



Virtual issue: Ecology and evolution of pteridophytes in the era of molecular genetics

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Abstract

The past quarter-century has witnessed a revolution in our understanding of the phylogenetics, systematics, and ecology of pteridophytes (ferns and lycophytes), particularly due to the rapid accumulation of plastid sequence data and a renewed interest in the ecology of the sexual phase of the life cycle. We here compile 19 papers recently published in the *Journal of Plant Research* dealing with the biology of pteridophytes, grouped into six categories: (1) breeding systems, (2) species complexes and polyploidization, (3) fossil taxa, (4) gametophyte ecology, (5) systematics, (6) biodiversity. We hope this collection of papers will be of value to researchers interested in this fascinating group of plants.

Our understanding of the phylogeny of pteridophytes (ferns and lycophytes) was revolutionized starting in 1995 with the sequencing and phylogenetic analysis of the plastid *rbcL* gene (Hasebe et al. 1995). This ushered in the modern era of pteridophyte systematics, which has witnessed increasingly sophisticated analyses of the evolutionary relationships of seed-free vascular plants (Pryer et al. 2001; Qi et al. 2018; Rothfels et al. 2015; Schneider et al. 2004; Shen et al. 2018). Correspondingly, important insights have also been made into pteridophyte ecology, particularly with regards to the sexual gametophytic phase of the life cycle (Ebihara et al. 2013; Farrar et al. 2008; Nitta et al. 2017; Pinson et al. 2017; Pittermann et al. 2013; Watkins et al. 2007). The results of many dozens of molecular phylogenetic analyses of ferns and lycophytes over the past two decades or so have been synthesized in updated taxonomic treatments that more accurately reflect our understanding of pteridophyte evolution (Smith et al. 2006), updated as new information becomes available (PPG I 2016).

In this virtual issue of the *Journal of Plant Research*, we have compiled a list of 19 recent papers published in this journal that have contributed to the modern understanding of pteridophyte ecology and evolution. These include papers in the areas of: (1) breeding systems, (2) species complexes and polyploidization, (3) fossil taxa, (4) gametophyte ecology, (5) systematics, (6) biodiversity.

1. Breeding systems: Since the gametophytes of pteridophytes grow independently of the sporophyte, they have a wide range of breeding system flexibility, with important ecological and evolutionary implications (Klekowski 1973). Several studies in this journal have investigated various aspects of fern breeding systems. Yatabe-Kakugawa et al. (2009) clarified the population structure of hybrids between *Osmunda japonica* and *Osmunda lancea*, demonstrating partial fertility and the presence of F₂ and later backcrosses amongst the hybrids. Yatabe-Kakugawa et al. (2013) utilized the same species as an experimental system to investigate transmission ratio distortion (TRD) by developing a set of EST-derived nuclear markers for linkage mapping, and compared rates of TRD between selfing and crossing gametophytes and sporophytes. Ootsuki et al. (2012) conducted extensive screening of the apomictic *Cyrtomium fortunei*, experimentally demonstrating that genetic segregation can occur in apogamous, supposedly clonal, ferns. Nakato et al. (2012) investigated the production of partially fertile spores in a population of

