

Life Strategies and Adaptations in Bryophytes from the Near and Middle East

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Abstract: A review article on life strategies and ecomorphological adaptations (xerothermal and xeropotoid life syndromes) of bryophytes is given, based on the hitherto known and analysed terrestrial, saxicolous and epiphytic communities of the Near and Middle East. The examples given impressively demonstrate common adaptive trends that arise convergently but independently in unrelated taxa when they evolve under similar habitat conditions. These functional types are important for the establishment, habitat maintenance and dispersal of species and indicate the relationships between site ecology, niche differentiation and species evolution. Their differentiation is a prime example of parallel evolution.

Key Words: Adaptive traits, bryophytes, ecomorphological adaptations, functional type, life strategy, xerothermal and xeropotoid life syndrome

Introduction

Bryophytes belong to a highly specialised group of plants, neglected by most botanists due to their small size. They can survive under a wide variety of environmental conditions, and often form a striking part of the vegetation in forests, wetlands, terrestrial and on rocks habitats. Even in most areas of the Near and Middle East they are obvious, as in the *Liquidambar* L. forests of western Turkey (Kürschner et al., 1998), in extended rocky areas (Frey & Kürschner, 1995a) or, more surprisingly, in true deserts, such as the wadi terraces in the Dead Sea area (Frey & Kürschner, 1991a, b). Here, thallose liverworts especially form extended mats and are an obvious part of the microphytic crusts.

Living under demanding environmental conditions, most species evolve special ecological, morphological and physiological adaptations to survive and evolve under special habitat conditions (Frey & Kürschner, 1991b, 1998; Kürschner & Ghazanfar, 1998). Over the last few decades, several attempts have been made to define bryophytes as functional types based on a system of co-evolved adaptive traits (Stearns 1976) that can be used successfully in characterising organisms, communities and the particular ecological niche they occupy. These adaptive traits are mainly based on the complex life forms (cf. Mägdefrau, 1982), life strategies (During, 1979;

Frey & Kürschner, 1991a), and ecomorphological adaptations (Frey & Kürschner, 1988, 1998) that arise convergently but independently in quite unrelated taxa when they evolve under similar habitat conditions. From their analysis it is possible to summarise bryophytes as functional types which are based on groups of species from unrelated taxa, suggesting adaptive evolution. The differentiation of bryophytes therefore is a prime example of parallel evolution.

1. Life forms

Mägdefrau (1982) classified 10 life forms – annual, cushion, short turf, tall turf, dendroid, fan, mat, pendant, tail and weft – typical for mosses and liverworts, suggesting adaptive evolution. They are supplemented by the category ‘solitary plants, forming gregarious herds’ (Frey & Kürschner, 1991b), which is typical for arid habitats.

The strong correlation of life forms, community structure and ecological site conditions have been repeatedly demonstrated (Bates 1998; Frey & Kürschner, 1991a, c, 1995a, b; Gimingham & Birse, 1957; Kürschner, 1994, 1999; Kürschner & Parolly, 1999a, b; Kürschner et al., 1998; Zippel, 1998) and is obvious with regards to sun-exposed, epilithic communities, where acrocarpous short turfs and cushions dominate.

Within desert areas, species that frequently grow as gregarious solitary plants in herds are most striking. Examples can be given from the Arabian Peninsula, the Dead Sea area and the Pannonian loess cliffs, where solitary plants are obvious in the terrestrial communities (Frey & Kürschner, 1991a, b; Kürschner & Ghazanfar, 1998; Kürschner & Pócs, 2002; Kürschner 2002). The plants are mostly deeply embedded in the substrate during the dry season and then are hardly visible. Various *Pottiaceae*, such as *Aloina* Kindb., *Crossidium* Jur., *Pterygoneurum* Jur. and *Tortula* Hedw. spp., belong to this life form which frequently occurs under desertic conditions. It is possible that, as with the well-known root competition in desert flowering plants, the conspicuous occurrence of solitary mosses in desert sites is a result of subterranean rhizoidal competition. Most of the mentioned taxa show a characteristic rhizoid dimorphism (Fig. 7b) that consists of thick, long macrorhizoids and a fine network of subterranean microrhizoids. While the macrorhizoids anchor the plant in the often unstable substrate, the net of microrhizoids helps with the absorption of water by capillary action from the upper soil layer after dew fall (Frey & Kürschner, 1998; Kürschner & Ghazanfar, 1998).

As a general tendency, an increase in solitary plants, short turfs and cushions, as is typical for numerous

acrocarpous mosses, can be observed in sunny, dry and xeric habitats, whereas mat-, weft-, tail- or fan-forming pleurocarpous mosses dominate in shady, humid and mesic to hygric sites (Fig. 1).

2. Life strategies

In addition to life forms, the life history strategy of a species is of great importance for habitat establishment and maintenance. A general concept of a life strategy system for bryophytes has been established by During (1979), who distinguished six categories: annual shuttle species, fugitives, colonists, short lived and perennial shuttle species, and perennial stayers. This system has been extended by Frey & Kürschner (1991a, c) who added a seventh category, geophytes, and was further subdivided with respect to reproductive tactics.

In general, the life strategy system is based on characters such as life form, life span (avoidance versus tolerance strategy of the gametophyte), reproduction [age of first reproduction, reproductive effort (sexual reproduction, e.g. regular formation of sporophytes versus asexual reproduction by propagules), size and number of spores, dormancy of spores], and dispersal strategy [few, large spores (> 25 µm), indicating decreasing long-range dispersal versus many, small spores (< 25 µm) providing chance dispersal] (cf. During, 1979; Frey & Kürschner, 1991a).

