

# Poikilohydry in mosses: an ecological limitation or opportunity?

## Introduction

The most significant evolutionary event in the history of the plant kingdom began with the migration of aquatic photosynthetic organisms on to land approximately 475 Myr ago<sup>1,2</sup>. Terrestrial embryophytes (referred to as embryophytes) derived from algal ancestors constitute two divisions, the bryophytes (lacking vascular tissue) and the tracheophytes (possessing vascular conducting tissues)<sup>2</sup>. The evolutionary transition from aquatic photoautotrophs heralded the innovation of morphological and physiological characteristics critical for success in the terrestrial habitat, and consequent diversification of land plants. It has been hypothesised that early bryophyte related groups pioneered the transition from water to life on land<sup>1,2,4</sup>. The mosses appear to be among the most ancient divisions of the land plants. Fossils of spores and gametophytes dating from the Mid Ordovician (~476 Myr) and Mid Silurian (~432 Myr) have been discovered that closely resemble some modern bryophytes<sup>4</sup>. Furthermore, the remains of fossilised spore-bearing organs and vascular tissues from the Lower Devonian (~410 Myr) reveal similarity in anatomical details to living mosses<sup>4</sup>. This paleobotanical evidence combined with phylogenetic studies suggests that groups related to extant mosses are primitive ancestors of the major taxonomic groups of terrestrial plants.

In the comparatively uniform environment of aquatic life there is much less scope for variation in abiotic factors and hence natural selection. Light availability vertically through the water column is the major limiting factor. Photosynthetic organisms surrounded by water have no requirement for specialised anatomical features for water absorption, as diffusion occurs across the whole cellular surface, nor do aquatics require adaptive measures to protect against water loss through evaporation. Furthermore, a submerged plant requires no mechanical tissues as the buoyant force of water provides the necessary support<sup>1,5</sup>. In contrast, plants entering the terrestrial environment are exposed to a greater variation in the fundamental abiotic conditions including moisture, temperature (rainforest and tundra), light and gravitation. In particular, the land environment exhibits dehydrating affects from the atmosphere and water may be continually lost through evaporation. Water and nutrients may be continuous underground, however, dependence on light requires the aboveground presence of photosynthetic tissue where water is often irregular<sup>1,5</sup>. Therefore, suitable water relations are a prerequisite to survival on land.

Embryophytes are able to tolerate the desiccating affects of the land environment and exhibit numerous morphological and physiological departures from the ancestral aquatic state. Depending on their ability to compensate for fluctuations in water supply and rate of evaporation, embryophytes may be classified as poikilohydric or homoiohydric<sup>5</sup>.

## Poikilohydry as a limitation

Mosses represent the oldest living remnants of initial land colonisation. It can be viewed the mosses represent a primitive condition of plant development<sup>4</sup>. Mosses can be said to represent an evolutionary intermediate between algal ancestors and the vascular plants, manifested in features that may be more in common with aquatic algae or lichens and are said not to be fully 'terrestrialised' or having a greater reliance on water<sup>4,5,7,8</sup>. However, moss gametophytes do exhibit innovations such as tissue differentiation (leaves, rhizoids) and primitive vascularisation<sup>3</sup>.

It is in the gametophyte form of mosses where the potential for land development in some ecological scenarios may be limited. The gametophyte does not possess a true root and vascular system (xylem or phloem) or outer cuticle, having no control over loss which can be rapid, and internal water content is in equilibrium with that of the atmosphere<sup>3,5</sup>. This condition is said to be poikilohydric. Due to this intimate coupling with environmental moisture, mosses may dehydrate completely in dry air (i.e. no barrier to

water loss represented by the cuticle in higher plants)<sup>3</sup>. Although many moss species can withstand desiccation by dormancy, this comes at an expense of suspending growth and metabolism. They are dependent on availability of free water and mineral salts at the land surface as they do not possess true roots, with rhizoids present for anchorage on the substratum<sup>3</sup>. As the root system is deficient, mosses depend largely upon the direct absorption of water through the leaves. Owing to the failure of the gametophyte to produce true vascular tissue with support structures they are unable to attain large dimensions or growth above ground exhibited in higher plants<sup>3,5</sup>.

