

In: Ferns

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## *Chapter 1*

# **ECOPHYSIOLOGY AND ADAPTABILITY OF TERRESTRIAL FERNS: PERSPECTIVES IN A CHANGING GLOBAL CLIMATE**

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## **ABSTRACT**

During millions of years of biological evolution, fern species have exhibited remarkable adaptive radiation, inhabiting environmental niches in all of the major biomes of the world, exclusive of the most formidable polar regions; although some occur in less hostile portions of the Arctic. Fern species occur widely in a variety of ecosystems including moist temperate and tropical forests, dry forests, wetlands, arid lands or deserts, and mountain domains, and have become highly specialized to exploit

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niches that complement their particular life profile. Some have become entirely aquatic. However, this chapter focuses on epiphytic and terrestrial ferns to highlight peculiar challenges that global climate change may bring for their adaptation or survival. Unlike seed-bearing plants, where the seed gives rise directly to a second generation of seed-producing plants, ferns produce haploid spores that germinate to produce an intermediate, less obvious, haploid reproductive stage known as a gametophyte (or prothallus). Upon maturation, the gametophyte produces sexual reproductive organs, i.e., egg-containing archegonium and sperm in the antheridium. Released sperm swim to the archegonium of the same prothallus, or a nearby one, where the egg is fertilized producing a diploid zygote. The zygote matures to form, once again, a more prominent diploid spore-producing plant known as a sporophyte; thus completing the entire reproductive cycle. Each of the reproductive stages (sporophyte, spore, and gametophyte) has particular characteristics that can enhance fern adaptation, or during challenging environmental conditions may be the weak link in reproductive success. Although some fern species are broadly distributed globally, and are robustly adapted to changing climate conditions, many have become highly adapted to their particular environmental niche and may be particularly vulnerable to changing environmental conditions. This review examines the possible effects of three aspects of global climate change (elevated atmospheric CO<sub>2</sub>, increasing temperatures, and changes in precipitation), focusing on how each of these may affect fern reproductive adaptation and success; especially with respect to: (1) spore vitality and germination; (2) gametophyte growth and reproductive success; and (3) sporophyte growth and maturation. This is followed by five selected examples of fern groups that illustrate the ways ferns may be affected by a changing climate, namely: *Hymenophyllum* and relatives (filmy ferns), the *Osmunda* ferns (e.g., *Osmunda regalis*), *Asplenium nidus* (tropical epiphytic and terrestrial fern), *Lygodium* (climbing invasive fern), and *Cheilanthes* (*Myriopteris*) spp. (arid-adapted ferns). Finally, some comments are presented on a future outlook for conservation and management.

## INTRODUCTION

This is a review of current knowledge about the ecophysiology and adaptability of homosporous, leptosporangiate ferns, specifically related to climate change effects. Among the pteridophytes (ferns and allied plants) homosporous, leptosporangiate ferns, are characterized by a relative limited number of spores of only one size, dispersed from sporangia that

arise from a single initial cell. These are among the more abundant terrestrial ferns. The other major group of “ferns” includes the eusporangiate ferns (e.g., *Ophioglossum* spp.) that produce typically more spores in each sporangium that develops from many initial cells. Background information on fern classification can be found in Smith et al. (2013). Hereafter to be concise, the term “fern” will be used to mean homosporous leptosporangiate ferns. In this treatise, topics are specifically selected to address the theme of climate change and less emphasis is placed on broad ecological principles. There are excellent published sources on general fern biogeography and ecology including books (e.g., Mehltreter et al., 2010; Moran, 2004; Ranker and Haufler, 2013; Tryon and Tryon, 2012), and articles or chapters in books (e.g., Farrar et al., 2013; Mehltreter, 2013; Page, 1979; Parris, 1985; Sharpe et al., 2010; Tryon, 1986; Watkins et al., 2007a). Research on the autecology of individual fern species (as with many vascular plants) is limited, thus hampering strong inferences about climate change effects on particular species. However, much more information is available on functional groups of ferns (ferns occupying particular ecological niches or habitats), and some inferences are possible about climate change effects for these broader groups. Moreover, where current information is more limited, potential research questions or research topics are presented to encourage further inquiry into effects of climate change on fern communities.

Additional challenges for making predictions arise due to the limited scope of current climate change predictions. Much of the climate change modeling and global predictions are limited to making fairly robust predictions about large regions of the planet (e.g., IPCC, 2014); and less certainty exists for particular geographic regions, especially localized regions such as particular biomes or biogeographic domains where ferns are commonly most abundant (e.g., temperate and tropical forest understories, montane cloud forests, and other localized habitats of endemic fern species). Nonetheless, it is clear that atmospheric concentrations of CO<sub>2</sub> are increasing, global temperatures are expected to rise above current levels, and changes in precipitation patterns are predicted for large regions of the planet (IPCC, 2014). Additionally, many ferns have become adapted to mesic habitats in cool or tropical humid

environments; and it is clear that rising temperatures, and possibly trends toward less precipitation for some biogeographic domains, could offer substantial challenges for fern adaptation and survival.

Current paleobotanical evidence indicates that ferns originated from moniliforms in ancient tropical habitats during the Middle Devonian 390 mya (Rothwell and Stockey, 2013), and flourished during the Carboniferous (355-290 mya). After three mass extinctions and reduction in fern diversity, seed plant species emerged and increased in dominance, especially the angiosperms (Cenozoic, 65 mya to present). Thus, the extant ferns are believed to have expanded and began to diversify at the same time as angiosperms (Schneider et al., 2004), largely as understory growth beneath the canopies of seed plants (e.g., Sharpe et al., 2010). Consequently, many modern fern species are found in humid, relatively cool understories of forests, or in montane cloud forests, that represent habitats more closely like those of their ancient biogeographic origins (Kessler, 2010). However, through radiation and adaptation, extant fern species are found in most every major habitat (e.g., Figure 1), including arid and desert regions (e.g., cheilanthoid ferns), tropical and arctic locales, and mountain forests, among others (Kessler, 2010; Moran, 2004). Cheilanthoid xeric ferns include the genus *Cheilanthes*. The taxonomy of this genus has been revised, and some of the species moved to the reconstituted genus *Myriopteris* based on molecular phylogenetic evidence (Grusz and Windham, 2013). Because the genus *Cheilanthes* is so widely referenced in the literature, the species transferred to *Myriopteris* will be presented here as *Cheilanthes (Myriopteris)* spp. to allow cross-reference to previous publications.

The life cycle of ferns is unique compared to seed plants, and has a profound influence on the dispersal and adaptability of ferns. Ferns exhibit a characteristic alternation of generations (e.g., Sheffield, 2013). Haploid dust-like spores produced by meiosis in spore producing organs (sori) of mature diploid sporophyte leaves are dispersed by wind or water and give rise in suitable environments to a haploid, leaf-like gametophyte (prothallus), that eventually produces sexual reproductive organs (i.e., egg-containing archegonium, and sperm in the antheridium) where after

fertilization of the egg, a diploid zygote is formed giving rise to a new diploid young sporophyte (Figure 2).



Figure 1. Examples of ferns from varying temperate and tropical habitats. **A.** *Polystichum acrostichoides* (Christmas fern) in the understory of a deciduous tree stand; **B.** *Dryopteris* sp. (wood fern) growing from a crevice in a rock face; **C.** *Cheilanthes* (*Myriopteris*) *lanosa*, a xeric, rock-dwelling fern (note the thickened and small-sized pinnae); **D.** *Osmunda cinnamomea* (cinnamon fern) growing in a partially flooded swamp area; **E.** *Osmunda regalis* (royal fern) growing at the edge of a stand of deciduous trees; **F.** Thicket of a spreading fern in a shallow ravine beneath a partially open tree canopy. **G.** *Asplenium nidus*; **H.** *Lygodium japonicum*. A.-F. All locations in New York State: A., B., F., Torrey Cliff, Palisades, N.Y.; C. New York Botanical Garden, Bronx, N. Y.; D, E. Babylon, Long Island. G and H, Tropical greenhouse plantings.

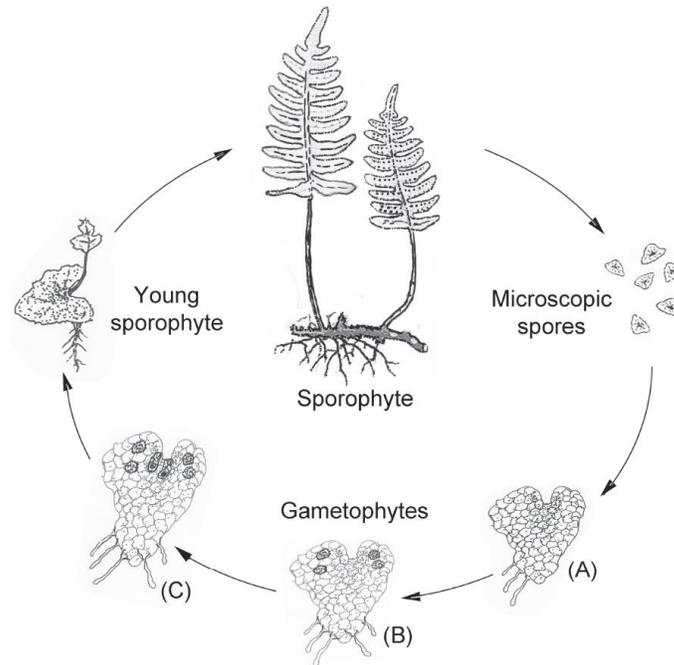


Figure 2. Stages in the life cycle of leptosporangiate ferns. The mature diploid sporophyte ( $2N$ ) produces fine haploid ( $1N$ ) microscopic spores in sori on the ventral surface of a fertile leaf. When a disseminated spore deposits on a suitable moist substrate, it germinates as a slender cellular extension, known as a protonema, that matures into a gametophyte (A). Some gametophytes initially produce globose, sperm-containing antheridia typically near the margins of the ventral side (B), and some produce vase-shaped archegonia, each containing an egg, situated in the thickened pad area beneath the cleft (C). A sperm released from antheridia can swim to and fertilize an egg in an adjacent gametophyte, or sometimes in the same gametophyte, producing a zygote ( $2N$ ) that undergoes repeated cellular division and differentiation to yield a young sporophyte. The gametophyte withers, and the young sporophyte with root matures into a second generation sporophyte ( $2N$ ).

Compared to seed plants, the haploid gametophyte generation interspersed between diploid generations, provides an additional adaptive stage in the fern life cycle where processes of natural selection and gene recombination can lead to evolutionary advances and biogeographic spread of the species to new environments beyond their current range (Farrar et al., 2013). However, the gametophyte (as explained more fully in a subsequent section) is typically less robust morphologically than the

sporophyte phase, and may incur greater survival risks than the sporophytes. Gametophytes are poikilohydric (forming desiccation resistant stages among many species) and lack anatomical features to regulate water conservation found in the sporophyte, and in most vascular plants. Remarkably, in some species the gametophyte is more desiccation resistant than the sporophyte (Hietz, 2010, p. 159-160). In general, the desiccation tolerance of the gametophyte corresponds to the desiccation tolerance of its sporophyte; i.e., desiccation-resistant sporophyte species have desiccation-tolerant gametophytes, and vice versa (e.g., Kappen, 1965). Tropical epiphytic species tend to have gametophytes that are more desiccation resistant than some of the terrestrial species, possibly because growth in the canopy, or at the ends of branches of trees, incurs more frequent periods of drought-like conditions. As may be expected, xeric fern species in general tend to have desiccation-tolerant gametophytes.

The dust-like spores of ferns, compared to most seeds of flowering plants (except for orchids, among others, with dust-like seeds), are relatively easily dispersed and can be carried by wind to distant locations including across major biogeographic distances, such as from mainland to islands (Walker and Sharpe, 2010). Fern spore viability and resistance to environmental stress, however, are major factors in determining the dispersal and adaptive capacity of a fern species (Sharpe et al., 2010, p. 15-16). The sporophyte is typically the more obvious, leafy stage most of us recognize as “a fern plant.” The sporophyte is more closely related anatomically to other vascular plants, including the presence of vascular bundles for water conduction, and stomata on the leaves to regulate water conservation. Thus, the sporophyte stage is homeohydric (with exceptions of some “filmy ferns” lacking stomates). Filmy ferns, as explained more fully in later sections, have one-cell-thick leaf lamina and are found typically in humid, shaded habitats of tropical and subtropical regions, although some are epiphytes in the crown of tropical trees. The root system of many ferns (consisting of secondary produced, wiry surface-foraging roots) emerges from a typically thickened rhizome that supports the emergent leaves (Sharpe et al., 2010, p. 8). Some rhizomes bear a thick sheath of organic scales that eventually decay, along with older portions of

the rhizome, contributing to enriched organic matter in the soil, in addition to soluble organic molecules secreted by the root system. Soil surrounding the fern rhizosphere has been shown to support robust microbial growth (e.g., Anderson, 2009). Also the roots of many fern species form mycorrhizal associations with fungi, thus gaining the affordances of this mutualistic relationship that can enhance nutrient and water availability to the fern (e.g., Richardson and Walker, 2010, p. 115).