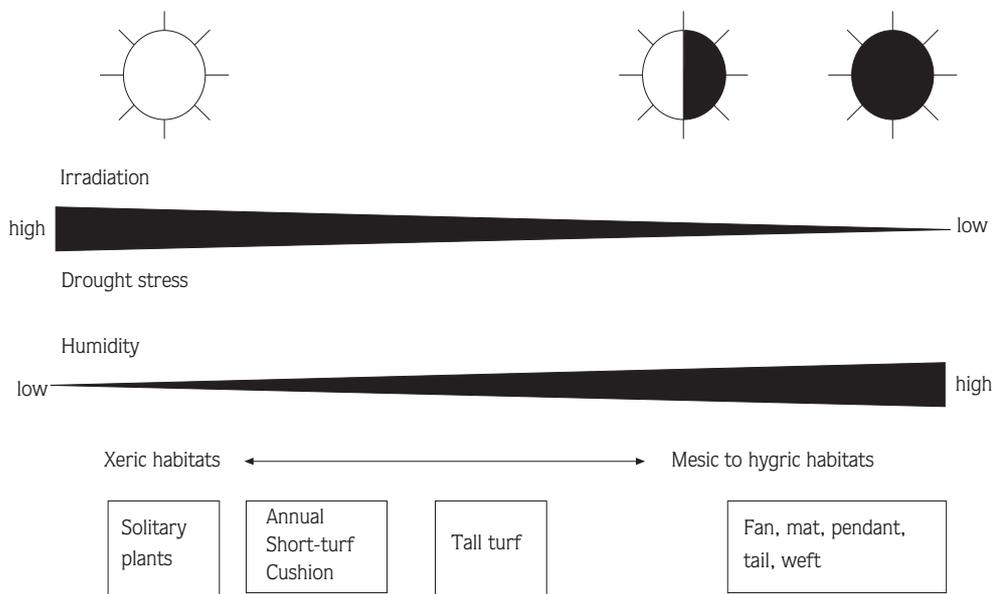


Figure 1. Distribution of life forms in bryophytes: general tendencies.

Two examples will demonstrate the system (Fig. 2), the first being 'colonists with high sexual reproductive effort'. Species with the colonists strategy are characterised by a moderately short life span of only a few years, i.e. 1-3 years with a resting stage as spore (pauciennial), or several years (pluriennial), a high sexual reproductive effort by regular formation of sporophytes, and small spores, less than 25 µm. The small spores are very persistent in most species, are produced in large amounts, and long-distance dispersal is frequent.

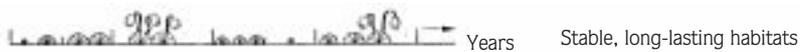
In terrestrial communities, species with this life strategy often consist of truly colonising species with a pioneer character, appearing in early successional series. Examples are found within *Aloina*, *Barbula* Hedw., *Didymodon* Hedw., *Bryum* Hedw., *Orthotrichum* Hedw. and *Tortula* species.

The second example is, short lived shuttle species, which comprises taxa with rather large spores which enable them to shuttle to another site, even within the same community. Several experiments have shown that the probable dispersal distance rapidly decreases for spores larger than 25 µm, indicating short-range dispersal and an enzy- to achorous tendency (Kürschner & Parolly, 1999a; Miles & Longton, 1992; Stoneburner et al., 1992).

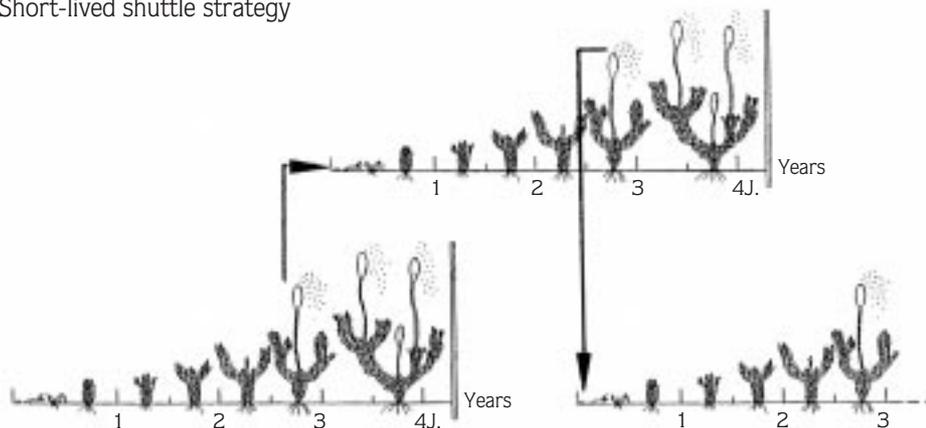
Shuttle species are typically found in unstable habitats and anthropogeneous sites that do recur predictably within the community or neighbourhood. Their life cycle is often strongly determined by seasonal fluctuations and a severe stress period, for example summer drought, which is avoided by being present in the spore stage. Most of the spores remain near the parent plant and a diaspore bank is built to increase the chance of habitat maintenance and re-establishment.

A good example for the dominance of shuttle species was given by Kürschner & Parolly (1999a) from the Beşparmak Dağları of western Turkey, where this life strategy is characteristic for the Epipterygio-Riccietum *frostii*. This ephemeral community, dominated by *Sphaerocarpus texanus* Austin, *Epipterygium tozzeri* (Grew.) Lindb. and *Riccia frostii* Austin, periodically borders brooklets and overflowed streambanks. Its life strategy analysis clearly shows the high proportion of shuttle species typical for this community (Fig. 3). Imagining the site conditions of the steep stream and cutbanks of the brooklets, heavily flooded and disturbed during winter rains, it is quite obvious that species following the shuttle strategy have competitive advantages. They occupy the recurring sites by large spores in diaspore banks, which primarily provide a

Colonists strategy



Short-lived shuttle strategy



Unstable habitats, that do recur predictably within the same community or in the neighbourhood

Figure 2. Life strategies in bryophytes: examples (re-drawn after Frey & Hensen, 1995).

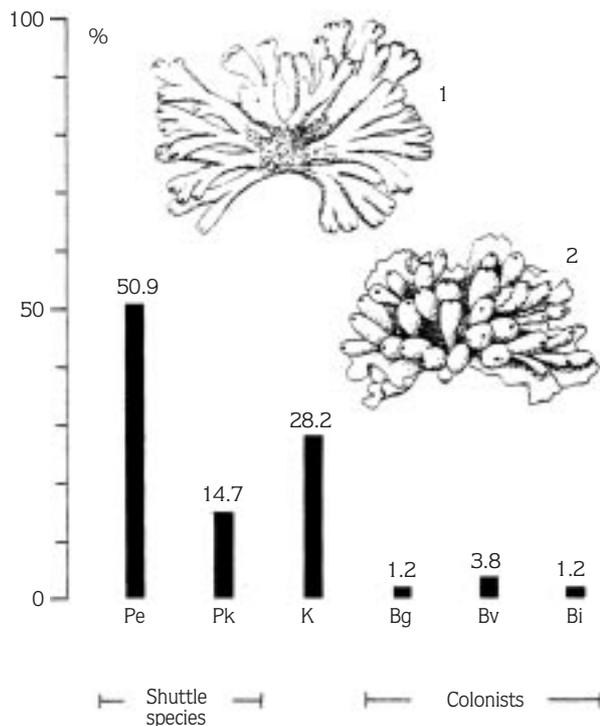


Figure 3. Life strategy spectrum (mean percentage cover) of the Epipterygio-Riccietyum frostii of western Turkey [Pe, annual shuttle species; Pk, short-lived shuttle species; Pv,g, perennial shuttle species with high asexual and sexual reproductive effort; K, fugitives; Bg, colonists with high sexual reproductive effort; Bv, colonists with high asexual reproductive effort; Bi, colonists with basitonic innovations; 1 *Riccia frostii*, 2 *Sphaerocarpus texanus* (after Kürschner & Parolly, 1999a)].

safeguard for years against unfavourable conditions. In addition, diaspore banks bridge gaps between favourable and infrequent periods, and lower the risk of local extinction (During, 1997; Longton, 1997). A further example has been analysed in Israel and Jordan, where again shuttle species play an important role by the establishment of microphytic crusts on the wadi terraces of the Dead Sea area (Frey & Kürschner, 1991a).

