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REVIEW ARTICLE

Desiccation Tolerance in Bryophytes: Evolutionary Origins, Poikilohydric Adaptation and Cellular Mechanisms

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Abstract: Desiccation tolerance represents a fundamental adaptive strategy that enables Bryophytes to withstand fluctuations in water availability. Liverworts, mosses and hornworts predominantly exhibit poikilohydric water relations, whereby tissue hydration closely follows ambient environmental conditions. The present review synthesises the structural, physiological and cellular mechanisms associated with desiccation tolerance in Bryophytes and examines their evolutionary significance in the transition from aquatic to terrestrial environments. During dehydration, Bryophytes undergo progressive metabolic downregulation and cellular reorganisation, while structural characteristics such as cell wall elasticity and tissue water-retention properties help minimise mechanical injury. At the cellular level, protection involves maintenance of membrane integrity, accumulation of protective proteins and compatible solutes, dissipation of excess excitation energy, and activation of antioxidant mechanisms that limit photo-oxidative and cellular damage. The persistence of these mechanisms provides an ecologically effective strategy for survival under fluctuating and extreme moisture regimes. From an evolutionary perspective, desiccation tolerance may have provided an important alternative to complete internal water regulation during early terrestrialisation by enabling early land plants to survive periods of atmospheric water loss while retaining the capacity for rapid recovery following rehydration. Thus, Bryophytes provide valuable systems for understanding the integration of structural, physiological and cellular adaptations that underpin plant resilience to dehydration and illuminate key innovations associated with the evolution of life on land.

Keywords: Bryophytes; desiccation tolerance; poikilohydry; dehydration stress; rehydration; cellular protection; terrestrialisation

Introduction

Bryophytes — the mosses, liverworts, and hornworts — comprise the second-largest photoautotroph group on Earth and have been shaping terrestrial ecosystems since the late Cambrian era through a distinctive suite of anatomical, physiological, and morphological traits (Slate *et al.*, 2024; Stanton & Coe, 2021). Despite their small physical apperance, they have large control over planetary biogeochemistry: they fix substantial amounts of carbon, contribute to nitrogen cycles across forests, tundra, peatlands, and deserts, and act as effective traps for water and nutrients owing to uptake over their entire body

