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Unexplored dimensions of variability in vegetative desiccation tolerance

Rose A. Marks[1,2,3,5], Jill M. Farrant[3], D. Nicholas McLetchie[4], and Robert VanBuren[1,2]

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[1] Department of Horticulture, Michigan State University, East Lansing, MI 48824, USA

[2] Plant Resilience Institute, Michigan State University, East Lansing, MI 48824, USA

[3] Department of Molecular and Cell Biology, University of Cape Town, Rondebosch 7701, South Africa

[4] Department of Biology, University of Kentucky, Lexington, KY 40506, USA

[5] Author for correspondence (e-mail: marksr49@gmail.com)

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Desiccation tolerance has evolved recurrently across diverse land plant lineages as an adaptation for survival in regions where seasonal rainfall drives periodic drying of vegetative tissues. Growing interest in this phenomenon has fueled recent physiological, biochemical, and genomic insights into the mechanistic basis of desiccation tolerance. Although, desiccation tolerance is often viewed as binary and monolithic, substantial variation exists in the phenotype and underlying mechanisms across diverse lineages, heterogeneous populations, and throughout the development of individual plants. Most studies have focused on conserved responses in a subset desiccation-tolerant plants under laboratory conditions. Consequently, the variability and natural diversity of desiccation-tolerant phenotypes remains largely uncharacterized. Here, we discuss the natural variation in desiccation tolerance and argue that leveraging this diversity can improve our mechanistic understanding of desiccation tolerance. We summarize information collected from ~600 desiccation-tolerant land plants and discuss the taxonomic distribution and physiology of desiccation responses. We point out the need to quantify natural diversity of desiccation tolerance on three scales: variation across divergent lineages, intraspecific variation across populations, and variation across tissues and life stages of an individual plant. We conclude that this variability should be accounted for in experimental designs and can be leveraged for deeper insights into the intricacies of desiccation tolerance.

KEY WORDS drought; genetic diversity; natural variation; plasticity; resiliency; resurrection plants.

INTRODUCTION

Plants have evolved diverse and elegant strategies for life in water-limited environments. At the extreme, some plants can survive typically lethal levels of water loss by becoming quiescent or dormant during prolonged drought events. Vegetative tissues that can withstand drying to or below an absolute water potential of −100 MPa without dying (Bewley, 1979) are considered desiccation tolerant. Plants with this ability are referred to as resurrection plants because of their dramatic ability to revive from a dry and seemingly dead condition. In the current literature, the term resurrection plants is commonly reserved for vascular plants (distinguishing them from nonvascular plants), but in this review, we refer to all land plants with vegetative desiccation tolerance as resurrection plants. Resurrection plants are phylogenetically diverse, exhibit contrasting anatomy, drying kinetics, and survival frequencies, but they typically co-occur in specific habitat types. Over 90% of vascular resurrection plants inhabit rocky outcrops or inselbergs in Africa, Asia, Australia, and South America, and it is common to find species spanning ~400 million years of divergence growing as complex intertwined communities (Porembski and Barthlott, 2000).

Vegetative desiccation tolerance is an ancestral adaptation that facilitated the colonization of terrestrial habitats by early land plants. Subsequently, this trait was lost (or suppressed) in the ancestor of vascular plants as a trade-off for more complex water management and transport systems such as vasculature

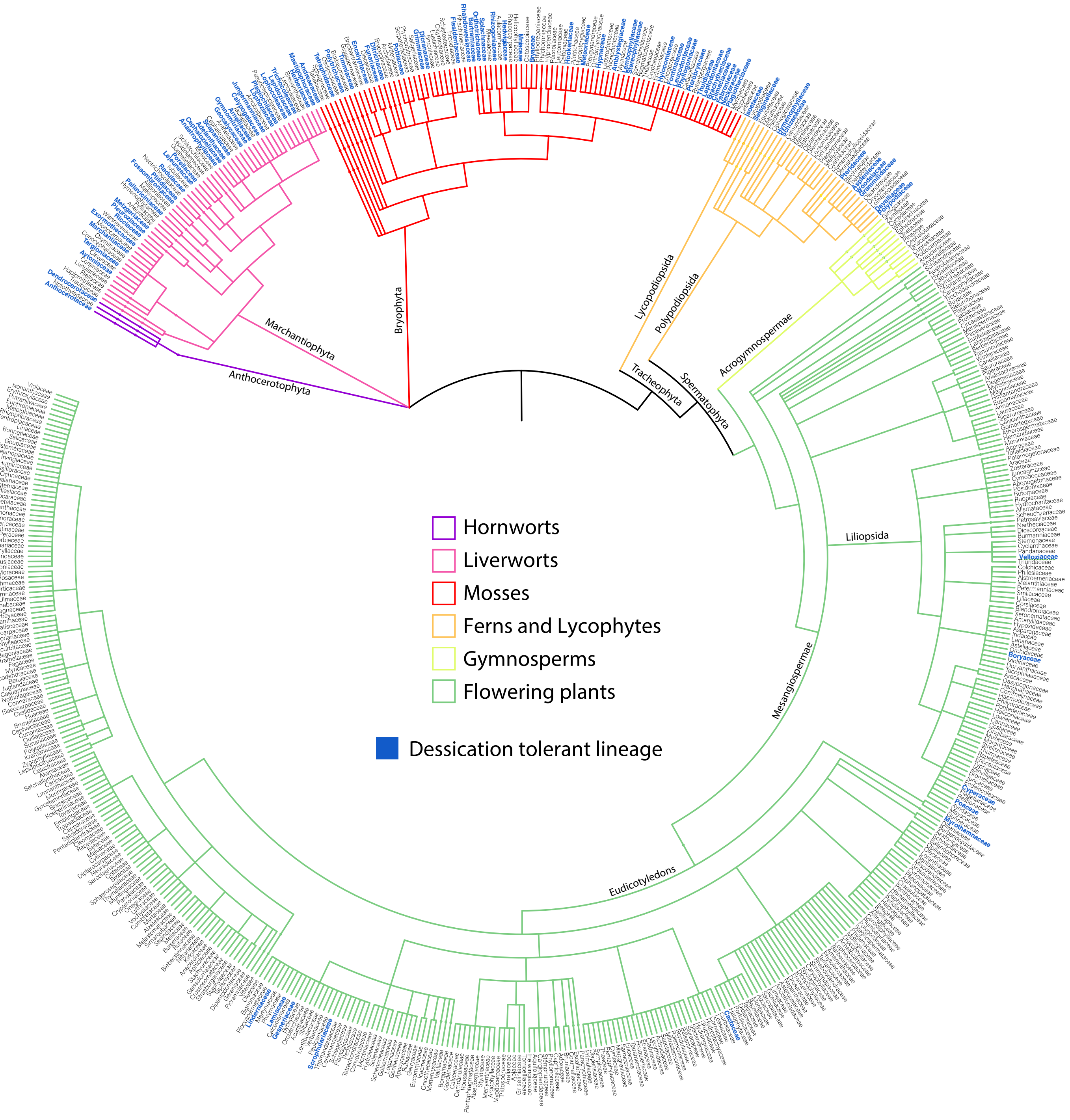


FIGURE 1. Species tree showing the distribution of desiccation tolerance across all land plant families. Families in blue have at least one desiccation tolerant lineage. Major clades are designated by color. The complete list of plant families was retrieved from The Plant List (2013). The species tree was generated with phyloT (2019) and visualized using iTOL (Letunic and Bork, 2019). Desiccation-tolerant lineages were identified via a literature review; the complete list is in Appendix S1 (with citations in Appendix S2).