Quite different life strategies can be observed in one of the commonest rock communities of acidic schist in western Turkey: the Homalothecio aurei-Pleurochaetetum squarrosae (Kürschner & Parolly, 1999b). This community, which is also reported from south-eastern Spain, is restricted to shady and humid sites in the Mediterranean climate and consists mainly of species following the Perennial stayer and Perennial shuttle strategy (Fig. 4). Perennial stayers show a long

life span, a rather low sexual and asexual reproductive effort with a variable age of first reproduction, but several years at least. The spores are small, providing chance dispersal. A majority of perennial stayers rarely or never produce sporophytes. They are most frequent in late successional stages or long-lasting habitats under more or less constant environmental conditions. The species show low growth and are stress-tolerant.

Interesting are the life strategies typical for epiphytes. Several studies from Israel, Jordan and Turkey have shown that life strategies clearly correlate with site conditions (Frey & Kürschner, 1995b; Kürschner et al., 1998; Kürschner, 1999). This is well demonstrated by the analysis of the Brachythecio olympici-Dicranoweisietum cirratae of west Anatolian *Pinus* L. woodland, and the Orthotricho franzoniani-Antitrichietum breidlerianae of *Platanus orientalis* L. alluvial forests – two communities of rather dry and sunny and humid and shady sites, respectively (Fig. 5).

The drought-resistant, photo- and xerophytic Brachythecio-Dicranoweisietum is characterised by xerotolerant cushion- and short turf-forming acrocarpous perennial stayers with regular sporophyte production and small spores, providing chance dispersal. These epiphytes are very successful in colonising the widespread xeric *Pinus* woodlands and are able to reach new habitats easily. Sexual reproduction produces a wider range of genotypes among the spores, some of which may prove adaptive in new and possible remote habitats (Longton, 1994). The relatively high proportion of colonists within this community, a strategy which in general is typical for pioneers, indicates the high disturbance frequency by fire in these *Pinus* woodlands.

By contrast, tail-, mat- and fan-forming pleurocarpous mosses and liverworts belonging to the passive perennial shuttle and perennial stayers strategy dominate the shady, meso- to hygrophytic Orthotricho-Antitrichietum of *Platanus* alluvial forests. These passive species are characterised by low sexual and asexual reproduction, and sporophytes are seldom seen. Their dominance on the phorophyte is mainly a result of clonal growth of the often unisexual populations, which is supported by the humid and well-balanced climatic conditions within the alluvial forests (Kürschner, 1999). Co-dominant are species with a high asexual reproductive effort, such as *Leucodon sciuroides* (Hedw.) Schwägr. This species maintains its population at these sites by

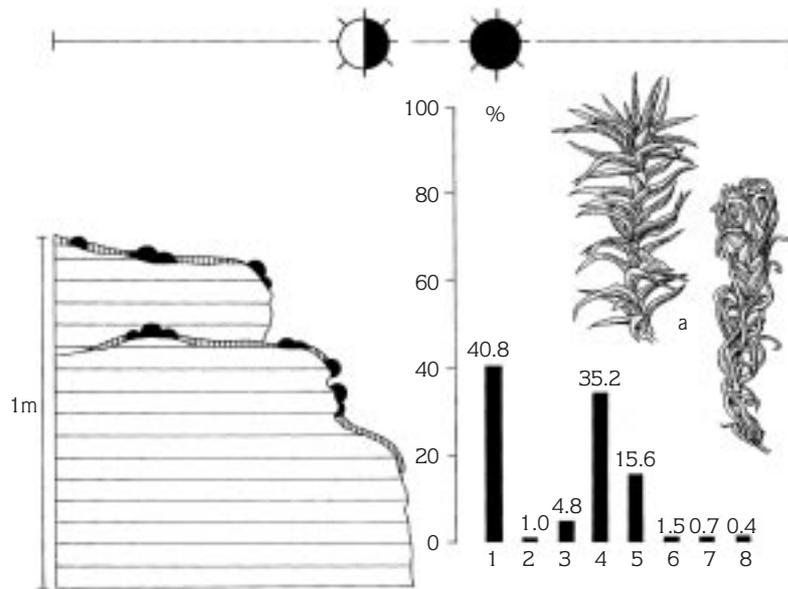


Figure 4. Life strategy spectrum (mean percentage cover) of the Homalothecio aurei-Pleurochaetum squarrosae of western Turkey [1 perennial stayers with low sexual and asexual reproductive effort; 2 perennial stayers with high sexual reproductive effort; 3 perennial stayers with high asexual reproductive effort; 4 perennial shuttle species with low sexual and asexual reproductive effort; 5 perennial shuttle species with high sexual reproductive effort; 6 colonists with high asexual and sexual reproductive effort; 7 colonists with high sexual reproductive effort; 8 pauciennial colonists; a *Pleurochaete squarrosa* (after Kürschner & Parolly, 1999b)].

