the mitochondrial cristae disappear on dehydration and the remaining ones appear to decompose within 30 min after rewetting. This is mirrored by a loss in insoluble or structural proteins (almost 50%), which is much less marked (generally *c.* 10%) in HDT plants (Gaff & Hallam, 1974).

On re-wetting *X. scabrida*, reconstruction of thylakoids has already begun by the time the tissue has reached full saturation. Chlorophyll synthesis starts 8–10 h after rehydration (Tuba *et al.*, 1993a). In this process, osmiophilic lipid material is used up. Primary thylakoids with a small stacking ratio make up an intermediate step in resynthesis. Regeneration of the photosynthetic apparatus is complete within 72 h after rewetting. The restitution of cristae in mitochondria was faster than that of chloroplast internal membranes. Net CO₂ assimilation was first measurable after 24 h rehydration. At this point, chlorophyll content was just 35% of that in fully active control plants (Tuba *et al.*, 1993b).

CO₂ gas-exchange of desiccating *Xerophyta scabrida* leaves was studied by Tuba *et al.* (1996, 1997). Photosynthetic activity declined steeply to zero through the first 4 d of drying. By this time the leaves had lost approx. 60% of their water content. The fall in net CO₂ assimilation was caused mainly by the rapid stomatal closure, but it was the decrease in chlorophyll content (as shown by the fluorescence signal) that finally brought photosynthesis to a halt. Dark respiration continued until the 14th day of dehydration, at 24% of the original water content. The declines in water content and respiration were closely correlated. The prolonged respiration during desiccation may cover the energy demand of controlled disassembly of the internal membrane structures in PDT plants (Tuba *et al.*, 1997). In rehydrating *Xerophyta scabrida* leaves, respiratory processes are fully operational before full turgor is achieved (Tuba *et al.*, 1994); fast recovery of respiration is important as the only ATP-source during the primary phase of rehydration (Gaff, 1989). A high initial respiration rate on re-moistening, so called 'resaturation respiration' (Smith & Molesworth, 1973), is seen in lichens, bryophytes and HDT vascular plants, but this elevated rate persists much longer in PDT species – 30 h in the case of *X. scabrida* (Tuba *et al.*, 1994).

The HDT and PDT strategies solve the same ecological problem, but cover a broad temporal range of adaptation. The HDT pteridophytes and angiosperms are generally adapted to longer drying–wetting cycles than bryophytes and lichens, but to more rapid alternations of wet and dry periods than the PDT monocot species (Schwab *et al.*, 1989; Ingram & Bartels, 1996; Sherwin & Farrant, 1996; Tuba *et al.*, 1998), though some can survive dry for very long periods of time. The PDT strategy has evolved in habitats where the plants remain in the desiccated state for 5–8(–10) months. Under

these conditions it is evidently more advantageous to dismantle the whole photosynthetic apparatus and reconstitute it after rehydration. Of course there is variation within each category and the categories overlap in their ecological adaptation, and two or more may coexist in one habitat, for example on inselbergs (Ibisch *et al.*, 1995). Both ends of this ecological spectrum have particular points of interest. There is probably a trade-off between the 'cost' of protection and repair to the photosynthetic apparatus if this is kept in a quickly recoverable state through prolonged periods of desiccation, and the 'cost' of reconstituting the photosynthetic apparatus *de novo*.

