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Edited by Klaus Mehltreter, Lawrence R. Walker and Joanne M. Sharpe

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# 1

## Ecological importance of ferns

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### 1.1 Introduction

Ferns immediately capture the imagination of all who are fortunate enough to notice them. With their large, highly dissected and shiny green leaves, ferns are so visually appealing that many are sold as ornamentals. Most moist woodlands will have a number of fern species blanketing the understory with their pungent foliage. In tropical woodlands, ferns are often at eye level or above, providing an aesthetic and delicate subcanopy. Even in arid lands or on newly exposed surfaces such as burns, clear-cuts or landslides, ferns can be present and sometimes dominant, catching your full attention as you push through fern thickets or get snagged by their spines. Beyond their immediate visual appeal, ferns are curious objects. How do plants of such ancient origin persist in the modern world? How can something so fragile survive trampling, burning, logging or grazing? Ferns and lycophytes were long considered as mystical plants, because people did not understand how they could reproduce without ever producing a flower, a fruit or a seed (Moran, 2004). In this book, we address the mystique that surrounds ferns by exploring fern ecology, or how ferns relate to their environment. Throughout the world, whenever ferns are the focus of ecological research, important and often surprising findings emerge.

We present four approaches to fern ecology. First, we provide a conceptual synthesis of the rapidly expanding field of fern ecology in order to establish a framework for future research and to encourage interdisciplinary approaches to studies of ferns. For example, modern molecular and genetic tools are used to probe the linkages of extant ferns to their fossil progenitors while evolutionary ecologists explore how ferns have coexisted with seed plants for so long. Second, we highlight key aspects of the rapidly expanding literature on fern ecology in order to provide a solid background for both researchers and teachers who inspire the next generation. We address the ecological underpinnings of such questions as how ferns reproduce, grow and successfully invade such a diversity of habitats. Third, we hope to broaden the nascent appreciation

of the ecological importance of ferns among natural resource professionals such as ecologists, conservationists and land-use managers. The remarkable adaptations of ferns to various disturbances, including their abilities to accumulate toxins in their environment, suggest an important role for ferns in conservation and restoration. Fourth, we provide an in-depth focus on ecological processes with examples and details to further educate and intrigue anyone who is already fascinated by ferns.

Humans use ferns for food, medicine, agriculture and horticulture. For example, the unfurled croziers (immature leaves) of *Matteuccia struthiopteris* (ostrich fern) are eaten in the USA. In medicine, the lycophyte *Huperzia serrata* (Chinese club-moss) provides an alkaloid that has been important for the control of epilepsy. Agricultural uses of ferns include the aquatic nitrogen-fixing ferns in the genus *Azolla* (mosquito fern) that are used in parts of Asia as green manure for rice fields and in India where they are fed to cows to increase milk production. Leaves of the South African fern *Rumohra adiantiformis* (leatherleaf fern) are grown commercially for their ornamental value for flower arrangements. Horticultural research has resulted in hundreds of fern species being grown as ornamentals and successfully cultivated in greenhouses and fields throughout the world (Jones, 1987; Rickard, 2000; Hoshizaki and Moran, 2001; Mickel, 2003; Olsen, 2007) but less is known about how ferns interact with their environment. Recent human activities have also enhanced the long distance dispersal capabilities of ferns that are weedy colonizers. Introduced fern species have displaced native plants in some parts of the world. Successful control measures for invading species, as well as the conservation of rare ferns, have an important role in many natural ecosystem management strategies and require a thorough understanding of fern ecology.

Novel insights can be gained about whole ecosystem interactions and species links to abiotic components by focusing on the spore-producing ferns and lycophytes as a group (see Section 1.4.3) that has a unique reproductive system but an ecology that is both similar and distinct from that of the better known plants for which reproduction depends on seeds. In this introductory chapter, we highlight some of the trends in the study of fern ecology and provide a brief overview of the topics included in the remaining chapters of this book. Because ferns (Plates 4–6, 8) and lycophytes (Plate 3) may be groups of plants that are unfamiliar to some of our readers, we then discuss (1) important differences between the elements of the fern life cycle and those of the more commonly studied seed plants, (2) the history of ferns on a geologic timescale and (3) recent changes in phylogenetics and systematics that have redefined the classification of ferns and lycophytes.