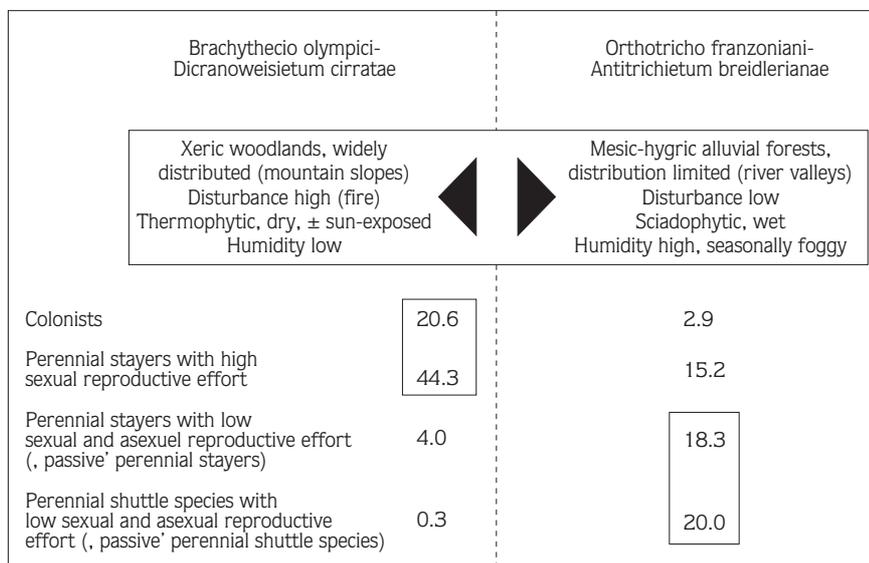


Figure 5. Main life strategies in two West-Anatolian epiphytic bryophyte communities (mean percentage cover, after Kürschner, 1999).

asexual propagation, i.e. a rich production of deciduous, axillary shootlets. None of these perennial shuttle species occur in the Brachythecio-Dicranoweisetum owing to the much more xeric conditions in the *Pinus* woodlands.

Similar results were obtained within the epiphytes of the *Liquidambar orientalis* forests of south-western Anatolia (Kürschner et al., 1998). In addition, several studies outlined in the subtropics and tropics revealed that among epiphytes the perennial shuttle strategy is typical for habitats with constant ecological conditions and long-lasting microsites (Frey & Kürschner, 1991d; Frey et al., 1995; Kürschner & Parolly, 1998; Kürschner et al., 1999; Zippel, 1998), as are provided in the humid alluvial forests of the Near and Middle East.

These few examples impressively demonstrate that life forms and life strategies are crucial characters for successfully occupying different habitats.

3. Ecomorphological adaptations

A third complex closely connected to life forms and life strategies is the ecomorphological adaptations of the species. The majority of semi-desert and desert bryophytes exhibit a drought-tolerance strategy, involving a variety of structural adaptations for the retention of water and the maintenance of photosynthesis under arid conditions. These adaptive structures have been summarised as the xerothalloid and xeropotioid life syndromes (Frey & Kürschner, 1988, 1998).

The xerothalloid life syndrome (Fig. 6) consists of a variety of morphological and anatomical structures typical for most of the highly specialised thallose liverworts growing under xeric conditions (cf. Frey & Kürschner, 1998; Kürschner & Ghazanfar, 1998). Examples are found in *Asterella* Lindb., *Exormotheca* Mitt., *Mannia* Opiz, *Plagiochasma* Lehm. & Lindenb., *Riccia* L. and *Targionia* L. The most conspicuous characters are the rolled-up, shrivelled or folded thalli exposing the intensely anthocyanin-pigmented or hyaline ventral scales (Fig. 6f). Thus, the dorsal photosynthetic surface is well protected from the sun. Often, the complete plant is sunk into the soil surface, appearing only after a shower of rain or heavy dew. Such plants were called “resurrection plants” by Volk (1984). Hyaline scales, as in many *Riccia* or *Oxymitra* Bisch. Species, probably help to protect against desiccation. A similar effect is produced by the balloon-like epidermis cells of various *Riccia* spp. and the chimney-like, hyaline air-chambers of the *Exormotheca*

spp. (Fig. 6b-e). The later form a so-called Fensterthallus which can be compared with the windows in the leaves of some South African *Mesembryanthemaceae* (e.g., *Lithops* N.E. Brown spp.). They help to reduce the light intensities reaching the photosynthetic active layer. In cross-section, most of the thalli are very thick, nearly semi-circular and consist of dense, parallel assimilatory pillars in air-chambers (Fig. 6a). The thickness of these green pillars is frequently correlated with the degree of insolation.

Several species, such as *Plagiochasma rupestre* (R.&G. Forst.) Steph. have a non-wettable thallus surface due to the presence of hydrophobic wax globules. The xerophytic *Marchantiales* are thus not able to take up water with the thallus surface, but do so by pegged rhizoids. Wax globules perhaps also prevent the entry of water into air-chambers, thus avoiding reduced photosynthesis due to a downing in the desert effect. In many species, this is prevented by hydrophobic cuticular ledges around the pores (Schönherr & Ziegler, 1975).

The xeropotioid life syndrome consists of a variety of morphological structures typical for the *Pottiaceae* and *Grimmiaceae* (Fig. 7). The most common characteristics of this syndrome are crisp, contorted leaves accompanied by a considerable shrinkage of the lamina and increased rolling-up of the recurved margins. The whole leaf winds helically round the stem, so that the dried leaf is protected both from insolation and desiccation. Often, the leaf movement is so pronounced that the plant almost disappears in the soil. After rainfall, sand particles and other material are removed by the twisting of the leaves (Scott, 1982). Additionally, the shining abaxial surface of the costa is exposed (e.g., *Timmella* (De Not.) Limpr., *Tortella* (Lindb.) Limpr. spp.). This may increase the reflection of incoming radiation and thus reduce evaporation and heat-stress.

A unique feature of several desert mosses is the presence of lamellae, filaments or other outgrowths of the leaf and costa surface as demonstrated by *Aloina*, *Crossidium*, *Pterygoneurum* or *Tortula* sect. *Crassicostatae* Mönk. species (Fig. 7a-c). This increases the photosynthetic surface of the leaves and acts as a sun-shade, providing a thick and opaque cover. In addition, the leaf lamina cells often become hyaline, and the strongly infolded leaf lamina protects the photosynthetic active filament cushion (Fig. 7c). This protects against insolation, desiccation and mechanical damage. The filament-cushions and lamellae also act as a capillary water conduction system and are able to store water.