6. Constitutive and induced tolerance

In the bryophytes and lichens of habitats that frequently dry out, desiccation tolerance appears to be essentially constitutive and influenced to only a limited extent by previous desiccation history or rate of drying. Recovery takes place quickly, and depends essentially on reactivation of components conserved undamaged through the drying–rewetting cycle. By contrast, in DT angiosperms tolerance is generally induced in the course of slow drying (Gaff, 1980, 1989, 1997). These plants may tolerate severe and prolonged desiccation under appropriate conditions, but show little or no tolerance if they are dried rapidly. This antithesis may at least in part reflect different evolutionary origins of desiccation tolerance, primitive in bryophytes (and lichens), secondary and polyphyletic in vascular plants (Oliver *et al.*, 2000a), where it has probably often evolved as a fall-back in plants already more or less tolerant of drought stress. Slow drying is a natural consequence of the vascular-plant habit, and in some cases elements of the induction process are obvious, as in the conversion of 2-octulose to sucrose in *Craterostigma*, and the controlled dismantling of the photosynthetic system in *Borya* and *Xerophyta*. However, the antithesis is not clear-cut. Leaf cells of mosses in exposed sunny situations switch from full turgor to air dryness with a few minutes, but many forest bryophytes dry much more slowly, and a degree of drought hardening is readily demonstrated (Höfler, 1946; Abel, 1956; Proctor, 1972; Dilks & Proctor, 1976). Also, desiccation tolerance appears to be essentially constitutive in various small saxicolous ferns (*Hymenophyllum tunbrigense*, *H. wilsonii*, *H. sanguinolentum*, *Asplenium trichomanes*, *A. ruta-muraria*) and *Selaginella* species (*S. cf. underwoodii*) which can dry out and recover as quickly as many bryophytes (Kappen, 1964; M.C.F. Proctor, unpublished). These species dry out quickly once water becomes limiting, and show no conventional adaptations to conserve water within the plant, a habit probably related to the high temperatures reached in their saxicolous habitats in the absence of evaporative cooling. By contrast the taller (and often epiphytic) polypody ferns (*Polypodium vulgare* agg.) show strong stomatal control over water loss and dry out slowly (Lange *et al.*, 1971; M.C.F. Proctor, unpublished).

It is generally accepted that ABA produced in roots under water stress induces various drought responses in vascular plant shoots (Schulze, 1986; Zeevaert & Creelman, 1988). Molecular-biological evidence (Ingram & Bartels, 1996) has tended to confirm earlier speculation that ABA may have a general role in evoking desiccation tolerance in DT plants. However physiological evidence for this is equivocal. *Chamae-gigas intrepidus* and *Craterostigma lanceolatum* increased their ABA content 20–30-fold on drying (Schiller *et al.*, 1997). On the other hand, ABA concentration did not increase in drying leaves of *Polypodium virginianum*, but exogenous ABA enhanced survival of rapid drying (Reynolds & Bewley, 1993b). Gaff & Loveys (1984) found a substantial rise in ABA levels (along with increased desiccation tolerance) in detached leaves of both (homoichlorophyllous) *Myrothamnus flabellifolia* and (poikilochlorophyllous) *Borya nitida* equilibrated at 96% rh; cell survival was significantly promoted by exogenous ABA without concurrent water stress in *B. nitida*, and slightly so in *M. flabellifolia*. In the grass *Sporobolus stapfianus* isolated leaves became DT only if detached below 61% relative water content (RWC), but ABA peaked in shoots at 15% RWC, and originated in the leaves rather than the roots (Gaff & Loveys, 1992). In the same species, Ghasempour *et al.* (1998) found desiccation tolerance was promoted only marginally by exogenous ABA, whereas brassinolide and methyljasmonic acid had much larger effects. In the DT thalloid liverwort *Exormotheca holstii*, high levels of ABA went with high desiccation tolerance under field conditions, ABA level and desiccation both declining under well-watered cultivation, but desiccation tolerance could be restored by exogenous ABA (Hellwege *et al.*, 1994). Tolerance of water stress was increased significantly by ABA treatment even in the aquatic thalloid liverwort *Riccia fluitans* (Hellwege *et al.*, 1996). Similar effects of ABA in promoting desiccation tolerance have been found in protonema of the moss *Funaria hygrometrica* (Werner *et al.*, 1991; Bopp & Werner, 1993) and leafy shoots of *Atrichum androgynum* (Beckett, 1999). In the highly DT moss *Tortula ruralis* ABA is undetectable (Oliver *et al.*, 1998). A systematic search for endogenous ABA in bryophytes is much needed.

7. Recovery; re-establishment of water-relations and metabolism

Highly DT bryophytes growing in exposed situations typically re-moisten quickly and diffusely. The thin leaves of bryophytes (and lichen thalli and algal mats) equilibrate rapidly with the humidity of the surrounding air, and can regain turgor from overnight dewfall even if no obvious deposition of liquid water has taken place (Lange *et al.*, 1968, 1990, 1991, 1994; Csintalan *et al.*, 2000). Liquid water from rain or cloudwater deposition is imbibed by the leaves directly as it spreads by capillarity over the surface of the shoots. In species with well-developed internal conduction and water-repellent leaf surfaces, such as many large Polytrichaceae and

Mniaceae, imbibition is slower and may take an hour or two to complete even when liquid water is present. The water-conducting hydroids of mosses collapse without embolising on drying (J.G. Duckett, pers. comm.), so they are able to refill immediately through their lateral walls as the stem re-imbibes water.

