

Review

Physiological ecology of ferns: Biodiversity and conservation perspectives

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Ferns have a long geological record extending over millions of years, and they are distributed in diverse environments worldwide; including swamps, coastal locations, open grasslands, mountain terrains, drylands and deserts. Consequently, their physiological ecology is rich with examples of the fern species diversity, and remarkable adaptive variability. This is a review of some major aspects of their physiological ecology (that is, water relations and desiccation tolerance, light and photosynthesis, and temperature and physiological responses), focusing on terrestrial and epiphytic ferns in diverse global geographic locales. Ferns are important economically in horticultural commerce and provide significant ecological services. Climate change and destruction of their natural habitats may lead to extensive loss of fern biodiversity; and some of the current issues related to the protection of their natural habitat and conservation of fern species are addressed.

Key words: Biological adaptation, climate change, geographic distribution, human impact, plant evolution.

INTRODUCTION

Ferns, encompassing approximately 12,000 species (PPG 1, 2016), represent only about 4% of vascular plant diversity (Mehltreter, 2010); nonetheless, they provide important ecological services (Sharpe et al., 2010), and comprise a substantial portion of commercial ornamental plant production as well as horticultural economic development (Hoshizaki and Moran, 2001; Singh and Johari, 2018). Their evolutionary and paleobiological history is extensive beginning in the Middle Devonian, approximately 390 million years ago (mya) with expanded diversity during the Cenozoic (65 mya), when angiosperms were becoming more dominant (Schneider et al., 2004; Schuettelpelz and Pryer, 2009). Ferns were

dominant flora in the Carboniferous, later losing space to gymnosperms and angiosperms. Increasing forests provided suitable protective, shady environments where ferns flourished on the forest floor or as epiphytes on tree trunks and limbs (Watkins and Cardelús, 2012). Subsequently, over geological time spans, through adaptation and evolutionary radiation (Sessa, 2018), ferns proliferated to occupy a wide diversity of terrestrial environments; ranging from swamps and coastal locations to more open grasslands, mountain terrains, drylands and deserts. Consequently, their biodiversity and life histories (Figure 1) have commensurately expanded to include a rich panoply of different life forms,

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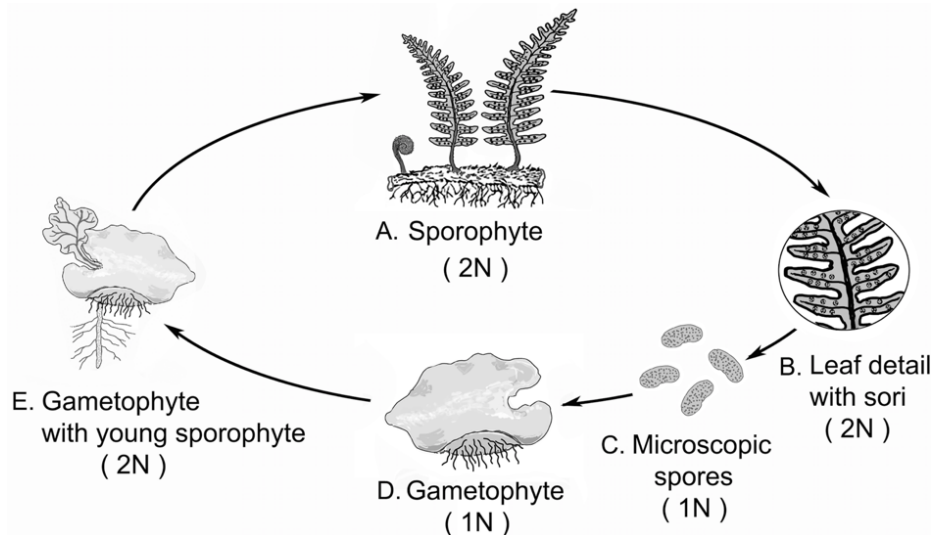


Figure 1. Fern life cycle diagram. **A.** Sporophyte, diploid phase of fern life cycle. **B.** Detail of leaf with rounded sori containing spore-producing sporangia. **C.** Spores that have been released from the sporophyte. **D.** Heart-shaped gametophyte, a haploid phase of the fern life cycle, producing sperm in antheridia and egg in archegonia; fertilized egg produces a zygote that develops into a young sporophyte. **E.** Gametophyte with first growth of a young sporophyte.

physiological adaptive strategies, and wide global habitats.

A brief comment about terminology: in prior publications, the leafy photosynthetic portion of the fern (including the stipe) was referred to as 'fronds' and this is still appropriate; but increasingly the term used is 'leaves' as applied to other vascular plants. Therefore hereafter, the term 'leaves' will be used largely, except where frond may be more appropriate.

In comparison to seed-bearing plants, spore-bearing ferns have a characteristic life cycle with alternating generations of a diploid (2N) spore-bearing sporophyte and a free-living, haploid (1N) gametophyte (prothallus) that produces egg and sperm. After fertilization of the egg producing a zygote, it gives rise to a new sporophyte generation (Figure 1). The dominant phase of the fern life cycle is the sporophyte that produces haploid spores in sporangia, typically occurring on the lower surface of fern leaves (Figure 2a, b), or in separate spikes (sporangiophores) with more specialized, usually reduced and modified fertile sporophylls. The cinnamon fern, *Osmundastrum cinnamomeum* (L.) C. Presl, observable in the natural environment and commonly grown in gardens, is an example of such a dimorphic fern. A crown of green, pinnate leaves surrounds central sporangiophores with brown, reduced fertile leaves bearing sporangia and spores.

The photosynthetic gametophyte (prothallus) that develops from the fern spore is typically thin (one-celled thick) and lacks extensive surface protective covering. Therefore, it is particularly subjected to environmental

pressures. Consequently, it can be a precarious link in the alternation of generations in the fern life cycle; because its failure would interdict development of the sporophyte stage, especially if environmental conditions are challenging. Although many species have a chordate (heart-shaped) prothallus as shown in Figure 1, it is important to recognize that in other species the prothallus is strap-shaped, ribbon-like, or even filamentous at maturity, especially varying with the habitat where the species have become adapted.