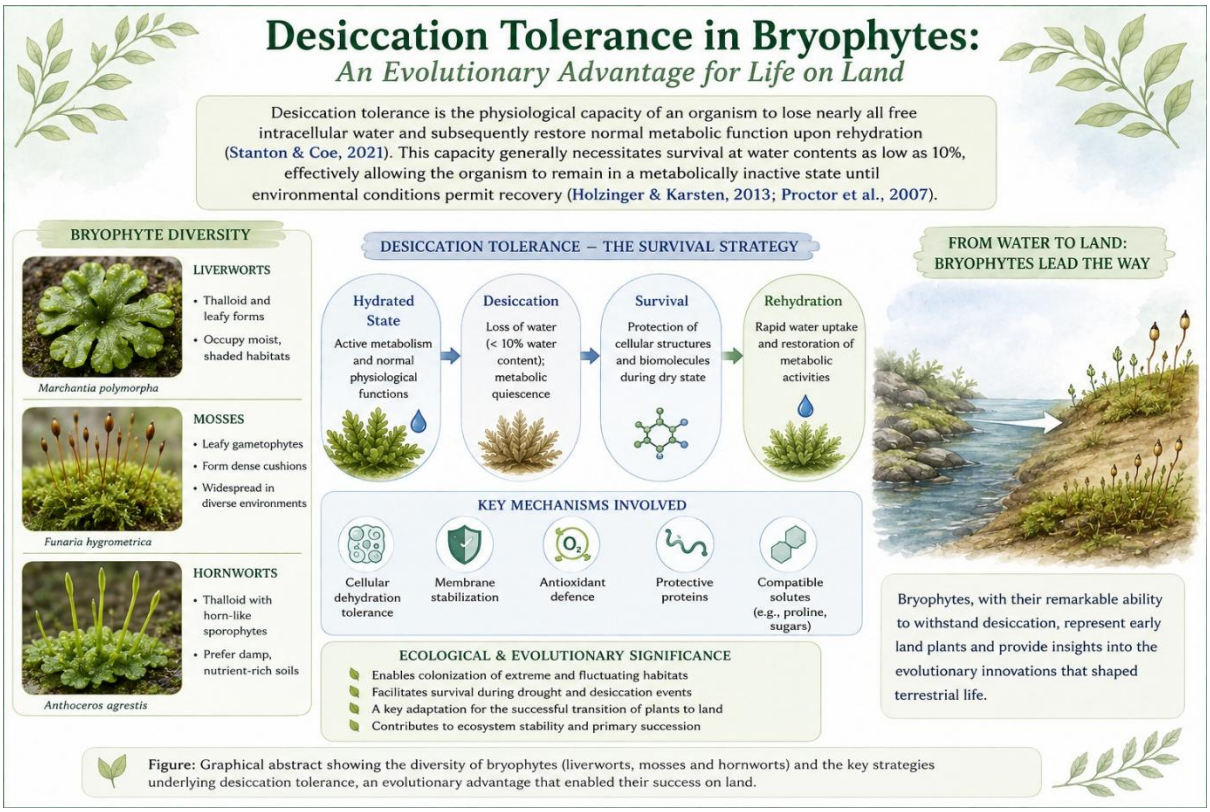

Figure: Graphical abstract showing the diversity of bryophytes (liverworts, mosses and hornworts) and the key strategies underlying desiccation tolerance, an evolutionary advantage that enabled their success on land.

surface *(Slate et al.,* 2024; Turetsky, 2003). Their ability to retain and control water, in particular, positions them as key regulators of ecosystem hydrology and as potential buffers against the hydrological consequences of climate change (Abay & Gül, 2025; Slate *et al.*, 2024). The conquest of land presented early plants with a fundamental physiological dilemma: the irregular supply of water in terrestrial environments. Vascular plants resolved this challenge principally through internal transport from soil to canopy — the homoiohydric strategy, in which shoot water status is buffered from soil moisture deficits (Proctor & Tuba, 2002). Bryophytes pursued the alternative, scale-dependent strategy: poikilohydry, in which the leafy shoot equilibrates rapidly with the water potential of its surroundings and therefore exists in one of only two states — fully hydrated and metabolically active, or desiccated and metabolically inactive (Proctor *et al*., 2007; Proctor & Tuba, 2002). Survival in the desiccated state depends on desiccation tolerance, defined as the ability to lose virtually all free intracellular water and still recover normal function upon rehydration — arguably the most remarkable physiological feature of the Bryophytes (Proctor *et al*., 2007).Desiccation tolerance is a striking but far from universal trait. Of the estimated 21,000 bryophyte species, only about 210 — roughly 1.0% — have been experimentally confirmed to possess vegetative desiccation tolerance, comprising 158 mosses, 51 liverworts, and a single hornwort (Wood, 2007). Tolerant forms nonetheless occur from tropical to polar regions, and some mosses and lichens can dry out and recover within an hour or less, far outpacing the one-to-few-day response times of tolerant vascular plants (Proctor & Tuba, 2002). Ecologically, DT allows Bryophytes to occupy substrates largely unavailable to tracheophytes — rock surfaces, dense or vertical bark, and shallow, drought-prone soils — and to capitalize on brief wet periods through rapid resumption of physiological function (Abay & Gül, 2025; Stanton & Coe, 2021). Evolutionarily, DT in Bryophytes is widely regarded as a primitive character of land plants: a reflection of the strategy that accompanied the invasion of terrestrial habitats, subsequently lost during the evolution of the homoiohydric vascular-plant shoot system but retained in spores, pollen, and seeds and re-evolved in the vegetative tissues of vascular "resurrection plants" (Oliver, 2005; Proctor *et al*., 2007). Across the plant kingdom, vegetative DT

has evolved independently at least twelve times, and the mechanisms observed in modern Bryophytes appear to have changed remarkably little from their earliest manifestations (Oliver, 1996, 2005). Understanding this ancient trait therefore offers insight into one of the pivotal transitions in the history of life — the terrestrialization of plants, which selected for morphological, physiological, and molecular innovations permitting survival under limited water and extreme temperatures (Ghosh *et al*., 2026).