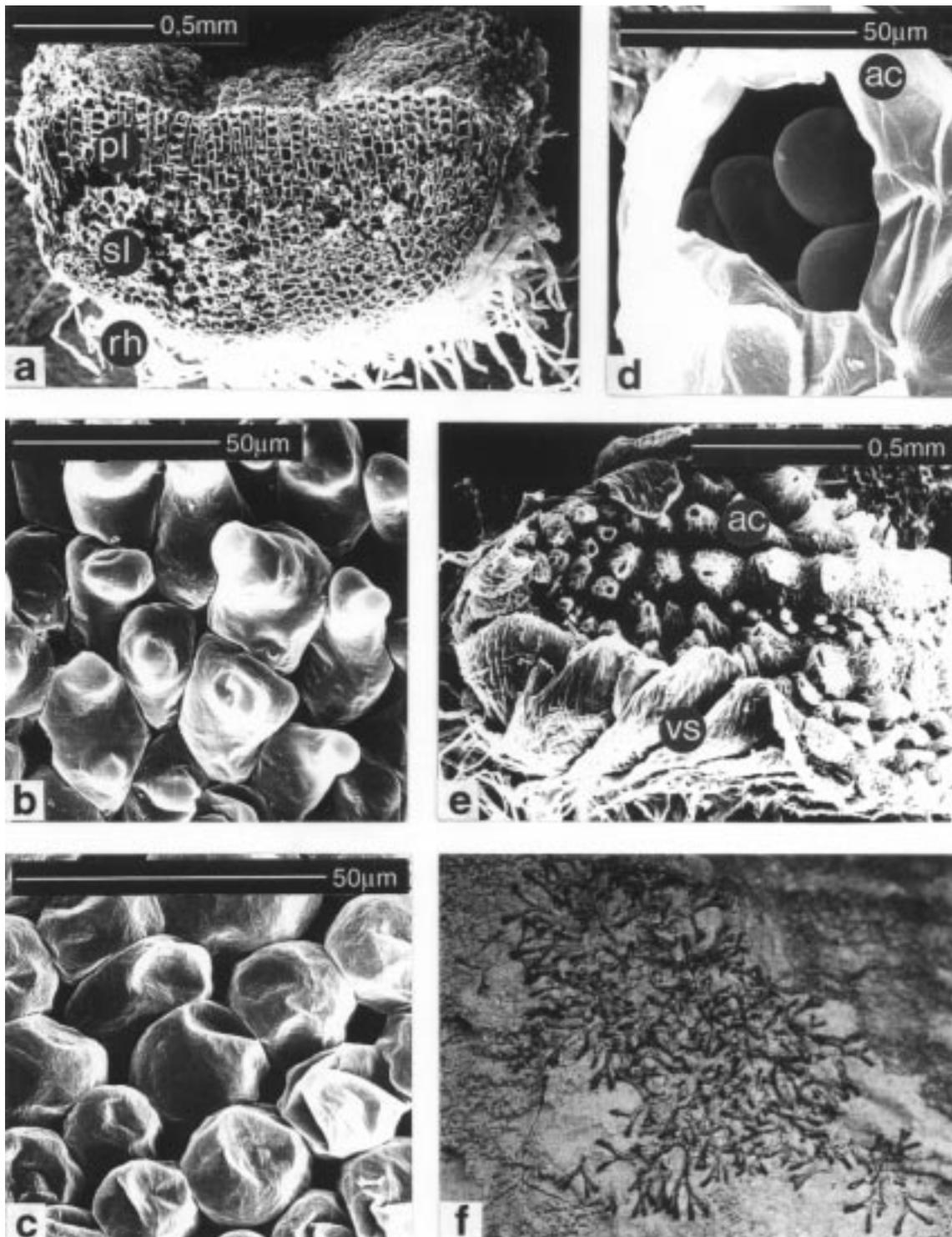


Figure 6. Xerothermal life syndrome. a, *Riccia crenatodentata*, cross-section of thallus (pl, photosynthetic pillars; sl, storage layer; rh, rhizoids); b, *Riccia atromarginata*, balloon-like epithelial cells (end-cells of photosynthetic pillars) with papillae and air pores; c, *Riccia lamellosa*, balloon-like epithelial cells and air pores; d, e *Exormotheca pustulosa*: d, hyaline chimney-like air chambers (ac) inside end cells of photosynthetic pillars; e, thallus with ventral scales (vs) and chimney-like air chambers (ac); f, *Targionia hypophylla*, rolled-up and shrivelled thalli exposing intensely pigmented ventral scales (from Kürschner & Ghazanfar, 1998).