and stomata (Oliver et al., 2005; Alpert, 2006; Gaff and Oliver, 2013). Vegetative desiccation tolerance re-evolved in a subset of diverse vascular plants as an adaptation for survival in regions where seasonal rainfall causes plants to dry periodically. Resurrection plants are represented in every major lineage of land plants, except gymnosperms (Alpert, 2000, 2006). Despite this widespread taxonomic distribution, vegetative desiccation tolerance is a relatively rare trait confined to select lineages. To date, vegetative desiccation tolerance has been documented in ~600 land plants across 68 bryophyte (mosses, liverworts, and hornworts), 10 fern and fern ally, and 10 angiosperm families (Fig. 1; Appendix S1). Interestingly, desiccation tolerance has been retained in the seeds and spores of nearly all land plants, suggesting that most plants have the genetic potential to be desiccation tolerant, but are limited by anatomical, physiological, and regulatory constraints. Consequently, it has been proposed that the convergent re-evolution of vegetative desiccation tolerance in vascular plants occurred through the rewiring of ancestral desiccation tolerance pathways maintained in seeds and spores (Illing et al., 2005; Costa et al., 2017; VanBuren, 2017; VanBuren et al., 2018). Throughout the remainder of this review, we use desiccation tolerance as shorthand for vegetative desiccation tolerance.

Although resurrection plants are remarkably diverse, it seems that their evolution has been shaped by common selective forces. Resurrection plants have successfully colonized extremely xeric habitats unsuitable for most other organisms where they are subjected to long and/or frequent periods in a desiccated state (Alpert, 2000; Porembski and Barthlott, 2000). Specialized communities of phylogenetically diverse resurrection plants are common on inselbergs throughout Africa, Asia, Australia, and South America. These habitats are characterized by shallow and nutrient-poor soils, intense solar radiation, high temperatures, sporadic water availability, and low relative humidity (Porembski and Barthlott, 2000; Porembski, 2007, 2011). Desiccation-tolerant plants (particularly bryophytes, ferns, and fern allies) are also abundant in the epiphytic niche, which is characterized by a similar lack of soil, intense solar radiation, and extreme water limitation (Hosokawa and Kubota, 1957; Proctor, 2002; Leon-Vargas et al., 2006; Pardow et al., 2012). The observation that resurrection plants often co-occur and are found in characteristic habitat types suggests that environmental selection has been a strong driving force in the retention and re-evolution of desiccation tolerance (Alpert, 2000). It is likely that similar selective forces continue to drive the contemporary evolution of desiccation tolerance on a local scale, but this possibility has rarely been tested. A more comprehensive understanding of the phylogenetic and geographical distribution of desiccation tolerance would shed light on the forces driving the evolution thereof, but the relative inaccessibility of inselbergs and epiphytic habitats continues to limit the discovery and characterization of new resurrection plants.

The substantial life history, anatomical, and physiological differences that exist across diverse desiccation-tolerant lineages have imposed inherent constraints on the kinetics and mechanistic basis of desiccation tolerance in individual species. Consequently, desiccation tolerance is not a monolithic trait, and unique tolerance strategies exist across divergent lineages. Commonalities in desiccation tolerance mechanisms have been documented, but there is also evidence of lineage- and species-specific mechanisms (Oliver et al., 2020), likely driven by evolutionary baggage accrued over millions of years of independent evolution. These differences are most apparent between vascular and bryophyte resurrection plants, but unique strategies are also evident on smaller phylogenetic scales. In fact, responses to desiccation can vary within a single species (Stieha et al., 2014; Marks et al., 2019), and even among different development stages of an individual plant (Proctor et al., 2007a, b; Blomstedt et al., 2018; Radermacher et al., 2019). This complex variability highlights the intricate physiology underlying desiccation tolerance.

Substantial progress has been made in understanding the molecular biology and biochemistry of desiccation tolerance. A number of informative reviews cover recent advances in this area (see reviews by Vicré et al., 2004; Farrant et al., 2007; Moore et al., 2009; Morse et al., 2011; Dinakar et al., 2012; Gechev et al., 2012; Dinakar and Bartels, 2013; Zhang and Bartels, 2018; and Oliver et al., 2020); however, this knowledge is based on a small subset of resurrection plants that have been studied in great detail, with most studies conducted under laboratory conditions using a single or limited number of accessions. Consequently, multiple knowledge gaps and questions remain, particularly regarding the genetic diversity, plasticity, and trait variability of desiccation tolerance. Although broad differences in gene expression (e.g., constitutive vs. inducible) and photosynthetic processes (e.g., chlorophyll degrading vs. retaining) have been noted across lineages, few studies have explicitly characterized the additional scales of variability in desiccation tolerance, and a lack of consistent methodology across existing studies makes identifying such differences retrospectively challenging.

Characterizing the many dimensions of variability in desiccation tolerance is critical for accurate mechanistic understanding of this complex trait. Desiccation tolerance is not a binary trait and exists along a gradient spanning divergent lineages, diverse genotypes, and complex tissues. Here, we review current understanding of variability in desiccation tolerance on three levels: across lineages, populations of a single species, and tissues of an individual plant. We argue that each of these scales of variation can be leveraged to provide unique insight into desiccation tolerance. Specifically, detailed comparison of divergent lineages will aid in untangling the central or "core" components of desiccation tolerance from those that are species-specific. Characterizing differences within a single species will provide insight into the roles of plasticity and local adaptation in desiccation tolerance. Finally, understanding differences among tissues and life stages of a single plant can provide insight into the regulatory mechanisms underlying desiccation tolerance. We summarize information collected from resurrection plants described in the literature and suggest that the variability contained within these diverse lineages can be leveraged for deeper understanding of this complex and elegant trait.

Variation in how desiccation tolerance is assessed

Many factors can impact the outcome of a desiccation event including the minimum water content of dried tissues (i.e., the intensity of drying) (Gaff, 1989; Watkins et al., 2007; Marks et al., 2016), the rate of drying (Oliver et al., 1998; Farrant et al., 1999; Cruz de Carvalho et al., 2011, 2019; Stark et al., 2013; Greenwood and Stark, 2014; Greenwood et al., 2019; McLetchie and Stark, 2019), the light and temperature conditions during drying and rehydration (Hearnshaw and Proctor, 1982; Seel et al., 1992; Guo and Zhao, 2018), the duration that tissues are maintained in a dry state (Benkő, 2002), and the condition of tissues before drying (Schonbeck and Bewley, 1981; Beckett et al., 2005a, b; Brinda et al., 2016) (Fig. 2). Subtle modifications to these variables are common across studies and can impact the ultimate survival of tissues, complicating comparisons and highlighting the intricacy of desiccation tolerance. In a natural context, many of these variables are impacted by local environmental conditions as well as anatomical and physiological constraints at a species level. Depending on the species and the conditions under which the tissues were dried and stored, resurrection plants can remain viable for months, years, or even decades in a desiccated state (Hosokawa and Kubota, 1957; Gaff, 1989; Alpert, 2000; Farrant and Kruger, 2001; Benkő, 2002; Proctor, 2003). Artificial manipulation of these variables can lead to contrasting recovery outcomes within a single species (Farrant et al., 1999; Cruz de Carvalho et al., 2011, 2019; Stark et al., 2013; Greenwood and Stark, 2014).