## 1.2 Advances in the study of fern ecology

Early ecological studies rarely included ferns, instead concentrating on seed plant ecology. However, a survey of the recent fern literature (International Association of

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Pteridologists, 1994–2007) shows a threefold increase in the number of publications devoted to fern ecology over the 14-year period. The study of fern ecology began with taxonomy. Early collectors in the tropics sent fern specimens with field notes to taxonomists at temperate herbaria for examination and comparison. Using such annotated herbarium collections in Switzerland, Christ (1910) wrote the first biogeographical treatment of ferns, even though he had never traveled further than to the Canary Islands. It became clear that there were many more species of ferns and lycophytes in tropical than in northern temperate climates (Plates 1, 2). Today, most fern species are found in the humid tropics where their ancestors originated, although some groups have adapted to cooler climates of tropical mountains or temperate latitudes. Furthermore, the tropics provided a wider range of habitats in which ferns developed a variety of growth forms such as tree ferns, water ferns, epiphytes, hemiepiphytes, and climbers (Plates 6, 8). Notable centers of fern diversity include mountainous tropical islands.

Holtum, a tropical fern taxonomist who went to Malaya in 1922 and directed the Singapore Botanical Gardens for several years, described fern habitats, their light conditions and associated seed plants based on his own observations (Holtum, 1938). These descriptions were a major contribution to tropical fern ecology that is still recognized today (Price, 1996). Following in this tradition, Tryon and Tryon (1982) integrated extensive ecological field notes into their treatment of the genera of ferns and lycophytes in the neotropics. The focus of fern ecology shifted from simple habitat descriptions to more detailed observations of plant growth and population dynamics when Watt (1940) published the first of his many ecological studies of *Pteridium aquilinum* (bracken) in Britain (see Watt, 1976 for a review). *Pteridium* is an extremely successful colonizer worldwide and can form dense, nearly impenetrable stands. *Pteridium* generally contains several biochemical compounds such as high levels of carcinogens that make it a health hazard when eaten by livestock or humans although the early Maori of New Zealand used *Pteridium esculentum* rhizomes as a crop. Where it is unwanted (i.e., considered an invasive weed), *Pteridium* is difficult to eradicate. *Pteridium* therefore continues to be an important subject for ecological research (Robinson, 2007). Studies of *Pteridium* and other abundant ferns have helped to develop an understanding of the complex relationships between ferns and their environments.

An early assessment of a forest understory in a northern New England watershed emphasized the potential ecological significance of ferns. Siccama *et al.* (1970) reported that ferns comprised 37% of annual understory biomass production (shrubs and herbaceous plants) and that species of *Dryopteris* (wood fern) contributed 70% of the biomass of the herbaceous layer. One difference between ferns and seed plants was highlighted in the 1960s during an experiment in which a section of a Puerto Rican rain forest was irradiated with cesium (Odum and Pigeon, 1970). This study

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was sponsored by the United States Atomic Energy Commission in order to understand the consequences of nuclear warfare or major reactor accidents on rain forests. Many plant species were negatively affected by the radiation, but ferns and lycophytes were unexpectedly resistant (Sorsa, 1970). More recently, ecologists have turned their attention to the high fern diversity of the tropics.

The temporal and spatial dimensions of fern growth have attracted interest recently. For example, there were unexpectedly strong seasonal patterns detected in mangrove ferns (Mehltreter and Palacios-Rios, 2003), climbing ferns (Mehltreter, 2006) and tree ferns in Mexico (Mehltreter and García-Franco, 2008). Also unexpected was the discovery of year-to-year variation in spore production in a rheophytic (i.e., flood-adapted) fern in the rivers of Puerto Rico (Sharpe, 1997). The spatial dynamics of tropical ferns have been examined in the Amazonian lowlands of Peru and Ecuador (Tuomisto *et al.*, 1995; Tuomisto and Ruokolainen, 2005). These studies have led to a better understanding of the intricate pattern of edaphic variability in a rain forest that was thought to be quite homogeneous because of its more uniform tree canopy composition. Portugal Loayza (2005) detected very distinctive fern abundance patterns in a 16-ha grid at a long-term research area in a Puerto Rican rain forest and linked specific fern species to areas of the forest where coffee had been grown more than 70 years earlier. These studies have shown that unexpected spatial and temporal patterns can be explained by evaluating fern growth and distribution.

