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Bryophytes in Desert Regions

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ABSTRACT: Bryophytes are a proposed taxonomic division containing three groups of non-vascular land plants (embryophytes): the liverworts, hornworts and mosses. They are characteristically limited in size and prefer moist habitats although they can survive in drier environments. The bryophytes consist of about 20,000 plant species. Bryophytes produce enclosed reproductive structures (gametangia and sporangia), but they do not produce flowers or seeds. They reproduce sexually by spores and asexually by fragmentation or the production of gemmae.

In case of bryophytes in thar, on the basis of compilation of earlier reports and results of fresh exploration, the present work provides a list of 113 bryophyte taxa from Mount Abu, thar including 24 taxa as new to the Mount Abu area. Out of these, 14 are new records to Rajasthan state, while 07 taxa are new to Central Indian bryo-geographical region. Bryophytes are most abundant and conspicuous in moist habitats, but are also found in grasslands and deserts where they endure prolonged dry periods. Number of Bryophyte species like Funaria hygrometrica, Marcantia palmata,Riccia robusta are collected from Thar desert of Rajasthan particular from Ganganagar district for the studies on morphological and anatomical adaptation. These studies reveal the anatomical adaptations of bryophytes to xeric conditions (like presence of tufts of tough rhizoids and longer rhizoids etc.). The study was carried out through section cutting using rotary microtome. Different photographs of these sections have been taken from microscope with the help of digital camera.

KEYWORDS: moss, bryophytes, flora, rajasthan, areas, xeric, dessert, taxa, rhizoids, adaptation

I. INTRODUCTION

Studies on the mosses of hot and arid Indian Thar Desert revealed the occurrence of five moss species viz. Tortula muralis Hedw., Gymnostomiella veronicosa (Hook.) Fleisch., Hyophila involuta (Hook.) Jaeger., Semibarbula orientalis (Web.) Wijk. & Marg. and Fissidens flaccidus Mitt. Among these taxa Fissidens flaccidus Mitt. is a new record for Rajasthan and it distinguishes from its allies in having leaves with complete limbidium and percurrent costa, ending far below apex. The present work deals with a morphotaxonomic studies of these taxa along with the adaptive strategies to survive in severe xeric environmental conditions of Thar Desert. This is the first consolidated record of bryophytes from Indian Thar Desert.[1,2,3]

Drought is an important abiotic environmental condition that occurs when potential evapotranspiration is more than incoming precipitation and is often associated with the loss of water from tissues and cells causing dehydration stress. Plants can avoid deficit stress either by the evolution of a complex set of morphological (structural growth forms) and physiological features. e.g. C4 and CAM photosynthetic pathway and anatomy or by temporally escaping drought through shortened their life cycles. Another strategy for avoiding water deficit stress is physiological tolerance when in plants have evolved the physiological abilities to survive desiccation. Mosses with 12,700 species [1] and liverworts with about 7,500 species [2] form the second and fourth largest groups of land plants respectively. In mosses the gametophyte has stem, leaves and the most species of mosses have at least some form of internal water conducting tissues, but these are usually poorly developed whereas the gametophytes of all hornworts and liverworts are fairly simple thalloid. Mosses and leafy liverworts have other features in common that apparently have evolved independently. Among these features, (i) leaves with simple cell thickness, (ii) leaves that never have a petiole and are attached to the stem along a wide insertion and (iii) a lack of ability to retain water (poikilohydric) and cell turgor for an extended length of tome but a remarkable physiological ability to tolerate desiccation. The two different major strategies for survival are first avoiding desiccation through various morphological traits and the second of tolerating desiccation by physiological shutting down cell functions. Although most liverworts and mosses are desiccation tolerant to some extent, they also avoid drought through a number of morphological avoidance mechanisms. Indian Thar Desert is the biggest desert in India, lies between 24° to 28° N latitude and 68° to 71° E longitude. More than 60 per cent of the desert lies in the state of Rajasthan. It extends into southern part of Haryana and Punjab states and northern Gujarat. In hot and dry areas of Indian Thar Desert, water is typically scarce with unpredictable rainfall. Strong winds and dust storm activities are common feature of this region. Desert ecosystem presents the considerable