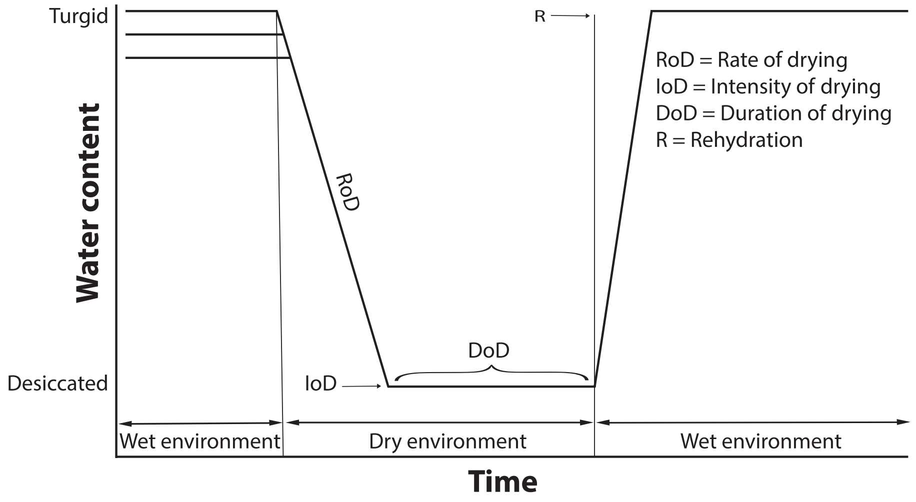


FIGURE 2. Schematic diagram of the desiccation–rehydration processes in resurrection plants. The *y*-axis represents water status of the plant tissue; the *x*-axis represents time. For simplicity, the moisture of the environment is categorized as either wet or dry, although in reality the status is rarely so simple. Drying begins when the environment becomes dry, and rehydration occurs when the environment becomes wet. The initial water content of the plant tissue can vary within a normal physiological range, indicated by the three parallel lines before drying commences. Factors that can impact recovery from desiccation are indicated, including the rate of drying (RoD), the intensity of the drying event (IoD), and the duration of desiccation (DoD). Rehydration (R) is rarely manipulated in studies, but among bryophytes pre-hydration in high relative humidity can increase recovery.

Normal metabolic and physiological functions typically resume within minutes of a rehydration event in bryophytes (Proctor et al., 2007a, b) and within several hours to days in vascular plants. Methods of assessing recovery from desiccation events also vary greatly, with some studies monitoring photosynthetic performance (by various methods) (Dilks and Proctor, 1974; Leon-Vargas et al., 2006; Pressel et al., 2009; Proctor, 2010), some tracking the resumption of protein synthesis (Oliver et al., 1993; Farrant and Kruger, 2001) or cell survival (Clausen, 1964) and others monitoring downstream establishment, growth, and reproduction of treated tissues (Stieha et al., 2014; Greenwood et al., 2019). Furthermore, some studies assess the intensity of drying treatments by reporting the relative humidity to which tissues equilibrated, while others report the minimum water content of tissues either as relative water content (RWC) or on a dry mass basis. The diverse life forms of resurrection plants coupled with a lack of consistent methodology across studies make it difficult to directly compare desiccation responses across lineages and studies.

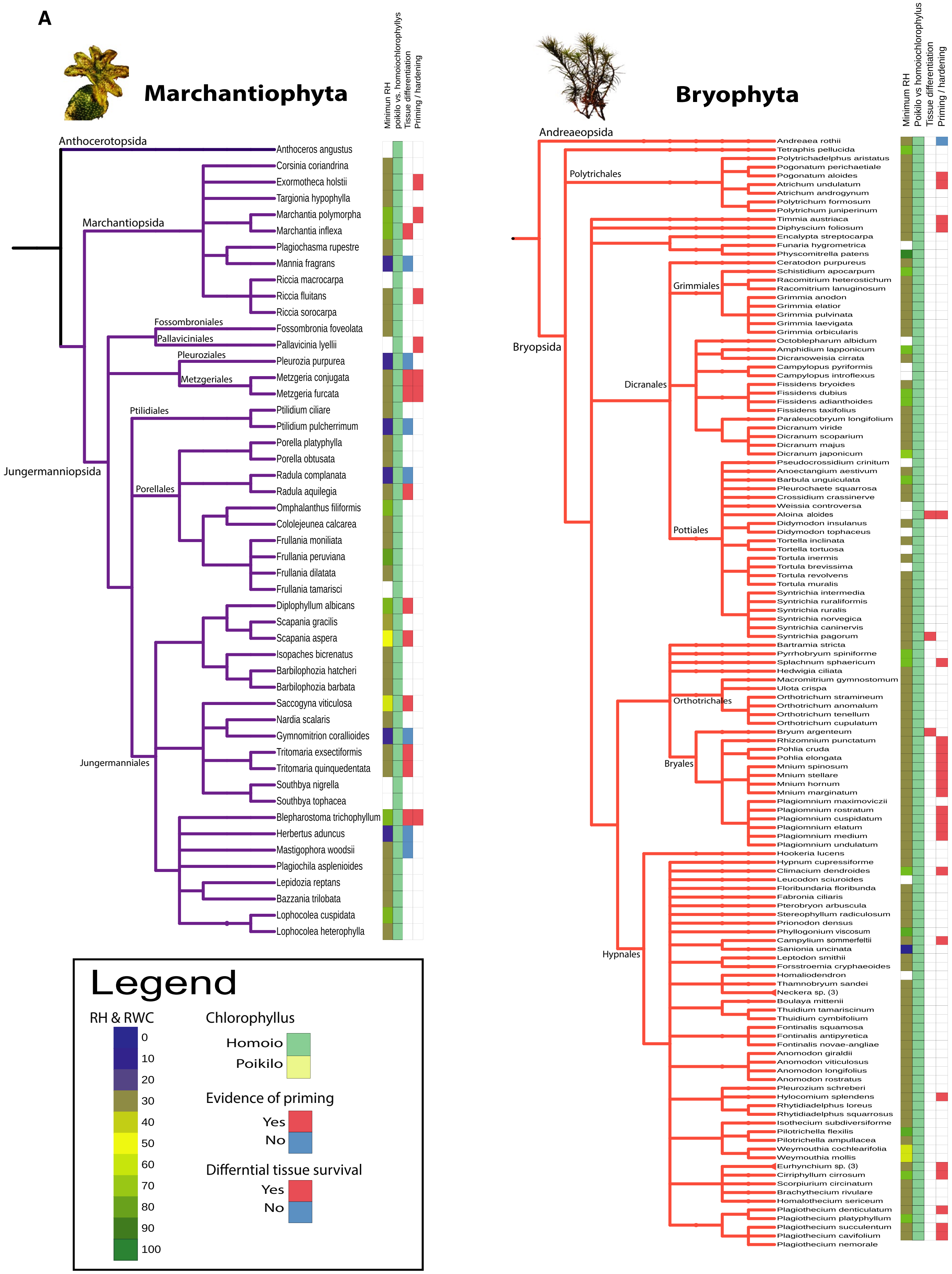
Variation among species

There are approximately 600 desiccation-tolerant land plants currently described in the literature (Appendix S1), but taxonomic characterization is likely incomplete. Desiccation tolerance is most common among bryophytes, with representatives in a least 68 families (e.g., Frullaniaceae, Grimmiaceae, Mniaceae, Orthotrichaceae, Pottiaceae, Ricciaceae, Thuidiaceae), followed by ferns and fern allies with desiccation-tolerant species distributed across 10 families (e.g., Hymenophyllaceae, Polypodiaceae, Pteridaceae, Selaginellaceae). Comparatively few angiosperm lineages are reported to be desiccation tolerant, but four monocot (Boryaceae, Cyperaceae, Poaceae, Velloziaceae) and six eudicot families (Cactaceae, Gesneriaceae, Lamiaceae, Linderniaceae, Myrothamnaceae, Scrophulariaceae) contain resurrection plants (Fig. 1). The phylogenetic distribution of desiccation tolerance suggests that ancestral desiccation tolerance was retained in many early-diverging lineages (indicated by the widespread occurrence of this trait across bryophyte families) and supports the hypothesis that desiccation tolerance was lost (or suppressed) in the common ancestor of vascular plants and only re-evolved in a unique subset of lineages (indicated by the multiple independent origins of desiccation tolerance across vascular plant lineages) (Fig. 1).