The number of spores released by the sporophyte is usually copious, and most spores are distributed in near vicinity to the mother plant (sporophyte). Consequently, a relatively dense population of gametophytes may develop in surrounding suitable locations, thus increasing the probability of successful completion of the life cycle. However, the density of gametophytes may lead to competition and only a portion of the more vigorous gametophytes survive. Moreover, there is increasing evidence that the powdery spores can be carried by wind to distant locations (including distant oceanic islands); thus, increasing dispersion of the species, assuming the new location is suitable for gametophyte survival (Sharpe et al., 2010). The evolution of very light-weight spores has promoted wide-spread dispersion of some fern species and contributed to their establishment broadly across continents and islands of the oceans in highly diverse geographic locales. Furthermore, the capacity for some gametophytes to self-fertilize also ensures that even a single gametophyte from a spore carried to distant lands may successfully give rise to a new generation at



Figure 2. Examples of fern biodiversity. **A.** *Phlebodium pseudoaureum* (Cav.) Lellinger, with large pinnatifid (lobed) leaves and rounded sori where spores are produced. **B.** *Pyrrosia lingua* (Thunb.) Farw. (Cristata cultivar), an epiphyte growing on tree bark exhibiting the abaxial surface with dense deposits of sori within a dark, purplish indumentum. **C.** *Adiantum* sp.: typically, shade adapted ferns with thin leaf laminae that have one to two celled thick mesophylls. **D.** *Davallia fejeensis* Hook. with finely divided pinnate leaves.

these distant locations. Depending on the genetic composition of the individual and potential for adaptation in the new locale, a new population may thrive and in some cases through evolution become established as endemics in that geographic locale.

The biogeography and systematics of ferns have a relatively richer, and historically longer, record of research than physiological ecology that largely expanded in quantity and sophistication during the twentieth and twenty-first centuries. There appears to be few recent reviews of fern physiological ecology addressing the particular topics treated here, although there are other substantial sources on fern ecology, more broadly (Mehltreter et al., 2010). Some representative examples of published research on fern physiological ecology are reviewed here. Ferns have diversified to occupy widely different ecological niches; including, aquatic, terrestrial, epiphytic (growing on other plants)

and epilithic (growing near to or upon rocks) species occurring in diverse geographical and climatic locales. Thus, there is a rich source of potential evidence for fern physiological ecology research. A more general treatment of fern research and natural history is provided by Fernández (2018) and Moran (2004). For information on horticultural and cultivation aspects consider Jones (1987). A comprehensive review of gametophyte developmental biology is given by Raghavan (2005). Each of the particular life forms of ferns has evolved specialized morphological and physiological adaptations to better survive in their particular habitat. With increasing concerns about the possible aversive effects of climate change for life on Earth, there is also particular interest in the likely challenges for survival of many fern species that have become adapted to particular environmental niches (Anderson, 2018). Consequently, there are enhanced efforts to better understand the physiological ecology of

ferns to more fully document and monitor the distribution and survival of biodiverse fern populations, and the biological communities where they occur.

This review of current research on fern physiological ecology focuses on terrestrial and epiphytic ferns, with particular emphasis on examples of biodiverse groups of ferns that have been published in recent decades. During the literature search, an online survey using the keywords 'Fern ecophysiology' was made for each year from present (2021) back to 1900. To delimit the categories of articles reviewed, three main topics were identified: 1) Water relations and desiccation tolerance, 2) Light and photosynthesis, 3) Temperature and physiological responses, and finally 4) Issues of conservation. These were chosen as particularly relevant aspects of physiological ecology for ferns, and consistent with the intent of a review article focusing on diverse groups of ferns in broad global environments. Additionally, articles were selected that were representative of the habitat (terrestrial or epiphytic) and addressed life stages (spores and germination, gametophyte stage, and sporophyte stage). In so far as possible, representative articles were chosen that included varied global locations (geographically and environmentally) that may be of interest to an international audience of readers.

WATER RELATIONS AND DESICCATION TOLERANCE

In addition to appropriate illumination for photosynthesis, adequate moisture is one of the most important environmental variables controlling the distribution and abundance of terrestrial and epiphytic ferns. Some species (*Acrostichum aureum* L., known as golden leather fern or swamp fern) are found in freshwater and mangrove swamps or other wet locations. By contrast 'Cheilanthoid ferns,' e.g., *Cheilanthes* spp., *Myriopteris* spp. (separated from *Cheilanthes*, sensu stricto), and *Asplenium ceterach* L., are adapted to dryland and desert locales. For example, xerophytic *Myriopteris lanosa* (Michx.) Grusz & Windham (hairy lip fern) has very small leaves, tightly curled (approximating a ball), and is covered with a dense, lanose (wooly) surface coat – particularly adapted to reduce water loss by leaf transpiration. A substantial amount of ecological and laboratory experimental research has focused on water relations and desiccation tolerance of ferns. A useful review of the topic for 'resurrection plants' in general is presented by Deeba and Pandey (2017); and more specifically for resurrection ferns by Hietz (2010), Kavitha et al. (2017), and López-Poso et al. (2018). Relevant published research topics are summarized here for terrestrial and epiphytic ferns. Subtopics within each section address environmental and physiological factors or, where relevant, cellular and biochemical adaptations. In general, review of research related to the gametophyte

is presented before addressing research with sporophytes.

Terrestrial ferns

Gametophyte environmental physiological responses

Because of the delicate and potentially fragile state of gametophytes in the fern life cycle, research attention has been given to their tolerance for desiccation stress and adaptive response to water stressful environments, including adaptive variations in tropical species (Watkins et al., 2007) and the role of competition and climate change with particular to the rare fern *Asplenium scolopendrium* var. *americanum* (Fernald) Reichst., Rasbach & Viane published by Testo and Watkins (2013). Compared to six other species, gametophytes of *A. scolopendrium* var. *americanum* had the lowest rates of germination and sporophyte production and exhibited the greatest sensitivity to interspecific competition, temperature increases, and desiccation. Given these potentially precarious characteristics, possibly threatening its survival, greater attention to conservation of this species is warranted. Particular attention has been given to gametophyte desiccation tolerance by other rare or endangered species including *Camptosorus rhizophyllus* (L.) Link, typically growing with mosses and lichens on the shaded surface of dry limestone slabs and on detached limestone slabs in open ravines and torrent beds – particularly challenging environments (Pickett, 1913).