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- Thelypteris decursivepinnata*, suggesting the importance of this type of spore formation in polyploid speciation.
2. Species complexes and polyploidization: Polyploid species complexes are common in pteridophytes, and represent a major challenge to taxonomy and accurate characterization of biodiversity (Sigel 2016). Recent studies have combined plastid and nuclear genes, often in combination with observations of spore size and morphology, to trace hybrid origins and revise taxonomy. Chang et al. (2018) utilized a “diploids-first” approach (Beck et al. 2010) within an integrative framework including morphology and plastid and nuclear DNA to clarify the taxonomy of the widespread *Asplenium normale* species complex. Fujiwara et al. (2018) incorporated cytology and plastid and nuclear DNA to infer the evolution of *Lepisorus* in Japan. Hori et al. (2014) disentangled a particularly diverse group, the *Dryopteris varia* complex, which includes multiple sexual and apogamous taxa. Ebihara et al. (2012) showed that a member of the *D. varia* complex previously thought to be extinct, *Dryopteris shibipedis*, is a hybrid that actually exists in cultivation.
 3. Fossil taxa: Pteridophytes are well known for their relatively rich fossil record (Niklas et al. 1983; Rothwell 1996). Several papers recently reported on newly discovered fossil ferns from China, with implications for modern fern systematics and ecology. Naugolnykh et al. (2016) reported a new fossil *Cyclosorus* from South China, which indicates that the climate during the Eocene may have been similar to modern conditions, i.e., relatively warm and humid. Tian et al. (2014) described a fossil rhizome belonging to the Osmundaceae, which provides insights into the systematics of this group with more extinct than extant species. Wang et al. (2015) described fertile material from a dipterid fern and compared it with extant species, demonstrating that fossil taxa had more elaborate spores than their modern counterparts.
 4. Gametophyte ecology: Detailed studies of fern gametophyte ecology have long been neglected because of their small size and cryptic morphology. Recent studies are applying molecular methods to gain new insights into gametophyte ecology (e.g., Duffy et al. 2015; Ebihara et al. 2013; Nitta et al. 2017). One important result of these approaches is the identification of “independent gametophytes”, gametophyte populations that occur separately from their conspecific sporophytes, or lack sporophytes altogether (reviewed in Pinson et al. 2017). Kuo et al. (2017) used molecular techniques to identify independent vittarioid gametophytes in East Asia. Another common theme of papers investigating gametophyte ecology in this journal is their symbiosis with arbuscular mycorrhizal (AM) fungi in the Glomeromycotina (glomalean fungi) (Winther and Friedman 2007). Winther and Friedman (2009) used molecular techniques to clarify the phylogenetic affinities of AM fungi associated with both gametophytes and sporophytes in cultivated *Psilotum nudum*. Ogura-Tsujita et al. (2013) detected glomalean fungi in field-collected gametophytes of *Angiopteris lygodiifolia* and *Osmunda japonica*, and identified the thickened part of the gametophyte known as the cushion as an important site for hosting AM fungal symbionts. Ogura-Tsujita et al. (2019) recently detected another fungal symbiont belonging to the Murcoromycotina in gametophytes of the same two host fern species, indicating that fern gametophytes form symbiotic relationships with fungi from multiple, deeply phylogenetically divergent lineages.
 5. Systematics: Plastid sequences have been a mainstay of pteridophyte systematic studies over the past ca. 20 years. Two recent papers in this journal utilized plastid sequences to investigate fern systematics. Lu et al. (2012) sampled 80% of Chinese *Adiantum* to test various taxonomic concepts in this large subclade of Pteridaceae and verify its monophyly with respect to vittarioid ferns. Chen et al. (2018) resolved the phylogenetic placement of the hitherto unsampled *Aenigmopteris*, providing both strong molecular and morphological data that show it is deeply nested within *Tectaria*. Other papers mentioned under ‘2. Species complexes and polyploidization’ have also contributed to systematics of various groups.
 6. Biodiversity: Pteridophytes are an important group for understanding biodiversity because they are widely distributed and occupy a variety of habitats. Two recent studies in this journal have investigated pteridophyte biodiversity patterns and processes at different scales. Kessler and Lehnert (2009) compared fern communities on tropical montane slopes vs. ridges, and found that ridges tended to have more specialized assemblages with fewer species compared to slopes. Ebihara and Nitta (2019) compiled the most comprehensive database of fern and lycophyte distributions in Japan to date, and reviewed and re-analyzed patterns of fern and lycophyte biodiversity in Japan.

We hope this collection of papers is useful to researchers interested in this fascinating group of plants, and spurs additional insightful studies.

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