The water conducting xylem elements of many ferns are typically composed of tracheids, lacking vessels (except for *Pteridium aquilinum* and several other species), and thus have less efficient water conduction compared to many vessel-containing seed plants (Hietz, 2010, p. 147-149); although water transport efficiency in some ferns can overlap with woody plants (e.g., Pittermann et al., 2013). This anatomical feature of water transport may interact strongly with environmental conditions, such as varying precipitation patterns and available soil moisture, thus influencing fern distribution and adaptability in changing environments. Economy of water use in ferns is attributed to varying degrees of stomatal control of transpiration, modifications of the leaf epidermis and thickening of the cuticle that provide greater resistance to changing available moisture, conferring some remarkable adaptive advantages for this old lineage of plants (e.g., Pittermann et al., 2013). Nobel et al. (1984) examined the influences of photosynthetically active radiation (PAR), temperature and water vapor concentration on gas exchange by 14 fern species from diverse habitats compared to the results with other vascular plants, and commented on the adaptive mechanisms of ferns that prevent excessive transpiration, a characteristic not previously reported in other plant groups. These, and other aspects of fern adaptability, are addressed in subsequent sections of this chapter in relation to climate change variables.

Considerable attention has been given recently to the importance of climate change broadly in plant ecology (e.g., Bazzaz, 1996; Csergő et al., 2017; Maschinski and Haskins, 2012; Nicotra et al., 2010), but less attention has been given to fern conservation and environmental challenges (e.g., Mehlreter, 2010). In the next section (Fern Life Stages in a Changing Climate), possible impacts of climate change on fern adaptability

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and survival are examined for each of the major reproductive stages (spore, gametophyte, and sporophyte) drawing on available ecophysiological, biogeographic, and experimental evidence. This is followed by a section on five case examples of ferns from diverse habitats to highlight what is known about their ecology and adaptability. The last portion of the chapter presents a future outlook for conservation and management, and a final section on overall conclusions.

## **FERN LIFE STAGES IN A CHANGING CLIMATE**

Current research information on the ecophysiology of fern spores, gametophytes, and sporophytes is reviewed in the subsequent three sections, respectively. Particular attention is given to the possible effects of elevated CO<sub>2</sub>, increasing temperatures, and changes in precipitation patterns, as pertinent to each topic.

### **Spore Vitality and Germination**

There are two major kinds of fern spores produced by different fern species: (1) chlorophyll-containing (green) spores (hereafter called green spores) and (2) non-green spores (Wada, 2013). In addition, cryptochlorophyllous spores, that appear to be non-green, may contain small amounts of chlorophyll (Tseng et al., 2017). Green spores (of grammitid ferns, Hymenophyllaceae, Onocleaceae, and Osmundaceae) are apparently more vulnerable to climatic extremes (e.g., drought and temperature) and are less viable (48 days on average), compared to non-green spores without developed chloroplasts that may survive for months to years (Lloyd and Klekowski, 1970). The reasons for less viability in green spores are not fully determined, but differences in amount of water content, respiration rate, and desiccation resistance have been suggested (Lloyd and Klekowski, 1970; Windham et al., 1986). Depending on the species, spores without chlorophyll remain viable for periods ranging from

several months (Lloyd and Klekowski, 1970) to approximately 100 years (Johnson, 1985) in spore banks or even dried herbarium specimens. However, the 100-year estimate was for sporocarps of the aquatic species *Marsilea*. More conservative estimates have been made for terrestrial ferns e.g., in *Pellaea* spp. 25 to 50 years or more (Windham et al., 1986).

The longevity of green spores (e.g., from *Osmunda* spp.) can be substantially increased by dry storage at lower temperatures, such as 4°C compared to less viability at 25°C (Ballesteros et al., 2011). This evidence further suggests that high respiration rates may account for the limited longevity of many green spores, and the reduction in resting respiration at lower temperatures may conserve stored energy reserves and increase spore longevity. Moreover, green spores germinate rapidly when they settle on a suitably moist site, further suggesting that they have limited dormancy, are metabolically active, and capable of immediately germinating. Ballesteros et al. (2011) found, remarkably, that green spores stored at temperatures as low as -80°C to -196°C maintained high viability, rapid germination, and normal growth throughout the study period of 24 months, but not comparable to freshly collected spores. Furthermore, longevity of green spores is seriously impaired by storage at low relative humidities and with increasingly less moisture content of the spores (e.g., Mikula et al., 2015). Given the decreased survival of green spores exposed to increased temperatures, current rising global temperatures may seriously affect the survival of some mesic ferns, and their ranges may be markedly reduced. Nonetheless, with sufficiently favorable large-scale environmental conditions, fern species with green spores can achieve broad ranges extending from mainland to islands (e.g., Kessler, 2002).

### ***Fern Spore Longevity and Soil Spore Banks***

Substantial evidence suggests that fern spores with sufficient longevity can survive for long periods of time in soil banks as mentioned above. For a general review see Ranal (2003). The species composition and estimates of spore densities in habitats from widely different geographic locales in temperate regions in North Carolina and Scotland were reported by Dyer and Lindsay (1992), indicating that: (1) fern spore banks are widespread;

(2) spore banks contain two or more species; (3) size and composition of the spore bank varies between sample sites (especially in relation to the nearest mature fern source); and (4) the size and composition of the spore banks vary with soil depth. However, there is evidence that viable fern spores can be distributed to substantial depths (50 to 80 cm) by soil mixing or streams of water percolating through the soil (e.g., Esteves and Dyer, 2003). Soil disturbance by animals or other natural events can bring deeply buried spores to the soil surface where they may germinate under favorable conditions, especially available light and moisture.

The viability of fern spores and favorable conditions required for spore germination have been tested by germinating spores in laboratory experiments, because of potential contamination in field or greenhouse studies (Halpern et al., 1999; Miller, 1968). Miller (1968) summarizes some of the requirements for fern spore germination including water, temperature, mineral nutrients, pH, specific chemical effects, light, and other factors. Among these, temperature and water requirements are of particular relevance to a discussion of climate change effects. In addition to Miller's review, there are relevant current research contributions (e.g., Brum and Randi, 2002; dos Santos et al., 2010; Mertens et al., 2008; Psaras and Haupt, 1989; Quintanilla et al., 2000; Ranal, 1999; Richard et al., 2000; Viviani and Randi, 2008).

### ***Soil Moisture and Fern Spore Germination***

Spore germination requires adequate moisture, including appropriate humidity. For example, spores of bracken (*Pteridium aquilinum*) sown on moist substrate in a closed space with no air currents germinated equally well in a range of relative humidities of 15.5 to 100 percent; whereas, spores sown on soil open to air currents occasionally germinated poorly even at 75-80 percent relative humidities (Conway, 1949). *Pteridium aquilinum*, however, grows robustly in drier environments, and this must be considered in evaluating evidence based on its spore germination. Spores of *Dryopteris* require at least 15 hours of water imbibition before they become responsive to light-induced changes, mediated by phytochrome far red, that signal onset of germination (Haupt and Psaras,

1989). Thus, sufficient constant moisture is likely to be required to ensure full germination of many fern spores from species in both mesic and wet environments.

The moisture requirements for germination of *Cheilanthes feei* (*Myriopteris gracilis*; per Grusz and Windham, 2013), an arid tolerant species found in open sun in rocky locations, was examined for varying levels of moisture (0, 10, 20, 30, 40, and 50  $\mu\text{l cm}^{-2}$ ) by Nondorf et al. (2003). Although the spores germinated in the dark, even on dry filter paper, germination rates were optimal in the light at moisture levels of 20-50  $\mu\text{l cm}^{-2}$ . However, there was a significant decrease in germination in the dark with moisture levels between 20-50  $\mu\text{l cm}^{-2}$ . During spore germination, the filamentous protonema (thread-like cellular extensions) that emerged from the germinating spores were approximately 200  $\mu\text{m}$  in length and developed a more mature planar shape; but, filamentous protonema in a moisture of 40 and 50  $\mu\text{l cm}^{-2}$  were only 100  $\mu\text{m}$ . Additional research is needed to more fully evaluate the autecology of fern spore germination in relation to hydration across a broader range of terrestrial fern species. But it is clear, with the possible exceptions of xeric fern species, that major changes in precipitation including recurring droughts or extended periods of low moisture can seriously diminish fern spore germination among a broad range of more mesic species.

### ***Temperature Effects on Fern Spore Germination***

Optimal temperature for fern spore germination varies among species, but generally is in the range of 15 to 30°C (Miller, 1968; Ranal, 1999). Brum and Randi (2002) analyzed the effects of temperature ranges (15, 20, 25, and 30°C) on the germination of spores from *Rumohra adiantiformis* (a fern commonly used in floral arrangements) harvested from Ilha Comprida, São Paulo, Brazil. The most favorable, lowest mean germination time (7.93 days) was observed at 25°C, followed by 20°C (9.21 days). The highest mean germination time was observed at 15°C (12.10 days), followed by 30°C (10.63 days). The latter inhibited germination. The effects of temperature on spore germination in some species are complicated due to interactions with light (e.g., Raghavan, 1980, 1989). For example, high

temperatures following irradiation with a saturating dose of red light inhibited the spore germination process, possibly due to inactivation of phytochrome molecules, but degree of hydration and changes in membrane properties are probably involved in the temperature sensitivity of the spores (Towill, 1978).

Although the spores of some mesic species of ferns can germinate at temperatures as high as 30°C, it is clear that many ferns dwelling in the cooler, humid habitats of forest understories or shaded locales require more moderate temperatures for successful spore germination. Even with some of the moderate projections for increasing global temperatures, it is clear that many locales will incur seasonal temperatures well above 30°C (86°F) for extended periods of time. And, moreover, with likely increased solar radiation (depending on cloud cover) higher temperatures and decreased moisture effects may be exacerbated. However, even without solar radiation, the surface temperature of soil and other growth substrates can be in close equilibrium with ambient air temperatures, but may be significantly different depending on local microclimates. Inhibition of spore germination resulting from either insufficient moisture, or lethal temperature effects, due to climate change will threaten the dispersal, recruitment, and survival of many mesic fern species. However, the particular biogeographic locales that may experience these extremes remain to be determined by more detailed climatological modeling and analyses (e.g., IPCC, 2014).

### **Gametophyte Growth and Reproductive Success**

There are several useful published sources on gametophyte biology (e.g., Banks, 1999; Dyer, 1979; Farrar et al., 2013; Nayar and Kaur, 1971; Verma, 2003; Voeller, 1971) and a major monograph on fern gametophyte developmental biology (Raghavan, 1989). Germination of the fern spore gives rise to a thread-like outgrowth (protonema) that elongates, and eventually becomes more flattened and expanded to produce the mature morphology of the “leaf-like” gametophyte (prothallus). The chordate or

heart-shaped gametophyte commonly presented in textbooks is more characteristic of prothalli that last for one growing season (annuals), especially for ferns of temperate climates. Other fern species, including epiphytic ferns (e.g., growing on trees) especially in the tropics produce more robust strap-shaped or ribbon-like prothalli (Farrar et al., 2013). The strap-shaped prothalli as the name implies have axes longer than the width, and sometimes bifurcate at the growing edge. Ribbon-like prothalli produce multiple thin ribbon-like extensions that protrude at varying places from the growing edge due to the presence of interrupted marginal meristems. Eventually, when mature, prothalli produce antheridia containing sperm, and archegonia containing a single egg cell. As prothalli mature, they secrete antheridogen (a gibberellin-like molecule) that induces antheridium formation, not only within the source prothalli, but also less mature prothalli growing sufficiently close to the more mature ones. Eventually, archegonia are typically produced. Flagellated sperm released from antheridia swim in a thin film of water to fertilize the egg, either in the archegonium of the same prothallus, or more likely by cross-fertilization of nearby prothalli. For successful fertilization to occur, there must be a sufficient water film to permit the sperm to swim the distance from the antheridium to an archegonium that contains an egg (Sharpe et al., 2010).

As an alternative to the typical sexual reproductive cycle, some gametophytes of fern species produce vegetative, bead or bud-like, gemmae at the periphery of the prothallus. The gemmae separate from the prothallus and can be carried some distance by disturbance, rain rivulets, or wind and establish new populations of gametophytes at more distant locales. In some species the gemmae can produce sporophytes directly. In other species, sporophytes are produced by the prothallus without fertilization (apogamy) giving rise to haploid sporophytes. At maturity, these haploid sporophytes undergo chromosome doubling, before reduction division during meiosis to produce the more typical haploid spores (e.g., Raghavan, 1989, p. 261), thus ensuring continuation of the typical alternation of generations.

### ***Atmospheric CO<sub>2</sub> Concentration Effects***

In general, mature chordate prothalli are one-cell thick, but become multi-cell layered near the apex where a thickened pad develops, typically in the region where archegonia form. Strap-like and ribbon-shaped prothalli may be thicker than chordate prothalli. All are “leaf-like” but without surface pores or stomates. Consequently, CO<sub>2</sub> diffuses directly into the cells of the thin lamina of the prothallus. However, more research is needed to determine the physiological factors affecting CO<sub>2</sub> diffusion into the prothallus. Among other factors, thickness of surface water films, cell wall thickness, membrane permeability, enzyme mediated uptake by carbonic anhydrase (for example), and membrane pores (e.g., aquaporins) could be involved (e.g., Uehlein et al., 2017). Fern prothalli are photosynthetic, and some fern spores do not germinate unless there is sufficient light. Many epiphytic and terrestrial ferns are adapted to fix carbon at relatively low light levels. For example, in laboratory experiments, carbon fixation was substantially higher in eight species of fern subjected to low light intensities (100  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) compared to a higher intensity (500  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) (Farrar et al. 2013). Maximum carbon fixation ranged from approximately 30 to 80  $\mu\text{mol C g}^{-1} \text{s}^{-1}$  at the lower light intensity. Hagar and Freeberg (1980) reported a photosynthesis rate of  $2.36 \pm 0.29 \mu\text{l CO}_2 \text{ h}^{-1} \text{ mg dry wt}^{-1}$  for *Todea barbara* gametophytes. In general, increasing atmospheric CO<sub>2</sub> concentrations would be expected to enhance gametophyte photosynthesis within the limitations of other physiological and environmental factors, but I have found no published information on the effects of variations in atmospheric CO<sub>2</sub> on gametophyte photosynthesis. More information is available on the effects of differences in atmospheric CO<sub>2</sub> concentrations on sporophyte photosynthesis as reviewed below in the sub-section on *Sporophyte growth and maturation*.