At the mechanistic level, nearly five decades of research have established a two-part framework combining constitutive cellular protection with an inducible recovery-and-repair program activated upon rehydration (Oliver, 2005). Constitutive protection involves late embryogenesis abundant proteins, high contents of non-reducing sugars, and effective antioxidant and photoprotection systems that control oxidative damage during drying, while repair following rehydration is coordinated at the level of mRNA sequestration and translational control (Oliver, 2005; Pizarro *et al.,* 2019; Proctor *et al.,* 2007). Recovery of respiration, photosynthesis, and protein synthesis occurs within minutes to hours, whereas restoration of the cell cycle and cytoskeleton may require 24 hours or more (Proctor *et al.*, 2007). Yet major gaps persist: a synthesis of 337 desiccation–rehydration studies covering 351 species found surprisingly low convergence among experimental protocols, with 40% of the 52 bryophyte orders never studied, underscoring the need for standardized methods and expanded taxonomic and geographic coverage (Sánchez *et al*., 2022). Ecological studies echo this concern, emphasizing that outcomes depend critically on the rate of drying, water content at equilibration, duration dry, and rate of rehydration — factors still frequently conflated (Stark, 2017).

The relevance of this field has never been greater. Global climate change is intensifying drought, shifting rainfall distributions, and driving desertification of once-moist regions, subjecting Bryophytes — and the ecosystems they stabilize — to unprecedented stress (Marschall, 2017; Slate *et al.*, 2024). At the same time, the haploid, desiccation-tolerant tissues of mosses offer rare opportunities for functional gene analysis via homologous recombination, with obvious biotechnological potential for engineering stress tolerance in crops (Fernandez *et al.*, 2006). This review synthesizes current knowledge of desiccation tolerance in Bryophytes across three domains: it first establishes the conceptual foundations of the poikilohydric strategy that makes DT necessary; it then traces the evolutionary origins of the trait, from early terrestrialization to its phylogenetic conservation across modern lineages; and finally, it details the cellular protection mechanisms — from protective molecules and antioxidant systems to gene-expression and repair programs — that together constitute the bryophyte desiccation tolerance syndrome. A comprehensive literature search was conducted using major scientific databases, including Web of Science, Scopus, PubMed, Google Scholar and ScienceDirect. The search covered publications available up to 2026.

Poikilohydric Strategy

Desiccation tolerance is defined as the physiological capacity of an organism to lose nearly all free intracellular water and subsequently restore normal metabolic function upon rehydration (Stanton & Coe, 2021). This capacity generally necessitates survival at water contents as low as 10%, effectively allowing the organism to remain in a metabolically inactive state until environmental conditions permit recovery (Holzinger & Karsten, 2013; Proctor *et al*., 2007). This trait fundamentally distinguishes Bryophytes from tracheophytes, as the former exhibit a poikilohydric water strategy characterized by the direct equilibration of tissue water potential with the surrounding environment (Mishler & Oliver, 2009). In contrast, homoiohydric plants utilize complex internal regulatory mechanisms to maintain relatively constant water status despite external fluctuations, a strategy that often precludes the levels of dehydration tolerance found in Bryophytes (Oliver *et al*., 2004). While vascular plants rely on an endohydric, xylem-based system to restrict transpiratory water loss (Raven, 2002), Bryophytes typically employ poikilohydry, which allows for rapid recovery through external capillary conduction (Liepiņa & Ievinsh, 2013). This strategy confers a scale-dependent advantage by enabling rapid tissue equilibration, thereby avoiding prolonged