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challenges, to survive the plants. Bryophytes are moist and shade loving plants and can successfully exploited many habitats. These are the nonvascular cryptogams,[4,5,6] and play an important role in ecosystem function [3]. Bryologists had avoided the desert for a long period with the preconceived notion that desert is devoid of life and harboring, few species if able to tolerate the heat, drought and severity of weather. Knowledge of Bryophytes from Indian Thar Desert is so fragmentary, and only few studies have been undertaken such as [4, 5]. It is interesting to note that from last two decades rainfall and humidity is continuously increasing in this part of Rajasthan due to considerable amount of rainfall every year. This has been increased availability of water and humidity also in the environment and probably this condition favored the growth of bryophytes in this particular studied area [5]. There is little information concerning with the bryophytes, its habitat and survival strategies in arid and semi-arid environment of Indian Thar Desert. So, the adaptations relating to habitat, life form and leaf architecture among the bryophytes from the Indian Thar Desert were studied. Particularly this region of Rajasthan remains dry for considerable part of the year thus bryophytes found here spend long periods of time in desiccated state, when they are rehydrated with rain or dew they regain normal function. Unfortunately, these are the regions where species diversity among bryophytes is less abundant and the bryophytes living there adopt various survival strategies to cope up with great heat and harsh climatic conditions.

An updated account of 51 taxa of mosses of Rajasthan and Punjab plains is provided along with a note on delimitation of boundaries of this unique bryo-geographical zone. Family Pottiaceae is most dominant and diversified with 17 taxa under 11 genera while genus Fissidens (Fissidentaceae) has the maximum diversity with 7 species followed by Physcomitrium (Funariaceae) and Bryum (Bryaceae) with 6 species each.

II. DISCUSSION

Perennation is the ability of plants to survive especially in unfavorable or harsh situation such as drought and cold by developing specific perennating organs. Rajasthan remains dry for a considerable part of the year and most of the plant species appear just after the first rain complete their life cycle within a short period of one to three months. Most of the species get dry before competing their life cycle due to high temperature and low rainfall. It was reported that the species found in the arid or semi arid regions are annuals and depends entirely on the spores for perennation and survival as the temperature during the summer is quite high and plants get completely dry but at the approach of favorable condition the plant parts like stem, rhizoids, leaves and other external or underground perennating organs revive their growth with the first shower of rain and multiply through regeneration because bryophytes have high potential of resurrection or revive. Each plant part give rise one or more apical shoot while older portion dies by death and decay mechanism. It was observed that in plants, growing under xeric condition after few days of drought, the leaves become enrolled and scattered on the soil or on the rocks along with their small portions of stem. Such plant organ readily revive and resume their growth after first rain in any season It was observed that sterile plants were in great abundance then fertile parts. In species like Physcomitrium japonicum underground gemmae are formed in unfavorable condition which help the plant to survive in dry situation and act as perennating organ [6]. These gemmae develop on underground rhizoids, Multicellular and red in colour (10,11,12). Bryologists some time confuse it with the spore of fungus Alternaria species. During dry condition, the parent plant die but these gemmae remain in the resting or dormant stage throughout the unfavorable period and at the approach of favorable condition, this gemnae sprout to form new gametophytes. Gemmae formation has also been observed in Semibarbula orientalis and Hyophila rosea. In S. orientalis these gemmae are aerial axial i.e they develop on the apex of shoot and in the axil of leaves whereas in H. rosea these gemmae are although aerial but at the axil of leaves at the middle part of axis [7]. Gemmae are also quite abundant in the members of Hepaticopsida and they may occur on thallus or in gemma cups such as in Marchantia polymorpha and certain species of Riccia. There is a great variations in the structure and forms of these gemmae but it is a characteristic feature of a particular species. They may be one or two celled, multicellular stalked etc. It is also reported that perennation may take place by adventitious branches, primary and secondary protonema. The colorless or green, filamentous primary and secondary protonema develop in certain mosses that may break into small fragments by any external or internal activity and may remain as perennating organ. These perennating organs may grow into a new protonema latter on which is converted in caulonema (brown colored). On these caulonema buds are developed and each bud give rise new leafy gametophytes. Protonema develops from other parts of plants instead of spores are known as secondary protonema. It may develop from rhizoids, injured portion of leaves; stem e.g. in Funaria hygrometrica, Physcomitrium japonicum and some species of Bryum. Thalloid liverworts are common in hot and dry areas. When these plants are wet in favorable condition the thallus are open and green but under harsh situation or in drier condition the thallii rolled inwardly along their length, so that only fairly thin, black lines and on the underside of each strap there are blackish scales that act as a protecting covering for inrolled thallus. The thallii of Riccia species are generally Y