Vascular resurrection plants in general require liquid water for rehydration (Gaff, 1977), and the continuity of water within the xylem must be restored as the tissues rehydrate if the leaves are to remain turgid for more than a few hours after rain. Embolism in xylem vessels has been assumed to hinder resaturation of the photosynthetic tissues in some species (Sherwin & Farrant, 1996). The fact that resurrection plants are generally low herbs or shrubs (Gaff, 1977; Kappen & Valladares, 1999) is consistent with the idea that restitution of xylem transport is a real challenge for these plants, and probably imposes a practical limit on their height. If normal function of the vascular system is to be re-established, it is vital that the vascular bundles remain essentially undamaged in the desiccated state. Rosetto & Dolder (1996) found that vascular bundles of the desiccation tolerant *Nanuzia plicata* showed no significant changes due to dehydration. By contrast, drought stress severely impaired vascular bundles in nonDT barley leaves (Pearce & Beckett, 1987), which would preclude the reestablishment of water flow even if all the other factors necessary for rehydration were present. In *Myrothamnus flabellifolia*, a DT shrub with a height of at most a few decimetres (Figs 3g and 4a), Sherwin *et al.* (1998) considered capillary rise in the narrow reticulate xylem vessels sufficient to achieve continuity of water column, but Schneider *et al.* (2000) and Wagner *et al.* (2000) presented evidence that root pressure is implicated in the initial filling of a proportion of xylem elements, water then moving radially in a complex manner into the adjacent xylem and other tissues. In *Pellaea calomelanos*, Gaff & Hallam (1974) found capillary rise unable to transport water even into the lowest leaves, and concluded that root pressure must also play a part. In *Borya nitida*, the leaves on the upper half of the shoots had still not rehydrated from the soil after 6 d (Gaff & Churchill, 1976), so in this case rehydration through the leaf cuticle seems also to be essential. *Xerophyta scabrida* roots die back when desiccated, therefore rehydration can only occur via the leaves. In this species leaf turgor is regained within 6 h and maximum water content after 12 h in immersed leaves (Tuba *et al.*, 1994). After re-establishment of metabolism in the leaves, adventitious roots develop and ensure continuous water supply (Tuba *et al.*, 1993a). The relative importance of the water received by the roots and water absorbed through leaves varies from species to species (Gaff, 1977).

In desiccation-tolerant mosses that have been air dry for a few days, respiration recommences almost instantaneously on remoistening and net photosynthetic carbon fixation typically reaches two-thirds or more of normal levels within the first few minutes. The initial respiratory carbon loss is typically

made good within 30 min or so (Tuba *et al.*, 1996; Proctor & Pence, 2002). Chlorophyll-fluorescence measurements show that initial recovery of the photosystems is extraordinarily rapid, and independent of protein synthesis (Csintalan *et al.*, 1999; Proctor & Smirnoff, 2000). Complete return to unstressed levels of fluorescence parameters may take a number of hours, but is unaffected by protein-synthesis inhibitors in the dark. There are indications that some cytoplasmic protein synthesis following remoistening is needed for return to predesiccation levels of CO₂ fixation (Proctor & Smirnoff, 2000), but this may be 'maintenance' repair of ongoing photo-damage during recovery in light, rather than the repair of damage from desiccation. Over all, the results suggest that recovery of respiration and photosynthesis in these plants is largely a matter of reassembly and reactivation of components which have survived drying and re-wetting essentially intact. A substantial 'repair' element in the recovery of DT bryophytes was suggested by Bewley (1979) and Bewley & Krochko (1982) primarily in relation to restoration of membrane integrity. Oliver & Bewley (1984, 1997) postulated that desiccation tolerance in 'fully DT plants' (primarily bryophytes) is essentially 'repair based', while that in 'modified DT plants' (vascular plants) is based on inducible 'protection' systems set in place in the course of slow drying. This division broadly reflects the phylogenetic distribution of DT plants (Oliver *et al.*, 2000a), but its value depends heavily on how 'repair' is defined – and it underplays not only the wide range of behaviour within both bryophytes and DT vascular plants and the speedier recovery of many bryophytes, but also the features in common between the two groups. Leakage of membranes for a short time after re-wetting occurs in all desiccation-tolerant organisms (Crowe *et al.*, 1992), and 'repair' processes in the limited sense originally envisaged by Bewley must be common to all DT plants. Indeed the greatest commitment to repair is seen in the poikilochlorophyllous vascular plants where much of the photosynthetic system must be rebuilt each time the plant dries out. Much further research is needed on the distribution and mechanisms of inducible desiccation tolerance in both bryophytes and vascular plants. Oliver and colleagues have reported the synthesis of many rehydration-specific proteins in *Tortula ruralis* (Oliver, 1991; Oliver *et al.*, 1998; Wood *et al.*, 1999; Oliver *et al.*, 2000b), and this too is an area in which we may expect interesting developments in the future.