The peculiar American species *Vittaria appalachiana* Farrar and Mickel, growing densely on shaded rock surfaces, exists only in the gametophyte form. It is sometimes known as a 'gameto-only' fern, lacking a sporophyte stage in the life cycle and reproducing asexually by photosynthetic propagules (gemmae) produced by the gametophyte. Chambers et al. (2017) report that this unique species, while limited to local sites, shows considerable adaptive variability to desiccation; indicating that it may have greater survival potential than suggested by its limited geographic range. Sato (1992) studied the effects of seasonal variables, especially spring desiccation, on survival and size of gametophytes of *Athyrium brevifrons* Nakai ex Kitag. in a transplant garden of Sapporo Japan. Gametophytes of all sizes decreased with decreasing soil moisture ($r = 0.878$, $p < 0.01$). In a similar study in the natural environment, the carbohydrate, lipid content and biomass of the gametophyte stage of the xerophytic hairy lip fern, *Myriopteris* (*Cheilanthes*) *lanosa*, collected from a sandstone bluff in midwestern U.S.A., was reported by Crow and Mack (2011). They found that each gametophyte increased in percent of total biomass (w/w) throughout development; concomitant with ability to better manage water balance during maturation.

Moreover, young gametophytes, with high carbohydrate and low lipid content, were located on substrates with a potential for small but continuous water source.

Sporophyte environmental physiological responses.

Extensive research has been given to the sporophyte stage of the fern life cycle. Mesophytic ferns, growing in environments with ample precipitation, have been investigated to determine effects of intermittent desiccation events. Liao et al. (2008) examined the effects of variation in soil moisture (80, 60, and 40%) on adaptive characteristics of *Adiantum reniforme* var. *sinensis* Y.X. Lin, an endangered species endemic to the Three Gorges Region in China. They found that drought stress decreased leaf growth and photosynthetic capacity, and hence reduced total mass, specific leaf area (SLA) and leaf area ratio (LAR). However, there was an increase in dry matter allocation into the root fraction with decreasing soil moisture. Leaf relative water content (RWC) decreased marginally as soil water was depleted. The authors concluded that these results might be the result of a physiological balance between the demand for water by the leaves and the water uptake from soil by the roots.

During the period of 2012 to 2016, California incurred severe seasonal drought. Holmlund et al. (2016) examined tissue-water relations among eight ferns in the Santa Monica Mountains to examine differential mechanisms of drought survival. They reported that five chaparral species had a wider range of tolerance (e.g., water potentials, root depths and leaf phenological traits) than two evergreen species. The evergreen species, nonetheless, were especially diverse, exhibiting wide variations in seasonal tissue water potentials. With respect to conservation perspectives, the authors predict differential survival among fern species as future drought events in California intensify, with desiccation-tolerant resurrection ferns being the most resistant and possibly leading to a reduction in diversity if less tolerant species succumb. Further research by Holmlund et al. (2020) with two species of 'resurrection ferns' documented that sufficient moisture is essential during desiccation recovery to ensure sufficient positive root pressure to drive whole-plant desiccation recovery; that is, hydration of the dried leaves alone was insufficient. Changing climate patterns that include only sporadic and limited precipitation may not be adequate to provide sufficient amount and duration of moisture at the roots to fully activate root pressure needed to revive desiccation-tolerant ferns, thus leading to their demise and decreasing biodiversity of the relatively sparse vegetation in these dryland habitats.

A rather interesting adaptive response to seasonal desiccation was reported by Farrant et al. (2009) for the unusual fern, *Mohria caffrorum* (L.) Desv., a South

African endemic, growing on Table Mountain in Western Cape, South Africa. Samples were collected during the rainy and dry seasons to determine differential responses to the changing seasonal available precipitation. Remarkably, the physiological response varies seasonally; that is, this species is desiccation tolerant during the dry season and becomes desiccation-sensitive in the rainy season, showing a differential physiological adaptive mechanism activated by changing seasonal patterns of precipitation. Its threat status is categorized as 'Least Concern' though it is growing in this rather formidable environment, and may be attributed partially to its supple capacity to alter its physiological demands to complement the changing seasonal climate.

The desiccation tolerance of ten British fern species was studied by Proctor (2009) who examined the response of excised leaves to drying. *Asplenium rutamuraria* Michx., *A. septentrionale* (L.) Hoffm., *A. trichomanes* (L.), *A. ceterach*, *Polypodium cambricum* (L.), and *P. interjectum* Shivas withstood drying for periods of a week or more to a RWC of ca. 4-7%, suggesting that they are much more tolerant to drying than most vascular-plant tissue that is irretrievably damaged at an RWC of ca. 30%. Moreover, small *Asplenium* species and *A. ceterach* dried quickly (half-drying times a few hours), suggesting little stomatal control over drying. The much slower drying of the *Polypodium* species may indicate that their stomata close under water stress. Similarly, Kessler and Siorak (2007) conducted desiccation and rehydration experiments on detached leaves of 37 fern species and six lycophytes obtained from the Botanical Garden at University of Göttingen, Germany, including a range of adaptive life forms (that is, mesomorphic, poikilohydric, xeromorphic and drought-deciduous). They reported the studied species exhibited wide variation in all measured parameters. Desiccation resistance (percentage of water loss before lethal effect) varied from 30% in the mesophytic species *Asplenium nannii* Hook. (L) to 99% in poikilohydric *Cheilanthes myriophylla* Desv. (L) and intermediate state *Adiantum macrophyllum* Sw. (L). On the other hand, the desiccation resistance of a clearly mesophytic species, *Adiantum trapeziforme* L. (L), was 51%.

Further studies by Banupriya et al. (2020) were done on the physiology of a desiccation tolerant species (*Adiantum raddianum* C. Presl) occurring widely in the Devarayanadurga forest region of Karnataka, India. They reported that during desiccation of detached leaves from healthy plants, the RWC decreased to as low as 16% after four hours with intense inward curling. Upon rehydration, the RWC of the leaves regained 85% of the initial water content within four hours; and approximated the original morphology. Physiological activities of antioxidant enzymes and molecular constituents (superoxide dismutase, peroxidase, catalase, glutathione reductase, lipid peroxidation, and proline) increased

during desiccation; however, sucrose and starch content showed differential response. Additional evidence of desiccation-protective organic constituents was reported by de Moraes et al. (2014) who analyzed the sugar content of ferns, with comparison to a lycophyte (club moss), growing in extreme rocky outcrops on the southeastern coast of Brazil. The ferns largely had glucose, fructose, and sucrose as protective osmotic compounds, and the lycophyte had glucose and trehalose. Among the ferns, the total sugar content ranged from 81.31 to 200.92 (mg g⁻¹ DW) and the RWC ranged from 80 to 88.3%.