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shaped when open and green in normal natural favorable condition. During drought or in hot condition thallii of this plant also fold up along their axis. A number of typically arid areas bryophytes are individually shot lived but persistent as a species in given are. In these bryophytes the gametophytes, typically small, develop quickly from spores, produce sporophytes and large spores and then die such as in many species of Riccia and other liverworts. The spores are often quite large and incapable of long distance dispersal. These species are commonly described as annual shuttle species. The annual shuttle species do not tolerate drought but evade it by the production of drought resistant propagules. The gametophytes of annual shuttle species tend to appear after first rain in micro habitats that are ephemeral but which tend to recover with some degree of regularity. At the other extremes, are the perennial stayers, with far more robust gametophytes and with various adaptations to ensure long term survival as individuals e.g. certain Riccia species. Bryophytes are most abundant and conspicuous in moist habitats, but are also found in grasslands and deserts where they endure prolonged dry periods. Number of Bryophyte species like Funaria hygrometrica, Marcantia palmata,Riccia robusta are collected from Thar desert of Rajasthan particular from Ganganager district during 2008-2010 for the studies on morphlogical and anatomical adaptation. These studies reveal the anatomical adaptations of bryophytes to xeric conditions (like presence of tufts of tough rhizoids and longer rhizoids etc.). The study was carried out through section cutting using rotary microtome. Different photographs of these sections were taken from microscope with the help of digital camera.

III. RESULTS

Resurrection potential of bryophytes In contrast to other plants, many bryophytes have an ability to survive in drought, typically by folding up when dry and unfold when moistened or survive complete desiccation without dying known as resurrection. These resurrection plants when rehydrated they can able to recover their normal metabolism activity including photosynthesis etc This remarkable property is essential because1. Bryophytes leave have a thin cuticle or without cuticle, they rapidly gain loss of water and equilibrium with their environment (Poikilohydric). 2. They also have various types of physiological and morphological adaptations to delay water loss and mitigate damage due to water stress. a. Most bryophytes have large amount of water retaining capacity (% of wet mass related to dry mass). b. They can produce proteins and other organic compounds which help to protect cell membranes from damage during desiccation and dehydration. c. They are also able to efficiently repair damage caused by drying and recover quickly upon rehydration.[13,14,15]

Desiccation tolerance strategies Desiccation tolerance or drying without dying is the most among phenomena in biology and has been the topic of number of reviews [8, 9, 10] . Mosses occur in all of the major biomes of the world. They dominate the ground layer in boreal forest and are foundational species of northern peat lands. They are among the abundant epiphytes in higher elevation tropical rain forests and with liverworts. Specific plant canopy Mosses like vascular plants, have variable canopies of leaves, branches and stems, all of these are important in controlling water balance and gas exchange; especially important are surface roughness, stem diversity and position [11, 12]. These different canopies can provide protection from evaporation stress. Further complex canopy development allows the expansion of colonies in both horizontal and vertical directions providing a competitive advantages to the plants. Canopy in mosses are two types- (i). Unbrached dendroid This type of canopy is mostly abundant in terrestrial habitats. The leafy branches are present only at the upper part of the main shoot. (ii). Branched dendroid This canopy is found in epiphytic or terrestrial habitat. These are frequently branched, erect, leafy shoot. Short life cycle of plants One life history strategy widely used by mosses is to avoid drought by shortening the functional life cycle, thereby temporally escaping periods of drought. Annuals and species even shorter, ephemeral life styles largely avoid periods of drought by completing the gametophytic life cycle phase or by having short- lived gametophores during a brief moist growing season and weathering the dry season as a Diaspore. Several mechanisms are also present in mosses, including leaves with adaxial costal surface having (i) photosynthetic pads, (ii) filaments, (ii) lamellae and (iv) adaxial leaf laminal surface having concave cell walls. Shortened life cycle not only include modification to the gametophyte generation [13 but also to the sporophytic generation. Such modifications are reduction in seta length, resulting in capsules immersed in the vegetative leaves, capsule axis compressed to a globose shape, loss of peristomes function and lack of an operculum that results in spores being deposited in the same place as the parent plant such as in Physcomitrium japonicum. Multistratose leaves Many mosses inhabiting a variety of xeric habitats having photosynthetic cells in with 2-3 layers or strata. The correlation between habitat and multistratose leave suggests that this could be a method of extending the length of time that cells can be active by reducing the ratio of evaporative surface to cell volume. Leaf cell structural modifications Mosses that occur in harsh environmental conditions such as on rock faces, dry lands, soil crusts and tree trunks and branches all appear to have a high level of desiccation tolerance, but also have asset of morphological attributes that are associated with these severe habitats. These species have thick cell walls, thus a higher