### ***Desiccation Effects***

The desiccation tolerance of fern gametophytes has been studied extensively, particularly given their apparent fragile morphology, and the likely stresses that terrestrial and epiphytic ferns may encounter during

drought or periods of less than optimal precipitation (Farrar et al. 2013, p. 236-240). Watkins (2006) and Watkins et al. (2007b) examined the effects of different desiccation intensities and multiple desiccation cycles on gametophyte recovery ability. Desiccation intensity (increasingly dry air) was studied by exposing the gametophytes to three different desiccation intensities: (1) The typical vapor pressure deficit (VPD) in natural environments (0.53 kPa); (2) a VPD typical of a drought event (1.32 kPa); and (3) An extremely low VPD (2.12 kPa) that species at the study site rarely encountered. Desiccation tolerance was closely linked to species ecology. *Diplazium subsilvaticum* (a low-light mesophyte) had little tolerance of desiccation intensities imposed by a relative humidity of approximately 50%. An epiphyte, *Microgramma reptans*, (situated typically on the distal ends of emergent twigs of trees) exhibited essentially no adverse effect to desiccation of this intensity. A similar pattern was reported when these two species were subjected to multiple desiccation cycles - *Microgramma reptans* was least affected. With climate change including increasing periods of droughts, and likely continuous drier conditions in mesic fern environments, additional studies of this kind are needed with various functional groups of mesic ferns to better predict the responses of their gametophytes to desiccation.

Even if the gametophytes are desiccation resistant, unless there is sufficient moisture at the growing site to produce the necessary continuous film of water beneath the sexually mature prothallus to support motility of the sperm, fertilization will fail; and there will be no succeeding generation of sporophytes. Under these conditions, entire populations of some fern species could be decimated. Alternatively, in some geographic regions, climate change may bring increased annual rainfall, thus promoting the survival and range expansion of some mesic fern species. Additional published sources on gametophyte desiccation resistance include the following (Chambers et al., 2017; Ong and Ng, 1998; Quirk and Chambers, 1981; Riaño and Briones, 2015). However, with rising global temperatures, the issue of temperature tolerance among fern species needs to be considered in addition to soil moisture effects.

### *Temperature Effects*

A search of the literature produced only a few published results of studies where varying temperature was examined for its affect on development and growth of fern gametophytes. Indeed, there is evidence that we have little information in general on fern heat tolerance (e.g., Hietz, 2010, p. 169). Overall, published results (mainly with tropical fern gametophytes) indicated that for most species optimal gametophyte development occurred at approximately 25°C, and temperatures as high as 30°C, were either deleterious or eventually lethal (e.g., Marcon et al., 2017; Perez-Garcia et al., 2007; Wan et al., 2010). This is consistent with results reported in the above section on temperature tolerances for spore germination. In gametophytes of *Gleichenella pectinata*, gametophyte growth was best at 25°C, but the highest percentages of gametophytes with developed rhizoids were observed at 22°C and 5% natural light (dos Santos et al., 2010). However, in a study by Testo et al. (2013), mature gametophytes of *Asplenium scolopendrium* var. *americanum* (a rare temperate species) grown at 25°C were 84.6% smaller than those grown at 20°C, and only 1.5% produced sporophytes after 200 days in culture; similar responses were not observed in other species examined in their study.

Warne and Lloyd (1980) reported that the optimal temperature for temperate and tropical gametophytes corresponded to their preferred habitat, with gametophytes of tropical species thriving at warmer temperatures, even as high as 30°C in some cases. Whereas, temperate fern gametophytes with lower optimal temperatures survived in the range of 20 to 25°C. However, some cool, temperate ferns such as *Matteuccia struthiopteris*, that sporulate in spring, produced sexually mature gametophytes (female and hermaphroditic, with antheridia and archegonia) only at cooler temperatures (11 and 16°C). These data indicate, as may be expected, that temperate ferns, adapted to cooler and humid environments, are most likely to be seriously affected by rising environmental temperatures associated with climate change, and that some tropical ferns may have more flexibility. In general, xeric ferns have gametophytes that

tolerate much higher temperatures than those of temperate ferns (Hietz, 2010).

As mentioned above, light also influences the development and maturation of fern gametophytes and more attention is needed to elucidate the interaction of light with other abiotic variables in the optimal growth of fern gametophytes. In general, it is clear that we need much more experimental and field-based research on the effects of abiotic variables on fern gametophyte ecophysiology; particularly among various functional groups based on habitat, ecophysiology, morphology, and molecular genetics, to increase the confidence of our predictions about climate change effects across the broad panorama of leptosporangiate ferns. This also pertains to the fern sporophyte generation.

### **Sporophyte Growth and Maturation**

The green, leafy, typically prominent, fern sporophyte is anatomically and physiologically similar to other vascular plants, with some exceptions as partially noted in the Introduction. Consequently, some of the challenges that other vascular plants confront during climate change are likely to also affect fern sporophytes. However, variations are to be expected attributed in part to the fern-specific habitats, specialized adaptations, and genetic aspects inherited from their ancient evolutionary origins. In this section, as in the previous one, the three themes of: (1) elevated concentrations of atmospheric CO<sub>2</sub>; (2) changing patterns of precipitation; and (3) rising temperatures will be explored in relation to fern sporophyte adaptation and survival. A considerable amount of recent work has been done on fern sporophyte ecology (e.g., Sharpe et al., 2010, p. 2-5), including climatic factors (e.g., Bystriakova et al., 2014; de Gasper et al., 2015; Khrapko and Tsarenko, 2015; Mehltreter, 2006; Mehltreter and Garcia-Franco, 2008; Mehltreter and Palacios-Rios, 2003; Pouteau et al., 2016; Richard et al., 2000; Sharpe, 1997), and only some relevant citations pertaining to likely climate change scenarios related to the three cited themes are summarized in the next subsections.

### *Atmospheric CO<sub>2</sub> Concentrations*

Fern sporophytes exhibit photosynthesis responses to changes in CO<sub>2</sub> concentrations and light intensity similar to other vascular plants. For example, laboratory studies of the effects of light level, CO<sub>2</sub> enrichment, and concentration of nutrient solution on photosynthesis and growth of the Boston fern (*Nephrolepis exaltata*) demonstrated that microleaf cuttings grown at higher irradiance accumulated more leaf fresh and dry weights than microcuttings grown at low irradiance; and CO<sub>2</sub> enrichment enhanced dry weight accumulation and plant height (Nowak et al., 2002). Whitehead et al. (1997) compared the effects of elevated CO<sub>2</sub> concentrations (539  $\mu\text{mol mol}^{-1}$ ) in relation to ambient concentrations (355  $\mu\text{mol mol}^{-1}$ ) on the growth and photosynthesis of two perennial plants: (1) bracken (*Pteridium aquilinum*); and (2) an angiosperm, heather (*Calluna vulgaris*). They found, under controlled laboratory conditions, when plants were grown at high CO<sub>2</sub>, both species had higher rates of net photosynthesis than those grown in ambient CO<sub>2</sub>. This increase was greater in heather than in bracken; and resulted in a large stimulation of growth in the heath, but there was no significant change in plant size or phenology of the bracken.

Hew and Wong (1974) reported that the maximum photosynthetic rates ( $P_{\text{max}}$ ) of some sun and shade epiphytic and terrestrial ferns ranged from 1.1 mg CO<sub>2</sub> hr<sup>-1</sup> g<sup>-1</sup> fresh weight (shade tolerant) to 6.0 mg CO<sub>2</sub> hr<sup>-1</sup> g<sup>-1</sup> fresh weight (sun tolerant), in a pattern that would be expected in general for sun and shade adapted plants, including seed plants. However, one of the more important physiological adaptations of leaves in seed plants is the regulatory control of stomatal size (pore opening) in relation to the concentration of CO<sub>2</sub> in the atmosphere relative to the CO<sub>2</sub> concentration in the leaf interior mesophyll. There has been an on-going controversy about the evolutionary origins of these active regulatory mechanisms controlling stomatal closure and whether ferns exhibit such physiological responses (e.g., H $\ddot{o}$ rak, et al., 2017). Current evidence is mixed, showing that some ferns possess sensitive regulatory control of stomatal closure related to changing CO<sub>2</sub> concentrations, but others do not; or in some cases, if present, it is less sensitive than in most angiosperms (e.g.,

Brodribb, et al., 2009; Doi and Shimazaki, 2008; Flexas et al., 2014; Franks, et al., 2012; Lammertsma et al., 2011).

In general, it is difficult to predict on an ecosystem level how ferns will respond to increasing concentrations of CO<sub>2</sub>. In those species that have sensitive stomatal regulatory control, increasing concentrations of atmospheric CO<sub>2</sub> can lead to smaller stomatal openings, thus conserving water loss through transpiration and potentially increasing water use efficiency (Brodribb, et al., 2009), but this also depends on how efficient the photosynthesis response is to other environmental variables accompanying climate change. Because decreased transpiration is energy efficient, only if energy gained through photosynthesis remains stable and reasonably high. On the other hand, Flexas et al. (2014) predict that plant species with lower photosynthetic capacity (such as some ferns and gymnosperms) would be proportionally more favored under these foreseen environmental changes. They conclude that the main reason for this difference is the lower diffusion limitation imposed by stomatal conductance ( $g_s$ ) and mesophyll conductance to CO<sub>2</sub> ( $g_m$ ) in plants having high capacity for photosynthesis among the angiosperms, which reduces the positive effect of increasing CO<sub>2</sub>. However, this apparent advantage of low-diffusion species would be canceled if the two conductances ( $g_s$  and  $g_m$ ) acclimate and are down regulated in high CO<sub>2</sub>. At present, it would appear we need substantially more ecophysiological research on the response of various groups of fern species to elevated CO<sub>2</sub> before we can make conclusive claims about the benefits or disadvantages of increasing CO<sub>2</sub> atmospheric concentrations on fern communities.

### ***Changing Patterns of Precipitation and Desiccation Effects***

Drought and aridity tolerance varies widely among fern species, reflecting the broad climatic differences among fern habitats (e.g., Kessler, 2010; Hietz, 2010), as also reported above for fern gametophytes. Much is known about the physiological mechanisms and tolerance levels of ferns adapted to arid or periodically dry environments; e.g., temperate and tropical wetlands that occasionally dry out, dry forests, savannas, forest margins, and rocks (e.g., Nobel, 1978). Less information is available on

desiccation effects on mesic fern species. Epiphytic ferns also incur periods of low humidity in sunlit tree canopies; and at some points in time, even brief periods of dryness depending on frequency of precipitation (Hietz, 2010). The physiological adaptations of some epiphytic species to these sporadic dry conditions have been carefully studied (e.g., Hietz and Briones, 1998, 2001; Sinclair, 1983).

Examples of desiccation-tolerant ferns have been reported in a broad range of fern families, including: Anemiaceae, Aspleniaceae, Cyatheaceae, Dryopteridaceae, Pteridaceae, Hymenophyllaceae, Polypodiaceae, Schizaeaceae, Tectariaceae, and Woodsiaceae; but in some cases there are only one or a few genera that are truly desiccation tolerant in each family (Hietz, 2010, p. 145-146). However, this diverse range of families with evidence of genetic diversity toward desiccation resistance suggests that there might be sufficient genetic variability for some fern genera to adapt to future periods of less precipitation in some areas that are presently more mesic.

Some examples of research on the various ways ferns adjust to desiccation stress are summarized to illustrate the potential for ferns to adapt to future scenarios of a drier habitat, including examples from tropical and more temperate environments. Farrant et al. (2009) studied *Mohria caffrorum*, typically found growing at forest margins in the Western Cape, South Africa, where it is exposed to desiccation conditions only during the dry season. Their data show that the vegetative tissues of this fern are desiccation-tolerant during the dry season, and desiccation-sensitive in the rainy season, thus affording maximum adaptive flexibility to exploit survival in both seasons. Tolerant fronds acquire protection mechanisms during drying that are largely similar to those reported for angiosperms. These include: (1) chlorophyll masking by abaxial scales and frond curling; (2) increased antioxidant capacity that is maintained in dry tissues; (3) mechanical stabilization of vacuoles in the dry state; (4) de novo production of heat stable proteins; and (5) accumulation of protective carbohydrates (e.g., sucrose, raffinose family oligosaccharides, and cyclitols).

Liao et al. (2013) examined the relative drought tolerance of two species of *Adiantum* in China (*Adiantum reniforme* var. *sinensis* and *Adiantum capillus-veneris*). They report that drought stress decreased total mass of *A. capillus-veneris*, but no significant effect on total mass of *A. reniforme* var. *sinensis*. However, *A. reniforme* var. *sinensis*, compared with *A. capillus-veneris*, had significantly higher root to shoot ratios, but lower values for other analyzed traits. These results suggest that *A. reniforme* var. *sinensis* is relatively superior in drought tolerance, but inferior at low light, allowing it to persist in habitats with low soil moisture and high light availability, but only when there are few coexisting species.