metabolic activity under limiting water potentials that would be lethal to more complex, drought-stressed vascular organisms (Marschall, 2017).The poikilohydric strategy is defined by the absence of significant homeostatic control over internal hydration status, forcing internal water potential to track ambient humidity levels closely. Although this reliance on ambient equilibrium is often considered passive, recent investigations indicate that structural traits such as high capacitance and cell wall properties can provide a degree of active regulation over transpiratory water loss. This physiological flexibility allows Bryophytes to modulate their rate of drying, which is critical for the activation of protective mechanisms before reaching lethal dehydration thresholds (Perera-Castro *et al*., 2025). In this state, the plant shifts from an active metabolic regime to a desiccated, quiescent phase, effectively entering a protective dormancy that minimizes cumulative cellular damage during prolonged drought (Mundree *et al.,* 2002). During this transition, metabolic processes such as photosynthesis decline rapidly with moisture loss, yet the structural integrity of the cellular apparatus is preserved to ensure a swift physiological reactivation upon subsequent rehydration. This recovery trajectory is mediated by the intensity and duration of the desiccation event, often influenced by drought-hardening processes that occur during the initial stages of water loss (Proctor, 1990). Across liverworts, mosses, and hornworts, these protective adjustments help preserve fundamental cellular components through repeated cycles of drying and rewetting, thereby preventing irreparable damage to vital physiological functions (Oliver, 2005). These responses facilitate controlled anhydrobiosis, enabling these non-vascular plants to partition water storage from vital processes like gene expression and protein assembly (Pointing *et al*., 2015). Specifically, cell wall elasticity serves as a primary mechanical determinant of this resilience, as it allows tissues to accommodate the physical strains of dehydration and rehydration independently of bulk cell wall thickness. This capacity is phylogenetically widespread, with documented evidence of vegetative desiccation tolerance across the mosses, liverworts, and hornworts (Wood, 2007). Recent experimental evidence suggests that species residing in hyper-arid habitats, such as specific hummock-forming mosses, exhibit enhanced recovery rates during rehydration, indicating that these lineages have evolved mechanisms to optimize the energetic costs associated with repairing damage incurred during prolonged metabolic quiescence (Hájek & Beckett, 2007).

Evolutionary Origins

Desiccation tolerance is widely hypothesized to be an ancestral trait of early land plants, essential for surviving the transient aquatic-to-terrestrial transitions of the Paleozoic era. This physiological capacity, largely maintained in the diaspores of most Bryophytes, likely persists as a foundational module that predates the diversification of vascular lineages (Marks *et al.*, 2026). The widespread retention of desiccation tolerance in the spores and other reproductive structures of liverworts, hornworts, and mosses suggests that its underlying genetic architecture has remained conserved, despite the trait's frequent secondary loss from vegetative tissues in tracheophytes (Proctor *et al*., 2007). Within Bryophytes, this evolutionary continuity is reflected in the modular recruitment of spore-specific protective mechanisms for the vegetative body, a process that has occurred repeatedly across the three lineages (Oliver *et a*l., 2020). This convergent evolutionary trend is evidenced by the discovery of shared biochemical and regulatory signatures between vegetative and reproductive desiccation-tolerant tissues (Artur & Kajala, 2021). Such phylogenetic convergence indicates that while desiccation tolerance represents a primitive, basal trait, its repeated deployment in Bryophyte gametophytes suggests a sophisticated evolutionary exaptation of ancestral regulatory pathways to accommodate varying ecological pressures (Pizarro *et al.,* 2019; Wang *et al.,* 2022). By retaining the capacity for vegetative anhydrobiosis, these Bryophyte lineages effectively bridge the mechanistic gap between the latent desiccation tolerance of ancestral spores and the specialized drought-avoidance strategies characterized by complex vascular systems (Bowles, 2021; López-Pozo *et al.,* 2018). Consequently, Bryophytes serve as essential models for understanding how the primordial toolkit for desiccation tolerance was refined to support vegetative survival in diverse, fluctuating habitats (Oliver & Goffinet, 2010). Given the complex,

multigenic nature of these traits, the emergence of vegetative desiccation tolerance likely arises from the co-option and differential regulation of conserved gene expression pathways, rather than the acquisition of entirely novel molecular innovations (Marks *et al*., 2019).