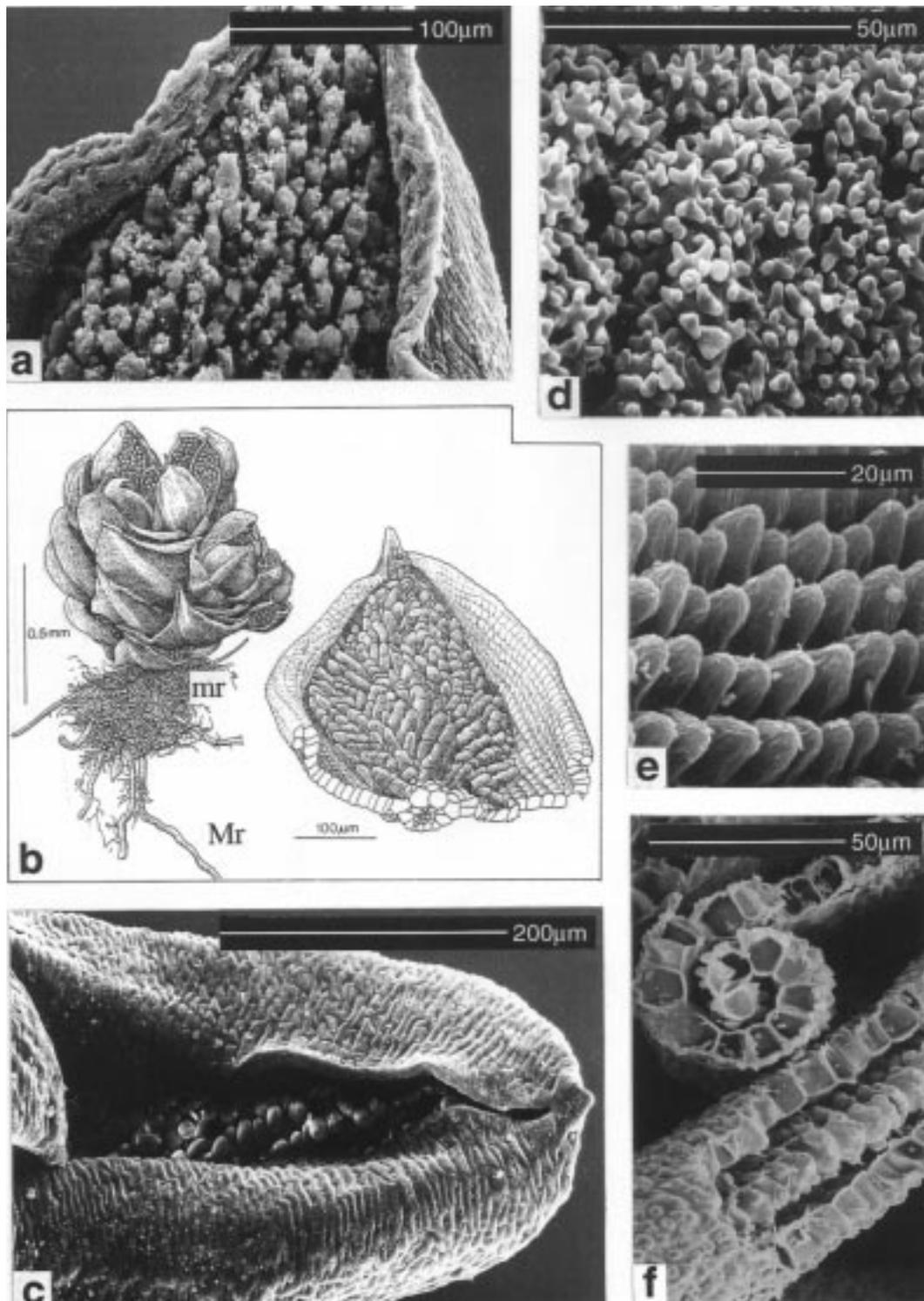


Figure 7. Xeropottioid life syndrome. a, *Crossidium squamiferum* var. *pottioideum*, leaf apex with filament cushion; b, *Crossidium laevipilum*, bulbiferous plant with dimorphic rhizoids (Mr, macrorhizoids, mr, microrhizoids) and leaf with filament cushion; c, *Aloina rigida*, cucullate leaf apex with infolded lamina; d, *Tortula atrovirens*, papillae; e, *Timmiella barbuloides*, papillae; f, *Pseudocrossidium hornsuschianum*, spirally rolled leaf margin (cross-section and longitudinal section of leaf margin), marginal cells differentiated into a specialised photosynthetic region (from Kürschner & Ghazanfar, 1998).

Several taxa, such as *Pseudocrossidium* R.S.Williams. spp., or *Tortula porphyreoneura* (Müll. Hal.) Townsend. have highly developed chlorophyllous marginal cells forming a special photosynthetic region, protected by their location in the spirally-revolute leaf margins ['Assimilationsstreifen' Herzog (1926), Fig. 7f].

Also common among xerophytic mosses are hair-points formed from dead cells at the tip of the leaves. These reflect sunlight and may help in the absorption of condensed water vapour from fog and dew. In this context papillae (Fig. 7d, e) are also of importance, accelerating water uptake when water is available. These often curious and bizarre structures are present in nearly all pottioid genera, acting as a rapid capillary water movement system (Longton, 1988; Proctor, 1979).

Summarising examples

A synopsis of all three complexes, life forms, life strategies and adaptations is well demonstrated by the analysis of the *Tortula atrovirens* (Sm.) Lindb.-*Crossidium squamiferum* (Viv.) Jur. synusium of central Saudi Arabia (Kürschner & Ghazanfar, 1998; Fig. 8). This synusium occurs in a very arid region with only 60-100 mm rainfall per year and grows under limestone boulders, where shade and water runoff from the rock surface sometimes create a mesic microhabitat. A strong micro-zonation of morphological adaptations and life strategies occurs along the gradient of soil texture, moisture, temperature and irradiation.

The *Plagiochasma rupestre*- and *Riccia trabutiana* Steph. micro-zone consist of short-lived or perennial shuttle species with drought-resistant gametophytes. These form dense mats and occur only on soil beneath overhanging rocks. In both micro-zones, the incidence of sexual reproduction is rather high. However, the spores are large, up to 120 µm, indicating short-range dispersal (engychory). Most of the spores remain near the parent plant and may permit survival of the populations if the gametophytes are destroyed. This is especially obvious in the *Riccia trabutiana* micro-zone where capsules are totally embedded in the thallus and are cleistocarpous (achory). In addition, most of the spores remain in tetrads and were released only after the thalli were destroyed. Asexual reproduction is rare in both zones and the thalli show adaptations of the before-mentioned xerothaloid life syndrome.

The following *Tortula-Crossidium* micro-zone (Fig. 8) is dominated by acrocarpous mosses with a colonists strategy. These taxa have a moderately short life span, i.e. 1-3 years with a resting stage as spores, and build predominantly short-turfs or solitary plants on the clayey-sandy crusts. During the dry season they are deeply embedded in the substrate. The colonists have a high rate of both asexual and sexual diaspore production. The spores are small and long-distance dispersal is frequent. Two life strategies can be observed: sexual colonists with a high degree of sexual reproduction within the first year as in *Crossidium squamiferum* (Viv.) Jur. and *Tortula atrovirens* (Sm.) Lindb. and vegetative colonists that rely largely on asexual reproduction by subterranean rhizoid gemmae (e.g., *Bryum* spp.). These colonists often appear in primary successional series as pioneers and are important forerunners in crust stabilisation. Morphologically, they can be characterised by the xeropottioid life syndrome.

Meanwhile, more than 20 bryophyte communities of the Near and Middle East have been analysed with respect to the three complexes mentioned. They comprise desert communities from Israel, Jordan and Saudi Arabia, ephemeral communities of Israel and Turkey, rock communities of Jordan and Turkey, as well as various epiphytic communities. They outline very similar adaptive trends and life strategies that generally are subjected to selection pressure. They can be summarised as follows (Fig. 9):

Within xerophytic, terrestrial communities a broad variety of life strategies can be observed. Most prominent is the colonists and shuttle strategy. Especially colonist with basitonic innovations are frequent, which are nearly absent in all other communities. In addition, the geophytic strategy, which hitherto is known only from a single moss, *Gigaspermum mouretii* Corb. (Frey & Kürschner, 1991c), is confined to terrestrial communities.

Against that, in humid to subhumid terrestrial communities in Mediterranean areas, colonists with high sexual and asexual reproduction are obvious, underlying chance dispersal. Species following the perennial stayer strategy were not observed within the communities analysed.