Prange et al. (1983) conducted experiments on the ostrich fern (*Matteuccia struthiopteris* (L.) Todaro) in a gas exchange system to examine the effect of a water stress, induced by  $-200$  kPa polyethylene glycol (PEG) solution. They measured carbon dioxide and water vapor flux, frond diffusive resistance, intercellular carbon dioxide concentration, carbon dioxide residual resistance and leaf water potential. Measurements were taken one day after the application of PEG. The measurements were made on young leaves (8 days old) and mature leaves (20–24 days old) illuminated at Photosynthetic Photon Flux Densities (PPFDs) from 0–1400  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . Water stress decreased the net photosynthesis rate in mature leaves at PPFDs of 210  $\mu\text{mol m}^{-2} \text{s}^{-1}$  or greater, and increased the net photosynthesis rate below 210  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in young leaves. The net photosynthesis increase in stressed young leaves was associated with a significant reduction in the dark respiration rate. Water stress and decreasing PPFDs increased leaf diffusive resistance. The residual resistance to carbon dioxide flux was not significantly affected by either leaf age or water stress. Leaf water potential was significantly lower in mature leaves than in young leaves.

Zhang et al. (2009) studied the effect of drought on two epiphytic and two terrestrial tropical fern species. Potted fern plants of the two epiphytic (Ep) species (*Neottopteris nidus* and *Microsorium punctatum*), and two terrestrial (Tr) species (*Asplenium finlaysonianum* and *Paraleptochilus decurrens*), collected from a seasonal tropical rainforest, were grown in a screen house with 5% irradiance for four months. They were treated by

withholding water for five to seven weeks, and subsequently re-watered. During the water stress, the two Ep species completely closed stomata when frond relative water content (RWC) reached about 70%, with fairly constant maximum photochemistry efficiency ( $F_v/F_m$ ), while the two Tr species kept stomata partially open until RWC reached 45% and, moreover,  $F_v/F_m$  was reduced during the late stage of the drought treatment. Physiological recovery was completed after three days of re-watering for the Ep species, which was more rapid than for the Tr species. The gas exchange measurements and regression analyses indicated higher photosynthetic water use efficiency in the Ep species than in the Tr species. Overall, studies of fern richness in mountain zonal ecosystems (e.g., Nepal) indicate the importance of moisture on fern distributions, with peaks coinciding spatially with climatic factors that enhance moisture levels, maximum number of rainy days, and the cloud zone (Bhattarai et al., 2004). With increasing changes in montane climates, especially increasing shifts upward of climate maxima supporting optimal fern growth, it is essential to know to what extent fern adaptations, dispersal, and recruitment will be able to keep pace with the upward drift of their likely optimal altitudinal climate zones (e.g., Colwell et al., 2008).

Given the diversity of habitats of ferns, and the uncertain predictions about future precipitation patterns resulting from climate change, it is difficult to make strong predictions about changing distribution and survival of major fern groups resulting from variations in available soil moisture. Fern species that are already adapted to limited moisture are most likely to persist and perhaps expand their range in regions of increasing temperature and decreased precipitation, but the exact patterns of survival cannot be fully predicted. Brodersen et al. (2012) reported interesting data on how the physiology and anatomy of vascular bundles in primary xylem may predict a fern species' response to increasing moisture deficits. They report that the drought-deciduous pioneer species, *Pteridium aquilinum*, had fronds composed of 25 to 37 highly integrated vascular bundles with many interconnections among them, a high  $g_s$  and moderate cavitation resistance ( $P_{50} = -2.23$  MPa). This species has increased risk of drought-induced vascular cavitation. By contrast, the evergreen

*Woodwardia fimbriata* had sectoried frond steles, with 3 to 5 vascular bundles and infrequent connections, low  $g_s$ , and a high resistance to cavitation ( $P_{50} = -5.21$  MPa). If this pattern can be shown to be more general, it may be a convenient anatomical and physiological means of predicting a fern's survival in increasingly drier environments.

### ***Temperature Effects***

Given the paucity of information on the effects of elevated temperatures on ferns (e.g., Hietz, 2010) predictions about fern adaptation and survival are seriously limited. However, some inferences can be made about the most likely optimum temperature for growth and survival of many fern groups based on the geographic locales where they are most abundant and diverse, for example the regions of maximum species richness and diversity along mountain elevation gradients, especially in tropical and subtropical regions (Kessler, 2010). However, humidity, soil properties, slope and exposure variables, and other abiotic factors also may partially account for part of the fern distribution patterns (e.g., Nettesheim et al., 2014). In general, it would appear that favorable growth conditions parallel those found for gametophytes, though the latter may be more resilient than the sporophyte generation for some fern species as summarized in the previous section on gametophytes.

A search of the literature provided very few relevant reports of research studies that provide insights into how some fern species may respond to increasing temperatures, or provide cues to where future research may go to better document rising temperatures effects on major groups of ferns. However, some examples of current state of research are reviewed below as possible sources of insight for further research, as well as important indicators that may be productive in examining temperature optima and upper limits for various functional groups of ferns.

Studies of temperature effects on the tropical fern *Nephrolepis exaltata* 'Corditas' indicated that effects on photosynthesis assessed as chlorophyll fluorescence ratio ( $F_v / F_m$ ) was significantly less (0.28) when grown at 40°C than growth at 25°C (0.78) (Sivanesan et al., 2014). Similarly, Mortensen and Larsen (1989) reported that *Nephrolepis exaltata* grown at

a range of temperatures from 21 to 32°C had an optimal day temperature of 24°C, and an optimal night temperature of 27°C based on dry weight measurements, in agreement with findings of Hvoslef-Eide (1986). However, at a night temperature approaching 32°C, there was a major decline in dry weight to as much as one-third of the weight at 27°C. Moreover, the weight per leaf was reduced 55 to 60% by increasing the day or night temperature from 21 to 32°C. Shoot length also was substantially decreased when night temperature was increased from 27 to 32°C. Overall, these data suggest that even modest increases in temperature above the optimal, can have major effects on the productivity and growth of *Nephrolepis exaltata*. However, data published by Poole and Conover (1981) indicated that excursions in temperature as high as 44°C under good ventilation, and with adequate irrigation, can be tolerated by *Nephrolepis exaltata*.

Soil temperatures also are likely to be important in fern growth. Flinn and Pringle (1983) assessed the heat tolerance of rhizomes of several understory plant species, including bracken fern (*Pteridium aquilinum*) and some angiosperms, by immersing the rhizomes in a constant temperature water bath for five minutes at either 45, 50, 55 or 60°C. They reported that *P. aquilinum* was among the least tolerant to the high temperatures, and had the least mean regrowth index (- 2.0) compared to the most tolerant (4.0) for *Rhododendron canadense*. Zero growth occurred when the fern rhizomes were treated at 55°C.

Tree ferns are a major component of many tropical and subtropical forests (e.g., Brock et al., 2016), and their vitality during a possible warming climate raises questions about their response to temperature gradients. For example, current evidence based on correlative species distribution models suggests that the macro-scale distribution of tree ferns across New Zealand is largely determined by temperature (mean annual temperatures of 1.5–15.9°C) and solar radiation (11.7–15.3 MJ m<sup>-2</sup> day<sup>-1</sup>) (Brownsey, 2001; Lehmann et al., 2002). The growth and reproduction of two Australian tree ferns, *Cyathea australis* and *Dicksonia antarctica*, have been consistently associated with temperature and precipitation (Syfert et al., 2013; Fedrigo et al., 2014). Tree ferns in New Zealand show

interspecific elevational habitat preferences (as a function of climate), with the species distribution along latitudinal and elevational gradients suggesting that temperature is a major niche discriminator.

Volkova et al. (2009) examined the effects of high irradiance and moderate heat treatments on photosynthesis of the tree-fern *Dicksonia antarctica* in a climate chamber under two contrasting irradiance regimes (900 and 170  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ) and three sequential temperature treatments (15°C, 35°C, and back to 15°C). Temperature increase to 35°C resulted in further decreases in  $F_v/F_m$  (0.45) and in chlorophyll bleaching of high irradiance plants. Critical temperature for thylakoid stability ( $T_c$ ) of *D. antarctica* was comparable with other higher plants (c. 47°C), and increases of  $T_c$  with air temperature were greater in high irradiance plants.

Crassulacean acid metabolism (CAM) is an adaptation of some heat and drought tolerant plants, including ferns (e.g., Sayed, 2001), but only a few ferns (mainly epiphytic species) have been identified definitely to have CAM (e.g., Martin et al., 2005). Stomates in CAM plants are closed during the heat of the day, thus conserving water and energy, but open at night when  $\text{CO}_2$  is assimilated and chemically stored for use in photosynthesis on the following day. Additional research is needed to explore the presence of CAM in ferns that may be subjected to extremes in heat during climate change, especially for those already living in warmer environments.

## Summary

Overall, we have only limited evidence of how increasing frequency of droughts, extended periods of dryness, and increasing temperature may affect the reproductive stages of many groups of ferns during projected major changes in the climate, but it is evident that there is considerable diversity in fern resilience to habitats that exhibit occasional or recurrent periods of desiccation stress. Likewise, biogeographic and laboratory studies have shown the remarkable diversity among fern species adapted to differences in optimal light intensity, varying from the twilight of the dense tropical forest floor, to the extreme illumination of epiphytic habitats in the

tree crowns, and in open ground of arid and rocky environments. Further research is needed to better understand the biological bases for these adaptive differences. In addition to temperature tolerance studies, much more field-based and experimental research is needed to determine more clearly the range in intensities of water stress that many species, or functional groups, of ferns can successfully endure. Given that global increases in temperature are likely to be one of the most significant forcing functions on the ecophysiology and adaptability of ferns, especially for more mesic and cooler climate ferns, a much more focused research agenda is needed with major functional groups of ferns to better document their temperature optima and maxima.

## CASE STUDIES OF FIVE GROUPS OF FERNS IN VARYING HABITATS

### *Hymenophyllum* spp. and Relatives (Filmy Ferns)

The filmy ferns are characterized by leaves that are extremely thin with lamina composed of a single cell layer, lacking stomata. They include, for example, *Hymenophyllum* and *Trichomanes* in the family Hymenophyllaceae. However, ferns in other families also have acquired this reduced leaf morphology including *Hymenophyllopsis* (Cyatheaceae), *Leptopteris* (Osmundaceae), as well as several species of *Asplenium* (Aspleniaceae), *Cystopteris* (Woodsiaceae), and some *Danea* (Marattiaceae) (Kramer et al., 1995; Hietz, 2010). Consequently, their leaves are translucent and appear film-like, and they are largely found in very humid, often shaded environments, or as epiphytes on trees in humid, tropical regions. However, some species are found in temperate regions (Morton, 1947; Richards and Evans, 1972) as well as tropical and semi-tropical regions (Young and Leon, 1991; Ebihara and Iwatsuki, 2007; Mehltreter, 1995; Moore et al., 2010).

In temperate locales, such as Britain, *Hymenophyllum tunbrigense* are found locally abundant on rocks, more rarely on trees and on peaty soil among bryophytes, in moist, well-sheltered situations (Richards and Evans, 1972). Moreover, they have been found in *Abies alba* forests in the French, Vosges Mountains on moist and small (less than 2.5 m high) sandstone rocks, generally located near running water in wet valleys, at altitudes between 400 and 640 meters (Muller et al., 2006). In the Eume Valley (northwest Spanish region of Galicia) the lower part of the valley has an unusually warm, wet microclimate with very low frost risk, and is an important refuge for a number of endangered fern species including *H. tunbrigense* (Vázquez and Norman, 1995). In tropical regions, they occur in humid, terrestrial locations, but also vertically within forest trees, including high canopy species (e.g., Krömer and Kessler, 2006).

Because the leaves have become so morphologically reduced, the ecophysiology of these vascular ferns is more comparable to that of Bryophyta (e.g., mosses). They are poikilohydric and some are desiccation resistant, but only to a limited degree in many cases; and environmental factors such as available moisture and relative humidity can be determining factors in their abundance, especially for epiphytes in tree canopies.

Previous studies have focused on the ecophysiology of the Hymenophyllaceae (Härtel, 1940; Gessner, 1940; Proctor, 2003) and general ecology (e.g., Dubuisson et al., 2003), but very little is known about the vertical distribution of tropical species within the forest strata, although Krömer and Kessler (2006) have examined their distribution in the high canopies of tropical forest trees in Bolivia. Furthermore, Parra et al. (2009) examined the microhabitats of epiphytic Hymenophyllaceae species among host trees in a temperate rain forest in Chile, and reported that canopy openness and relative humidity differed significantly with height in trees. While canopy openness increased with height in a host tree, relative humidity decreased. DCA analysis showed that filmy fern species distribution within and among trees was mainly explained by the relative humidity of the microhabitat.

In a more general perspective, Proctor (2012) examined light and desiccation responses of Hymenophyllaceae in various tropical or semi-

tropical regions and made some conclusions about their worldwide ecological niche space and its limits. Overall, he reported that light and desiccation responses of filmy ferns can be interpreted as an integrated system. At low light and wind speed in humid forests, net radiation and saturation deficit are low, and diffusion resistance is high. Simultaneously, transpiration water loss is slow, and can be supported by modest conduction from the substratum. However, with higher irradiance, selection pressure for desiccation tolerance increases progressively, and there is greater evidence for recovery after water loss. Proctor (2012) further noted that in an environment with low light and high humidity, the filmy fern pattern of adaptation is probably optimal, and there is likely no major gain in having the more complex features of thicker leaves with mesophyll and stomata found in other vascular plants. Overall, trade-offs between light adaptation and desiccation tolerance, and between stem conduction and water absorption through the leaf surface, underlie adaptive radiation and niche differentiation of species within the Hymenophyllaceae.