V. Time-scale considerations and ecological adaptation

1. The time scale of drying–wetting cycles: low-inertia and high inertia responses

Rates of both water loss and rehydration vary enormously between different DT plants. Mosses of exposed situations such as *Tortula* (*Syntrichia*) *ruralis* or *Grimmia pulvinata*

can dry from full turgor to a water content of 10% d. wt or less within 30 min without damage, and return to a near-normal rate of net CO₂ fixation within a similar time on remoistening. Lichens of comparable habitats respond similarly fast (Ried, 1960a,b; Lange, 1988; Tuba *et al.*, 1996); indeed some lichens of exposed rock surfaces seem able to 'switch' on and off within a minute or two (e.g. *Rhizocarpon geographicum*, Fig. 5a). However, even amongst bryophytes of relatively open habitats, many species respond more slowly; substantial differences are apparent in the rate of recovery of the chlorophyll-fluorescence parameter F_v/F_M following remoistening (Fig. 5b; Proctor, 2001). Forest-floor bryophytes such as *Rhytidiadelphus loreus* (Dilks & Proctor, 1976; Proctor & Smirnoff, 2000), *Mnium hornum* or *Polytrichum formosum*, experiencing higher ambient humidity and lower windspeeds and net radiation exchange, dry out relatively slowly, and full recovery of normal rates of photosynthesis may take many hours. Drying and recovery rates do not necessarily correlate with either relative tolerance of different intensities of desiccation or with maximum survival times.

Vascular DT plants typically dry out and re-moisten on a longer time scale than bryophytes and lichens, but there is much overlap between the two groups (Fig. 6). The filmy ferns (e.g. *Hymenophyllum* spp.) behave much like bryophytes of similar sheltered humid habitats; they lose and absorb water readily over the whole leaf surface and water conduction by the vascular system is limited (Härtel, 1940); they recover remarkably quickly from periods of a few days dry (Fig. 6). In the field there is probably rather little difference between rates of drying and recovery of bryophytes such as *Polytrichum*, *Dawsonia* or the big Mniaceae, and some species of *Selaginella* and small DT ferns such as *Polypodium polypodioides* (Stuart, 1968) or *Asplenium trichomanes* (Fig. 6). However, drying and recovery rates of vascular DT plants are generally slower. *Craterostigma wilmsii* regains substantially normal photosynthetic function within 24 h; the woody *Myrothamnus flabellifolia* requires rather longer (Fig. 6b; Sherwin & Farrant, 1996). Recovery of PDT plants is slower again. *Xerophyta* spp. (Velloziaceae) generally need 3–4 d to re-establish fully normal metabolism (Fig. 6b; Sherwin & Farrant, 1996; Dace *et al.*, 1998; Tuba *et al.*, 1998). *Borya nitida* (Liliaceae (Anthericaceae); Gaff & Churchill, 1976) and *Eragrostis nindensis* (Poaceae; Vander Willigen *et al.*, 2001) recover on a similar time scale).

Taking DT plants as a whole, we thus see a wide spectrum of time responses to alternating wet and dry periods. At the 'low-inertia' end are the lichens and bryophytes of exposed situations, responding within minutes to rapid changes of water content. At the 'high-inertia' end are the PDT vascular plants, adapted to an essentially predictable annual 'wet-season–dry-season' pattern in which quick response to brief dry spells or isolated showers would be counterproductive, and times of response to drying and re-wetting are measured in days. A majority of DT plants lie somewhere between these extremes.