Early Terrestrialization

The successful colonization of land was predicated on the evolution of morphological innovations that mitigated the dual pressures of water limitation and atmospheric temperature extremes (Renzaglia *et al.,* 2000).Desiccation tolerance therefore provided an alternative to the evolution of complete internal water regulation during terrestrialization: by preserving cellular membranes, photosynthetic machinery, and other essential components during near-total dehydration, early land plants could survive periods when atmospheric water loss exceeded external water supply and rapidly resume metabolism after rewetting (Oliver, 2005; Oliver & Goffinet, 2010). This strategy was especially compatible with the small, low-growing bodies of Bryophyte-like plants, which could absorb water across their surfaces and exploit humid boundary layers near soil, rock, or bark, while entering a metabolically quiescent state when those sources disappeared (Proctor & Tuba, 2002; Renzaglia *et al.,* 2000). The persistence of comparable protective mechanisms in spores and vegetative tissues further supports the view that vegetative tolerance was recruited from an ancestral reproductive program, allowing early gametophytes to withstand fluctuating hydration during establishment and dispersal (Oliver, 2005; Proctor *et al.*, 2007). By contrast, the later evolution of cuticles, vascular water-conducting systems, and homoiohydric regulation reduced reliance on vegetative desiccation tolerance in vascular plants, indicating that Bryophytes retained an ancestral but ecologically effective route to life on land (Holzinger & Karsten, 2013; Oliver et al., 2020). Furthermore, genetic research indicates that these lineages have evolved through a combination of reductive genome evolution and the proliferation of accessory gene families, which support the modular deployment of stress-responsive pathways in vegetative tissues (Harris *et al*., 2022).

Phylogenetic Conservation

The conservation of these protective mechanisms is punctuated by significant instances of lineage-specific loss, particularly within the evolutionary transition toward complex tracheophyte morphologies.In contrast to non-vascular Bryophytes, vascular lineages evolved sophisticated water-conducting systems and transpiration-regulatory mechanisms that reduced the need for constitutive vegetative desiccation tolerance (Proctor *et al*., 2007). This transition resulted in the widespread replacement of constitutive desiccation tolerance with inducible mechanisms, or its eventual loss entirely within the lineages leading to modern gymnosperms and angiosperms (Gechev *et al*., 2021). However, the intermittent reappearance of this trait in select "resurrection plants" across diverse angiosperm families and fern lineages suggests that the ancestral genetic circuitry remains dormant rather than entirely eliminated, capable of being redeployed under specific selection pressures *(Xue et al.,* 2022). This genetic potential is further underscored by the role of conserved transcription factors, such as the ABI3/VP1 family, which originally facilitated seed maturation and now coordinate systemic desiccation responses in both Bryophyte gametophytes and select vascular species (Zhang *et al.*, 2020).

Cellular Protection Mechanisms

The survival of Bryophytes during extreme dehydration is facilitated by the strategic deposition of cell wall components, such as hemicelluloses and specialized proteins, which prevent irreversible mechanical collapse and plasma membrane rupture as turgor pressure declines. These structural modifications, alongside the accumulation of Early Light-Induced Proteins, serve to dissipate excess excitation energy, thereby preventing photo-oxidative damage to the photosynthetic apparatus as cellular water content drops (Mitra *et al*., 2013; Xiao *et al.*, 2025). Simultaneously, the accumulation of compatible solutes, particularly sucrose and raffinose, facilitates the formation of a biological glass phase that stabilizes cellular architecture and preserves the structural integrity of membrane-bound organelles by replacing