Such perennials, perennial stayers as well as perennial shuttle species, are very frequent in epilithic communities. Co-dominant here are pauciennial colonists. This strategy

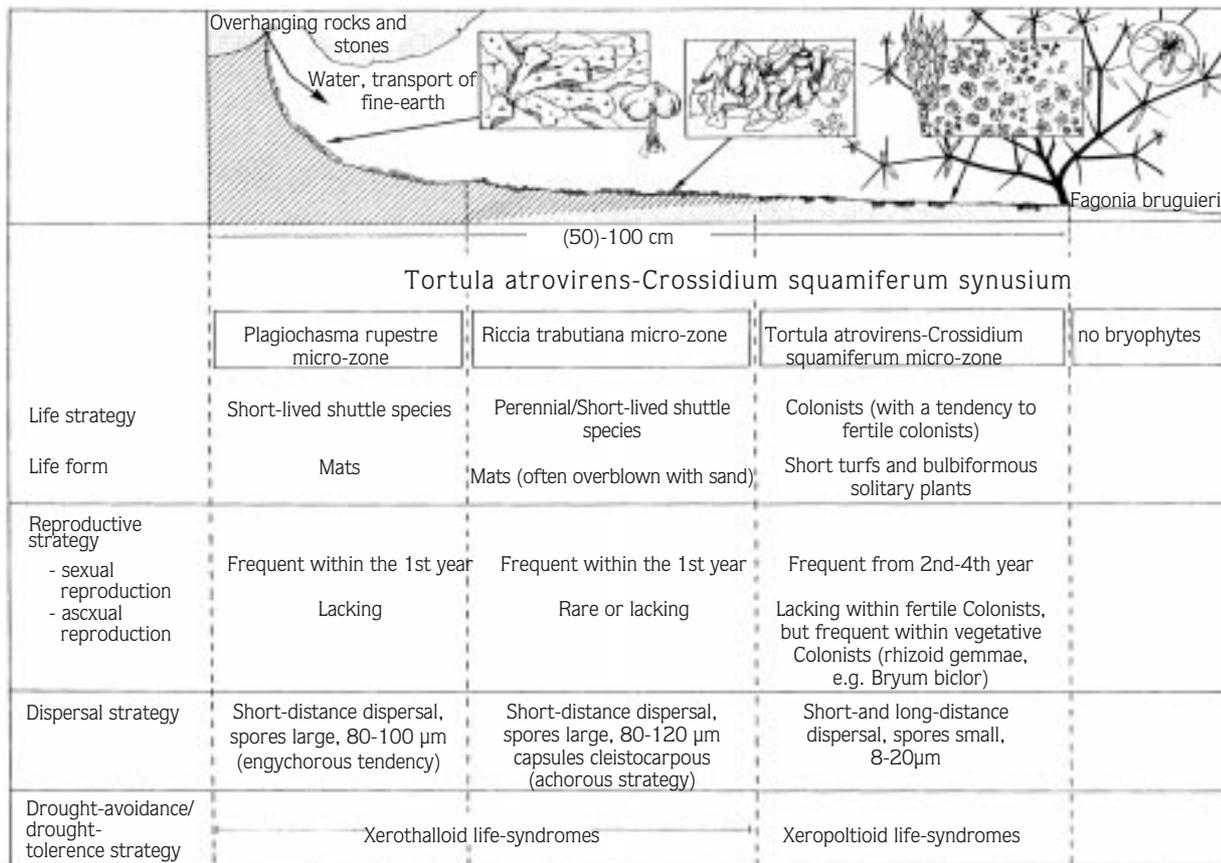


Figure 8. The *Tortula atrovirens-Crossidium squamiferum* synsium of Jebel Tuwayq (Central Saudi Arabia). Life strategies, life forms, reproductive, and dispersal strategies of the different micro-zones (after Kürschner & Ghazanfar, 1998).

is characterised by a longer life span, monoecy, regular sporophyte production, and the production of large quantities of small spores. This functional type is typical for saxicolous bryophytes, which compensate the high mortality rates of the gametophytes, often caused by the summer-drought or erosional effects, by a regular formation of sporophytes. Other strategies occur, but are of minor importance.

Within epiphytic communities, the seven examples analysed indicate a high proportion of perennial stayers with sexual reproductive effort within xerophytic communities. Additionally, a high number of colonists may occur here, dependent on the degree of disturbance. Within mesophytic communities growing under well-

balanced humid conditions perennial stayers and perennial shuttle species with a low sexual and asexual reproductive effort are frequent (so-called passive species). Their dominance on the phorophytes is mainly a result of clonal growth.

The analysis of life forms, life strategies and morphological adaptations indicate common adaptive trends that arise convergently but independently in unrelated taxa when they evolve under similar habitat conditions. It provides a basis for hypothesis concerning the establishment of species, habitat maintenance and dispersal strategies and impressively indicates the relationships between site ecology, niche differentiation and species evolution.

		Terrestrial communities		Epilithic communities	Epiphytic communities				
		xeric	humid		xeric	humid			
Number of associations considered		8	2	5	4	3			
Life strategies (Frey & Kürschner 1991)	Colonists	Annual shuttle species	●	●					
		Fugitives	●						
	Colonists with high sexual and asexual reproductive effort	●	●	●	●	●			
	pauciennial Colonists	●		●					
	Colonists with basitonic innovations	●	●	●					
	Perennial	Short lived shuttle species	●	●	●				
		Perennial shuttle species	●		●	●	●	Pg	
		Perennial stayers			●	●	●	Pp	
						●	●	Ag	
	Geophytes	●					Ap		

Figure 9. Summarised trends in life strategies (mean percentage cover) of bryophyte communities in the Near and Middle East (based on 23 communities; Ag, perennial stayers with high sexual reproductive effort; Ap, passive perennial stayers; Pg, perennial shuttle species with high sexual reproductive effort; Pp, passive perennial shuttle species; dominant, $\leq 25\%$; frequent, 5-25%; rare, $< 5\%$).