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amount of carbon is allocated to structural components than the species of mesic habitats. They mostly have papillae cell wall protuberances in a variety of forms, from mere finger like bumps to branched, forked or C to U shaped structures. They may create capillary channels that efficiently move to water along the leaf surface allowing rewetting of the leaf to occur more quickly [14]. They are hollow and create an increased cell surface to volume ratio allowing being absorbed and loss more quickly and they create an elevated surface for enhanced gas exchange. Habitat The bryophytes living in such harsh and dry climatic condition, found to be grown in more protected microhabitat, especially in moist habitat such as grass tussocks, under boulder overhang, in rock crevices etc. Such microhabitat creates a tolerable environment for such delicate plants. The grass tussocks and xeric plants inhabiting Indian Thar Desert provides the shade and holds the water for long and makes the condition favorable for the growth of these plants. During rainfall, there will be runoff from the boulder which moisten the soil around the base and hence provides the suitable habitat to bryophytes [5]. The Indra Gandhi Canal which was constructed to rejuvenate the Thar region had various ecological impacts. It also provided the suitable habitat and environmental condition to the various bryophytes to grow in nearby seepage areas and ponds and thus also helps in dune stabilization. Biological features Bryophytes found in Indian Thar Desert showed a number of morphological, anatomical and biological features which allow them to tolerate and withstand in such an extreme arid environment [15, 16]. (i). Protective feature in Gametophyte Gametophyte is long lived and dominating stage in life cycle of bryophytes. All the conspicuous vegetative organs, including photosynthetic leaf-like structures, thallus, stem, rhizoids belong to the gametophytic stage. a. Cushion forming habitat It has been reported that many bryophytes such as species of Riccia (Fig 1, B), Semibarbula and Bryum (Fig 1, A) always grow in cushion habitat which prevent the water loss and provide moist condition for the survival of these plants in comparatively dry and hot condition. A few plants grow in loose tufts on wet and moist soil near seepage areas. The cushions are of two types in bryophytes- (i). Large cushions This type of cushion attains a diameter of about 5 cm; in Gmnostomiella vernicosa and Bryum species. (ii). Small cushions This type of cushion attains a diameter of less than 5 cm.

b. Mats Mats are formed of creeping shoots and their branches which are firmly affixed to the substratum with the help of rhizoids. The mats frequently occur on forest floor and are of various types such as rough, smooth, thread like and thalloid etc. These different types of mats help in more water retention and to survive in dry condition. c. Water sacs and ventral appendages The universal occurrence of inflated ventral lobules or water sacs is an example of Pottiales (Bryaceae) which are also known as water storing structures like water sacs, large ventral under leave and foliar scales which increase capillarity along the ventral side of the stem in prostrate taxa. In erect taxa they function in photosynthesis just like the ventral leaves, but in the prostrate they likely are not effective in photosynthesis. In general, increasing the volume of capillary spaces, promotes the maintenance of volume and turgidity through brief periods of atmosphere drying, but is not a mechanism to avoid long term drought [17]. d. Rhizoids, stolen and other subterranean structures In hepatics, the term rhizomes is applied for an underground stem bearing reduced leaves and stolen for leafless, hyaline subterranean system of the Haplomiriales. The modification of leafy stem apices into tubers is another mean of persisting by perennation during drought or any other unfavorable growing conditions. These tuber like rhizomes are densely covered with rhizoid sand bear thick walled epidermal cells, but they are fleshy, determinant in growth and filled with starch filled parenchymatous cells [18]. e. Cell modifications Liverworts of xerophytic habitats leaf and stem cells typically possess especially large trigones or corner thickenings and nodular intermediate thickenings on their interior walls and producing papillae on their dorsally exposed, superficial walls. These modifications limits both water uptake and evaporation in plants and they help to maintain an interface gas exchange and also prevent wetting of fully dry plants when water is insufficient for recovery. f. Shape and Arrangement of Leaves on stem This is one of the most important protective methods against dryness. In this pattern shoots radially form a central pint forming a rounded tuft. Most of the xerophilous mosses have a concave leaf and forms a cuspidate tuft (1, C & D) and serves as a condensation point. In Fissidens (1, E) the lower part of leaf is conduplicate which forms the small chamber that retains water and make it available to the plant for long period. During moist condition, leaves absorb water and open out but in the dry condition they place themselves close to the stem, enroll or curl which makes the surface less available for evaporation [15]. Spiral twisting of leaves around the stem is common amongst the acrocarpous mosses and is well shown in Tortula muralis, Semibarbula orientalis, Bryum capillare. Similarly, Bryum argenteum shows the imbrications of leaves and exposes the apices and thick nerve and thus facilitates the desiccation tolerance. g. Thickening of leaf cells The papillosity of leaf margin and incrassate cell wall is also an important adaptive character in xerophilous species such as in Tortula muralis (1, G) and Semibarbula orientalis (1, H). Thickening and widening of costa is also a common occurrence in xerophilous mosses. h. Investment of dead cells Hyaline hair point may be formed by excurrent costa as in Tortula muralis (1, G) and Bryum argenetum (1, F). These hyaline hair points protect the colony against overheating by reflecting some of incident radiation and also provide numerous condensation points. Similarly hyaline cells at leaf bases act as water storing cells, as in Physcomitrium sps.