Sexual reproduction is facilitated by water (as in algae) via motile male gametes. Only when mosses are covered water can the reproductive organs open and permit the sperm to escape and penetrate the open neck of the archegonium, and thus reach the egg cell. In this regard mosses are essentially amphibious in nature, i.e. they require uninterrupted access to water for reproductive success<sup>3,8</sup>. As a result mosses may typically be found 'hugging' wet soil, or living in permanently moist habitats, avoiding exposure to turbulent drier air found above the land surface<sup>3,8</sup>.

Mosses are also set apart from vascular plants on the basis that the non-sexual sporophyte is permanently associated with the gametophyte and never establishes on the substrate. Within higher plants it is recognised that dominance in the land environment is derived from sporophyte of basal archegoniate lineages<sup>2,8</sup>. It is evident that in the evolution of the sporophyte, the most significant fact is the progressive reduction of the spore product and increasing dominance of the sporophyte generation in the plants life-cycle, compared with the gametophyte<sup>2</sup>. In liverworts the life-cycle of the sporophyte is brief, its exclusive function being in spore production. In mosses the growth period of the sporophyte is greatly prolonged and spore production becomes less important. This trend towards increasing subordination of the gametophyte and increasing importance of the sporophyte in mosses may be manifested in tissue differentiation found in the sporophyte<sup>2</sup>. It is evident that the sporophyte of mosses possesses vascular tissue with photosynthetic cells<sup>3</sup>. Although the sporophyte is able to prolong growth on account of the production of green tissue, it is still dependent on the gametophyte for water. In higher plants, by the development of the root to acquire water from subterranean sources, the sporophyte becomes truly independent<sup>4</sup>.

In contrast to the level of developmental complexity present in mosses, it can be argued that homiohydric characters exhibited in the tracheophytes; a lignified vascular system of xylem and phloem, an impermeable cuticle surrounding vegetative tissues, stomata and seed in higher tracheophytes are a higher state of plant organisation and the ultimate solution to the problem of adaptation to life on land, providing greater independence from water<sup>5</sup>. The properties of vascular tissue allow the formation of a transport system conducting water and photosynthate around the multicellular body, thus allowing the development of large complex bodies of roots and leaves<sup>7</sup>. Additionally, lignified vascular tissue provides a means of mechanical support in large tracheophytes allowing for the erect habit, in contrast to the dorsiventrally flattened posture in mosses<sup>7</sup>. With an extensive root network, the homiohydric system allows the maintenance of activity despite sudden changes in humidity as roots penetrate readily available subterranean sources of water i.e. greater period of growth than mosses<sup>7</sup>. The waterproof cuticle provides a means of reducing water loss through evaporation and also a barrier to gaseous diffusion. The stomata perforating the cuticles provide avenues for gas exchange, however, also presenting a sight of water loss. The guard cells limit the rate at which water is lost through stomatal openings via transpiration<sup>7</sup>. These adaptations exert greater control over water economy and are thus seen to be more effective and dependable than the bryophytic strategy.

The tendency in tracheophytes has been to develop reproductive strategies which did not depend on the existence of standing water (e.g., pollen, seeds, flowers). Instead of developing swimming sperm, male

gametes are carried in pollen grains from microsporangia with pollination achieved via entrainment into wind or through insects. The development of the seed habit has facilitated the adjustment of plants to strictly terrestrial conditions, with the angiosperms reaching the most perfect expression of the plant organism. Seeds are specialised to resist adverse conditions and can remain dormant until conditions are suitable for germination. Furthermore, the seed may be modified to facilitate dispersal from the parent gametophyte. Thus tracheophytes have become sufficiently productive to form closed cover over large areas, and is ultimately manifested in the enormous global coverage of phytomass.

### Poikilohydry as an opportunity

Without a doubt, vascular plants are adaptive optimums within habitats characterised by adequate soil water. However, the homoiohydric system has success within certain limits defined by temperature and the availability of water<sup>5,7</sup>. Mosses are the successors of ecological niches characterised by intermittent water availability due to their ability suspend metabolism during periods of drought (escaping the need for metabolic function) and resume activity rapidly with available water<sup>3,5,6</sup>. This feature is known as desiccation tolerance (DT) and is common to various functionally dissimilar species. For poikilohydrous organisms in general, and bryophytes in particular, DT can be argued to be an optimal adaptation to habitats characterised by extreme fluctuations in water availability (i.e. functionally specialised stress-tolerators)<sup>3,5</sup>. The pervasiveness of mosses in dry habitats provides an alternative perspective on mosses in contrast to the tone already set in this paper.

