Commentary

Resurrection plants revisited: bridging the gap between bryophytes and angiosperms to decode desiccation tolerance

Desiccation tolerance is widespread on the phylogeny, but rare in seed plants, found only in select species that occur in the most water-limited environments (Marks *et al.*, 2021). Desiccation tolerance is thought to have evolved over 500 million years ago and likely played a critical role in enabling the transition of early land plants from aquatic to terrestrial environments (Oliver *et al.*, 2000). As land plants diversified to colonize the earth's surface, they evolved numerous alternative adaptations to cope with water scarcity, such as vasculature, roots, stomata, and seeds. In parallel, some lineages lost their ability to tolerate desiccation as they adopted drought escape and avoidance strategies instead. However, desiccation tolerance re-evolved in a select subset of seed plants, likely through the rewiring of pathways maintained in seeds (Costa *et al.*, 2017; VanBuren, 2017; VanBuren *et al.*, 2017). Although most vascular plants lost desiccation tolerance in their vegetative tissues as they adapted to more mesic environments, most bryophytes retained vegetative desiccation tolerance throughout time. Thus, bryophytes serve as important landmarks for studying the origin, conservation, and divergence of desiccation tolerance mechanisms. In a paper by Zhang *et al.* (2024; doi: 10.1111/nph.19620), recently published in *New Phytologist*, the authors leveraged the tractable bryophyte model, *Syntrichia ruralis*, to identify a deeply conserved regulator of water stress tolerance in plants. Their work sheds light on fundamental biological processes underlying desiccation tolerance and highlights the utility of bryophytes, not just as evolutionary models, but as important reference points for the discovery of deeply conserved genetic networks for the fundamental biology of life.

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But what exactly is desiccation tolerance? Desiccation tolerance, or anhydrobiosis, is the ability to maintain life without water, and it represents one of the most remarkable adaptations to water scarcity observed in nature. Decades ago, Derek Bewley defined desiccation tolerance in a biological context, as the ability to revive from equilibration with the water potential of the air, which is predominantly low (Bewley, 1979; Oliver *et al.*, 2020). In practice, this equates to the ability to survive equilibration to 50% relative humidity or *c.* −100 MPa and generally corresponds to the point where the monolayer of water molecules around cellular organelles breaks down (Alpert & Oliver, 2002; Oliver *et al.*, 2020). However, there are many subtle nuances and complex variations under this broad definition. For example, we know that desiccation-tolerant grasses and other angiosperms can survive drying to −250 MPa, but experience damage at water potentials below this. Most bryophytes, on the other hand, can survive much lower water potentials, up to −600 MPa, without incurring damage. A revision of the definition of desiccation tolerance that accounts for these types of variability is sorely needed, but we'll save that discussion for another day. For now, I simply want to make the point that bryophytes are as, if not more, tolerant of drying than seed plants.

The poetic, albeit scientifically inaccurate, term 'resurrection plant' is frequently used to describe plants with desiccation-tolerant vegetative tissues. The term draws attention to these plant's dramatic ability to recover from what looks like death after long periods of drought. Historically, this terminology was reserved exclusively for vascular plants (Gaff, 1971, 1977; Rascio & Rocca, 2005; Griffiths *et al.*, 2014). However, many, if not most, bryophytes are just as desiccation-tolerant as vascular plants and exhibit similar 'resurrection' abilities (Wood, 2007; Stark, 2017; Marks *et al.*, 2021). Why then, are bryophytes not included in 'resurrection plants'? Surely, we can all agree that bryophytes are plants, and we can observe that many bryophytes are desiccation-tolerant, so shouldn't they too be considered 'resurrection plants'? I would argue that the exclusion of bryophytes from the terminology of 'resurrection plants' stems from deeply held biases that discount the complexity and value of bryophytes broadly. There are, in fact, many examples of this bias woven into the language and literature on bryophytes. For example, bryophytes are often referred to as 'basal', 'primitive', or 'lower' plants, while angiosperms are called 'higher' plants. Of course, these biases are likely multidirectional and communities working within any taxonomic group tend to focus on and promote their organism of choice. Sadly, this dynamic creates silos, which in turn perpetuate misconceptions, reduce the flow of knowledge, and exacerbate inefficiencies. Given the current push to re-examine our biases broadly and foster a more inclusive scientific society, perhaps it is time that we reconsider the term 'resurrection plant' and work to increase the inclusivity of our language? The study by Zhang *et al.*, is a prime example of why we should include bryophytes in 'resurrection plants' and celebrate their value more broadly. This study not only highlights the utility of bryophytes as models for desiccation tolerance but also identifies

This article is a Commentary on Zhang *et al.* (2024), doi: 10.1111/nph.19620.

a deeply conserved regulatory mechanism of water stress tolerance that is shared across millions of years of evolution and divergence. These findings highlight the conservation and convergence of desiccation tolerance mechanisms and 'resurrection' phenotypes across extremely diverse plant lineages.

Regardless of semantics, understanding the mechanisms underlying desiccation tolerance holds immense promise for various practical applications, including the improvement of crop plants, as well as the production, storage, and utilization of agricultural, medicinal, and material products. Consequently, biologists have been intrigued by the phenomenon of anhydrobiosis for many decades (Bewley, 1979; Tebele *et al*., 2021). Despite the long-standing interest in desiccation tolerance, unraveling the genetic basis of anhydrobiosis has proven to be a formidable challenge due to its inherent complexity. Fortunately, recent advancements in multi-omics techniques open the door to exploring the intricate molecular pathways associated with anhydrobiosis in greater depth. Zhang *et al*. took advantage of this opportunity by integrating high-resolution genomic and transcriptomic data to provide a nuanced understanding of the molecular pathways involved in desiccation tolerance. While numerous previous studies have investigated desiccation tolerance using omics techniques, few have taken the extra step of validating candidate genes in a model system. Zhang *et al*. took this extra step, they combined multi-omics with traditional genetics rooted in an evolutionary framework to identify a previously uncharacterized regulator of water stress tolerance, the R2R3 MYB regulator (Sr_g19809), which was then validated in *Arabidopsis thaliana*. By combining insights from evolutionary biology with cutting-edge omics technologies, the authors identified key regulatory networks governing anhydrobiosis to pinpoint a promising target for bioengineering desiccation and drought tolerance. This work is an exciting example of how to bridge the gap between genomic discoveries and functional insights to accelerate the development of drought-resistant crops to improve global food security.

The study by Zhang *et al*. represents a significant milestone in understanding desiccation tolerance and underscores the utility of bryophyte models in unraveling complex biological traits. Looking ahead, future studies should build upon this foundation by combining insights from evolutionary biology with cutting-edge omics technologies. By leveraging the genetic resources in both bryophytes and seed plants, researchers can explore the molecular mechanisms underlying vegetative desiccation tolerance and apply this knowledge to improve the resilience of crops, among other applications. This research opens new avenues for biotechnological advancements to enhance the resilience of economically important plants and underscores the value of using bryophyte models in evolutionary-informed studies to address global challenges related to climate change and food security.

Acknowledgements

This work was supported by NSF grant no. DBI-2213983 to the Water and Life Interface Institute. The author's ideas have been shaped by numerous interactions and conversations with colleagues.

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Key words: bryophytes, desiccation tolerance, resurrection plant, *Syntrichia ruralis*, water stress tolerance.