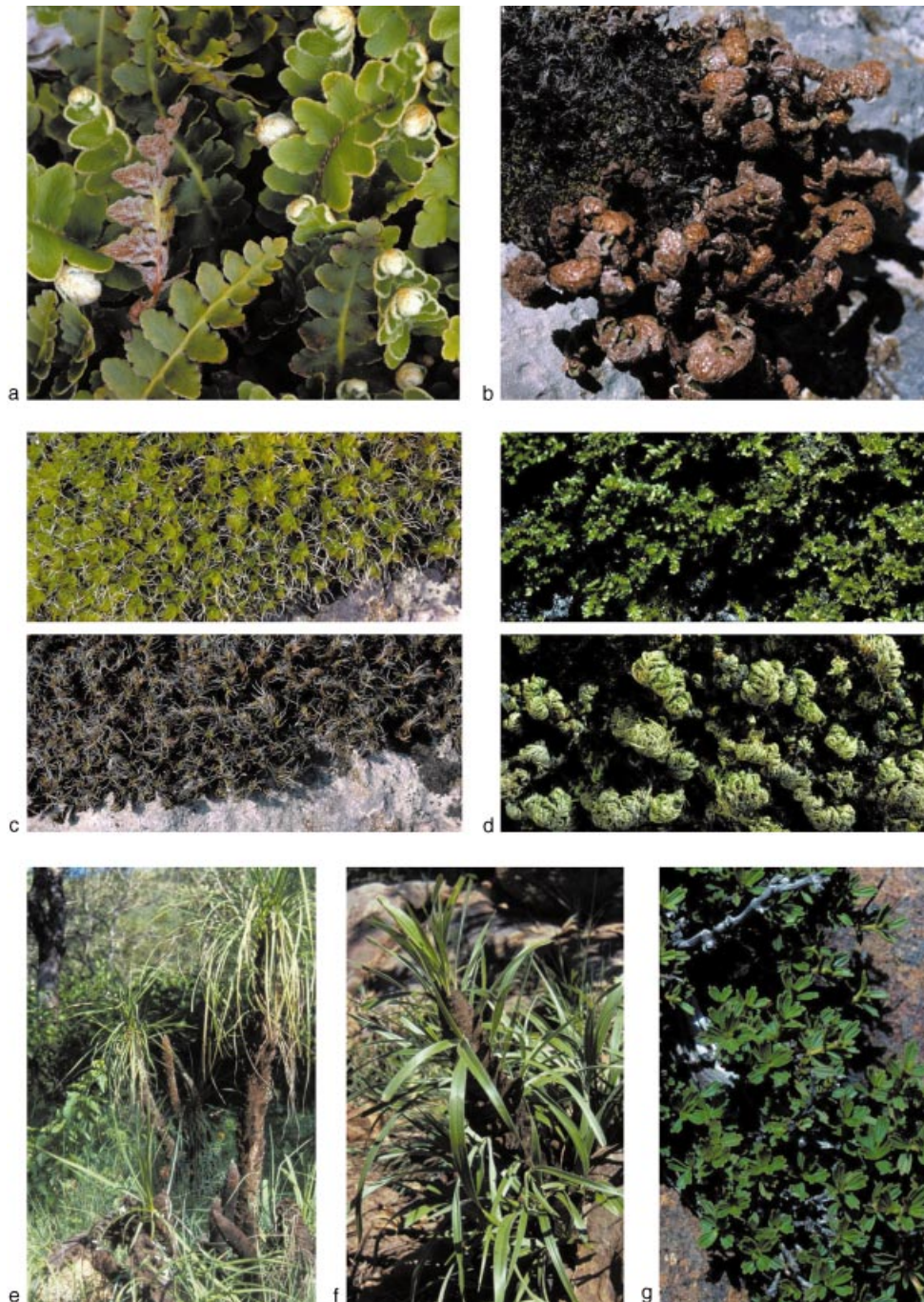


Fig. 3 (a) The desiccation tolerant (DT) fern *Ceterach officinarum* fully hydrated and metabolically active, and (b) dry during summer, with the leaves tightly rolled and the densely scaly undersides exposed. Chudleigh, Devon, UK. (c) *Tortula* (*Syntrichia*) *intermedia*, a DT moss (above) fully hydrated, and (below) dry. Chudleigh, Devon, UK. (d) The DT moss *Leptodon smithii*; (above) hydrated and fully expanded, and (below) dry, with the shoot systems tightly rolled in characteristic balls recalling the growth habit of *Selaginella lepidophylla*. Locronan, Brittany, France. (e) *Xerophyta retinervis*, a tall (c. 2 m) member of the Velloziaceae, seen here fully hydrated with green leaves, in open seasonally dry forest, Itala Game Reserve, KwaZulu-Natal, South Africa. (f) *Xerophyta villosa*, a lower-growing species, on sun-exposed rock outcrops, here hydrated and green. Itala Game Reserve, KwaZulu-Natal, South Africa. (g) The DT shrublet *Myrothamnus flabellifolia*, hydrated, with fully expanded leaves. Louwsburg, KwaZulu-Natal, South Africa. (For photographs of *Craterostigma* in hydrated and desiccated states see Bernacchia *et al.* (1996); Bohnert (2000); Scott (2000)).