Cea et al. (2014) using molecular genetic, proteomic analysis of desiccation tolerant species found that the desiccation tolerant properties of these filmy ferns are constitutive and not an inducible response. Moreover, the rate at which desiccation takes place precludes the induction of protective systems, further suggesting that there is a constitutive mechanism of cellular protection. Overall, however, the desiccation tolerance of many filmy fern species is limited; and extended periods of desiccation can be fatal. Given their likely fragile response to major climate change variables, though some are tolerant for short durations of desiccation, the filmy ferns are susceptible to major loss by increasing temperatures and decreasing available moisture, especially for those found in cool and humid present-day environments. However, in otherwise favorable environments, increasing atmospheric concentrations of CO<sub>2</sub> may enhance survival through increased primary production, and this aspect of filmy fern physiology deserves much more attention, among other responses to current climate change variables.

***Osmunda* spp. (e.g., *Osmunda regalis*)**

*Osmunda* spp. (Figure 1 D & E), in the family Osmundaceae, have one of the richest fossil records ranging as far back as the Late Triassic (e.g., Rothwell and Stockey, 2013) and many representative species are distributed globally (Kato, 2007). For example, *Osmunda regalis* (Figure 1 E) is a cosmopolitan species distributed worldwide. A general survey of osmundaceous plants has been published by Sharma et al. (2012). Landi and Angiolini (2010), who studied populations of *O. regalis* in Italy, reported that it performed best in conditions of full sunlight, but also could persist and recruit young sporophytes under closed canopy. Because many marsh and lake environments have disappeared or been altered by human activity in portions of Italy, more populations were located under high canopy cover in the forest than in open habitats. However, fewer and smaller fronds were found in plots with high forest canopy cover. Light seemed to promote fertility, as the number of fertile fronds decreased with increasing canopy cover.

Landi and Angiolini (2011) examined the structure of 42 natural populations of *O. regalis* in the Mediterranean area, and reported some insights into ecological factors for their distribution and community structure that may be insightful for predicting effects of changing environments. They reported the following findings: (1) dynamic populations, characterized by a large proportion of sporelings and vegetative adults, are associated with streams and nemoral species; (2) stable populations, with a higher proportion of generative adults, were found prevalently in habitats rich in hygrophilous grasses and shrubs, with lower tree cover; and (3) spring swamps, with populations that provide a clear example of remnant dynamics, are the habitat with the most stable conditions for *O. regalis*. They conclude that these dynamic populations can only survive by virtue of a continuous supply of propagules from spring swamps. Therefore, the maintenance of unaltered spring swamps is an indispensable requisite for the regional conservation of *O. regalis* under the current Mediterranean climate.

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***Asplenium nidus* (Tropical Epiphytic and Terrestrial Fern)**

*Asplenium nidus* (bird's nest fern) forms a funnel-shaped crown of long, erect and stiff, lance-shaped, bright green leaves emanating from a central basal point on the erect rhizome (Figure 1G). It is a widespread epiphytic fern in the Old World tropical rain forests. Zhang et al. (2010) examined factors affecting the distribution and abundance of *A. nidus* in a tropical lowland rain forest in Malaysia. They found that *A. nidus* was present on a wide diversity and size range of host taxa, but was more abundant in the understory, and on hosts with smooth bark and relatively flat branch angles. Larger individuals occurred higher in the canopy and were more common in the hilly area. They suggest that the distribution of *A. nidus* may represent a trade-off between the availability of suitable microsites for establishment in the understory and better growth conditions higher in the canopy. Fayle, et al. (2009) studying epiphytic ferns in a tropical rain forest reported that *A. nidus* was found at all heights in the canopy and was associated with emergent trees and areas with an open understory. A larger species *Asplenium phyllitidis* was found higher in the canopy, while larger *A. nidus* was found on trunks and branches with a wider diameter. They surmised that *A. nidus* seems adapted to withstand the hot dry conditions in the upper canopy and in gaps, and its size is consequently limited only by the size of its support.

Freiberg and Turton (2007) concluded, based on experimental and natural field-based data, that drought is probably a more important abiotic factor to control the population of *A. nidus* than air temperature, relative humidity, wind or sunlight. In a more general study of *A. nidus* ecophysiology, Martin et al. (2004) provided evidence of varying plant sizes on several ecophysiological parameters. They reported that although rates of net CO<sub>2</sub> exchange of the leaves measured in situ in the field appeared to increase with plant size, this increase and other size-related differences in gas exchange parameters were not significant. Leaf stomatal densities were higher in larger plants. However, experimental studies by Ainuddin and Nur Najwa (2009) using pot experiments showed that *A. nidus* was able to adapt and survive without watering for 16 weeks,

suggesting its adaptive hardiness to periodic limited moisture. Moreover, varied patterns of applying water (once every day extending to withholding water entirely) showed that watering every day produced the highest dry matter production, and the plants allocated more growth to the shoot under optimum conditions, but more growth to the root under stress conditions. When water was withheld for 16 weeks, all growth decreased; although the plants survived as stated above.

Overall, *A. nidus* appears to be an example of an epiphytic plant that has become adapted to the demands of high canopy existence, including extended periods of water deprivation, thus enhancing its likely survival potential for possible increased water stress and more elevated temperatures associated with global climate change.

### ***Lygodium* spp. (Climbing Fern)**

*Lygodium* (Figure 1H) is a genus of ferns, largely tropical, across the world, with a few temperate species in eastern Asia and eastern North America. It is called a “climbing fern” because the rachis (midrib) of each leaf is thin, flexible, and long, extending its length by indeterminate growth, due to a persistent apical meristem. The rachis of the leaf twines around its support such that each leaf forms a distinct vine. The vine-like leaves can reach lengths of many meters, and some species have become problematic invasive weeds in warmer regions of the U. S. A. *Lygodium microphyllum* (Old World Climbing Fern), introduced as an ornamental plant, has become a noxious weed in Florida (e.g., Beckner, 1968).

Among other factors contributing to its successful expansion is a symbiotic association with arbuscular mycorrhizal fungi (AMF) that promotes growth rate compared to plants without the symbiosis (Soti et al., 2014). Moreover, *L. microphyllum* is highly dependent on the mycorrhizal fungi for growth and phosphorus uptake. These results suggest that AMF play a significant role in vegetative reproduction and likely enhance the invasiveness of *L. microphyllum* in south Florida’s natural areas. Other contributing factors include a capability of intragametophytic selfing. That

is, each gametophyte is capable of producing both antheridia and archegonia, thus permitting self-fertilization. Lott et al. (2003) showed that 78% of *L. microphyllum* gametophytes in laboratory culture produced sporophytes by self-fertilization, while over 90% of the *L. japonicum* gametophytes self-fertilized and produced sporophytes. They conclude that the high intragametophytic selfing rate achieved by both species has likely facilitated their ability to colonize and spread through Florida as well as other warm climatic regions of the New World. Moreover, *L. microphyllum* is capable of both selfing and mixed mating. Thus, it appears to have the ability to invade distant habitats and then adapt to local conditions. The implications for this adaptability in relation to challenges presented by global climate change, especially global warming, deserve greater attention.

***Cheilanthes (Myriopteris) spp.***  
**(Arid-Adapted, Rock-Dwelling Ferns)**

Species of *Cheilanthes* (Figure 1C), and those transferred to the reconstituted genus *Myriopteris* (Grusz and Windham, 2013), are rock-dwelling and arid terrestrial ferns widely distributed globally; e.g., North and South America (Petrik-ott and Ott, 1982; Ponce and Morbelli, 1989; Rothfels et al., 2012), Europe (Berthet, 1987; Fuchs, 1961), Asia (Miyamoto and Ohba, 1997), Africa (Klopper et al., 2006; Scheipe, 1954), and Australia (Horton, 2004; Quirk et al., 1983).

*Cheilanthes* sporophytes are remarkably adapted to survive in harsh, xeric environments, including ultimate tops of mountain ridges in Costa Rica (e.g., Mehltreter, 1995), and have morphological features and reproductive mechanisms that aid their survival in dry climates and numerous xeric habitats. These adaptive features include carbohydrate and lipid contents in gametophytes that relegate them to substrates with a small but continuous water source (e.g., Crow et al., 2011). Additional features of gametophyte and sporophyte development in *Cheilanthes farinosa* have been studied by Srivastava and Uniyal (2014), who reported that this

species appears to be a good colonizer in nature. Moreover, *Cheilanthes* sporophytes produce abundant leaf-surface trichomes that help to prevent water loss (Quirk and Chambers, 1981). The leaves have a thick cuticle, and as a result some species appear bluish-green (Cobb et al., 2005). The leaf cells exhibit reduced surface area to volume (Gratani et al., 1998), hence there is a relatively small amount of cell surface area for water loss. They are desiccation-tolerant and can dry and rehydrate (Quirk and Chambers, 1981). The presence of mycorrhizal associations, as in other vascular plants, aid in water and nutrient uptake (Al-Karaki, 1998; Harley and Smith, 1983). Other physiological adaptive features of *Cheilanthes* spp. (e.g., *C. persica*) were reported by Gratani et al. (1998).

Various anatomical features also promote successful invasion and survival in xeric environments. The fundamental anatomy of the rhizome has been documented in 26 taxa in the genus *Cheilanthes* by McCulloch et al. (1974). Sen and Mukhopadhyay (2014) have shown that the vascular tissue of rhizomes contains tracheids as in most ferns and also vessels (but not in the stipes), thus enhancing efficient water and nutrient conduction to the base of the leaves. The vessel elements have distinct, obliquely elongated endplates, mostly provided with a compound perforation plate without a pit membrane. At least one species (*C. bolborrhiza*) has storage roots with enlarged pericycle cells containing starch grains that can provide energy reserves in coping with stressful arid environments (Schneider, 1999). At this time, *C. bolborrhiza* has not been assigned to the reconstituted genus *Myriopteris* by Grusz and Windham (2013). Additionally, leaf adaptive features of some *Cheilanthes* spp. (e.g., *Cheilanthes* [*Myriopteris*] *myriophylla*), and other ferns, include a possible passive hydraulic control of stomata in response to changes in leaf water status. This provides for efficient stomatal responses to vapor pressure deficit (VPD) between the leaves and the atmosphere, leading to closure rates as fast or faster than those seen in most angiosperms (Martins et al., 2016). This rapid stomatal response increases the adaptive potential for such arid plants when transient changes in atmospheric water vapor pressure could otherwise put higher water use demands on the plant.

The Cheilanthoid ferns and other “resurrection ferns” exhibit some of the remarkable adaptive features that allow them to persist during drought conditions, but also revive rapidly when moisture is sufficiently available as occurs with sporadic occurrences of precipitation characteristic of many deserts and other arid lands. Cheilanthoid ferns appear to be well adapted to survive during likely climate change scenarios, where increased atmospheric CO<sub>2</sub>, increased temperatures, and possibly limited precipitation are predicted.

## FUTURE OUTLOOK FOR CONSERVATION AND MANAGEMENT

Substantial attention has been given to challenges and policies of fern conservation, largely because of habitat destruction and also increasing concerns about climate change (e.g., Mehltreter, 2010). Given the diversity of fern habitats and the global distribution of some major groups, a coherent set of policies and plans may be difficult to assemble separate from the particular locale, and there are well-established conservation efforts underway in many geographic regions. However, some major conceptual strategies and guidelines have been published that provide sound advice for *in situ* and *ex situ* conservation efforts at local and national levels (e.g., Arcand and Ranker, 2013; Ibars and Estrelles, 2012; Mehltreter, 2010), including specific insights on conservation of fern spores (e.g., Ballesteros, 2011), and other *ex situ* techniques (Pence, 2013). Jermy and Ranker (2002) emphasize the importance of adopting an ecosystem approach to species conservation, while also considering regional approaches to *in situ* and *ex situ* methods of protection and restoration. Mehltreter (2010) has added six aspects of ecological data needed for risk assessment, in general: (1) fern abundance; (2) geographic range; (3) habitat specificity; (4) intrinsic biological factors (e.g., growth rates, dispersal or reproduction); (5) population dynamics and genetic diversity; and (6) environmental disturbances (such as fire, land use

change, etc.). Coordination of numerous governmental, legal, institutional and social entities are required to successfully implement conservation efforts. Ibars and Estrelles conclude “As we could observe in many conservation programmes already developed, coordination between scientists and government departments is necessary to develop, and especially to complete, effective conservation or recovery programmes” (p. 78). They provide an informative diagram of actions (Figure 4, p. 79) to guide future planners of fern conservation in a broad perspective.

In this chapter, I have especially emphasized the importance of scientific information; because a lasting and well-informed plan must include a sound knowledge of the basic biological and environmental properties of major plant groups if all of the other conservation efforts are to succeed. There are many reasons for a full commitment to conservation of fern communities, not the least is their remarkable beauty and importance to the integrity of plant ecosystems, worldwide. Much more coordinated effort among major botanical institutions is needed to provide the comprehensive scientific knowledge of ferns at the ecosystems level, as well as among functional groups, to properly guide coherent policies for their conservation for future generations.

## CONCLUSION

While it is clear many fragile fern habitats are undergoing major changes, and some fern species will incur increasing stress, we need additional field-based and laboratory experimental studies to more fully determine the primary effects of climate change on major functional groups of ferns, and to determine how antagonistic and synergistic relationships with other biota (animals and plants) will affect fern community dynamics in a changing environment. Given the expansive number of modern fern species, a judicious and systematic plan of research is needed, perhaps focusing on major functional groups to determine soil moisture requirements, temperature tolerance ranges, and light intensity optima. In this respect, Derzhavina (2015) has presented an interesting

discussion of possible ecologically relevant fern morpho-functional groups, especially for rock-dwelling ferns. Because ferns have a remarkable reproductive cycle with alternation of generations and dispersal by spores, there is an added complexity to understanding the likely climatic challenges for fern survival. Each of the reproductive stages (spore, gametophyte, and sporophyte) may be differentially affected by climate change variables, and each is an essential link in fern adaptability, dispersion, and recruitment. Current evidence, though limited, indicates that for a given fern species, each of these stages may have different environmental requirements for successful completion of the fern life cycle, and establishment of the next generation. This fundamental scientific knowledge is essential to informed and effective policies for conservation and management. Some ferns are becoming regional and international problem species requiring multi-pronged management strategies (e.g., Clements et al., 2014; Pemberton, 1998; Schmitz, 2007). Moreover, predicting possible future problem species accompanying climate change is a challenge, and vigilance and foresight in monitoring current, locally abundant species as potential problem ferns may be required.