Among the resurrection plants that have emerged as models for desiccation tolerance, the bryophytes *Syntrichia ruralis* and *Bryum argenteum*; the pteridophyte *Selaginella lepidophylla*; the eudicots *Craterostigma plantagineum*, *Boea hgroscopica*, *Haberlea rhodopensis*, and *Myrothamnus flabellifolia*; and the monocots *Xerophyta humils*, *Xerophyta schlechteri* (syn. *Xerophyta viscosa*), *Eragrostis nindensis*, *Sporobolus staphianus*, and *Tripogon lolioformis* have been best studied. Of the ~600 known resurrection plants, these represent a very small subset, and yet substantial variation in the mechanism of desiccation tolerance is evident even among these selected species. In fact, unique patterns of gene expression, metabolism, stress physiology, and genome structure have been observed within this subset (Dinakar and Bartels, 2013; Lyall and Gechev, 2018; Oliver et al., 2020). The variation contained within these species is a valuable source of information that can be leveraged to distinguish among the core vs. species-specific mechanisms of tolerance. Still, these species capture only a small portion of the existing diversity contained in all desiccation-tolerant lineages, hindering our ability to identify broadly conserved mechanisms.

On a broad scale, there are substantial differences in desiccation responses between vascular plants and bryophytes (Oliver et al., 2005), but more nuanced differences also exist within these groups (Tuba et al., 1998; Tuba and Lichtenthaler, 2011). Most bryophytes dry extremely rapidly (in minutes to hours), whereas vascular plants tend to dry slowly over several days or weeks. Similarly, rates at which metabolism and physiological competence resume upon rehydration vary from minutes in bryophytes (Proctor et al., 2007a, b)

FIGURE 3. Reconstructed phylogenies of desiccation-tolerant lineages. Genera with poorly resolved phylogenies are collapsed, and the total number of known desiccation-tolerant species is indicated. The complete list of species reported to have desiccation tolerance is in Appendix S1 (with citations in Appendix S2). Other traits of interest are mapped onto the phylogeny where data are available. Plant genera were retrieved from The Plant List (2013); the tree was generated with phyloT (2019) and visualized using iTOL (Letunic and Bork, 2019).


A
Marchantiophyta
Minimun RH
poikilo vs. homoiochlorophyllys
Tissue differentiation
Priming / hardening
Anthocerotopsida
Anthoceros angustus
Marchantiopsida
Corsinia coriandrina
Exormotheca holstii
Targionia hypophylla
Marchantia polymorpha
Marchantia inflexa
Plagiochasma rupestre
Mannia fragrans
Riccia macrocarpa
Riccia fluitans
Riccia sorocarpa
Fossombroniales
Fossombronia foveolata
Pallaviciniales
Pallavicinia lyellii
Pleuroziales
Pleurozia purpurea
Metzgeriales
Metzgeria conjugata
Metzgeria furcata
Ptilidiales
Ptilidium ciliare
Ptilidium pulcherrimum
Jungermanniopsida
Porellales
Porella platyphylla
Porella obtusata
Radula complanata
Radula aquilegia
Omphalanthus filiformis
Cololejeunea calcarea
Frullania moniliata
Frullania peruviana
Frullania dilatata
Frullania tamarisci
Jungermanniales
Diplophyllum albicans
Scapania gracilis
Scapania aspera
Isopaches bicrenatus
Barbilophozia hatcheri
Barbilophozia barbata
Saccogyna viticulosa
Nardia scalaris
Gymnomitrion corallioides
Tritomaria exsectiformis
Tritomaria quinquedentata
Southbya nigrella
Southbya tophacea
Blepharostoma trichophyllum
Herbertus aduncus
Mastigophora woodsii
Plagiochila asplenioides
Lepidozia reptans
Bazzania trilobata
Lophocolea cuspidata
Lophocolea heterophylla
Legend
RH & RWC
0
10
20
30
40
50
60
70
80
90
100
Chlorophyllus
Homoio
Poikilo
Evidence of priming
Yes
No
Differntial tissue survival
Yes
No
Bryophyta
Minimum RH
Poikilo vs homoiochlorophylus
Tissue differentiation
Priming / hardening
Andreaeopsida
Andreaea rothii
Tetraphis pellucida
Polytrichales
Polytrichadelphus aristatus
Pogonatum perichaetiale
Pogonatum aloides
Atrichum undulatum
Atrichum androgynum
Polytrichum formosum
Polytrichum juniperinum
Timmia austriaca
Diphyscium foliosum
Encalypta streptocarpa
Funaria hygrometrica
Physcomitrella patens
Ceratodon purpureus
Grimmiales
Schistidium apocarpum
Racomitrium heterostichum
Racomitrium lanuginosum
Grimmia anodon
Grimmia elatior
Grimmia pulvinata
Grimmia laevigata
Grimmia orbicularis
Bryopsida
Octoblepharum albidum
Amphidium lapponicum
Dicranales
Dicranoweisia cirrata
Campylopus pyriformis
Campylopus introflexus
Fissidens bryoides
Fissidens dubius
Fissidens adianthoides
Fissidens taxifolius
Paraleucobryum longifolium
Dicranum viride
Dicranum scoparium
Dicranum majus
Dicranum japonicum
Pottiales
Pseudocrossidium crinitum
Anoectangium aestivum
Barbula unguiculata
Pleurochaete squarrosa
Crossidium crassinerve
Weissia controversa
Aloina aloides
Didymodon insulanus
Didymodon tophaceus
Tortella inclinata
Tortella tortuosa
Tortula inermis
Tortula brevissima
Tortula revolvens
Tortula muralis
Syntrichia intermedia
Syntrichia ruraliformis
Syntrichia ruralis
Syntrichia norvegica
Syntrichia caninervis
Syntrichia pagorum
Bartramia stricta
Pyrrhobryum spiniforme
Splachnum sphaericum
Hedwigia ciliata
Orthotrichales
Macromitrium gymnostomum
Ulota crispa
Orthotrichum stramineum
Orthotrichum anomalum
Orthotrichum tenellum
Orthotrichum cupulatum
Bryales
Bryum argenteum
Rhizomnium punctatum
Pohlia cruda
Pohlia elongata
Mnium spinosum
Mnium stellare
Mnium hornum
Mnium marginatum
Plagiomnium maximoviczii
Plagiomnium rostratum
Plagiomnium cuspidatum
Plagiomnium elatum
Plagiomnium medium
Plagiomnium undulatum
Hypnales
Hookeria lucens
Hypnum cupressiforme
Climacium dendroides
Leucodon sciuroides
Floribundaria floribunda
Fabronia ciliaris
Pterobryon arbuscula
Stereophyllum radiculosum
Prionodon densus
Phyllogonium viscosum
Campylium sommerfeltii
Sanionia uncinata
Leptodon smithii
Forsstroemia cryphaeoides
Homaliodendron
Thamnobryum sandei
Neckera sp. (3)
Boulaya mittenii
Thuidium tamariscinum
Thuidium cymbifolium
Fontinalis squamosa
Fontinalis antipyretica
Fontinalis novae-angliae
Anomodon giraldii
Anomodon viticulosus
Anomodon longifolius
Anomodon rostratus
Pleurozium schreberi
Hylocomium splendens
Rhytidiadelphus loreus
Rhytidiadelphus squarrosus
Isothecium subdiversiforme
Pilotrichella flexilis
Pilotrichella ampullacea
Weymouthia cochlearifolia
Weymouthia mollis
Eurhynchium sp. (3)
Cirriphyllum cirrosum
Scorpiurium circinatum
Brachythecium rivulare
Homalothecium sericeum
Plagiothecium denticulatum
Plagiothecium platyphyllum
Plagiothecium succulentum
Plagiothecium cavifolium
Plagiothecium nemorale