References

- Bates JW (1998). Is 'life-form' a useful concept in bryophyte ecology? *Oikos* 82: 223-237.
- During HJ (1979). Life strategies of bryophytes: a preliminary review. *Lindbergia* 5: 2-18.
- During HJ (1997). Bryophyte diaspore bank. In: Longton R E (ed.) *Population studies. Advances in Bryology* 6, pp. 103-134. Berlin: J. Cramer.
- Frey W & Hensen I (1995). Lebensstrategien bei Pflanzen: ein Klassifizierungsvorschlag. *Bot Jahrb Syst* 117: 187-209.
- Frey W & Kürschner H (1988). Bryophytes of the Arabian Peninsula and Socotra. Floristics, phytogeography and definition of the xerothermic Pangaeian element. *Studies in Arabian bryophytes* 12. *Nova Hedwigia* 46: 37-120.
- Frey W & Kürschner H (1991a). Lebensstrategien von terrestrischen Bryophyten in der Judäischen Wüste. *Bot Acta* 104: 172-182.
- Frey W & Kürschner H (1991b). Morphologische und anatomische Anpassungen der Arten in terrestrischen Bryophytengesellschaften entlang eines ökologischen Gradienten in der Judäischen Wüste. *Bot Jahrb Syst* 112: 529-552.
- Frey W & Kürschner H (1991c). Das Fossombronio-Gigaspermetum mouretii in der Judäischen Wüste. 2. Ökosozioökologie und Lebensstrategien. *Crypt Bot* 2: 73-84.
- Frey W & Kürschner H (1991d). Lebensstrategien epiphytischer Bryophyten im tropischen Tieflands- und Bergregenwald am Mt. Kinabalu (Sabah, Nord-Borneo). *Nova Hedwigia* 53: 307-330.
- Frey W & Kürschner H (1995a). Bryosozioökologische Untersuchungen in Jordanien. 3. Lebensstrategienanalyse der terrestrischen und epilithischen Moosgesellschaften. *Fragm Flor Geobot* 40: 491-511.
- Frey W & Kürschner H (1995b). Soziologie und Lebensstrategien epiphytischer Bryophyten in Israel und Jordanien. *Nova Hedwigia* 61: 211-232.

- Frey W & Kürschner H (1998). Wüstenmoose: Anpassungen und Überlebensstrategien im täglichen Kampf mit der Sonne. *BIUZ* 28: 231-240.
- Frey W, Kürschner H & Seifert HU (1995). Scientific results of the BRYOTROP expedition to Zaire and Rwanda 7. Life strategies of epiphytic bryophytes from tropical lowland and montane forests, ericaceous woodlands and the *Dendrosenecio* subpáramo of the eastern Congo basin and the adjacent mountains (Parc National de Kahuzi-Biega/Zaire, Forêt de Nyungwe/Rawanda). *Trop Bryol* 11: 129-149.
- Gimingham CH & Birse EM (1957). Ecological studies on growth forms in bryophytes. I. Correlations between growth form and habitat. *J Ecol* 45: 533-545.
- Herzog T (1926). *Geographie der Moose*. Jena: Fischer.
- Kürschner H (1994). Adaptionen und Lebensstrategien in basiphytischen Gesteinsmoosgesellschaften am Nordrand der Schwäbischen Alb (Süd Deutschland). *Phytocoenologia* 24: 531-558.
- Kürschner H (1999). Life strategies of epiphytic bryophytes in Mediterranean *Pinus* woodlands and *Platanus orientalis* alluvial forests of Turkey. *Cryptogamie Bryol* 20: 17-33.
- Kürschner H (2002). Life strategies of Pannonian loess cliff bryophyte communities. Studies on the cryptogamic vegetation of loess cliffs, VIII. *Nova Hedwigia* 75 (in press).
- Kürschner H & Ghazanfar SA (1998). Bryophytes and lichens. In: Ghazanfar S A, Fisher M (eds.) *Vegetation of the Arabian Peninsula*, pp. 99-124. Dordrecht, Boston, London: Kluwer Academic Publishers.
- Kürschner H, Frey W & Parolly G (1999). Patterns and adaptive trends of life forms, life strategies and ecomorphological structures in tropical epiphytic bryophytes – a pantropical synopsis. *Nova Hedwigia* 63: 73-99.
- Kürschner H & Parolly G (1998). Lebensstrategien stammepiphytischer Moose in Regenwäldern am Andenostabhang und im Amazonas-Tiefland von Nord-Peru. *Nova Hedwigia* 67: 1-22.
- Kürschner H & Parolly G (1999a). The Epipterygio-Ricciatum frostii ass. nov.: ecology and life strategies of an ephemeral bryophyte community in western Turkey. *Lindbergia* 24: 84-92.
- Kürschner H & Parolly G (1999b). Syntaxonomy, synecology and life strategies of selected saxicolous bryophyte communities of west Anatolia and a first syntaxonomic conspectus for Turkey. *Nova Hedwigia* 68: 365-391.
- Kürschner H & Pócs T (2002). Bryophyte communities of the loess cliffs of the Pannonian basin and adjacent areas, with the description of *Hilpertio velenovskyi-Pterygoneuretum compacti* ass. nov. – Studies on the cryptogamic vegetation of loess cliffs, VI. *Nova Hedwigia* 75 (in press).
- Kürschner H, Tonguç Ö & Yayintas A (1998). Life strategies in epiphytic bryophyte communities of the southwest Anatolian *Liquidambar orientalis* forest. *Nova Hedwigia* 66: 435-450.
- Longton RE (1988). Adaptations and strategies of polar bryophytes. *Bot J Linn Soc* 98: 253-268.
- Longton RE (1994). Reproductive biology in bryophytes. The challenge and opportunities. *J Hattori Bot Lab* 76: 159-172.
- Longton RE (1997). Reproductive biology and life-history strategies. In: Longton RE (ed.) *Population studies. Advances in Bryology* 6, pp. 65-101. Berlin: J. Cramer.
- Mägdefrau K (1982). Life forms of bryophytes. In: Smith AJE (ed.) *Bryophyte ecology*, pp. 45-58. London, New York: Chapman and Hall.
- Miles CJ & Longton RE (1992). Spore structure and reproductive biology in *Archidium alternifolium* (Dicks. ex Hedw.) Schimp. *J Bryol* 17: 203-222.
- Proctor MCF (1979). Structures and eco-physiological adaptations in bryophytes. In: Clarke GCS, Duckett JG (eds.) *Bryophyte Systematics*, pp. 479-509. London: Academic Press.
- Scott GAM (1982). Desert bryophytes. In: Smith AJE (ed.) *Bryophyte Ecology*, pp. 105-122. London: Chapman and Hall.
- Schönherr J & Ziegler H (1975). Hydrophobic cuticular ledges prevent water entering the air pores of liverwort thalli. *Planta* 124: 51-60.
- Stearns SC (1976). Life history tactics: a review of the ideas. *Quart. Rev. Biol.* 51: 3-47.
- Stoneburner A, Lane DM & Anderson LE (1992). Spore dispersal distances in *Atrichum angustatum* (Polytrichaceae). *Bryologist* 95: 324-328.
- Volk O (1984). Beiträge zur Kenntnis der Marchantiales in Südwest Afrika/Namibia IV. Zur Biologie einiger Hepaticae mit besonderer Berücksichtigung der Gattung *Riccia*. *Nova Hedwigia* 39: 117-143.
- Zippel E (1998). Die epiphytische Moosvegetation der Kanarischen Inseln. Soziologie, Struktur und Ökologie. *Bryoph Bibl* 52: 1-149.