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Among the liverworts, the thallus of Marchantiales (Riccia) curves round during dryness, so as to expose the non-chlorophyllous ventral scales and remains in inactive state. Whenever there is rainfall these thalli absorbs water quickly and opens up and become photo synthetically active. Protective feature in sporogonium A sporogonium consists of foot, seta and capsule and is dependent on gametophyte for its nutrition. The sporogonium develops from the zygote in a female sex organ i.e. archegonium. Spores are formed in a capsule from cells of archeospore as a result of meiosis. The young sporogonium in mosses is protected by the perichaetial leaves of the gametophyte (1, K). The bell shaped calyptra forms a protective bonnet over the unripe urn or capsule and protects it from dryness, as in Physcomitrium (1, I) and Funaria hygomitrica (1, J). In the liverworts the sporogonium are sunken in the archegonial cavity (Riccia, 1, L) and hence protected from dryness.

IV. CONCLUSION

n hot, dry areas water is typically scarce, with rainfall unpredictable, and the bryophytes living there adopt various survival strategies. One is to grow in the more protected MICRO-HABITATS – such as at the bases of grass tussocks, on tree trunks, under boulder overhangs and in rock crevices, to give just a few examples. Consider the benefits provided by a tree trunk. A bryophyte growing on the predominantly shady side of a tree trunk will of course be protected from the full force of the sun. Additionally, the tree trunk concentrates some of the rain falling on the tree. During rainfall, some rain will fall directly on the trunk, some on the branches above, with some falling on the branches flowing down onto the trunk, so adding to the amount of water the trunk is exposed to. The benefits are greatly increased if the bark is rough and fissured. Such bark provides a much greater surface area (with numerous shaded micro-habitats) and slows down the flow of water, as well as providing numerous spots where a few droplets can be trapped, allowing any nearby bryophytes to benefit from the water over a longer period. Now turn your thoughts to a large boulder that is half buried in the soil in an otherwise barren area. During rain there will be runoff from the boulder. The soil around the base of the boulder gets water directly from the rain as well as the runoff. In a torrential downpour the contribution of the runoff may be irrelevant. But during light rain the runoff [16,17,18]is likely to ensure that the soil near the base of the boulder stays wetter for longer than the soil further away from the boulder. The advantages created by trees, boulders or tussocks may be slight but, for some species, enough to create a tolerable habitat or sufficient to prolong benign conditions long enough to allow spore production.

Of course, you do also find arid area bryophytes growing in the open, but even here there are different microhabitats. For example, in the Southern Hemisphere a north-facing slope would undergo more heating than a south-facing slope, and vice-versa in the Northern Hemisphere. While some species would be able to tolerate either aspect, others would survive only on the more benign slope.

Arid area bryophytes open up and actively photosynthesize when there is moisture available, but close up and become dormant when conditions become too hot and dry. Bryophytes are much more resistant to heat when dry than they are when moist. Experiments have shown that species which can tolerate temperatures of 80-100°C (or even more) when dry, die at temperatures of 40-50°C if they are kept moist.

It's a fact of physics that close to the ground the air is very slowly moving. This boundary layer is a result of the friction between moving air and the ground. It's well known that still or very slowly moving air is a good insulator and it is also the case that molecules (for example, water vapour) move slowly through the boundary layer, since diffusion rather than convection is the moving force. Thus water, evaporating from the ground, is retained for a while within the boundary layer and creates a slightly more humid micro-climate. Arid area bryophytes growing on the ground are typically low growing and within that somewhat protective boundary layer. There's more in the BOUNDARY LAYERS CASE STUDYreference link.

click to enlarge
Bryum argenteum top view
Many exposed mosses grow as dense carpets or small hummocks, each a colony of numerous plants. On the right is a close-up view of the top of a colony of Bryum argenteum. Each of those bumps is the top of a separate plant. Here click for photo is a side-on view of part of the same colony. In such dense colonies water is lost more slowly than in sparser growths. For one thing, the upper parts of such carpets or hummocks shade the lower parts and so slow down the loss of water from within the colony. Additionally, dense carpets or hummocks expand the boundary layer. Any roughened surface (such as the surface of a dense moss colony) that increases friction with the air will slow air movement and so modify the boundary layer. In effect, a moss carpet or hummock raises the boundary layer over itself.