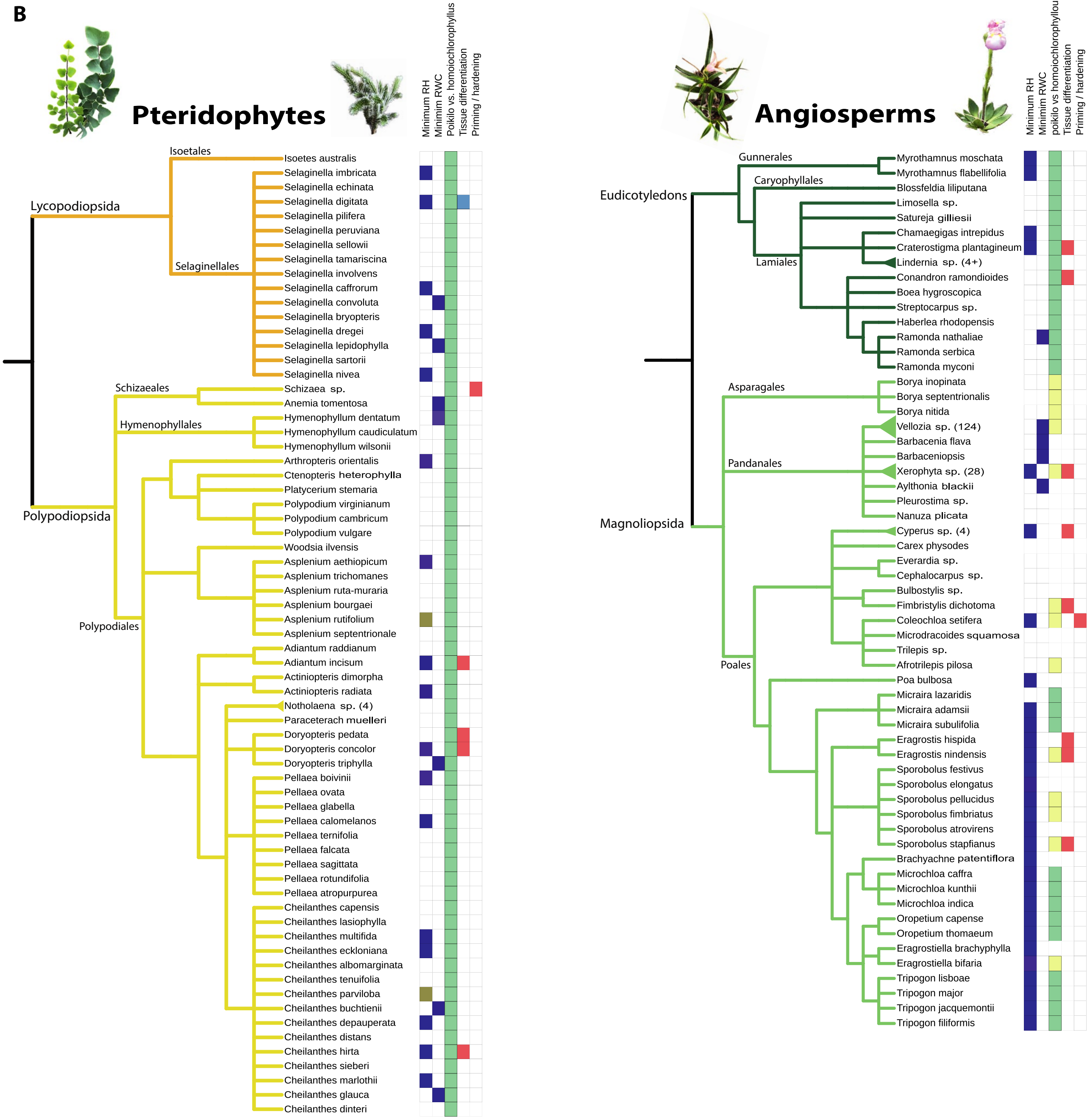


FIGURE 3 (Continued)

to hours and days in vascular plants. These differences in drying kinetics, seem to be driven by variation in tissue complexity, plant architecture, and morphology and are associated with contrasting dynamics in gene expression during desiccation and rehydration (Oliver et al., 2020). Most vascular plants slow the rate of drying through morphological and physiological mechanisms. During this time, the expression of genes involved in subcellular protection is initiated and cellular metabolism is shifted (Costa et al., 2017; Yobi et al., 2017; Liu et al., 2019). In contrast, bryophytes tend to dry rapidly, and they express desiccation-related transcripts constitutively (Oliver et al., 2000, 2005, 2020) and require considerable repair on rehydration (Alpert and Oliver, 2002).

Some bryophytes can survive desiccation to a lower water content than others (Fig. 3A) (Clausen, 1964; Streusand et al., 1986; Proctor and Tuba, 2002), and differences in the rate of drying (Dilks and Proctor, 1974), the duration of dry periods tolerated (Proctor, 2003), and tolerance of added stresses including high temperature (Hearnshaw and Proctor, 1982) have been noted. Additional differences in the speed and completeness of recovery, the extent of membrane damage, electrolyte leakage, and net photosynthetic rates have also been observed across diverse bryophyte lineages

(Dilks and Proctor, 1974; Alpert and Oechel, 1987; Harten and Eickmeier, 1987; Oliver et al., 1993; Proctor, 2002; Leon-Vargas et al., 2006). Although desiccation-tolerant bryophytes clearly have contrasting phenotypes, the physiological mechanisms behind this variation have rarely been studied, and the confounding effects of field-hardening and environmental plasticity have been largely overlooked. Recent work suggests that constitutive expression of desiccation-related transcripts in bryophytes may actually depend on priming or field-hardening of tissues (Fig. 3A) (Stark et al., 2014). In a natural context, bryophytes undergo rapid and frequent cycles of dehydration and rehydration because of the high surface to volume ratio of their tissues. Because bryophytes rapidly equilibrate to the ambient relative humidity, the constitutive expression of desiccation-related genes is favored. However, when cultured under mesic conditions, bryophytes may minimize the costly expression of desiccation-related transcripts in order to allocate those resources to other functions.