Overall, we have only limited evidence of how increasing frequency of droughts, extended periods of dryness, and increasing temperature may affect the reproductive stages of many groups of ferns during projected major changes in the climate, but it is evident that there is considerable diversity in fern resilience to habitats that exhibit occasional or recurrent periods of desiccation stress. In addition to temperature studies, much more field-based and experimental research (e.g., with controlled climate chambers) is needed to determine more clearly the range in intensities of water stress that many species, or functional groups, of ferns can successfully endure. Given that global increases in temperature are likely to be one of the most significant forcing functions on the ecophysiology and adaptability of ferns, especially for more mesic and cooler climate ferns, a much more focused research agenda is needed with major functional groups of ferns to better document their temperature optima and maxima. Further research is also needed on the moisture requirements, and

responses to light intensity across major ecologically significant groups of ferns. As with many groups of vascular plants, the effects of increasing atmospheric CO<sub>2</sub> on different environmental and ecophysiological groups of ferns requires additional research attention. In some cases, a positive response can be expected, not only through enhanced primary production, but also indirectly through morphological changes such as less surface density of stomates, thus increasing the likelihood of survival of species in increasingly drier habitats where they normally would be at risk due to transpiration losses. In general, an evidence-based strategy for selecting major groups of ferns to be studied is needed, because it is clear we cannot assess climate change effects for every fern species.

Provisionally, the designated groups to be studied could include a three-tiered, broad categorical sampling plan in selecting fern species for climate-related research: I. Those in Major Climate Regimes (e.g., Arctic, temperate, tropical); II. Secondarily, in Broad Biogeographic Ecosystems (e.g., dry and arid regions; deciduous and non-deciduous forests, and those in lowland and montane regions; grasslands and other open landscapes; marshes and wetlands); and III. More specifically, those in Taxonomic Groups, at least to the family level, based on modern molecular genetic cladistics. Ideally, selected species at the genus level may be needed to refine predictions where adaptive features are particularly varied at the family level. Such synoptic data may substantially enhance our ability to model and predict responses of ferns to future major climate changes.

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**REFERENCES**

- Ainuddin, N. A. & Nur Najwa, D. A. (2009). Growth and physiological responses of *Asplenium nidus* to water stress. *Asian Journal of Plant Sciences*, 8, 447-450.
- Al-Karaki, G. N. (1998). Benefit, cost and water-use efficiency of arbuscular mycorrhizal durum wheat grown under drought stress. *Mycorrhiza*, 8, 41-45.
- Anderson, O. R. (2009). Eukaryotic microbial communities associated with the rhizosphere of the temperate fern *Thelypteris noveboracensis* (L.) Nieuwl. *American Fern Journal*. 99, 176-181.
- Arcand, N. N. & Ranker, T. A. (2013). Conservation biology. In T. A. Ranker & C. H. Haufler (Eds.), *Biology and Evolution of Ferns and Lycophytes* (257-283). Cambridge: Cambridge University Press.
- Ballesteros, D. (2011). Chapter 12 Conservation of fern spores. In H. Fernandez, A. Kumar, & M. A. Revilla (Eds.), *Working with Ferns: Issues and Applications* (165-172). New York: Springer.
- Ballesteros, D., Estrelles, E., Walters, C., & Ibars, A. M. (2011). Effect of storage temperature on green spore longevity for the ferns *Equisetum ramosissimum* and *Osmunda regalis*. *CryoLetters*, 32, 89-98.
- Banks, J. A. (1999). Gametophyte development in ferns. *Annual Review of Plant Physiology and Plant Molecular Biology*, 50, 163-186.
- Bazzaz, F. A. (1996). *Plants in Changing Environments: Linking Physiological, Population, and Community Ecology*. Cambridge: Cambridge University Press.
- Beckner, J. (1968). *Lygodium microphyllum*, another fern escaped in Florida. *American Fern Journal*, 58, 93-94.
- Berthet, P. (1987). *Cheilanthes-marantae* L. Domin and *Asplenium-cuneifolium* Viv. (Fougères) Ferns in the Mont Pilat (massif central France). *Bulletin Mensuel de la Société Linnéenne de Lyon*, 56, 69-72.
- Bhattarai, K. R., Vetaas, O. R., & Grytnes, J. A. (2004). Fern species richness along a central Himalayan elevational gradient, Nepal. *Journal of Biogeography*, 31, 389-400.

- Brock, J. M. R., Perry, G. L. W., Lee, W. G., & Burns, B. R. (2016). Tree fern ecology in New Zealand: A model for southern temperate rainforests. *Forest Ecology and Management*, 375, 112-126.
- Brodersen, C. R., Roark, L. C., & Pittermann, J. (2012). The physiological implications of primary xylem organization in two ferns. *Plant Cell and Environment*, 35, 1898-1911.
- Brodribb, T. J., McAdam, S. A. M., Jordan, G. J., & Feild, T. S. (2009). Evolution of stomatal responsiveness to CO<sub>2</sub> and optimization of water-use-efficiency among land plants. *The New Phytologist*, 183, 839-847.
- Brownsey, P. J. (2001). New Zealand's pteridophyte flora – plants of ancient lineage but recent arrival? *Brittonia*, 53, 284–303.
- Brum, F. & Randi, A. M. (2002). High irradiance and temperature inhibit the germination of spores of the fern *Rumohra adiantiformis* (Forst.) Ching (Dryopteridaceae). *Revista Brasil Botanica*, 25, 391-396.
- Bystriakova, N., Ansell, S. W., Russell, S. J., Grundmann, M., Vogel, J. C., & Schneider, H. (2014). Present, past and future of the European rock fern *Asplenium fontanum*: combining distribution modelling and population genetics to study the effect of climate change on geographic range and genetic diversity. *Annals of Botany*, 113, 453-465.
- Cea, M. G., Claverol, S., Castillo, C. A., Pinilla, C. R., & Ramirez, L. B. (2014). Desiccation tolerance of Hymenophyllaceae filmy ferns is mediated by constitutive and non-inducible cellular mechanisms. *Comptes Rendus Biologies*, 337, 235-243.
- Chambers, S. M., Watkins, J. E. Jr., & Sessa, E. B. (2017). Differences in dehydration tolerance among populations of a gametophyte-only fern. *American Journal of Botany*, 104, 598-607.
- Clements, D. R., DiTommaso, A., & Hyvönen, T. (2014). Ecology and management of weeds in a changing climate. In B. S. Chauhan & G. Mahajan (Eds.) *Recent Advances in Weed Management* (13-37), New York: Springer.
- Colwell, R. K., Brehm, G., Cardelús, C. L., Gilman, A. C., & Longino, J. T. (2008). Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science*, 322, 258-261.

- Conway, E. (1949). The autecology of bracken (*Pteridium aquilinum*) (L.) Kuhn): the germination of the spore, and the development of the prothallus and the young sporophyte. *Proceedings of the Royal Society of Edinburgh B*, 63, 325-343.
- Cobb, B., Farnsworth, E., & Lowe, C. (2005). *Ferns of Northeastern and Central North America*, 2<sup>nd</sup> ed. Boston: Houghton Mifflin Co.
- Crow, W. E., Mack, M. R., Diamond, H. L., & Swatzell, L. L. (2011). Narrow substrate niche of *Cheilanthes lanosa*, the hairy lip fern, is determined by carbohydrate and lipid contents in gametophytes. *American Fern Journal*, 101, 57-69.
- Csergő, A. M., Salguero-Gómez, R., Broennimann, O., Coutts, S. R., Guisan, A., Angert, A. L., Welk, E., Stott, I., Enquist, B. J., McGill, B., Svenning, J.-C., Violle, C., & Buckley, Y. M. (2017). Less favourable climates constrain demographic strategies in plants. *Ecology Letters*, 20, 969-980.
- de Gasper, A. L., Eisenlohr, P. V., & Salino A. (2015). Climate-related variables and geographic distance affect fern species composition across a vegetation gradient in a shrinking hotspot. *Plant Ecology & Diversity*, 8, 25-35.
- Derzhavina, N. M. (2015). Adaptation of epilithic ferns on different levels of structural organization. *Contemporary Problems of Ecology*, 8, 141-147.
- Doi, M. & Shimazaki, K. (2008). The stomata of the fern *Adiantum capillus-veneris* do not respond to CO<sub>2</sub> in the dark and open by photosynthesis in guard cells. *Plant Physiology*, 147, 922-930.
- dos Santos, E. P. G., Lehmann, D. R. M., Santos, M., & Randi, A. M. (2010). Spore germination of *Gleichenella pectinata* (Willd.) Ching (Polypodiopsida-Gleicheniaceae) at different temperatures, levels of light and pH. *Brazilian Archives of Biology and Technology*, 53, 1309-1318.
- Dubuisson, J.-Y., Hennequin, S., Rakotondrainibe, F., & Schneider, H. (2003). Ecological diversity and adaptive tendencies in the tropical fern *Trichomanes* L. (Hymenophyllaceae) with special reference to

- climbing and epiphytic habits. *Botanical Journal of the Linnean Society*, 142, 41–63.
- Dyer, A. F. (1979). The culture of fern gametophytes for experimental investigation. In A. F. Dyer (Ed.) *The Experimental Biology of Ferns* (253-305). London, New York: Academic Press.
- Dyer, A. F. & Lindsay, S. (1992). Soil spore banks of temperate ferns. *American Fern Journal*, 82, 89-123.
- Ebihara, A. & Iwatsuki, K. (2007). The Hymenophyllaceae of the Pacific area. 1. *Hymenophyllum* subgenus *Hymenophyllum*. *Bulletin of the National Museum of Nature and Science Series B-Botany*, 33, 55-68.
- Esteves, L. M. & Dyer, A. F. (2003). The vertical distributions of live and dead fern spores in the soil of a semi-natural woodland in southeast Scotland and their implications for spore movement in the formation of soil spore banks. In S. Chandra & M. Srivastava (Eds.) *Pteridology in the New Millennium* (261-282). The Netherlands: Kluwer Academic Publishers.
- Fayle, T. M., Chung, A. Y. C., Dumbrell, A. J., Eggleton, P., & Foster, W. A. (2009). The effect of rain forest canopy architecture on the distribution of epiphytic ferns (*Asplenium* spp.) in Sabah, Malaysia. *Biotropica*, 41, 676-681.
- Farrant, J. M., Lenher, A., Cooper, K. & Wiswedel, S. (2009). Desiccation tolerance in the vegetative tissues of the fern *Mohria caffrorum* is seasonally regulated. *The Plant Journal*, 57, 65-79.
- Farrar, D. R., Dassler, C., Watkins Jr., J. E., & Skelton, C. (2013). Gametophyte ecology. In T. A. Ranker & C. H. Haufler (Eds.), *Biology and Evolution of Ferns and Lycophytes* (222-256). Cambridge: Cambridge University Press.
- Flexas, J., Carriqui, M., Coopman, R. E., Gago, J., Galmés, J., Martorell, S., Morales, F., & Diaz-Espejo, A. (2014). Stomatal and mesophyll conductances to CO<sub>2</sub> in different plant groups: Underrated factors for predicting leaf photosynthesis responses to climate change? *Plant Science*, 226, 41-48.
- Flinn, M. A. & Pringle, J. K. (1983). Heat tolerance of several understory species. *Canadian Journal of Botany*, 61, 452-457.

- Fedrigo, M., Kasel, S., Bennett, L. T., Roxburgh, S. H., & Nitschke, C. R. (2014). Carbon stocks in temperate forests of south-eastern Australia reflect large tree distribution and edaphic conditions. *Forest Ecology and Management*, 334, 129–143.
- Franks, P. J., Leitch, I. J., Ruzsala, E. M., Hetherington A. M., & Beerling, D. J. (2012). Physiological framework for adaptation of stomata to CO<sub>2</sub> from glacial to future concentrations. *Philosophical Transactions of the Royal Society B*, 367, 537-546.
- Freiberg, M. & Turton, S. M. (2007). Importance of drought on the distribution of the birds nest fern, *Asplenium nidus*, in the canopy of a lowland tropical rainforest in north-eastern Australia. *Austral Ecology*, 32, 70-76.
- Fuchs, H. P. (1961). The genus *Cheilanthes* Swartz and its European species. *British Fern Gazette*, 9, 38-48.
- Gessner, F. (1940). Die Assimilation der Hymenophyllaceen. *Protoplasma*, 34, 102–116.
- Gratani, L., Crescente, M. F., & Rossi, G. (1998). Photosynthetic performance and water use efficiency of the fern *Cheilanthes persica*. *Photosynthetica*, 35, 507-516.
- Grusz, A. L. & Windham, M. D. (2013). Toward a monophyletic *Cheilanthes*: The resurrection and recircumscription of *Myriopteris* (Pteridaceae). *PhytoKeys*, 32, 49-64.
- Hagar, W. G. & Freeberg, J. A. (1980). Photosynthetic rates of sporophytes and gametophytes of the fern *Todea Barbara*. *Plant Physiology*, 65, 584-586.
- Halpern, C. B., Evans, S. A., & Nielson, S. (1999). Soil seed banks in young, closed-canopy forests of the Olympic Peninsula, Washington: potential contributions to understory reinitiation. *Canadian Journal of Botany*, 77, 922-935.
- Harley, J. L. & Smith, S. E. (1983). *Mycorrhizal Symbiosis*. London: Academic Press.
- Härtel, O. (1940). Physiologische Studien an Hymenophyllaceen. II. Wasserhaushalt und Resistenz. *Protoplasma*, 34, 489–514.

