



## Xerophytic adaptations of bryophytes: Survival strategies against drought conditions in Indian Thar desert

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### Abstract

There is little information concerning with the bryophytes especially in relation to habitat and survival strategies in arid and semi-arid environment of Indian Thar Desert. In the present study adaptations relating to habitat, life form and leaf architecture were investigated. Cushion forms were more prevalent in the driest regions while small tufts dominating the wetter region nearby the water sources and seepage areas. The important adaptations were spiral twisting and imbrications of leaves on the stem, concave leaves, papillae, incrassate cell wall, rhizoidal and terminal gemmae etc. These adaptive characters favor the plant to survive under adverse xerophytic conditions in Indian Thar Desert.

**Keywords:** bryophytes xerophytic adaptations, Indian thar desert, drought condition, perennation, resurrection, gemmae

### Introduction

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. C<sub>4</sub> 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<sup>[1]</sup> and liverworts with about 7,500 species<sup>[2]</sup> 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 time 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 challenges, to survive the plants. Bryophytes are moist and shade loving plants and can successfully exploited many habitats. These are the non-vascular cryptogams, and play an important role in ecosystem function<sup>[3]</sup>. 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<sup>[4, 5]</sup>. 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<sup>[5]</sup>. 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.

### Materials and Methods

Plant material was collected after completion of rainy season during the period of 2017 to 2020 from different parts of Indian Thar Desert such as from various localities

of Jaisalmer, Barmer and Bikaner. The collected plant material was brought to the laboratory and preserved in Formo-Aceto- Alcohol (FAA) for study of xerophytic adaptations/characters. Photographs of different parts of plant such as leaves complete leaves, leaf apices, habitat, gemmae, rhizoids etc. were taken with help of microscopic attached Nikon FX-35A Japan camera. Xerophytic adaptive characters such as perennation, resurrection potential and desiccation tolerance were studied to find out the survival strategies of these delicate plants under adverse climatic conditions of Indian Thar Desert.

## Results and Discussion

### Perennation

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 (Fig.1 N,O). 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 gemmae 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 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.

### 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 (Fig.1.G). This remarkable property is essential because-

1. 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.

### 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 leaf 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 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 micro-habitat, especially in moist habitat such as grass tussocks, under boulder overhang, in rock crevices etc. Such micro-habitat 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 leaf 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 (Fig.1, C & D) and serves as a condensation point. In *Fissidens* (Fig.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**