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Carpets or hummocks are a feature of the community as a whole. The separate gametophytes also have various structural features that help maximise the use of any available moisture. When mosses dry out there are various ways in which they close up. In some the leaves bend inwards at the base, finishing up flat against the stem. In others they curl up around the stem. In dry plants there are numerous very narrow gaps between neighbouring leaves or between leaves and stems that are ideal conduits of tiny amounts of water by capillary action. When water (even early morning dew) becomes available these channels help move it quickly throughout the plant. The leaves of many arid area mosses have papillae. A papilla is a tiny protrusion on the cell surface. It may be just a simple bump or it may be split or forked in some way. In a densely papillose leaf the gaps between the papillae provide numerous channels for rapid water movement by capillary action and so help spread, and thereby maximise the use of, tiny amounts of water. At the same time the tips of the papillae are likely to remain above the watery film and so provide places where the gas exchange necessary for photosynthesis can take place. As an aside it's worth noting that papillae are not confined to arid area species, are also found in many of the leafy liverwort genera and are not always associated with capillary flow. For capillary flow the papillae need to be packed densely enough to create fine channels between the papillae and papilla shape may also be important. Studies have also shown that the tips of the papillae in various species are water repellent, thereby keeping them dry and available as sites for gas exchange. Many mosses of dry areas have slightly rolled up leaf margins. This creates a very narrow and somewhat tubular channel along the length of each leaf margin, Such channels also provide routes for capillary movement. The following drawing, by Judith Curnow, is of the moss Triquetrella papillata click for photo and shows part of a leaf surface in profile. You can see protruding papillae of various shapes. The black scale bar represents a length of 20 micrometres. Click on the drawing for another one showing the papillae of this moss.

scale = 20 µm (click to enlarge)

The moss family Pottiaceae has numerous genera and species, many of which are very common in harsh, exposed areas and are renowned for papillose leaves and curved leaf margins. To give you a rough idea of the prevalence of this family in dry areas, consider the book, by David Catcheside, given in the next reference button. It is a technical book with detailed descriptions of the mosses found in South Australia, predominantly a very dry state. The book deals with 31 families and has 184 pages of species' descriptions and 84 of those pages are devoted to the family Pottiaceae. The next largest family (with 36 pages) is the Bryaceae. Of course, there have been changes in taxonomy and additional discoveries since the book was published in 1980, but the relativities suggested by those page counts would still be much the same todayreference link.

The leaves of many arid area mosses have white hairpoints at their tips. When the leaves of Campylopus introflexus are closed up they are hard to see but the hairpoints show very well click for photo. Here click for photo is the species Tortula princeps (a member of the family Pottiaceae) with the plants moist and the leaves showing very clearly – but you can also see the hairpoints quite easily. Hairpoints have more than one role. Hot, arid areas often become quite cool overnight. Cold nights may result in early morning dew or at least a relatively high night-time or early morning atmospheric humidity, especially near ground level. The multitude of hair points in a moss colony provide numerous condensation points, which give the colony a very effective means of gathering water. Those numerous hairpoints are also a source of friction between the moss layer and the passing air. Friction slows the airflow so the hairpoints help thicken the boundary layer. Another feature of those hairpoints is that they help protect the colony against overheating by reflecting some of the incident radiation. Experimental studies on mosses, comparing plants with hair points with those where the hairpoints have been removed, have shown that hairpoints can reduce water loss by about a third.

Leafy liverworts show little variation with changes in atmospheric moisture but few leafy liverworts are found in dry areas, especially in the open exposed areas in which you may still find many moss species. In dry areas you'd look for leafy liverworts in the more sheltered microhabitats.

In contrast to the leafy liverworts several genera of thallose liverworts are common in hot, dry areas.

click to enlarge
Asterella drummondii - wet
click to enlarge
Asterella drummondii - dry