- Haupt, W. & Psaras, G. K. (1989). Phytochrome-controlled fern-spore germination, kinetics of Pfr action. *Journal of Plant Physiology*, 135, 31-36.
- Hew, C.-S. & Wong, Y. S. (1974). Photosynthesis and respiration of ferns in relation to their habitat. *American Fern Journal*, 64, 40-48.
- Hietz, P. (2010). Fern adaptations to xeric environments. In K. Mehlreter, L. R. Walker, & J. M. Sharpe (Eds.) *Fern Ecology* (140-176). Cambridge: Cambridge University Press.
- Hietz, P. & Briones, O. (1998). Correlation between water relations and within-canopy distribution of epiphytic ferns in a Mexican cloud forest. *Oecologia*, 114, 305-316.
- Hietz, P. & Briones, O. (2001). Photosynthesis, chlorophyll fluorescence and within-canopy distribution of epiphytic ferns in a Mexican cloud forest. *Plant Biology*, 3, 279-287.
- Hörak, H., Kollist, H., & Merilo E. (2017). Fern stomatal responses to ABA and CO<sub>2</sub> depend on species and growth conditions. *Plant Physiology*, 174, 672-679.
- Horton, H. (2004). A survivor fern, *Cheilanthes nudiuscula*. *Queensland Naturalist*, 42, 64-65.
- Hvoslef-Eide, T. (1986). *Nephrolepis exaltata* 'Bostoniensis' – growth and development. *Gartneryrket*, 76, 871-874 (in Norwegian).
- Ibars, A. M. & Estrelles, E. (2012). Recent developments in ex situ and in situ conservation of ferns. *The Fern Gazette*, 19, 67-86.
- IPCC (2014). Climate Change 2014: Synthesis Report. *Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* [Core Writing Team, R.K. Pachauri and L.A. Meyer (Eds.)]. Geneva, Switzerland: IPCC.
- Jermy, A. C. & Ranker T. A. (2002). Epilogue – the way forward. *The Fern Gazette*, 16, 417-424.
- Johnson, D. (1985). New records for longevity of *Marsilea* sporocarps. *American Fern Journal*, 75, 30-31.
- Kappen, L. (1965). Untersuchungen über die Widerstandsfähigkeit der Gametophyten einheimischer Polypodiaceen gegenüber Frost, Hitze und Trockenheit [Investigations on the resistance of the gametophytes

- of indigenous polypodiaceae to frost, heat and drought]. *Flora*, 156, 101-115.
- Kato, M. (2007). Distribution of Osmundaceae. *Bulletin of the National Museum of Nature and Science, Series B*, 33, 81-90.
- Kessler, M. (2002). Range size and its ecological correlates among the pteridophytes of Carrasco National Park, Bolivia. *Global Ecology and Biogeography*, 11, 89-102.
- Kessler, M. (2010). Biogeography of ferns. In K. Mehltreter, L. R. Walker, & J. M. Sharpe (Eds.) *Fern Ecology* (22-60). Cambridge: Cambridge University Press.
- Khrapko, O. V. & Tsarenko, N. A. (2015). Adaptive strategies of two species from the Family Onocleaceae. *Contemporary Problems of Ecology*, 8, 148-154.
- Klopper, R. R., Lemmer, P., & Nel, J. (2006). Notes on African plants: Pteridophyta: Pteridaceae - *Cheilanthes deltoidea*, a new locality in Gauteng, South Africa. *Bothalia-Pretoria*, 36, 173-174.
- Kramer, K. U., Schneller, J. J., & Wollenweber, E. (1995). *Farne and Farnverwandte*. Stuttgart: Georg Thieme.
- Krömer, T. & Kessler, M. (2006). Filmy ferns (Hymenophyllaceae) as high-canopy epiphytes. *Ectotropica*, 12, 57-63.
- Landi, M. & Angiolini, C. (2010). Ecological responses of *Osmunda regalis* to forest canopy cover and grazing. *American Fern Journal*, 100, 137-147.
- Landi, M. & Angiolini, C. (2011). Population structure of *Osmunda regalis* in relation to environment and vegetation: an example in the Mediterranean area. *Folia Geobotanica*, 46, 49-68.
- Lammertsma, E. I., de Boer, H. J., Dekker, S. C., Dilcher, D. L., Lotter, A. F., & Wagner-Cremer, F. (2011). Global CO<sub>2</sub> rise leads to reduced maximum stomatal conductance in Florida vegetation. *Proceedings of the National Academy of Sciences*, 108, 4035-4040.
- Lehmann, A., Leathwick, J. R., & Overton, J. McC. (2002). Assessing New Zealand fern diversity from spatial predictions of species assemblages. *Biodiversity Conservation*, 11, 2217-2238.

- Liao, J.-X., Jiang, M.-X., & Huang, H.-D. (2013). Growth characteristics of *Adiantum reniforme* var. *sinensis* and *A. capillus-veneris* in response to light and soil moisture. *Nordic Journal of Botany*, *31*, 500-504.
- Lloyd, R. M., & Klekowski Jr., E. J. (1970). Spore germination and viability in Pteridophyta: evolutionary significance of chlorophyllous spores. *Biotropica*, *2*, 129-137.
- Lott, M. S., Volin, J. C., Pemberton, R. W., & Austin, D. F. (2003). The reproductive biology of the invasive ferns *Lygodium microphyllum* and *L. japonicum* (Schizaeaceae): implications for invasive potential. *American Journal of Botany*, *90*, 1144-1152.
- Marcon, C., Silveira, T., Schmitt, J. L., & Droste, A. (2017). Abiotic environmental conditions for germination and development of gametophytes of *Cyathea phalerata* Mart. (Cyatheaceae). *Acta Botanica Brasiliica*, *31*, 58-67.
- Martin, C. E., Lin, T.-C., Hsu, C.-C., Lin, S.-H., Lin, K.-C., Hsia, Y.-J., & Chiou, W.-L. (2004). Ecophysiology and plant size in a tropical epiphytic fern, *Asplenium nidus*, in Taiwan. *International Journal of Plant Science*, *165*, 65-72.
- Martin, S. L., Davis, R., Protti, P., Lin, T.-C., Lin, S.-H., & Martin, C. E. (2005). The occurrence of crassulacean acid metabolism in epiphytic ferns, with an emphasis on the Vittariaceae. *International Journal of Plant Sciences*, *166*, 623-630.
- Martins, S. C. V., McAdam, S. A. M., Deans, R. M., DaMatta, F. M., & Brodribb, T. J. (2016). Stomatal dynamics are limited by leaf hydraulics in ferns and conifers: results from simultaneous measurements of liquid and vapour fluxes in leaves. *Plant, Cell and Environment*, *39*, 694-705.
- Maschinski, J. & Haskins, K. E. (Eds.) (2012). *Plant Reintroduction in a Changing Climate: Promises and Perils*. Washington, D. C.: Island Press.
- Mcculloch, J. E., Volz, P. A., & Knobloch, I. W. (1974). The rhizome anatomy of certain species of the genus *Cheilanthes*. *Botanical Gazette*, *135*, 132-139.

- Mehltreter, K. (1995). Species richness and geographical distribution of montane pteridophytes of Costa Rica, Central America. *Feddes Repertorium*, 106, 563-584.
- Mehltreter, K. (2006). Leaf phenology of the climbing fern *Lygodium venustum* in a semideciduous lowland forest on the Gulf of Mexico. *American Fern Journal*, 96, 21-30.
- Mehltreter, K. (2010). Fern Conservation. In K. Mehltreter, L. R. Walker, & J. M. Sharpe (Eds.) *Fern Ecology* (323-359). Cambridge: Cambridge University Press.
- Mehltreter, K. (2013). Phenology and habitat specificity of tropical ferns. In T. A. Ranker & C. H. Haufler (Eds.), *Biology and Evolution of Ferns and Lycophytes* (201-221). Cambridge: Cambridge University Press.
- Mehltreter, K. & Garcia-Franco, J. G. (2008). Leaf phenology and trunk growth of the deciduous tree fern *Alsophila firma* (Baker) D. S. Conant in a lower montane Mexican forest. *American Fern Journal*, 98, 1-13.
- Mehltreter, K. & Palacios-Rios, M. (2003). Phenological studies of *Acrostichum danaeifolium* (Pteridaceae, Pteridophyta) at a mangrove site on the Gulf of Mexico. *Journal of Tropical Ecology*, 19, 155-162.
- Mehltreter, K., Walker, L. R., & Sharpe, J. M. (Eds.) (2010). *Fern Ecology*. Cambridge: Cambridge University Press.
- Mertens, J., Beladjal, L., Alcantara, A., Fougnes, L., van der Straeten, D., & Clegg, J. S. (2008). Survival of dried eukaryotes (anhydrobiotes) after exposure to very high temperatures. *Biological Journal of the Linnean Society*, 93, 15-22.
- Mikula, A., Tomiczak, K., Makowski, D., Niedzielski, M., & Rybczynski, J. J. (2015). The effect of moisture content and temperature on spore aging in *Osmunda regalis*. *Acta Physiologia Plantarum*, 37, 229.
- Miller, J. H. (1968). Fern gametophytes as experimental material. *Botanical Review*, 34, 361-440.
- Miyamoto, F. & Ohba, H. (1997). *Cheilanthes wusukungii*, a new species resembling *C. rufa* in Himalaya and Thailand. *Journal of Japanese Botany*, 72, 168-171.

- Moore, S.-J., Chen, C.-M., & Wang, J.-C. (2010). *Hymenophyllum pilosissimum* C. Chr. (Hymenophyllaceae), a new recorded fern from Taiwan. *American Fern Journal*, 100, 180-183.
- Moran, R. C. (2004). *A Natural History of Ferns*. Portland OR: Timber Press.
- Mortensen, L. M. & Larsen, G. (1989). Effects of temperature on growth of six foliage plants. *Scientia Horticulturae*, 39, 149-159.
- Morton, C. V. (1947). The American species of *Hymenophyllum* section *Sphaerocionium*. *Contributions from the United States National Herbarium*, 29, 1-viii.
- Muller, S., Jérôme, C., & Mahevas, T. (2006). Habitat assessment, phytosociology and conservation of the Tunbridge filmy-fern *Hymenophyllum tunbrigense* (L) Sm. in its isolated locations in the Vosges Mountains. *Biodiversity and Conservation*, 15, 1027-1041.
- Nayar, B. K. and Kaur, S. (1971). *Gametophytes of homosporous ferns*. *Botanical Review*, 37, 295-396.
- Nettesheim, F. C., Damasceno, E. R., & Sylvestre, L. S. (2014). Different slopes of a mountain can determine the structure of ferns and lycophytes communities in a tropical forest of Brazil. *Anais da Academia Brasileira de Ciências*, 86, 199-210.
- Nicotra, A. B., Atkin, O. K., Bonser, S. P., Davidson, A. M., Finnegan, E. J., Mathesius, U., Poot, P., Purugganan, M. D., Richards, C. L., Valladeras, F., & van Kleunen, M. (2010). Plant phenotypic plasticity in a changing climate. *Trends in Plant Science*, 15, 684-692.
- Nobel, P. S. (1978). Microhabitat, water relations, and photosynthesis of a desert fern, *Notholaena Parryi*. *Oecologia*, 31, 293-309.
- Nobel, P. S., Calkin, H. W., & Gibson, A. C. (1984). Influences of PAR, temperature and water vapor concentration on gas exchange by ferns. *Physiologia Plantarum*, 62, 527-534.
- Nondorf, S. L., Dooley, M. A., Palmieri, M., & Swatzell, L. J. (2003). The effects of pH, temperature, light intensity, light quality, and moisture levels on spore germination in *Cheilanthes feei* of Southeast Missouri. *American Fern Journal*, 93, 56-69.

- Nowak, J., Sroka, S., & Matysiak, B. (2002). Effects of light level, CO<sub>2</sub> enrichment, and concentration of nutrient solution on growth, leaf nutrient content, and chlorophyll fluorescence of Boston Fern microcuttings. *Journal of Plant Nutrition*, 25, 2161-2171.
- Ong, B.-L. & Ng, M.-L. (1998). Regeneration of drought-stressed gametophytes of the epiphytic fern, *Pyrrosia pilosellodes* (L.) Price. *Plant Cell Reports*, 18, 225-228.
- Page, C. N. (1979). Experimental aspects of fern ecology. In A. F. Dyer (Ed.), *The Experimental Biology of Ferns* (552-581). London: Academic Press.
- Parra, M. J., Acuña, K., Corcuera, L. J., & Saldaña, A. (2009). Vertical distribution of Hymenophyllaceae species among host tree microhabitats in a temperate rain forest in Southern Chile. *Journal of Vegetation Science*, 20, 588-595.
- Parris, B. S. (1985). Ecological aspects of distribution and speciation in Old World tropical ferns. *Proceedings of the Royal Society of Edinburgh*, 86B, 341-346.
- Pemberton, R. W. (1998). The potential of biological control to manage Old World climbing fern (*Lygodium microphyllum*), an invasive weed in Florida. *American Fern Journal*, 88, 176-182.
- Pence, V. C. (2013). Ex situ conservation of ferns and lycophytes – approaches and techniques In T. A. Ranker & C. H. Haufler (Eds.), *Biology and Evolution of Ferns and Lycophytes* (284-300). Cambridge: Cambridge University Press.
- Pérez-García, B., Mendoza-Ruiz, A., Sánchez-Coronado, M. E., & Orozco-Segovia, A. (2007). Effect of light and temperature on germination of spores of four tropical fern species. *Acta Oecologica*, 32, 172-179.
- Petrik-ott, A. J. & Ott, F. D. (1982). *Cheilanthes lanosa* and *Cystopteris protrusa* in Florida. *American Fern Journal*, 72, 31.
- Pittermann, J., Brodersen, C., & Watkins Jr., J. E. (2013). The physiological resilience of fern sporophytes and gametophytes: advances in water relations offer new insights into an old lineage. *Frontiers in Plant Science*, 4, doi: 10.3389/fpls.2013.00285.