It has not escaped the attention of some ecophysiologicalists that ferns can be found in habitats featuring extremes of temperature, light or humidity. Bannister and Wildish (1982) found that native fern species in New Zealand were less likely to develop frost resistance than the non-native male wood fern *Dryopteris filix-mas*. They also showed that the shade tolerance in forest ferns in New Zealand is greater than had been reported for forest floor seed plants. With a positive gravitropic response facilitated by the low light environment of the rain forest floor, the fertile leaf of *Danaea wendlandii* stays flat on the ground during early development (Sharpe and Jernstedt, 1990). Growth of the leaf then dramatically reverses to the vertical direction during the very last stages of development, allowing spore dispersal from above the low layer of sterile leaves that had shaded it. Early work with fern water relations of a Colorado desert fern, *Notholaena parryi* by Nobel (1978) demonstrated that, in contrast to many other temperate ferns, only minimal growth occurs during the summer months of June, July and August when soil water potential is lowest and temperature is highest. More recently, Milius (2007) has discussed high tolerance for low humidity among the tiny green gametophytes of epiphytic ferns of the rain forest. There are, no doubt, many other unusual aspects of fern ecophysiology to be discovered.

Fern interactions with other species and their impacts on community dynamics are also beginning to be explored. On tropical landslides, Walker (1994) found that dense

thickets of scrambling ferns such as *Gleichenella pectinata* (syn. *Dicranopteris pectinata*) inhibited tree seedling growth early in succession but were likely to facilitate later stages of succession by stabilizing slopes and improving soil conditions. In a study of a temperate hardwood forest in the northeastern USA, George and Bazzaz (2003) discovered that a dense fern layer dominated by *Dennstaedtia punctilobula* (hay-scented fern) limited the growth of some species of tree seedlings but not others, thus controlling the ultimate structure of the upper canopy.

Human alteration of natural habitat, often combined with the appearance of fern species introduced from other parts of the world, is presenting new challenges to ecologists and land managers. *Lygodium microphyllum* (small-leaf climbing fern) from the Old World was introduced into gardens in the southeastern USA in the 1950s, escaped, and has now become a serious pest in vast areas where water regimes modified earlier by human disturbance are being restored (Hutchinson and Langeland, 2006). Researchers have had to conduct ecological studies of *L. microphyllum* (Plate 8D) in both its native and invaded habitats in order to understand how to control its spread. Tu and Ma (2005) recently reported that the hyperaccumulating *Pteris vittata* (Chinese brake fern, Plate 8B) can remove quantities of otherwise inaccessible arsenic from mined wastelands. While this plant process could be of great benefit, understanding the ecology of *P. vittata* before remediation is now essential because *P. vittata* has been identified as an invasive fern (Palmer, 2003).

The field of fern ecology has advanced from simple observation of fern habitat characteristics to long-term studies of their complex roles in nutrient cycling and successional dynamics of natural ecosystems. Recent human activities have required that the ecological role of ferns be better understood as ferns become increasingly important in the horticultural trade and as invaders of disturbed habitats. Issues regarding conservation of rare ferns and management of invasive ferns require a well-grounded understanding of fern dispersal, colonization and growth. Throughout the world, whenever ferns are the focus of ecological research, surprising and important findings emerge. While pioneering fern ecologists (e.g., Wagner, 1973; Page, 1979b) have highlighted the need for research in many areas of fern and lycophyte ecology, it is only in the last 20 years that these calls have been answered by ecologists. A productive trend in fern and lycophyte ecology is clearly emerging and we encourage readers with a wide variety of perspectives to contribute to the growth of this exciting field of research.

### 1.3 Fern ecology topics in this book

In order to encourage the inclusion of ferns in future ecological research, this book provides a comprehensive and updated review of fern ecology. This review

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integrates a broad range of topics and highlights questions that present new research opportunities and interdisciplinary approaches. Selected topics in fern ecology have been addressed in edited volumes about ferns (Verdoorn, 1938; Dyer, 1979; Dyer and Page, 1985; Kramer *et al.*, 1995, Camus *et al.*, 1996; Chandra and Srivastava, 2003; Ranker and Haufler, 2008) but the last comprehensive reviews on fern ecology were published nearly 30 years ago (Page, 1979a, 1979b). Since that time, there have been considerable advances and remarkable changes in the emphasis of ecological studies of ferns from the individual species and its habitat to studies at the population, community and ecosystem levels. In addition to the pteridologists who have traditionally conducted fern ecology studies in the past, general ecologists with interests in a wider variety of topics such as nutrient cycling, edaphic influences, spatial distribution and succession have begun to discover the importance of ferns. The scope of ecological studies of ferns is also changing, widening to include large-scale spatial and temporal dynamics as well as social and economic influences. While research on the individual species provides the fundamentals, it is within the larger context of global ecology that the role of ferns may prove vital to our future, given their long and successful history of adaptation to environmental change.