In addition to ferns typically found in mesophytic habitats, xerophytic ferns have been studied extensively to examine their desiccation tolerance and adaptive mechanisms. Hevly (1963) examined adaptations of cheilanthoid ferns in desert environments, largely in Arizona, and summarized the morphological and physiological properties that account for their success in extremely dry environments. These adaptive properties included leaf size in microphyllous species, surface cuticles and indument with wooly coating, osmotic properties, and heat tolerance mechanisms. Harten and Eickmeier (1987) examined the comparative desiccation tolerance of two desert ferns, *Cheilanthes tomentosa* Link and *Notholaena sinuata* var. *cochisensis* (Goodd.) Weath., growing in Big Bend National Park, Texas. The high-elevation species *C. tomentosa* was most sensitive to extended desiccation and had the slowest photosynthetic recovery and the greatest membrane damage; whereas, the mid-elevation species *N. sinuata* was consistently intermediate in response. They also compared the results of these two ferns to the low elevation lycophyte, *Selaginella lepidophylla* (Hooke. & Grev.), that was least sensitive to extended desiccation and had the fastest photosynthetic recovery with least membrane damage.

With increasing evidence that some ferns growing at low elevations in coastal regions may be subjected to hypersaline conditions due to ocean flooding, interest has turned to possible effects of salinity on cultivated and naturally occurring ferns. Salanchna and Piechocki (2021) examined the salinity tolerance of four hardy ferns in the genus *Dryopteris*; namely, *D. affinis* (Lowe) Fraser-Jenk., *D. atrata* (Wall. ex Kunze) Ching, *D. filix-mas* L., and one cultivar *D. filix-mas* cv. "Linearis-Polydactylon". All were grown under different light conditions. The species that were treated with 100 mM NaCl (ca. 5.9%) exhibited reduced height, less leaf greenness index and lower fresh weight of the above-ground part. Salinity caused leaf damage in *D. affinis* and *D. atrata*, which was not observed in the other two species. The effect of NaCl depended on light treatments and individual species. Among the investigated genotypes, *D. filix-mas* seemed the most tolerant, and *D. affinis* and *D. atrata* the least tolerant to salinity and light stress. Additional aspects of light-related adaptations in terrestrial ferns are presented

in a subsequent section on Light and Photosynthesis.

Epiphytic ferns

Epiphytes, growing on other plants (particularly tree trunks and branches) are vulnerable to desiccation stress because they are particularly exposed to atmospheric and meteorological variables. In regions with rather constant climate (e.g., tropical and some subtropical locales) with sufficient humidity, moderate temperatures and more predictable precipitation, epiphytic species may thrive without specialized adaptations to avoid aversive environmental conditions. In environments with varying climate, especially unpredictable precipitation patterns, epiphytic ferns typically have adaptations to endure periods of desiccation. Consequently, a broad range of adaptive mechanisms have evolved within many taxa of epiphytic ferns to enhance desiccation tolerance. In some cases they are deciduous, shedding leaves, to avoid transpiration and water loss; or in other cases they are desiccation tolerant and endure the dry period in a dormant state ('resurrection ferns').

A comment about taxonomic nomenclature to be used in the next section: presently the accepted taxonomic name for the common polypody fern is *Pleopeltis polypodioides* (L.) E.G. Andrews and Windham (previously, *Polypodium polypodioides* (L.) Watt.). Therefore, throughout this treatment, the currently accepted name will be used and abbreviated as *P. polypodioides*.

Gametophyte environmental and physiological responses

In general, studies of gametophyte physiological ecology are fewer than those of the sporophytes; and for epiphyte species, there appears to be proportionately fewer than for studies of terrestrial species' gametophytes.

However, Watkins et al. (2007) examined the photosynthetic response of laboratory cultured gametophytes of two epiphytic species, *Phlebodium pseudoaureum* and *Microgramma reptans* (Cav.) A.R. Sm., in comparison to 10 terrestrial species during desiccation. These tropical species were collected from La Selva Biological Station in the Atlantic lowlands of north-eastern Costa Rica (37-100 m above sea level). The rate of drying varied significantly among species, with the fastest dry down in the terrestrial *Thelypteris curta* (Christ) C.F. Reed, and slowest rates in two species – the terrestrial *Cyclopeltis semicordata* (Sw.) J. Sm. and the epiphyte *Microgramma reptans* (Cav.) A.R. Sm. Depression in photochemical efficiency (Fv/Fm), as measured by photosynthetic fluorescence, in desiccated gametophytes was nonlinear and varied among species. During recovery from desiccation, *Phlebodium pseudoaureum*, compared to the other species, exhibited

relatively less depression in Fv/Fm; indicating greater resistance to photoinhibition. Moreover, *Microgramma reptans* exhibited remarkable Fv/Fm stability – no significant Fv/Fm depression occurred at any of the desiccation intensities.

Compared to terrestrial fern species, typically found on the forest floor, the desiccation stress incurred among epiphytes in the canopy may have led to evolutionary adaptations for greater desiccation tolerance. This is further exemplified in a study by Ong and Ng (1998) who found that gametophytes of the epiphytic fern, *Pyrrosia piloselloides* (L.) M.G. Price, typically found on trunks and branches of wayside trees in Singapore, were able to tolerate 50 days of drought (though with some cell death), and after rehydration were capable of partial recovery forming new offspring gametophytes. However, gametophytes desiccated for only 1–21 days recovered completely upon rehydration, without the death of any cells, and continued growth and maturation.

Further studies on the influence of simulated drought on the functioning of the photosynthetic apparatus in gametophytes of *Platyserium bifurcatum* (Cav.) C. Chr. were published by Rut et al. (2003) who reported the presence of crassulacean acid metabolism (CAM) (that is, non-photosynthetic night fixation of CO₂) in this epiphytic fern. CAM was found in the sterile cover leaves, but not in the fertile spore-producing leaves.

The photosynthetic efficiency of the gametophyte phase in the fern life cycle may be critical for subsequent sporophyte development. There is evidence that the gametophyte provides photosynthetic nourishment of the young sporophyte during its early stages of development before the one-leaf stage (Sakamaki and Ino, 1999). Consequently, desiccation stress at the gametophyte stage may incur decreases in its photosynthetic efficiency and indirectly lead to less successful development of the young sporophyte.

Sporophyte environmental and physiological responses in epiphytic ferns

Changes in water content of epiphytic ferns are one of the most significant physiological indicators of the desiccation status of poikilohydric (resurrection) species. Potts and Penfound (1948) measured the water content of *P. polypodioides* and that of the tree bark where they were growing, and found that there is close correspondence. In the active state, the ferns had mean water content (percentage of oven-dry weight) of 207 ± 32 (bark = 52 ± 16), and when desiccated and dormant the fern water content was 86 ± 13 (bark = 18 ± 4). At varying dates, they measured the water content of the ferns and the relative humidity (RH) and also found a strong correspondence varying from 8% fern water content at RH = 65%, but a much higher 23% water content at RH 94%. They also measured the change in

water content of *P. polypodioides* in laboratory experiments under controlled drying conditions and reported that over 12 hours, the amount of water lost varied from 19% during the first hour to 1% by the twelfth hour, an average change of approximately 1.6% loss per hour.