- Ponce, M. M. & Morbelli, M. A. (1989). The *Cheilanthes dichotoma* group of South America. *American Fern Journal*, 79, 127-135.
- Poole, R. T. & Conover, C. A. (1981). Influence of maximum air temperatures and irrigation frequencies during high temperature periods of growth of four foliage plants. *Horticultural Science*, 16, 556-557.
- Pouteau, R., Meyer, J.-Y., Blanchard, P., Nitta, J. H., Terorotua, M., & Taputuarai, R. (2016). Fern species richness and abundance are indicators of climate change on high-elevation islands: evidence from an elevational gradient on Tahiti (French Polynesia). *Climatic Change*, 138, 143-156.
- Prange, R. K., Ormrod, D. P., & Proctor, J. T. A. (1983). Effect of water stress on gas exchange in fronds of the ostrich fern (*Matteuccia struthiopteris* (L.) Todaro). *Journal of Experimental Botany*, 34, 1108-1116.
- Proctor, M. C. F. (2003). Comparative ecophysiological measurements on the light responses, water relations and desiccation tolerance of the filmy ferns *Hymenophyllum wilsonii* Hook. and *H. tunbrigense* (L.) Smith. *Annals of Botany*, 91, 717-727.
- Proctor, M. C. F. (2012). Light and desiccation responses of some Hymenophyllaceae (filmy ferns) from Trinidad, Venezuela and New Zealand: poikilohydry in a light-limited but low evaporation ecological niche. *Annals of Botany*, 109, 1019-1026.
- Psaras, G. K. & Haupt, W. (1989). Light-induced fern-spore germination under reduced water potential. *Botanica Acta*, 102, 222-228.
- Quintanilla, L. G., Pajarón, S., Pangua, E., & Amigo, J. (2000). Effect of temperature on germination in northernmost populations of *Culcita macrocarpa* and *Woodwardia radicans*. *Plant Biology*, 2, 612-617.
- Quirk, H. & Chambers T. C. (1981). Drought tolerance in *Cheilanthes* with special reference to the gametophyte. *Fern Gazette*, 12, 121-129.
- Quirk, H., Chambers, T. C., & Regan, M. (1983). The fern genus *Cheilanthes* in Australia. *Australian Journal of Botany*, 31, 501-553.

- Ranal, M. A. (1999). Effects of temperature on spore germination in some fern species from semideciduous mesophytic forest. *American Fern Journal*, 89, 149-158.
- Ranal, M. A. (2003). Soil spore banks of ferns in a gallery forest of the ecological station of Panga Uberlândia, MG. Brazil. *American Fern Journal*, 93, 97-115.
- Ranker, T. A. & Haufler, C. H. (Eds.) (2013). *Biology and Evolution of Ferns and Lycophytes*. Cambridge: Cambridge University Press.
- Raghavan, V. (1980). Cytology, physiology, and biochemistry of germination of fern spores. *International Review of Cytology*, 62, 69-118.
- Raghavan, V. (1989). *Developmental Biology of Fern Gametophytes*. Cambridge: Cambridge University Press.
- Richard, M., Bernhardt, T. & Bell, G. (2000). Environmental heterogeneity and the spatial structure of fern species diversity in one hectare of old-growth forest. *Ecography*, 23, 231-245.
- Richards, P. W. & Evans, G. B. (1972). *Hymenophyllum Tunbrigense* (L.) Sm. *Journal of Ecology*, 60, 245-268.
- Richardson, S. J. & Walker, L. R. (2010) Nutrient ecology of ferns. In K. Mehlreter, L. R. Walker, & J. M. Sharpe (Eds.) *Fern Ecology* (111-139). Cambridge: Cambridge University Press.
- Riaño, K. & Briones, O. (2015). Sensitivity of three tree ferns during their first phase of life to the variation of solar radiation and water availability in a Mexican cloud forest. *American Journal of Botany*, 102, 1472-1481.
- Rothfels, C. J., Sigel, E. M., & Windham, M. D. (2012). *Cheilanthes feei* T. Moore (Pteridaceae) and *Dryopteris erythrosora* (D. C. Eaton) Kunze (Dryopteridaceae) new for the flora of North Carolina. *American Fern Journal*, 102, 184-186.
- Rothwell, G. W. & Stockey, R. A. (2013). Phylogeny and evolution of ferns: a paleontological perspective. In T. A. Ranker & C. H. Haufler (Eds.) *Biology and Evolution of Ferns and Lycophytes* (332-336). Cambridge: Cambridge University Press.

- Sayed, O. H. (2001). Crassulacean acid metabolism 1975-2000, a check list. *Photosynthetica*, 39, 339-352.
- Scheipe, E. A. C. L. E. (1954). The *Cheilanthes multifida* complex in southern Africa. *Journal of South African Botany*, 20, 127-13.
- Schmitz, D. C. (2007). Florida's invasive plant research: Historical perspective and the present research program. *Natural Areas Journal*, 27, 251-253.
- Schneider, H. (1999). Yet another fern with storage roots: *Cheilanthes bolborrhiza* Mickel and Beitel (Pteridaceae: Pteridophyta) from Mexico and El Salvador. *Fern Gazette*, 15, 269-273.
- Schneider, H., Schuettpelz, E., Pryer, K. M., Cranfill, R., Magallón, S., & Lupia, R. (2004). Ferns diversified in the shadow of angiosperms. *Nature*, 428, 553-557.
- Sen, K. & Mukhopadhyay, R. (2014). New report of vessel elements in *Aleuritopteris* and *Cheilanthes*. *Taiwania*, 59, 231-239.
- Sharma, B. D., Bohra, D. R., Suthar, O. P., & Harsh, R. (2012). An introduction and literature on osmundaceous plants. *Indian Fern Journal*, 29, 137-148.
- Sharpe, J. M. (1997). Leaf growth and demography of the rheophytic fern *Thelypteris angustifolia* (Willdenow) Proctor in a Puerto Rican rainforest. *Plant Ecology*, 130, 203-212.
- Sharpe, J. M., Mehltreter, K., & Walker, L. R. (2010). Ecological importance of ferns. In K. Mehltreter, L. R. Walker, & J. M. Sharpe (Eds.) *Fern Ecology* (1-21). Cambridge: Cambridge University Press.
- Sheffield, E. (2013). Alternation of generations. In T. A. Ranker & C. H. Haufler (Eds.) *Biology and Evolution of Ferns and Lycophytes* (49-74). Cambridge: Cambridge University Press.
- Sinclair, R. (1983). Water relations of tropical epiphytes I. relationships between stomatal resistance, relative water content and the components of water potential. *Journal of Experimental Botany*, 34, 1652-1663.
- Sivanesan, I., Son, M. S., Soundararajan, P., & Jeong, B. R. (2014). Effect of silicon on growth and temperature stress tolerance of *Nephrolepis exaltata* 'Corditas'. *Korean Journal of Horticultural Science and Technology*, 32, 142-148.

- Smith, A. R., Pryer, K. M., Schuettpelz, E., Korall, P., Schneider, H., & Wolf, P. G. (2013). Fern classification. In T. A. Ranker & C. H. Haufler (Eds.) *Biology and Evolution of Ferns and Lycophytes* (417-467). Cambridge: Cambridge University Press.
- Soti, P. G., Jayachandran, K., Purcell, M., Volin, J. C., & Kitajima, K. (2014). Mycorrhizal symbiosis and *Lygodium microphyllum* invasion in south Florida – a biogeographic comparison. *Symbiosis*, 62, 81-90.
- Srivastava, R. & Uniyal, P. L. (2014). In-vitro developmental studies of *Cheilanthes farinosa* (Forssk.) Kaulf. (Pteridaceae). *Journal of Plant Systematics*, 17, 87-91.
- Syfert, M. M., Smith, M. J., & Coomes, D. A. (2013). The effects of sampling bias and model complexity on the predictive performance of MaxEnt species distribution models. *PLoS One*, 8, e55158. doi:10.1371/journal.pone.0055158.
- Testo, W. L. & Watkins Jr., J. E. (2013). Understanding mechanisms of rarity in pteridophytes: competition and climate change threaten the rare fern *Asplenium scolopendrium* var. *americanum* (Aspleniaceae). *American Journal of Botany*, 100, 2261-2270.
- Towill, L. R. (1978). Temperature and photocontrol of *Onoclea sensibilis* spore germination. *Plant Physiology*, 62, 116-119.
- Tseng, M.-H., Lin, K.-H., Huang, Y.-J., Chang, Y.-L., Huang, S.-C., Kuo, L.-Y., & Huang, Y.-M. (2017). Detection of chlorophylls in spores of seven ferns. *Journal of Plant Research*, 130, 407-416.
- Tryon, R. M. (1986). The biogeography of species with special reference to ferns. *The Botanical Review*, 52, 117-156.
- Tryon, R. M. & Tryon, A. F. (2012). *Ferns and Allied Plants with Special Reference to Tropical America*. New York: Springer.
- Uehlein, N., Kai, L. & Kaldenhoff, R. (2017). Plant Aquaporins and CO<sub>2</sub>. In F. Chaumont & S. D. Tyerman (Eds.) *Plant Aquaporins, Signaling and Communication in Plants*. Cham, Switzerland: Springer International.
- Vázquez, A., J. & Norman, G. (1995). Identification of site-types important for rare ferns in an area of deciduous woodland in northwest Spain. *Vegetatio*, 116, 133-146.

- Verma, S. C. (2003). Some aspects of reproductive biology of the gametophyte generation of homosporous ferns. In S. Chandra & M. Srivastava (Eds.) *Pteridology in the New Millennium* (455-484). The Netherlands: Kluwer Academic Publishers.
- Viviani, D. & Randi, A. M. (2008). Effects of pH, temperature and light intensity on spore germination and growth analysis of young sporophytes of *Polypodium lepidopterist* (Pteridophyta, Polypodiaceae). *Rodriguésia*, 59, 751-760.
- Voeller, B. (1971). Developmental physiology of fern gametophytes: Relevance for biology. *BioScience*, 21, 266-270.
- Volkova, L., Tausz, M., Bennett, L. T., & Dreyer, E. (2009). Interactive effects of high irradiance and moderate heat on photosynthesis, pigments, and tocopherol in the tree-fern *Dicksonia antarctica*. *Functional Plant Biology*, 36, 1046-1056.
- Wada, M. (2013). Photoresponses in fern gametophytes. In T. A. Ranker & C. H. Haufler (Eds.) *Biology and Evolution of Ferns and Lycophytes* (2-48). Cambridge: Cambridge University Press.
- Walker, L. & Sharpe, J. M. (2010). Ferns, disturbance and succession. In K. Mehltreter, L. R. Walker, & J. M. Sharpe (Eds.) *Fern Ecology* (177-219). Cambridge: Cambridge University Press.
- Wan, X.-M., Lei, M., Huang, Z.-C., Chen, T.-B., & Liu, Y.-R. (2010). Sexual propagation of *Pteris vittata* L. influenced by pH, calcium, and temperature. *International Journal of Phytoremediation*, 12, 85-95.
- Warne, T. R. & Lloyd, R. M. (1980). The role of spore germination and gametophyte development in habitat selection: temperature responses in certain temperate and tropical ferns. *Bulletin of the Torrey Botanical Club*, 107, 57-64.
- Watkins Jr., J. E. (2006). *Comparative functional ecology of tropical ferns*. Unpublished Ph.D. Thesis. Gainesville FL: University of Florida.
- Watkins Jr., J. E., Mack, M. C. & Mulkey, S. S. (2007a). Gametophyte ecology and demography of epiphytic and terrestrial tropical ferns. *American Journal of Botany*, 94, 701-708.

- Watkins Jr., J. E., Mack, M. C., Sinclair, T. R., & Mulkey, S. S. (2007b). Ecological and evolutionary consequences of desiccation tolerance in tropical fern gametophytes. *New Phytologist*, 176, 708-717.
- Whitehead, S. J., Caporn, S. J. M., & Press, M. C. (1997). Effects of elevated CO<sub>2</sub>, nitrogen and phosphorus on the growth and photosynthesis of two upland perennials: *Calluna vulgaris* and *Pteridium aquilinum*. *New Phytologist*, 135, 201-211.
- Windham, M. D., Wolf, P. G. and Ranker T. A. (1986). Factors affecting prolonged spore viability in herbarium collections of three species of *Pellaea*. *American Fern Journal*, 76, 141-148.
- Young, K. R. & Leon, B. (1991). Diversity, ecology and distribution of high-elevation pteridophytes within Rio Abiseo National Park, North-Central Peru. *Fern Gazette*, 14, 25-39.
- Zhang, Q., Chen, J.-W., Li, B.-G., & Cao, K.-F. (2009). The effect of drought on photosynthesis in two epiphytic and two terrestrial tropical fern species. *Photosynthetica*, 47, 128-132.
- Zhang, L., Nurvianto, S., & Harrison R. (2010). Factors affecting the distribution and abundance of *Asplenium nidus* L. in a tropical lowland rain forest in peninsular Malaysia. *Biotropica*, 42, 464-469.

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