Fig. 4 (a) Habitat of *Myrothamnus flabellifolia*, *Cheilanthes* sp. and *Selaginella dregei* over flat-bedded sandstone slabs near Louwsburg, KwaZulu-Natal, South Africa. (b) Sandy dry grassland near Fülöpháza, Hungary; the desiccation tolerant (DT) moss *Tortula ruralis* carpets much of the ground under the sparse grass cover. (c) Arnavatnsheiði, C. Iceland: the DT moss *Racomitrium lanuginosum* dominant on stony slopes in foreground (with yellowish DT lichens, *Alectoria* sp.), and giving its grey-green colour to much of the rest of the landscape. (d) Lichen field dominated by the orange DT lichen *Teloschistes capensis*, near Cape Cross, Namibia. (e) *Quercus robur* wood under high rainfall, Black Tor Copse, Devon, UK; DT mosses and lichens cover almost every available surface. (f) Cool-temperate rainforest, Newell Creek, SW Tasmania; dense DT bryophyte cover on trunks, branches and fallen logs.

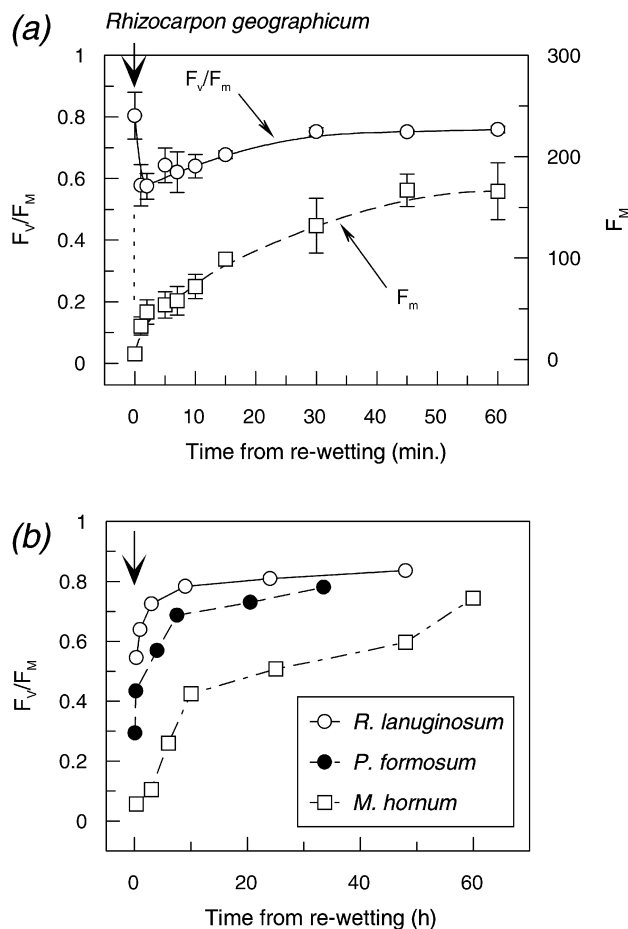


Fig. 5 Recovery rates in lichens and bryophytes. (a) A saxicolous lichen of exposed situations, *Rhizocarpon geographicum*: recovery of chlorophyll-fluorescence parameters following re-wetting (arrow) after 18 d dry (c. -100 MPa); F_v/F_m is at high levels throughout, and F_m reaches half its maximal value within 10 min. Plotted points are mean \pm s.d. ($n = 2$). (b) Recovery of F_v/F_m in three mosses after 10–16 d dry (c. -100 MPa): *Racomitrium lanuginosum*, Holne, Dartmoor, UK; *Polytrichum formosum*, Exeter, Devon, UK; *Mnium hornum*, Salcombe Regis, Devon, UK. For rapid recovery of mosses from short periods of desiccation see Proctor & Smirnov (2000), Proctor (2001, 2002).