Vascular resurrection plants are expected to exhibit contrasting mechanisms of desiccation tolerance due to the putative independent origins of the trait across these lineages. The most visually obvious and well-studied example of this variation is the manner in which photosynthesis is regulated during desiccation and recovery, where two contrasting strategies, termed homoiochlorophylly and poikilochlorophylly are evident. Homoiochlorophylly is typified by the retention of chlorophyll and the maintenance,and protection of the photosynthetic apparatus during desiccation, with minimal repair required on rehydration. In poikilochlorophyllous plants, chlorophyll is degraded, thylakoids are dismantled during desiccation, and subsequently regenerated during early rehydration. Homoiochlorophylly is an evolutionary ancient strategy present in all nonseed plants, all eudicots, and most C_4 monocots reported on to date. Poikilochlorophylly, on the other hand, is restricted to monocots (Fig. 3B) (Tuba, 2008), and its occurrence could be related to ecological patterns of drying. Poikilochlorophyllous plants may be better adapted to survive extended periods of dehydration and are expected to dominate in sites with fewer cycles of dehydration and rehydration. In contrast, homoiochlorophyllous plants are likely better adapted to capitalize on short periods of hydration (because their photosynthetic apparatus does not need to be reassembled during rehydration) and may outcompete poikilochlorophyllous plants in habitats with frequent cycles of dehydration and rehydration. *Xerophyta elegans* is the only *Xerophyta* species with homoiochlorophylly, and unlike its sister species, occurs in shaded niches, suggesting that light intensities may also play a role (J. M. Farrant, personal observation). However, this hypothesis has not been tested, and both poikilochlorophyllous and homoiochlorophyllous resurrection plants are often found side by side in the field (Rabarimanarivo and Ramandimbisoa, 2019).

Substantial differences in drying rate and relative resistance to water loss are easily observed among co-occurring resurrection plants (i.e., some plants dry in hours and others take several days to fully desiccate) (Gaff, 1977; Alpert, 1979; Sherwin and Farrant, 1996; Farrant et al., 1999; Proctor and Tuba, 2002; R. A. Marks, personal observation). Differences in drying rate may be related to ecological, phylogenetic, and anatomical variation among species. These differences are associated with variation in the nature and chemical composition of osmotic protection during the early stages of drying. During drying, most resurrection plants accumulate high levels of sucrose, but the nature of secondary sugars accumulated varies across species. For example, *Myrothamnus flabellifolia* contains substantial amounts of trehalose, arbutin, and glucopyranosyl-β-glycerol (Bianchi et al., 1993), whereas *Craterostigma plantagineum*, *Ramonda*, and *Haberlea* sp. accumulate an abundance of raffinose family oligosaccharides (Müller et al., 1997; Egert et al., 2015). Such metabolites are thought to not only slow the rate of water loss, but also to protect cells from the initial generation of reactive oxygen species as carbon fixation is hindered during the decline in water potential. Many resurrection plants exhibit elevated levels of sugars and amino acids in the hydrated state (Farrant et al., 2009; Oliver et al., 2011; Yobi et al., 2012, 2017; Suguiyama et al., 2014; Radermacher et al., 2019), implying a metabolic priming or state of readiness for incipient droughts.

There is additional variability among vascular resurrection plants in the means by which mechanical stabilization is progressively achieved. Some species minimize changes to cell volume during dehydration via increased vacuolation, whereas others depend on folding of the cell wall, usually in inverse proportions (Farrant et al., 2007; Oliver et al., 2020). Extreme folding of cell walls is typically accompanied by little or no increased vacuolation, as observed for *Craterostigma* sp. (Vicré et al., 2004), whereas many *Xerophyta* sp. have relatively inflexible walls and much of the cytoplasm is occupied by vacuoles during desiccation (Farrant et al., 2007). These enlarged vacuoles contain compatible solutes, the nature of which varies among species (Bianchi et al., 1993; Müller et al., 1997; Egert et al., 2015). The extent of cell wall flexibility can be related to the nature, relative quantities of, and modifications in pectin (particularly homogalacturonans), hemicelluloses, extensins, glycine-rich proteins, and arabinoglactan proteins present in each species (Moore and Farrant, 2012; Neeragunda Shivaraj et al., 2018), which results in considerable variation among species as to how cell wall flexibility is achieved.

Studies that seek to define detailed differences in the mechanisms of cellular protection and repair across diverse resurrection plants are needed. Applying standardized methods to additional species spanning the multiple independent origins of desiccation tolerance will shed light on the phenotypic and mechanistic variability of this trait. When combined with sister species comparisons of tolerant and sensitive taxa, these data could be leveraged to identify core components of desiccation tolerance. Differences in relative desiccation tolerance across lineages may also impact community dynamics and can be used to better understand ecological patterns, species distributions, and shifts under climate change.

Variation within species and across geography

The extent of intraspecific trait variability in desiccation tolerance is largely uncharacterized, but is likely significant, similar to other highly convergent adaptations to water deficit such as CAM and C_4 photosynthesis (Silvera et al., 2010; Schlüter and Weber, 2020). Many of the physiological and molecular studies on desiccation tolerance have used a single or limited number of accessions, inadvertently ignoring any variability found within individual species. Although this work has been fundamentally insightful, focusing on select accessions has hindered our understanding of the genetic and phenotypic variation in desiccation tolerance within species and across populations.

Screening natural populations to identify exceptionally tolerant ecotypes and mining the genetic variability contained within is a promising approach for identifying key genes for desiccation tolerance (Kovach and McCouch, 2008; Zamir, 2008). Many desiccation-tolerant angiosperms are widely distributed across central and southern Africa, Asia, Australia, or South America with stark differences in elevation, precipitation, and temperature across their native range (Bentley et al., 2019; Porembski and Barthlott, 2000). For example, annual precipitation across the distribution of *Myrothamnus flabellifolia* ranges from <250 mm in Namibia to >1000 mm in Malawi (Bentley et al., 2019). Other resurrection plants occur across similar geographical ranges, and it is possible that levels of desiccation tolerance vary in concordance. Surveying this variation would be a powerful way to leverage quantitative genetics to discover genes and regulatory elements underlying desiccation tolerance. Population-scale studies are advantageous over cross-species comparisons as they allow for the identification of discrete genetic variation underlying desiccation tolerance rather than conserved changes at the biochemical, physiological, or network levels that are correlated with this trait. In addition to facilitating fundamental research, this natural diversity can be leveraged more easily than systems-level approaches to identify bioengineering targets for improvement of drought-tolerance traits. Finally, while comparative studies across species can point to potential life history trade-offs, demonstrating the existence of trade-offs can best be done within a species or individual because confounding anatomical and physiological variation is limited.

Desiccation tolerance has a tremendous metabolic and physiological cost, and its induction requires limited resources to be allocated from one process to another in a complex growth defense trade-off. Based on the observation that desiccation tolerance is found primarily in small organisms, Alpert (2006) argued that desiccation tolerance trades off with growth and reproduction. Because the cost of tolerance must be balanced with the frequency of extreme drought events, resurrection plants are generally less competitive in regions with fewer prolonged drought events (Alpert, 2006). In these regions, desiccation-sensitive plants can outcompete the smaller, slow-growing resurrection plants using typical drought-avoidance strategies. Variation in climatic variables could drive diversification in desiccation tolerance, such that populations in wetter climates may sacrifice tolerance for faster growth rates or larger plant size. There are exceptions to this pattern, and desiccation tolerance has been maintained in some lineages that no longer encounter extreme drying such as the eudicots *Lindernia brevidens* and *Boea hygroscopica*. These species are endemic to montane rainforests in Tanzania and forest understories in North Queensland, respectively, that never experience seasonal drying (Gaff, 1981; Phillips et al., 2008). The retention of desiccation tolerance in these lineages suggests a productivity trade-off is not universal. However, any natural variation in desiccation tolerance can be used to test for trade-offs between desiccation tolerance and other life-history traits, which will provide insight into the potential consequences and pitfalls of engineering desiccation tolerance.