As mosses rapidly equilibrate internal moisture with that of the environment, mechanisms allowing tolerance of dry periods is essential<sup>6</sup>. DT is characteristic of a variety of moss gametophytes, and is common of both xeric and mesic habitats<sup>3</sup>. DT mosses may colonise rocky, thin soil (drought prone) substrates impenetrable to roots and the bark of trees<sup>5</sup>. DT is an obvious adaptive advantage in habitats characterised dry, sun-exposed rock surfaces with intermittent rain. Even in wet climates, moisture is not available continuously. For example, hard substrates dry quickly after rain stops, therefore, DT mosses would possess fitness in this niche<sup>5</sup>. In this situation it would be an advantage to be small in size<sup>1</sup>. Growth and reproduction occur only during these wet seasons, but upon drying the gametophyte can suspend metabolism for considerable time periods<sup>7</sup>. Desiccation tolerance is well documented in mosses. *Tortula ruralis* can be reduced to 20% of its original weight in 2 hours and even after prolonged periods (10 months) of desiccation resumes metabolic activity within minutes of receiving an adequate water supply<sup>7</sup>. *Andreadea rothii* is characteristic of hard acidic mountain rocks, and can recommence normal metabolism after 12 months desiccation at 32% rh and 20°C<sup>5</sup>. Recovery takes place quickly, and depends on the conservation of cellular components through the drying-re-wetting cycle<sup>5</sup>. Chlorophyll-fluorescence measurements show that photosystem recovery after re-hydration is rapid<sup>9</sup>. The recovery of respiration after prolonged desiccation similarly shows recovery in mosses<sup>5</sup>. It has been suggested that recovery after desiccation involves the reestablishment of membrane integrity and photosystems<sup>10</sup>.

At the scale of a moss gametophyte colony, surface tension is determines the distribution of water around the vegetative tissue<sup>5</sup>. Therefore, shoots and leaves tend to lie dorsiventrally flattened on the laminar atmospheric boundary<sup>5</sup>. The LAI of the moss leaf canopies tends to be greater than that of vascular plants and is comparable in some species (*Scleropodium* spp.) to the mesophyll/leaf-area quotients of vascular plants indicating scale as important determinants of morphology<sup>5</sup>. Additionally, it can be noted that mosses and vascular plants have similar rates of photosynthesis on a per-chlorophyll basis<sup>5</sup>. The physical structure of many mosses allows the short term storage of external capillary water<sup>3</sup>. The hydroid conducting cells of some large mosses (e.g. Polytrichaceae, Dawsoniaceae) may be an evolutionary

parallel to the xylem tissue of vascular plants in that both represent a low resistance pathway for water transport<sup>3,5</sup>. However, typically water movement is extracellular involving intricate conducting structures. The ability of bryophytes to survive desiccation is attributed to conservation of polyribosomes during desiccation period<sup>3,6</sup>. In *Tortula* after 90 minutes in a dry atmosphere, a decline in fresh weight by 20% was observed<sup>6</sup>. However, it retained distinct polyribosome pools which increased with increasing hydration time<sup>3</sup>. This is in contrast to vascular plants where extreme water stress induces an irreversible degradation in polyribosome activity. In addition there is evidence to suggest that the activity of antioxidant enzymes is a response in mosses and other DT organisms to oxidative stress induced by desiccation<sup>11</sup>. Oxidative damage has been shown to be less in DT organisms such as *Tortula* than desiccation sensitive vascular plants<sup>12</sup>.

In mosses there exists species specific differences in relation to their desiccation tolerance<sup>3</sup>. It has been observed that mosses characteristic of exposed habitats such as *Tortula ruralis* can recover rapidly after desiccation<sup>5</sup>. This may be an adaptation to maximise growth during a water regime that is transient. This is in contrast to forest-floor dwellers such as *Rhytidiadelphus loreus* where recovery of photosynthesis following drying takes several hours more<sup>5</sup>.

There exists approximately 14000 species of moss exhibiting world-wide distribution and are able to grow luxuriantly in the humid climate of temperate and tropical regions.<sup>3</sup> Fundamentally, mosses are able to persist in extreme conditions of arctic and alpine regions and can tolerate semi-arid conditions. Largely associated with their remarkable regeneration capacity, mosses exhibit great diversity in the ecological conditions in which they can pervade, proving in particular habitats to be the adaptively optimum plant organism.