2. Desiccation tolerance in an ecological and biogeographical context

What are the situations in which desiccation tolerance is an adaptive optimum? Obviously, the habitat must be at least intermittently dry. It must also at least sometimes be wet, and the wet periods should be at least predictably seasonal and the dry periods not too long. Many DT bryophytes and vascular plants can survive dry for 6 months or a year (sometimes more) but in general they do not remain viable as long as seeds, so the optimum niches for DT plants and desert ephemerals are different. ‘Dryness’ may arise from two causes. In even the wettest climate it does not rain continuously, and hard substrates impenetrable to roots quickly become dry

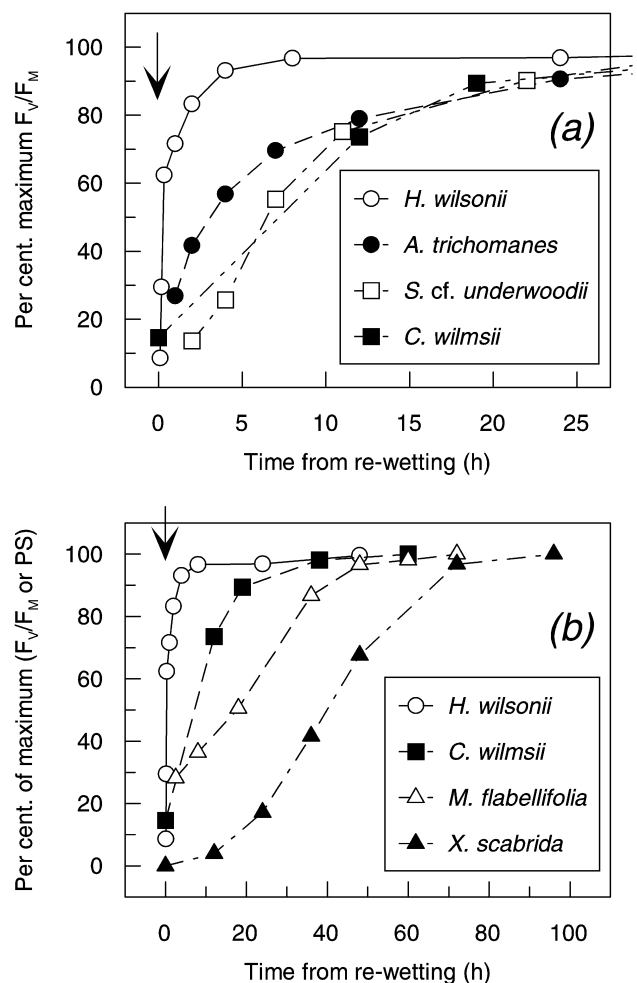


Fig. 6 Recovery rates in vascular desiccation tolerant (DT) plants, re-plotted for comparison as percentage of maximum value (F_v/F_m or PS) attained on full recovery. (a) Three pteridophytes and a homoichlorophyllous dicotyledon: *Hymenophyllum wilsonii*, Dartmoor, UK (15 d dry); *Asplenium trichomanes*, Chudleigh, Devon UK (8 d dry); *Selaginella cf. underwoodii*, Utah (8 months dry); *Craterostigma wilmsii*, South Africa (Sherwin & Farrant, 1996, > 1 month dry). (b) On a longer time scale, a pteridophyte, two homoichlorophyllous dicotyledons, and a poikilochlorophyllous monocotyledon; *H. wilsonii* and *C. wilmsii* as in Fig. 6(a) above; *Myrothamnus flabellifolia*, South Africa (Sherwin & Farrant, 1996, > 1 month dry); *Xerophyta scabrada*, Tanzania (Tuba *et al.*, 1998, several months dry). Original data unless otherwise indicated.