water molecules via hydrogen bonding (Challabathula & Bartels, 2013; Tripathi *et al.,* 2013). These solutes work in concert with Late Embryogenesis Abundant proteins and dehydrins, which shield vital enzymes and structural proteins from denaturation through molecular crowding (Mitra *et al*., 2013; Rascio & Rocca, 2005). Furthermore, these biochemical safeguards are complemented by the induction of reactive oxygen species scavenging systems that minimize oxidative degradation during the metabolic arrest associated with the dry state (Bechtold, 2018; Gechev *et al*., 2012). Specifically, the accumulation of non-reducing sugars serves to maintain membrane fluidity and prevent the formation of gel-phase lipids that typically occur during membrane desiccation (Kuroki *et al.*, 2019). Beyond these solute-mediated effects, the synthesis of poly-unsaturated phospholipids further enhances membrane plasticity, effectively mitigating the structural constraints of cell wall stiffening during severe water deficit (Griffiths *et al.*, 2014). Complementary to these membrane-stabilizing efforts, the accumulation of non-reducing sugars like trehalose serves as a vital safeguard by interacting with the amorphous glassy structure of the cytoplasm to shield proteins from irreversible denaturation *(Michalak et al.*, 2026). This stabilization process is critical for maintaining membrane integrity during slow drying, as it prevents the transition to a rigid, leakage-prone gel phase by keeping dehydrating membranes apart and limiting damaging fusion events (Koster *et al.,* 2010). In desiccation-tolerant mosses, membrane organization can remain sufficiently preserved to support the rapid restoration of osmotic function after rehydration, while membrane reservoirs formed from endoplasmic-reticulum vesicles accommodate changes in surface area during drying and rewetting (Singh *et al.,* 1984). Concurrent protection of chloroplast membranes and photosynthetic components, together with antioxidant activity, limits photo-oxidative and lipid-peroxidation damage, allowing photosynthesis to resume rapidly once water becomes available (Dhindsa & MATOWE, 1981; Oliver, 2005). These compatible solutes significantly lower the cellular water potential, thereby promoting water retention and maintaining turgor pressure during the initial phases of osmotic stress (Takahashi *et a*l., 2020). Moreover, by accumulating these organic osmolytes, cells can achieve osmotic balance without disrupting the native structure or function of intracellular macromolecules, because the solutes replace water at macromolecular surfaces while preserving protein conformation and enzymatic activity (Takahashi *et al*., 2020; Tripathi *et al.*, 2013). Their additional role as osmotic spacers limits the close apposition and fusion of dehydrating membranes, thereby reducing solute leakage and supporting the maintenance of cellular compartmentalization during prolonged water loss (Koster *et al.*, 2010).

Conclusion

Understanding dessication mechanism is essential for understanding Bryophyte evolution and their potential role in responding to future climate change. Future investigations should prioritize the integration of multi-omics approaches to elucidate the regulatory networks governing the transition between active metabolism and the quiescent, glass-like state. Elucidating the role of intrinsically disordered proteins and biomolecular condensates in this transition will be essential for understanding how these plants maintain spatial organization in the absence of a fluid solvent (Romero-Pérez *et al*., 2023; Rosete-Enríquez *et al.,* 2025). Furthermore, cross-species comparative analyses could reveal whether these molecular mechanisms represent convergent adaptations or the redeployment of ancestral pathways inherent to all land plants (Marks *et al*., 2025). By deciphering these conserved molecular blueprints, researchers may ultimately identify the specific genetic switches required to engineer enhanced drought resilience in commercially significant crop species (Hand *et al.*, 2011). Ultimately, such breakthroughs necessitate a synthesis of evolutionary developmental biology and metabolic engineering to transition these ancient, robust survival strategies into stable, high-yielding agricultural systems (Vicré *et al.,* 2004). Bridging these ecological adaptations with crop physiology could help mitigate yield volatility induced by climate-driven shifts in precipitation, although successful translation will require distinguishing broadly conserved protective mechanisms from traits dependent on Bryophyte-specific poikilohydry and small-body architecture (Proctor et al., 2007). Future studies should therefore evaluate candidate genes and metabolites under standardized dehydration–rehydration regimes that account for drying rate, tissue

water content, duration of the dry state, and rehydration conditions (Stark, 2017). Such validation could clarify whether Bryophyte-derived regulators can enhance water retention and protect photosynthetic function without imposing unacceptable growth or resource-allocation costs in crops (Xiao *et al.*, 2025).

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