Very few studies have explicitly tested for differences in relative desiccation tolerance among individuals of the same species, but those that have, identified measurable intraspecific variation (Newton, 1972; Stieha et al., 2014; Marks et al., 2016, 2019; Greenwood et al., 2019). This variation may derive from acclimation to specific sites (plasticity), local adaptation, or a combination of the two (Knight et al., 2006; Cavender-Bares and Ramírez-Valiente, 2017). As mentioned above, many resurrection plants are widely distributed across climates with vast differences in annual precipitation where they are subjected to unique local selective pressures that could drive contemporary evolution of desiccation tolerance in particular sites. Understanding the extent of plasticity vs. local adaptation to any observed phenotypic variation in desiccation tolerance will improve predictions about species persistence and range shifts under climate change. More broadly, these interactions can also inform farming practices by distinguishing among traits that can be modified through specific management practices vs. those that are genetically determined.

Evidence that priming (exposure to a mild stress before complete desiccation) (Lyall et al., 2014; Zhu et al., 2015) and field-hardening (Schonbeck and Bewley, 1981; Beckett, 1999; Beckett et al., 2005a) can increase desiccation tolerance, highlights the importance of plasticity in desiccation tolerance. Although the effects of priming and field-hardening have been investigated in very few species, Fig. 3 shows that in all but one case, these factors modulated relative desiccation tolerance. Studies of field hardening in bryophytes find that some highly desiccation-tolerant bryophytes lose tolerance when reared in mesic conditions (Stark, 2017), and that some desiccation-sensitive species can be made tolerant when dried under specific conditions (Khandelwal et al., 2010). Within vascular plants, there is substantial, although largely anecdotal, evidence that resurrection plants lose some degree of tolerance when reared under the relatively mesic conditions of a laboratory or greenhouse (Hellwege et al., 1994). Primed and unprimed plants are expected to have different physiological, metabolic, and gene expression dynamics under desiccation, but studies directly addressing these aspects are limited (Zhu et al., 2015). Similarly, few studies have attempted to screen for intraspecific genetic differences in resurrection plants, but those that have suggest that it exists (Newton, 1972; Stieha et al., 2014; Marks et al., 2016, 2019; Greenwood et al., 2019).

In vascular plants, much of the molecular work on desiccation tolerance has been carried out under controlled laboratory conditions. In contrast, many studies of bryophytes have relied on field-collected material. Few studies include both field-collected and cultivated material, but such studies are needed to better understand the magnitude of field-hardening, priming, and plasticity in desiccation tolerance. Additional insight into trait variability, local adaptation, and plasticity can be gained through the characterization of diversity panels, the use of common garden studies, and reciprocal transplants. This work, although labor intensive, time consuming, and limited by the slow growth rates of most resurrection plants, will shed light on the contribution of plasticity and local adaptation to any observed variability in desiccation tolerance.

Variation across development and time

Desiccation tolerance exists in specific spatial and temporal contexts, and not all tissues survive extreme dying. Most studies have surveyed desiccation tolerance at a whole plant level and inadvertently failed to measure or account for tissue-dependent tolerance (e.g., Farrant et al., 1999; Pardow et al., 2012; Marks et al. 2016, Zhang and Bartels, 2018). Direct comparisons among tolerant and intolerant tissues of the same plant could be a powerful approach for untangling the regulatory mechanisms of desiccation tolerance, identifying tolerance-enhancing traits, and ultimately improving our understanding of developmental plasticity and gene regulation in desiccation tolerance. In contrast, bulk collection of tolerant and sensitive leaf material may dilute any metabolic or gene expression signatures that distinguish death from survival. Few studies have attempted to isolate and compare specific tissues (but see Stark et al., 2004, 2016; Blomstedt et al., 2018; Greenwood et al., 2019; Radermacher et al., 2019; Marks et al., 2020); yet, careful separation of tolerant and sensitive tissue can be used in a comparative approach to identify critical cellular changes essential for survival.

The induction of desiccation tolerance requires the careful orchestration of numerous complex mechanisms that must be deployed at the correct times and in the right tissues throughout drying and recovery processes. These temporal and spatial preparations are not always successful, and some tissue-specific senescence is a common feature of resurrection plants. Interestingly, the degree of desiccation-induced senescence varies by tissue age, with younger tissues generally being more resilient. Older tissues are generally more prone to senescence, likely due to insufficient preparation during drying or failure to repair damage during recovery (Blomstedt et al., 2018). Some species lose tolerance completely at various points throughout their life cycle (e.g., immediately after germination and during reproductive development). Importantly, these developmental differences in desiccation tolerance can be plastic. Seedling desiccation tolerance is rescued in *Xerophyta schlechteri* through the application of abscisic acid (Costa et al., 2017), and exogenous abscisic acid can also induce desiccation tolerance in the otherwise sensitive moss *Physcomitrium patens* (Khandelwal et al., 2010). Together, these studies highlight, not only the plasticity, but also the conserved genetic architecture of desiccation tolerance. Tissue-specific also senescence varies across lineages, and eudicot leaves generally recover more completely than monocots. Only young leaf tissue is tolerant in the grasses *Eragrostis nindensis*, *Tripogon loliiformis*, and *Sporobolus stapfianus*, and older leaves and leaf tips senesce during desiccation (Gaff, 1977, 1989; Vander Willigen et al., 2001; Blomstedt et al., 2018). Senescence can also be avoided in a more controlled manner through leveraging autophagy to remove toxins and recycle nutrients as observed in *Tripogon loliiformis* and *Boea hygrometrica* (Williams et al., 2015; Zhu et al., 2015). Although differences in tissue survival have been described, the true extent of this variation is unknown. Untangling the contrasting mechanisms at play in senescent vs. nonsenescent tissues offers a promising approach for increasing tolerance in sensitive tissues through the manipulation of regulatory pathways.

Tolerance can also be seasonally regulated (Farrant et al., 2009) or modified by environmental cues. Seasonal variation in desiccation tolerance has been reported in multiple bryophytes (Hosokawa and Kubota, 1957; Dilks and Proctor, 1976; Beckett and Hoddinott, 1997; Stark, 2017) and the pteridophyte *Anemia caffrorum* (syn. *Mohria caffrorum*; Farrant et al., 2009), further reinforcing the importance of plasticity in desiccation tolerance. Other environmental perturbations affect tolerance and unusually fast drying or co-occurring stresses can increase senescence during desiccation (Farrant et al., 1999). The dynamic variability of desiccation tolerance within a single plant is an important consideration for experimental design and can serve as an additional comparative system to identify regulatory elements involved in desiccation tolerance.

CONCLUSIONS AND FUTURE DIRECTIONS

It is more critical now than ever before that we advance our agricultural practices, improve our crops, and make informed environmental management decisions to minimize the negative impacts of climate change, increasing drought, and associated reductions in agricultural productivity and environmental stability (Trenberth, 2011; Dai, 2013; Lesk et al., 2016). Unlocking the intricate mechanisms of plant resiliency is a promising approach for addressing these challenges that can inform crop improvement and management efforts. In an agricultural context, mechanisms to survive drought (including desiccation tolerance) are linked to survival and productivity in arid climates, on marginal lands, and in systems without advanced irrigation. Provided any productivity trade-offs associated with desiccation tolerance can be minimized, desiccation-tolerant crops are expected to survive better under drought, thereby reducing economic losses and improving food security. In a natural context, a better understanding of desiccation tolerance can inform predictions of species persistence and range shifts in increasingly arid and unpredictable environments. Despite major advances in our understanding of desiccation tolerance, many questions remain unanswered. Addressing the outstanding questions on natural diversity and plasticity in desiccation tolerance will provide important insights into the mechanisms of desiccation tolerance and is necessary for progressing towards applied objectives. We have highlighted some of the most pressing and exciting areas of research moving forward.