Subsequent studies by Voytena et al. (2015) reported that sporophytes of *Pleopeltis pleopeltifolia* (Raddi) Alston (commonly found in Brazil) subjected to desiccation for 0, 5, 10 and 15 days showed a sharp decline in water content when non-irrigated, reaching a final value of 9.6% after 15 days. As is typical, the ferns exhibited considerable wilting and frond rolling. A substantial increase was noted in sugar content of the fronds during desiccation – a possible osmotic adjustment and vitrification to protect tissues. During the five initial days of desiccation, the chlorophyll and carotenoid contents decreased abruptly. However, after 1 day of rehydration they partly recovered including resumption of photosynthesis.

The pliability of leaf cell walls during desiccation and folding of leaves was documented in *P. polypodioides* by Layton et al. (2010) who reported that a rise in the content of a putative 31-kDa dehydrin protein, present only during dehydration, may promote the flexibility and folding of the dehydrated leaves. They concluded that the ability to avoid cell wall damage in some desiccation-tolerant species may be partially attributed to cell wall localization of dehydrins enabling a pliable, reversible, large cell-wall deformation. This was further developed by Helseth and Fischer (2005) who derived a mathematical model to explain the physical mechanisms of changes in the pliable structure of the plant tissue during rehydration.

Further elucidation of the cellular mechanisms of dehydration and rehydration in *P. polypodioides* were reported by John (2017) using transcriptomic analysis of gene-activated protein synthesis. She found that *Pleopeltis* is prepared for desiccation at an early stage of dehydration by: a) accumulating various metabolites, b) reducing energy consuming metabolic activities, and c) subsequently catabolizing some metabolites after resumption of hydration. Additionally, many of the desiccation-induced gene transcripts are constitutively (continuously) expressed under hydrated conditions, which creates a constant supply of some essential molecules that allows the plant to adjust rapidly to desiccation.

Relatively less attention has been given to temperate epiphytic ferns. However, Klinghardt and Zotz (2021) analyzed the abundance and seasonal growth of polypod epiphytic ferns at three sites along a rainfall gradient in Western Europe; and reported, surprisingly, that seasonal frond productivity appeared to be unaffected by the amount of annual rainfall and average temperatures. Although it seems likely that these factors do play a role during gametophyte establishment. However, they reported that the abundance of epiphytic polypod ferns

strongly decreased from the wetter end of the rainfall gradient in Ireland towards the drier end in Germany; although, frond turnover was equally high at all study sites during summer months, and equally low during winter.

Considerable attention has been given to the so-called 'filmy ferns' (Hymenophyllaceae), sometimes with leaves only one-cell thick. Although they are constitutively delicate and typically grow in humid environments, some species of filmy ferns are desiccation tolerant. Other species of ferns growing in moist, shady terrestrial environments also have leaf lamina one to two cells thick; e.g., *Adiantum capillus-veneris* (L.) Hook. However, many of these are less desiccation tolerant. Ostria-Gallardo et al. (2020) applied molecular genetic analysis of gene networks to analyze desiccation tolerance mechanisms for two *Hymenophyllum* species (*H. caudiculatum* Mart. and *H. dentatum* Cav.) differing in their location within a forest canopy and experimentally studied at three different degrees of dehydration. While there were only a few distinctive genes activated comparatively in the two species, *H. caudiculatum* had ca. twice the number of activated genes than *H. dentatum*; and a higher proportion of increased-and-decreased abundance of genes occurred during dehydration. In contrast, the abundance of genes in *H. dentatum* decreased significantly when transitioning from dehydration to rehydration. Moreover, *H. caudiculatum* enhanced osmotic responses and phenylpropanoid related pathways; whereas, *H. dentatum* enhanced its defense system responses and protection against high light stress. Overall, these results provide evidence of the relationship between the species-specific response and the microhabitats that these ferns occupy in nature.

The correlation between water relations and within canopy distribution of epiphytic ferns in a Mexican cloud forest was examined by Hietz and Briones (1998). They reported that the filmy fern *Trichomanes bucinatum* Mickel & Beitel became desiccated completely within hours in moderately dry air and was confined to the stem bases; while *Asplenium cuspidatum* Lam., with no evident adaptations to cope with drought, grew in the second most shaded zone within the tree crowns. Likewise, Nitta et al. (2020) found a similar functional and habitat-specific diversity of a broad group of epiphytic ferns (including filmy ferns) in community analyses along mountain elevational gradients on the island of Moorea, French Polynesia.

Further findings include a variety of experimental and natural environmental studies as follows: a) Bravo et al. (2016) documented reversible cellular changes during desiccation and recovery of *Hymenophyllum* collected in the southern temperate rain forest of Chile; b) Flores-Bavestrello et al. (2016) made a comparative analysis of photosynthetic apparatus and responses to dehydration by *Hymenophyllum dentatum* and *Hymenoglossum cruentum* (Cav.) C. Presl isolated from different vertical

locations on a host tree in Chile; and c) Proctor (2012) published evidence of coordinated mechanisms of dehydration and photosynthetic light responses in filmy fern samples collected in New Zealand compared to those collected in Trinidad and Venezuela.

LIGHT AND PHOTOSYNTHESIS

Although available water is a major factor in fern physiological ecology, the quality and intensity of illumination is particularly important in determining fern distribution and productivity. As in previous sections, a review of research on terrestrial taxa is presented first followed by epiphytes. There is a substantial volume of published research on the topic of light and physiological adaptations of ferns. Examples of research were chosen that particularly highlight diverse geographic locales and climatic regions, globally.

Terrestrial ferns

Gametophyte environmental physiological responses

Spore germination initiates the gametophyte phase of the fern life cycle and substantial research on the effects of light on spore germination has been published, including: a) light induced spore germination (Life, 1907; Reynolds and Raghavan, 1982); b) spectral quality of light and the role of the light signaling molecule, phytochrome (Raghavan, 1971; Furuya et al., 1982; Zilberstein et al., 1984); and c) the interactions of light and temperature on spore germination (Pareek et al., 2005; Pérez-García et al., 2007). Moreover, Sugai et al. (1987) found that spores of species that normally require light to germinate can be activated by application of gibberellic acid or its methyl esters. Furthermore, complex effects are produced by adding abscisic acid (ABA) in interaction with auxin (indoleacetic acid, IAA) and kinetin (Chia and Raghavan, 1982). ABA can be inhibitory of full germination, leading to incomplete growth of the initial protonema. However, both IAA and kinetin, which alone do not promote full germination, reverse to some extent the inhibitory effect of ABA.