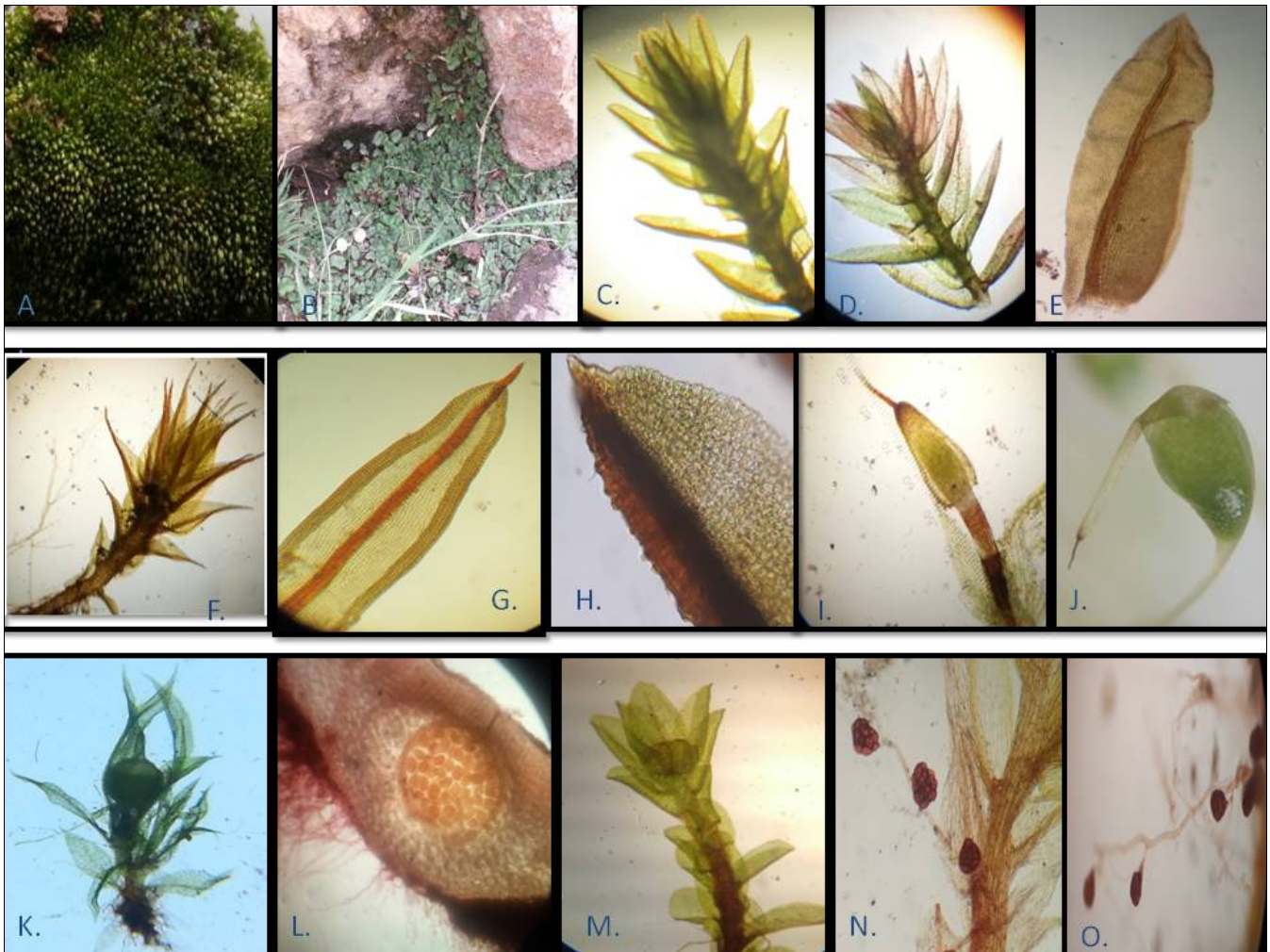
The papilosity of leaf margin and incrassate cell wall is also an important adaptive character in xerophilous species such as in *Tortula muralis* (Fig.1, G) and *Semibarbula orientalis* (Fig.1, H). Thickening and widening of costa is also a common occurrence in xerophilous mosses.

**h. Investment of dead cells**

Hyaline hair point may be formed by excurrent costa as in *Tortula muralis* (Fig.1, G) and *Bryum argenteum* (Fig.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. 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. archeogonium. 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 (Fig.1, K). The bell shaped calyptra forms a protective bonnet over the unripe urn or capsule and protects it from dryness, as in *Physcomitrium* (Fig.1, I) and *Funaria hygomitrica* (Fig.1, J). In the liverworts the sporogonium are sunken in the archeogonial cavity (*Riccia*, Fig.1, L) and hence protected from dryness.



**Fig 1:** Selected adaptive characters of some bryophytes from Indian Thar Desert. A. Cushion of *Bryum cellulare*; B. *Riccia* sps. in its natural habitat; C. & D. *Semibarbula orientalis* and *Bryum cellulare* shows concave leaf forming cuspidate tuft; E. Conduplicate leaf and vaginant lamina of *Fissidens flaccidus* forming water sac; F. Excurrent hair point in *Bryum argenteum*; G. Excurrent hair point and recurved margin in *Tortula muralis*; H. Pappilose cells on margins of *Semibarbula* leaf with incrassate cell wall; I. & J. Calyptra protecting young and mature sporophyte in *Physcomitrium japonicum* and *Funaria hygrometrica* respectively (K). Perichaetial leaves protecting the sporogonium of *Physcomitrium japonicum*; L. Sunken sporogonium in *Riccia* species; M. Terminal gemmae in *Gymnostomiella veronicosa* in axil of leaves; N. & O. rhizoidal gemmae in *Physcomitrium japonicum* and *Bryum plumosum* respectively.

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