Cataloging and comparing desiccation tolerance across and within species

More resurrection plants need to be identified and described. To this end, we have generated a list of known resurrection plants (Appendix S1). Although more than 240 bryophytes and 360 vascular plants have been identified as desiccation tolerant, the actual prevalence of desiccation tolerance is likely significantly greater. Vascular resurrection plants have been more comprehensively surveyed than bryophytes (Gaff, 1977, 1989; Gaff and Bole, 1986; Porembski and Barthlott, 2000; Porembski, 2006, 2011), but it is likely that many remain undescribed. Phylogenies of most desiccation-tolerant plant lineages are poorly resolved with missing taxa and tolerance phenotypes, limiting insights into the recurrent origin of this trait. Studies of additional desiccation-tolerant species will enable large-scale comparative analyses aimed at distinguishing between core and species-specific mechanisms of desiccation tolerance. Comparisons of sequenced resurrection plant genomes have identified gene duplication patterns indicative of convergent evolution (VanBuren et al., 2019), but extending these analyses to additional species will improve confidence in observed patterns.

We also need phylogenetically informed surveys targeting habitats and species complexes known to harbor desiccation-tolerant lineages. Field approaches, including portable protocols for assessing desiccation tolerance (López-Pozo et al., 2019), collections of live plant material, trait surveys, and physiological experiments are needed to better understand the breadth and variability of desiccation-tolerant phenotypes. Although numerous lineages with desiccation-tolerant taxa have been identified, only a few select species have been studied in detail. There is an opportunity to expand our knowledge base by targeting locally adapted relatives of known resurrection plants. Particular attention should be given to sampling underrepresented taxa including bryophytes (e.g., Dicranales, Grimmiales, Hypnales, Porellales, and Jungermanniopsida), ferns (e.g., *Selaginella* sp., *Palleae* sp., and *Cheilanthes* sp.), and monocots (e.g., *Vellozia* sp., *Borya* sp., *Microchloa* sp., and *Sporobolus* sp.). Comparative studies targeting sister taxa would allow for deeper understanding of the evolution and diversity of desiccation tolerance within and across these lineages.

Forest canopies and inselbergs remain underexplored due to the logistical difficulty of accessing these habitats. Available data describe a highly diverse community of desiccation-tolerant epiphytic ferns and bryophytes in moist tropical and temperate forests, but detailed studies of the taxa are lacking. Inselbergs are known to be hotspots for resurrection plants, and although many have been surveyed, remote destinations in western and northern Africa, South America, and Australia remain under sampled. The identification of new resurrection plants in remote areas could be expedited by leveraging local expertise and knowledge of floristic diversity to guide field and trait surveys. We suggest that curated collections of resurrection plants and live germplasm be maintained at local universities or community institutions in the country of origin to preserve natural-resource ownership, avoid the exploitation of indigenous knowledge, and promote international collaboration.

Standardize methods of characterizing desiccation tolerance

Standardized methods of imposing desiccation treatments are needed to facilitate cross-study comparisons. We suggest that the relative intensity of desiccation treatments is reported in terms of both the water content of desiccated tissues and the vapor pressure deficit (VPD) of the surrounding environment. Although many studies report the relative humidity of the surrounding air as a measure of desiccation intensity, evaporative demand of air is better represented by VPD, which takes into consideration the effect of temperature (Anderson, 1936; Ward and Trimble, 2004). Some studies solve this issue by using a single temperature within an experiment, but comparisons among studies are difficult because temperature conditions often vary. Thus, we suggest that VPD be provided to aid comparisons across studies. Relative water content is also frequently used as a measure of water loss. The original methodology, as outlined by Barrs and Weatherley (1962), uses the fresh and dry mass of plant material, measured gravimetrically. Dry mass is determined after oven drying at 70°C for 48 h and turgid mass is obtained by immersing the tissue in water in the dark for 24 h at 4°C. Although relative water content is informative and widely used, there are limitations. To begin with, it is not easily applied to bryophytes, and most bryologists report water content on a dry mass basis. In addition, some vascular plants, such as *Xerophyta schlechteri*, do not absorb water during tissue immersion, precluding the ability to obtain full turgor by this means. The method has also been criticized as a means for comparisons across species or tissues because values may be unrelated to their tissue water potential (Oliver et al., 2020). Thus, there is no one gold standard to assessing absolute water content, but reporting a combination of response measures can improve assessment.

Ideally, the performance of each desiccation-tolerant lineage or accession would be measured across a range of water contents and VPDs. While this work could be admittedly cumbersome, recent studies highlight the need for more comprehensive characterization of resurrection plants at additional water contents. It has been suggested that important metabolic shifts occur under moderate water deficit and can be an indicator of downstream survival, but detailed physiological data from multiple species at various water contents is needed to test how generalizable this phenomenon is. In addition, careful consideration must be given to the prior treatment of tissues used in experiments (i.e., field-collected vs. greenhouse-collected). Where possible, tests of both field-collected and cultivated material should be conducted. Recovery should be accessed by multiple measures including the proportion of tissue recovered, changes in photosynthetic responses, and downstream growth and fecundity. Where possible metabolomic, proteomic, and transcriptomic data should be generated to provide insight into the molecular underpinnings of desiccation tolerance.

Distinguishing among plasticity and genetic diversity in desiccation tolerance

Emerging work on priming, stress memory, and field-hardening suggest that desiccation tolerance can be highly plastic (Stark et al., 2014; Farrant et al., 2009). The multiple dimensions of plasticity in desiccation tolerance are exciting, underexplored research areas that should be investigated in more depth. Genetic variability in desiccation tolerance is also understudied, not surprisingly, given the broad variability in precipitation, temperature, and geography across the range of any given species. Surveying the genetic diversity in natural populations to identify exceptionally tolerant ecotypes will reinforce the current approach to identify the genetic basis of desiccation tolerance via comparisons of tolerant and sensitive species. Ultimately, these studies can be leveraged to identify causal genes and genetic elements underlying various tolerance phenotypes and may be used in breeding and bioengineering initiatives to quickly domesticate resurrection plants for food or fodder. For instance, the desiccation-tolerant grass *Eragrostis nindensis* is closely related to the orphan grain crop *Eragrostis tef*, and natural diversity of *E. nindensis* can be used to select for desirable agronomic traits such as plant size, yield, and nutrition to rapidly domesticate this wild species.

Our growing understanding of plant resiliency broadly, and desiccation tolerance specifically, has the potential to inform novel innovations in biotechnology, crop breeding, and environmental management. Building on the strong foundational work in the field, it is now possible to address more nuanced questions targeting the subtle natural diversity and variability in this complex phenotype. There are exciting opportunities to leverage new computational tools to interrogate data gathered from diverse resurrection plant lineages, accessions, and tissues over detailed timescales.

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AUTHOR CONTRIBUTIONS

R.A.M., J.M.F., and R.V. visualized the need for a review of this nature. R.A.M. compiled the species list (Appendix S1) and drew the figures. D.N.M., J.M.F., R.A.M., and R.V. contributed to the conceptual framework, writing, and interpretations presented.

DATA AVAILABILITY

The data used in this work are available online as Appendix S1 of the supporting information associated with this paper.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

APPENDIX S1. List of known resurrection plants and phenotypic information (where available) compiled from the literature and used to generate Figs. 1 and 3. In instances where individual species were not enumerated, the number of species in the genus reported to have vegetative desiccation tolerance is given.

APPENDIX S2. Literature cited in Appendix S1.

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