The importance of red light induced growth of spores is significant from a physiological ecology perspective, because overlying, shading plants absorb red light and thus may suppress underlying fern spore germination until there is sufficient full illumination to support the photosynthetic requirements of the gametophyte prothallus. It is worthy to note that ABA can take many roles, physiologically, but particularly as reported by Chia and Raghavan (1982) in the prior case, it may accumulate in spores under adverse conditions for germination, and thus delay premature germination in less than desirable environmental circumstances.

However, it is important that ABA is under regulatory control by other phytohormones (e.g., IAA and kinetins) to ensure that inhibition is released when environmental conditions are favorable for spore germination and survival of the gametophyte.

Sporophyte environmental physiological responses to light

There is a substantial literature base on this topic, and only some representative research is reviewed beginning with broad environmental factors and progressing to more detailed physiological response patterns. A rather comprehensive review of the effects of light on fern morphogenesis is presented by Kanegae and Wada (2006).

The effects of light intensity, temperature and nutrients on vernal frond emergence and biomass production in the temperate fern *Matteuccia struthiopteris* (L.) Tod. was reported by Prange (1985) who found that photosynthetic intensity, water availability, and nutrients affect frond productivity, but water availability appeared to be most critical. Maximum net photosynthesis rates of approximately $220 \mu\text{g CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ were reached at low light intensities of 300 to $600 \mu\text{mol m}^{-2} \text{ s}^{-1}$. Jordan and Kuehnert (1975), studying *Osmundastrum cinnamomea* reported that abrupt increases in light (e.g., through local deforestation) increased leaf primordial initiation to some degree, but there was greater primordial development in leaf bud primordia that were set in prior years, suggesting a carry-over effect from one year to the next.

In a further study of temperate ferns during the spring season, Tessier (2001) assessed the adaptive value of maintaining photosynthetic (wintergreen) fronds during winter in *Dryopteris intermedia* (Muhl.) A. Gray that were found growing in the Catskill Mountains of New York. He studied the photosynthetic productivity during April to May, particularly to explore the potential photosynthetic and retranslocational benefits of wintergreen fronds in sustaining the life of the fern. Net photosynthesis occurred throughout the study indicating a potential for movement of fixed carbon from winter-green fronds to other parts of the plant, though in this study the net photosynthesis was higher in April, immediately after snow melt, compared to May.

Saldana et al. (2007) examined the effects of varying light environments on the ecophysiological traits of *Blechnum chilense* (Kaulf.) Mett. occurring widely in Chilean temperate rainforests. They particularly studied contrasts of plants growing in gaps versus those in forest understories. In gaps with higher light intensity, the survival of *B. chilense* was positively correlated with water use efficiency (WUE) and negatively correlated with leaf size. In contrast, survival in shaded understories was positively correlated with leaf size. In understories, ferns of lower respiration rate and greater leaf size showed greater fecundity. Thus, whereas control of water

loss was optimized in gaps, light capture and net carbon balance were optimized in shaded understories.

Similarly, Zhu et al. (2016) examined the response of 16 fern species distributed between open gaps and shaded understories in sub-tropical forests of China. They found that a leaf cost-benefit analysis contributes to understanding the distribution pattern of ferns in contrasting light habitats. Ferns in the open habitat, employing a quick-return strategy, can pre-empt resources and rapidly grow in the high-resource environment of the open habitats; while a slow-return strategy of ferns in understory locations allows their persistence in the shaded understory of well-established canopies of old-growth forests.

Sun flecks, caused by flutter of canopy leaves and swaying branches, produce intermittent and transient peaks in light intensity in the understory habitats. Ferns growing on the forest floor produce concomitant fluctuations in productivity, that can be very rapid, as exemplified by the response of *Polypodium virginianum* L. ferns growing on cliff edges of the Niagra Escarpment, Canada (Gildner and Larson, 1992a). Further seasonal studies of *P. virginianum* at the Niagra site (Gildner and Larson, 1992b) showed that carbon gain in the spring greatly exceeded that of any other season. However, there was little change in the photosynthetic response to light on a seasonal basis, even though plants were exposed to highly variable and highly limited light most of the time.

Nishida and Hanba (2017) examined the photosynthetic response to drought stress among four temperate fern species from different habitats by withholding irrigation in laboratory experiments. Among other outcomes, they found that *Lepisorus thunbergianus* (Kaulf.) Ching (an epiphyte) had low stomatal density and showed high water-use efficiency (WUE) retaining photosynthetic activity with low relative frond water content under drought stress. This indicated they were highly adapted to drought. In contrast, low WUE with low light-saturated photosynthetic rate in *Adiantum pedatum* L. (growing in terrestrial, shady environments) was associated with much lower photosynthesis than in the other species under drought stress, suggesting lower adaptation to drought-prone habitats.

Epiphytic ferns

This subsection focuses largely on the sporophyte phase of the life cycle, where a substantial amount of research has been done. Photosynthesis of epiphytic ferns and their within-canopy distribution in a Mexican cloud forest revealed that there was a correlation between distribution of habitats within the canopy, and physiological traits (Hietz and Briones, 2001). Maximum rates of CO_2 uptake (Amax) and photon flux densities at light compensation points (LCP) were in the range of shade plants (Amax

$=0.6 \pm 5.2 \text{ mmol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; $\text{LCP} = 4 \pm 6.5 \text{ mmol m}^{-2} \text{ s}^{-1}$), but their saturation light photon intensities ($270 \pm 550 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$) were more typical for sun plants. Amax and nitrogen content per unit dry weight were correlated with the distribution of the species within the canopy; but LCP, apparent quantum yield and dark respiration were not.

Quinnell et al. (2017) examined the photosynthetic rate of *Davallia angustata* (Wall. ex Hook. & Grev.), an epiphyte on tree trunks and palm trees in south-east Asia. In this case it is not a crassulacean acid metabolic (CAM) plant as are some epiphyte fern species. Under well-watered conditions, *D. angustata* had a diurnal cycle of photosynthesis with maxima in mid-morning ~0900 hours (solar time). Under optimum irradiance ~45% of full sunlight (qualifying it as a 'sun plant'), the maximum photosynthetic electron transport rate (ETR_{max}) was $77.77 \pm 3.42 \text{ } \mu\text{mol e}^- \text{ m}^{-2} \text{ s}^{-1}$; or, expressed on a Chl *a* basis = $350 \pm 36.0 \text{ } \mu\text{mol g}^{-1} \text{ (Chl } a) \text{ s}^{-1}$.