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The photos above show the thallose liverwort Asterella drummondii with strap-like thalli. The species is often found well out in the open. When wet the thalli are open and green. Under much drier conditions that same colony takes on this appearance in the photo on the right. Now the thalli have rolled inwards, along their length, so that only fairly thin, black lines now show where previously there were green straps. On the underside of each strap there are blackish scales that act as a protective covering for the inrolled thallus. In the second photo the thalli have closed and all you see are the scales, which protect the thallus. Targionia hypohylla is another thallose liverwort found in fairly dry areas, though often in slightly protected micro-habitats. Many Riccia species are found in dry areas. The thalli are Y-shaped, the exact proportions (long and narrow, short and squat) varying between species. They are commonly found on damp soil in seasonally wet areas and this photo click for photo shows a colony of Riccia multifida in such a habitat. In this photo click for photo you can see a bryologist collecting specimens of Riccia. The habitat is the bare soil of a small dam in a forest in central New South Wales. The area is hot and dry for at least several months each year but in many years there is likely to be enough rain to raise the water level in this dam considerably. During the hotter months, as water evaporates from the dam, the water level will drop, leaving a temporary band of damp soil around the receding water's edge. It is in such a damp band that this bryologist is searching, for it is there that you may find Riccia thalli in various stages of development. You can see the slightly darker band of damp soil in the photo. The thalli of Riccia also fold up along their long axes. Here we see Riccia lamellosa open click for photo and closed click for photo. The black scales on the underside of a closed-up Riccia limbata click for photo are even more striking. However, not all Riccia species have black scales. Riccia crinita has white hairs, as you can see in this photo click for photo. When closed, the hairs provide a protective layer. and also a means of trapping moisture.

A number of typically arid area bryophytes are individually short-lived, but persistent as a species, in a given area. In these bryophytes the gametophytes, typically small, develop quickly from spores, produce sporophytes and large spores and then die. A number of Riccia species fall into this category and examples amongst the mosses are the genera Acaulon and Ephemerum. The spores are often quite large, at times over a tenth of a millimetre in diameter, and incapable of long-distance dispersal. Such species are commonly described as annual shuttle species. Like the annual vascular plants (especially of the daisy family) that are common in dry habitats, the annual shuttle species do not tolerate drought but evade it by the production of drought-resistant sexual propagules. Because the large spores tend to move only very short distances, the annual shuttle species tend to persist in a given area for many years – not as individuals but as a species. The gametophytes of annual shuttle species tend to appear after rain in micro-habitats that are ephemeral but which tend to re-occur with some degree of regularity. An example of this is the damp soil around the forest dam shown in a photo a little earlier. At the other extreme are the perennial stayers, with far more robust gametophytes and with various adaptations to ensure long term survival as individuals. In arid areas the perennial stayers are best represented by the desiccation-resistant mosses but there are perennial liverworts as well. For example, with the genus Riccia there are perennial stayers as well as annual species. There's a more detailed description of the various strategies in the LIFE-HISTORY STRATEGIES CASE STUDY.

click to enlarge
Fossombronia levieri showing two tubers
Fossombronia is a genus of seemingly delicate thallose liverworts and a number of Fossombronia species are found in hot, dry regions. This photo click for photo shows some Fossombronia plants growing in a recently wet Australian arid area. You can see a number of black spore capsules, each atop a translucent stalk. You can also see that parts of the gametophytes are white. They are beginning to die. Here's another photo click for photo showing a large number of white, dead Fossombronia gametophytes. Rapid spore production after a rainy period is one way in which a Fossombronia can perpetuate its species in an area. Fossombronia gametophytes, as they begin to dry out also produce tubers. The accompanying photograph shows such tubers. The plant in the photograph has been removed from the soil. When it was growing, all you would have seen above the ground was the long axis of the gametophyte with its flimsy, almost leaf-like outgrowths. The ends of the axis had turned down and produced swollen tubers beneath the ground. Eventually the above-ground gametophyte would die, leaving just the tubers within the soil. These tubers stay dormant in the soil until suitable rains come again, upon which the tubers produce fresh lettuce-like gametophytes.

Up the alps and near the poles
While many people will think of deserts when the word "arid" is mentioned the alps and the polar regions can also be considered arid. In very cold areas desiccation can be as great a problem as it is in arid areas. For example, in the polar regions water is abundant in principle, but much is locked away as ice, with free water being quite scarce in many places an it is free water that living organisms need. In all such areas strong, drying winds are another form of stress. Not surprisingly, you will also find polar bryophytes adopting many of the strategies outlined above.

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Experiments have shown that many drought-tolerant bryophytes also tolerate freezing, if the freezing happens slowly. That is usually the case in natural conditions, with water slowly removed from the cells so that freezing leads to the formation of extra-cellular, rather than intra-cellular, ice crystals. Since water expands when it freezes, there is a danger that water within bryophyte cells would freeze and so burst the cells. Temperate and desert areas can experience freezing temperatures but clearly freezing is a much more common danger in very cold areas, such as polar and alpine regions.