when the rain stops. In all but extreme arid climates, DT lichens and bryophytes colonise the surfaces of rocks and the bark of trees. Crustose lichens (together with some species of foliose and fruticose growth form) occupy bare rock surfaces from the polar regions to the equator, a mosaic of individual thalli of various species often completely covering the rock. Bryophytes are relatively more prominent in oceanic regions. Vast tracts of lava desert and stony morainic ground in the cold rainy climate of Iceland, and boulder fields on mountain summits in Scotland and Scandinavia, are dominated by

the moss *Racomitrium lanuginosum* (Fig. 4c), and bryophytes cover every available surface in humid forests in temperate hyperoceanic regions (Fig. 4e,f) and at high altitudes in the humid tropics. All of these plants must be able to endure periods of at least a few days desiccation. Even some DT vascular plants (e.g. *Ceterach officinarum* (Fig. 3a,b), *Asplenium trichomanes*, *Polypodium vulgare*) reach into humid temperate regions as epiphytes or on rock outcrops. In seasonally arid habitats the growth of nonDT vascular plants is limited by seasonal drought; bryophytes, lichens and vascular 'resurrection plants' are often prominent in such places, especially where the soil is shallow and nutrient poor; carpets of *Tortula ruralis* and other mosses commonly form an understorey to the thin cover of grasses on stabilising Atlantic-coast dunes, or in dry sandy steppe grasslands in central and eastern Europe (Fig. 4b), and in comparable habitats in other parts of the world. These two broad habitat types – rock (and bark) surfaces and thin drought-prone soils – intergrade, and some of the most characteristic situations for DT plants are on thin soils over and around rock outcrops in such areas as central and southern Africa (Fig. 4a), tropical South America and Australia; indeed the tropical inselbergs of South America and Africa are the principal centres of diversity for DT vascular plants (Porembski & Barthlott, 2000). Arid regions can be notably diverse in their plant life forms (Ehleringer, 1995; Ehleringer *et al.*, 1999), and DT plants often coexist with plants of other adaptive types, especially therophytes (adapted to seasonal drought by DT seeds rather than DT vegetative tissues), CAM plants, and in tropical and subtropical climates C4 grasses. In general they do not occur in true deserts with very low and unpredictable rainfall, with the interesting exception of those coastal deserts where cloudwater deposition from fog provides enough moisture for lichen growth, as in the extensive stands of *Teloschistes capensis* along the coast of Namibia (Fig. 4d; Lange *et al.*, 1990).

VI. Conclusion

Consideration of the morphological, ecological and geographical range of DT bryophytes and vascular plants suggests that simply to contrast 'poikilohydr' and 'homoihydr' is a quite inadequate way of looking at the diversity of physiological function that actually exists. Bryophytes are 'poikilohydr' primarily because at their scale vascular-plant structure (even if possible) would offer no adaptive advantage; with some 25 000 species and worldwide distribution they are a not unsuccessful group. Most vascular resurrection plants function as normal ('homoihydr') vascular plants until water becomes limiting. Like winter annuals and desert ephemerals (and other mesophytes), they then dry out within a few hours or days. The difference is that instead of dying and re-establishing from seed, their fall-back is to survive in a desiccated but still viable vegetative state. The critical contrast is not between

poikilohydr and homoihydr, but between plants that are desiccation tolerant and those that are not – and, over the whole range of DT plants, this is broadly associated with the contrast between ectohydr and endohydr as the predominant mode of water movement. Many 'poikilohydr' bryophytes maintain a rather constant water content and are sensitive to drying, and all DT vascular plants are 'homoihydr' under favourable conditions. Despite some argument to the contrary in particular groups (Schuster, 1984) bryophytes in general must certainly be primitively desiccation tolerant; all are C3 plants and they show few of the characteristics associated with drought tolerance in vascular plants. Virtually all vascular plants have desiccation-tolerant spores, pollen or seeds, but expression of desiccation tolerance in vegetative tissues has evidently evolved (or re-evolved) independently a number of times (Oliver *et al.*, 2000a), probably in most cases from 'homoihydr' but drought-tolerant antecedents. Accordingly, DT vascular plants, although themselves generally (perhaps invariably) C3 species, often have relatives showing C4 adaptation. A few even show indications of CAM behaviour or are closely related to CAM species (Barthlott & Porembski, 1996; Markovska *et al.*, 1997). DT bryophytes and vascular plants are not simply an odd sideline from mainstream homoihydr. They are an adaptive optimum in particular ecological situations, and (like 'normal' vascular plants) can be understood fully only in the context of a wide and multidimensional field of physiological and ecological possibilities.

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