Given the recurrence of desiccation stress in many epiphytic ferns, some have adapted stress tolerance by evolving CAM photosynthetic capacity, but overall for fewer species compared to many other vascular epiphytes. Winter et al. (1986) studied CAM in a tropical epiphytic fern, *Pyrrosia longifolia* (Burm. f.), in a fully sun-exposed and in a very shaded site in Northern Queensland, Australia. Maximum rates of net CO_2 uptake and the nocturnal increase in titratable acidity (attributable to dark fixation of the CO_2 into organic acids) were lower in shade than in sun leaves. Based on carbon stable isotopic data, $\delta^{13}\text{C}$ values of sun and shade leaves were not significantly different, and ranged between -14 and -15‰ (within the range of CAM plants) suggesting that, in the long term, carbon gain was mainly via CO_2 dark fixation by crassulacean acid metabolism. Sun leaves had a higher light compensation point of photosynthesis than shade leaves, but the same quantum yield.

Additional research on CAM in *P. longifolia* and *Drymoglossum piloselloides* (L.) Presl collected in Singapore (Ong et al., 1986), under controlled environmental conditions in laboratory culture chambers, showed that CO_2 exchange under water stress in *Pyrrosia* was less than in *Drymoglossum*; showing that *Pyrrosia* was more susceptible to water stress. During water stress, there was a continuous decrease of CO_2 uptake, both in light and darkness. Moreover, notably, in both plant species a residual diurnal acid rhythm remained, even if the drought stress caused stomatal closure and the nocturnal CO_2 uptake from the environment dropped to zero. This indicated 'CAM idling,' where CAM depended entirely on recycling of respiratory CO_2 ; that is, from respiration of existing carbon already fixed into organic acids during the night.

TEMPERATURE AND PHYSIOLOGICAL RESPONSES

Based on a global perspective, a published meta-analysis

of the relative effects of temperature versus precipitation on plant traits for a broad range of plant species worldwide has shown that temperature is the better predictor of plant traits than precipitation (Moles et al., 2014). However, as reported in the review of research above; at the local level within a reasonably well-defined climatic regime, the amount and pattern of precipitation is very significant for many fern species, particularly for epiphytes (Zotz and Hietz, 2001). Nonetheless, recognizing that temperature is a major environmental variable, it is remarkable that relatively little research has been done on the role of temperature in fern physiological ecology (Hietz, 2010; Anderson, 2018). Some illustrative studies are reviewed to provide information on the range of topics that have been published. Given the relatively limited coverage of temperature in the literature, this subsection is not subdivided by subtopics such as 'Terrestrial ferns' and 'Epiphytic ferns' as was, the case in preceding sections of this paper.

Epiphytic ferns have become adapted to dwelling on a relatively wide variety of tree species in subtropical and temperate mountainous regions, adapting to varied temperature and climate regimes, including in the Himalayas (Bhakuni et al., 2021; Joshi et al., 2020). In general, montane regions are likely hotspots for fern diversity (Suissa et al., 2021). Warne and Lloyd (1980) studied the role of temperature in the germination of spores and gametophyte development in some temperate and tropical ferns with the aim of understanding the correlation of temperature responses to the habitat of the ferns. They concluded, based on laboratory-based temperature controlled experiments, that characteristics of spore germination and gametophytic responses to temperature correlate with the natural distributions and life cycles of the studied species. The tropical taxa (*Ceratopteris* spp.) had optimum development at higher temperatures than observed for the temperate taxa. For example, the pattern of growth response of gametophytes of the temperate fern *Matteuccia struthiopteris* correlates with the winter and early spring discharge of spores in this species. Moreover, Warne and Lloyd's data suggest that a limiting factor controlling the southern distribution of this species may be the inability of its gametophytes to complete normal development in warmer climates.

Gildner and Larson (1992b) reported that temperature was a significant seasonal covariate in explaining the photosynthetic response of *Polypodium virginianum* to light intensity when growing in a forest floor location in Canada. Moreover, experiments conducted in the laboratory showed that the response of photosynthesis to temperature was broad. Ong et al. (1986), studying two obligate CAM metabolizing species (*Pyrrosia longifolia* and *Drymoglossum piloselloides*), reported that the effects of temperature on CO_2 exchange were inverse compared to other CAM plants. That is, in both ferns, dark CO_2 fixation increased when the night temperature was increased, and decreased with lower night

temperatures. Increase in day temperature reduced CO₂ uptake during phase IV (CO₂ uptake during the last part of the light period); and during the following night.

In Prange's (1985) studies of the ostrich fern (*Matteuccia struthiopteris*) a minimum amount of cold exposure was required to break winter dormancy – that is, a base temperature above 5.8°C is required and may be as high as 20°C. After the ostrich fern received its chilling requirement, vegetative emergence did not occur until temperatures were at or above ca. 9.3°C. Stamps et al. (1994), using experimental temperature regimes, examined the effects of temperature on growth of *Rumohra adiantiformis* (G. Forst.) Ching, also known as the leather leaf fern. When leaves of the leather leaf fern were produced under a high temperature regime (30°C day/ 25°C night), they grew faster and produced more sori earlier than those in a low-temperature regime (20°C day/ 15°C night). Transpiration and water-use efficiency (mass basis) at light saturation were similar for leaves from both temperature regimes.

Seasonal variations in temperature have a marked influence on fern phenology—the timing of leaf emergence and bioactivity. Lee et al. (2018) analyzed a phenological dataset of 225 fern species from around the world to illustrate the distribution of studies during the past half century into leaf and spore production seasonality and the correlation with climate factors. Seasonal patterns were found in most of the phenological phases, especially in temperate regions with cold winters. In tropical to subtropical regions, seasonal patterns vary, and the seasonality of growth and reproduction in ferns may correlate with temperature or precipitation (or both), depending on the habitat locations.

Temperate ferns are particularly prone to temperature stress during winter months. Fernández-Marín et al. (2021) assessed frond freezing tolerance and xylem anatomical traits in five wintergreen fern species. They report that only desiccation tolerant species that possessed a greater fraction of narrow tracheids (< 18 µm), compared to sensitive species, tolerated freezing. They concluded that adaptation for freezing tolerance is likely associated with desiccation tolerance through complementary xylem properties (which may prevent risk of irreversible cavitation) and effective photoprotection mechanisms.