At very high latitudes bryophytes are subject to very lengthy, even continuous light during the summer months. Experiments have shown that continuous illumination can cause some chloroplast disruption and so reduce photosynthetic activity. Continuous light is one stress that is clearly peculiar to the near-polar regions, the temperate and tropical parts of the world having distinct nights and days throughout the year.

On the subject of polar bryophytes and their adaptations, the bryologist RE Longton has noted that

None of these features, except perhaps tolerance of continuous light, can be regarded as a specific adaptation to polar conditions since all are shown by mosses growing in apparently more favourable environments ... The success of bryophytes in polar environments thus appears to derive from attributes that are widely represented among mosses (sic) in general rather than from specific adaptations to polar conditions.[18]

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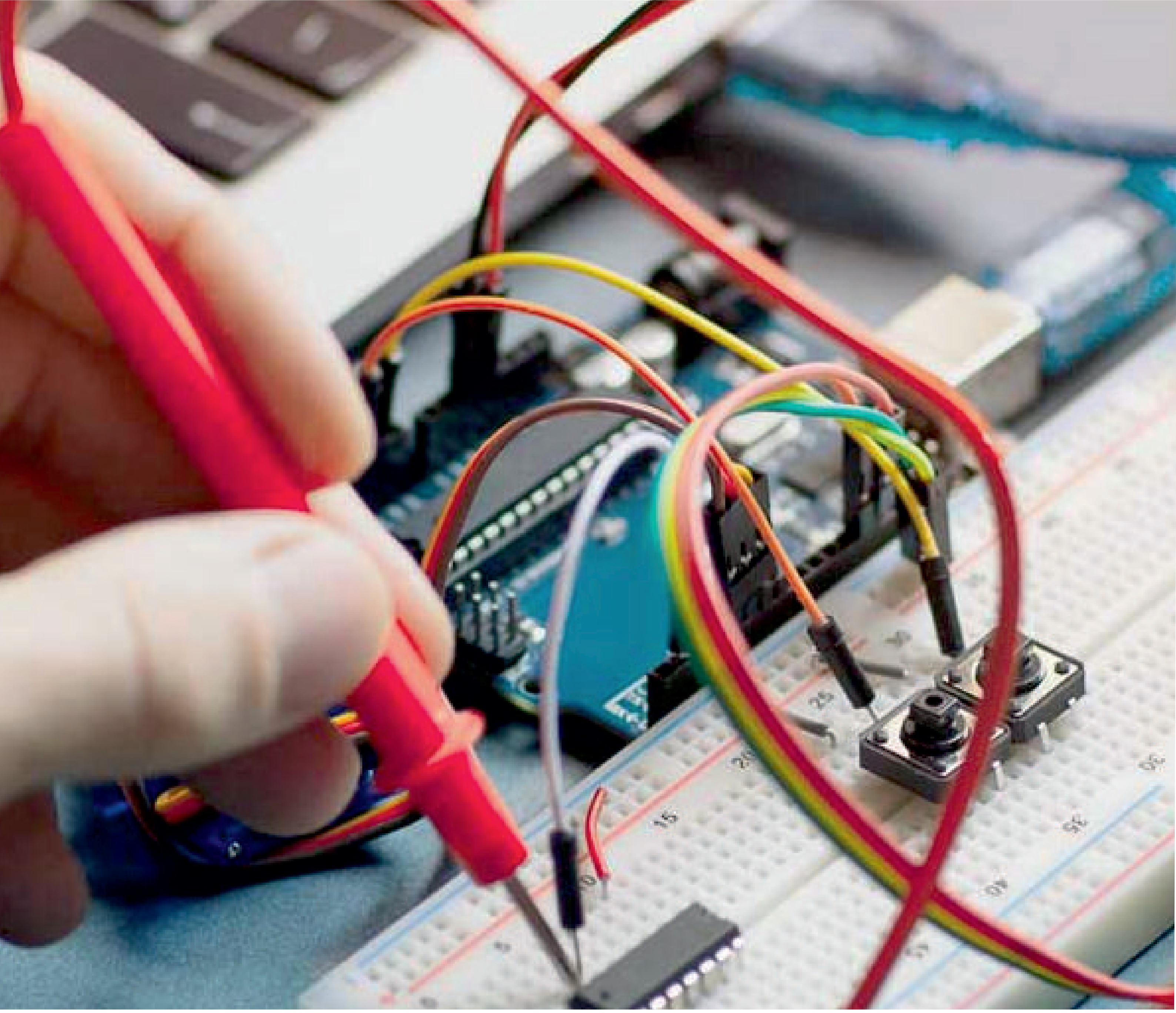

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