Rapp and Silman (2014), working in a Peruvian Andean cloud forest, examined the response of *Elaphoglossum* and other vascular epiphytes growing on trees to changes in temperature after being collected at varying elevations (800 m to over 4000 m), and then after they were transplanted to locations at lower elevations along the eastern slope of the Andes. When vascular epiphytes, with ramet-producing rhizomes, were transplanted down slope from the highest elevation within the cloud forest, they had lower ramet recruitment.

Furthermore, the number of ramets declined when transplanted to the lowest elevation, suggesting that

warmer temperatures, and lower cloud immersion, could cause community-level changes for species currently above the cloud base.

CONSERVATION PERSPECTIVES

A general review of current perspectives on fern conservation is given by Mehlreter (2010), including aspects of Risk assessment, Ecological data required for risk assessment and Management strategies for fern conservation. More specific issues of fern conservation related to changing climates are considered by Anderson (2018) and Sharpe (2019). The broad biogeographic distribution and wide habitat diversity of ferns, accompanied by highly diverse taxa adapted to environments ranging from aquatic to dry lands and deserts, exemplifies the remarkable evolutionary radiation of species in this group of vascular plants (Kessler, 2010). Diverse taxa such as those adapted to aquatic, xerophytic, rocky, and dryland environments further exemplify fern exploitation of widely different habitats. The presence of a broad range of epiphytic species living on the branches and trunks of trees, spanning tropical to temperate locales, provides additional witness to their adaptive capacity. Nonetheless, as with other highly evolved vascular plants, many fern species have become specialized to thrive only within particular optimal conditions. Others are endemic to limited geographic regions and in some cases have environmental requirements peculiar to their geographic locale. While all of this diversification and specialized adaptation make ferns a very attractive group of vascular plants for horticultural uses and scientific research, escalating threats by human exploitation, increasing climate change due to anthropogenic sources, and massive destruction of natural habitats (such as burning, agricultural cultivation, logging and commercial development in otherwise pristine natural environments) threaten the survival of many fern species (Arcand and Ranker, 2013; Nowicki and Kowalska, 2018).

Desert and dryland species may be considered less threatened due to their robust adaptive response to a hostile environment. However, increasing encroachment of construction for commercial purposes, and land development for human dwelling, puts ferns under additional survival pressure. Furthermore, possible increasing temperatures, and changing precipitation patterns due to climate change, may exceed the resilience of some species. Logging and massive destruction of forested regions pose particular threats to ferns in the understory of trees, where they are adapted to the usually shady, sometimes humid, and typically more constant soil moisture of the forest floor. Epiphytic ferns are particularly threatened by logging that destroys vast swaths of the forests where the epiphytes inhabit the trunks and limbs of trees. In other cases, tree thinning

increases light intensity in remaining trees. This favors invasion of open niches by high-light adapted species that proliferate to the exclusion of other species, and contribute to reduction of epiphyte biodiversity. Moreover, potential major alterations in precipitation patterns due to global climate change may produce protracted dry periods that exceed the epiphytic ferns' desiccation tolerances.

All of these potentially challenging scenarios, and many more documented in the literature, call to our attention how relatively little we know about the physiological ecology of ferns in broad and diverse habitats essential to estimating their risk status. Clearly, a more systematic research agenda is needed to categorize fern taxa into major groups that have particular environmental requirements; and better document their habitats, survival capacity and stress limitations (Anderson, 2018). For example, tree ferns (among other exotic fern species) are impressive plants and important members of plant communities, especially in tropical and sub-tropical environments; but increasing evidence suggests that their survival in some global regions is under threat and additional research and conservation measures are needed (Ramírez-Barahona et al., 2011).

It is difficult to judge how effectively *ex situ* cultivation and preservation in botanical gardens and designated natural preserves can contribute to conservation of threatened or vanishing species. Nonetheless, horticultural and research institutions committed to cultivation and preservation of fern diversity may be one of our best solutions to saving representatives of some threatened fern species, but further efforts to enhance future conservation and biodiversity of ferns within the unique circumstances of botanical garden conservatories are recommended (Mounce et al., 2017). Interestingly, innovative ideas for use of homegardens (especially, in less-developed countries and regions of the world) may be one way to preserve some indigenous fern taxa (Amberber et al., 2014).

A variety of *ex situ* protocols and methods for preservation of fern spores, gametophytes and plants have been proposed (Ballesteros, 2011; Pence, 2013; Ballesteros and Pence, 2018), or through a combination of *ex situ* and *in situ* methods (Ibars and Estrelles, 2012). Moreover, some *in vitro* conservation methods for rare and threatened fern species have been recommended (Barnicoat et al., 2011). Overall, a concentrated and coordinated program of applied research and policy analysis by major plant societies and botanical institutions may be needed to ensure that globally, the remarkable diversity and aesthetic quality of ferns will be preserved for current and subsequent generations.

CONCLUSIONS AND POSSIBLE DIRECTIONS OF FUTURE RESEARCH

The broad diversity of fern taxa, and the remarkably

varied geographic and climatic regions where they have become adapted, provides increasing opportunities to use fern species as model organisms to study ecophysiological research on the dynamics of plant and environmental interactions. With changing climatic regimes, some that threaten the survival of uniquely adapted fern species, further research is warranted on understanding the fundamental morphological and physiological processes that account for the adaptive qualities of different groups of ferns. This is especially true, if we are to better conserve environmentally threatened species.

Recent innovative approaches that combine trait analyses, functional types (that is, particular ecologically adapted taxa – some above species level) and modern molecular genetic techniques (such as transcriptomics, proteomics, and molecular phylogenetics) are particularly promising. Given the substantial diversity of ferns at the species level, and the challenges of studying species autecology in greater detail, a research strategy that focuses on broader functional groups and their ecophysiological characteristics may be a more productive approach than species-specific research. With modern experimental, controlled-environment facilities coupled with portable field-based physiological instrumentation, opportunities are open for more sophisticated combined laboratory and field-based research on fern physiological ecology. An endeavor to understand the adaptive mechanisms of ferns, that represent morphotypic and functional groups in varied environments, can be a more efficient and comprehensive approach to understanding fern physiological ecology than focusing on lower taxonomic classes of ferns, *per se*. Moreover, such comprehensive sources of evidence on the most significant ways ferns have adapted to their environmental niches may provide a more sound basis for conservation policies and practices.

CONFLICT OF INTERESTS

The author has not declared any conflict of interests.

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