Michael Kessler (see Chapter 2) presents a world map and an analysis of latitudinal and altitudinal gradients of fern distribution to explain the observed patterns and the reasons for their success throughout the world (Plate 1A, B). Joanne Sharpe and Klaus Mehlreter (see Chapter 3) discuss how elements of the life cycle and demography of individuals and populations respond to environmental triggers and document a wide array of phenological patterns in temperate and tropical ferns. Sarah Richardson and Lawrence Walker (see Chapter 4) describe fern responses to and impacts on ecosystem nutrient dynamics, while Peter Hietz (see Chapter 5) highlights the surprising success of ferns in xeric environments. Lawrence Walker and Joanne Sharpe (see Chapter 6) examine colonization and the negative and positive influences of ferns on successional processes that follow disturbance at several spatial and temporal scales. Klaus Mehlreter (see Chapter 7) highlights some of the strategies that ferns have developed to interact successfully with mutualistic and antagonistic fungi as well as animals.

Humans also have an impact on the role of ferns in many ecosystems. Roderick Robinson, Elizabeth Sheffield and Joanne Sharpe (see Chapter 8) present some of the most widespread but aggressive ferns that have a negative influence for humans as they invade natural ecosystems and impact agriculture. Fern and lycophyte lineages have survived millions of years by adapting successfully to a multitude of natural, sometimes even catastrophic changes, but the challenges are even greater today because of human alterations of the environment. As Klaus Mehlreter explains (see Chapter 9), a well-integrated approach to fern conservation requires a more complete understanding of their ecology. Finally, Lawrence Walker, Klaus

Mehltreter and Joanne Sharpe (see Chapter 10) summarize the ecological role of ferns, identify central themes in current research and suggest avenues for future research. We hope that advances in fern ecology will not only increase our knowledge of ferns as model organisms to investigate general and applied ecological questions but also ensure the future of the diversity of ferns and lycophytes as important components of our world.

#### **1.4 Fern structure, life cycles, evolution and classification**

A general grounding in the basics of fern structure can be helpful in reading this book and can be found in most elementary botany books. Lellinger (2002) has written a multilingual (English, French, Portuguese and Spanish) glossary that includes many of the terms specific to ferns and this book includes a short glossary of terms relating not only to ferns, but to ecological topics as well. We will discuss elements of the fern life cycle and then compare the alternation of generations in ferns with that found in seed plants. The ancient history of extant fern lineages provides a perspective on several aspects of ecology including, for example, alliances between herbivores and their host plants. Recent changes in the understanding of the phylogeny of ferns and lycophytes (Fig. 1.1) have resulted in a modified classification requiring several nomenclatural changes at the generic level. A current list of fern and lycophyte taxa, including brief descriptions of their key characteristics (Appendix A) may prove helpful for their distinction. Alan Smith has provided an updated alphabetical list of genera with synonyms (Appendix B) that can be invaluable in following the most recent taxonomical and nomenclatural changes.

##### ***1.4.1 Life cycle and alternation of generations***

Background information on ferns and lycophytes compared with the much more diverse and numerous seed plant groups, particularly the angiosperms (i.e., flowering plants), is essential to a complete understanding of the ecological importance of ferns. Functionally, ferns are no different from other green plants that capture the energy needed for photosynthesis. But differences in structure, life cycle and dispersal can result in unique roles for ferns.

Fern sporophytes are common and very distinctive plants in the vegetation of many parts of the world while a gametophyte is quite inconspicuous. The general sexual life cycle of ferns (Fig. 1.2) is characterized by the alternation of two generations consisting of (1) a prominent sporophyte plant and (2) a much smaller but independent plant, the gametophyte. The sexual life cycle requires (1) that the sporophyte leaf produces asexual spores (Fig. 1.3, Plate 5B) that can germinate into

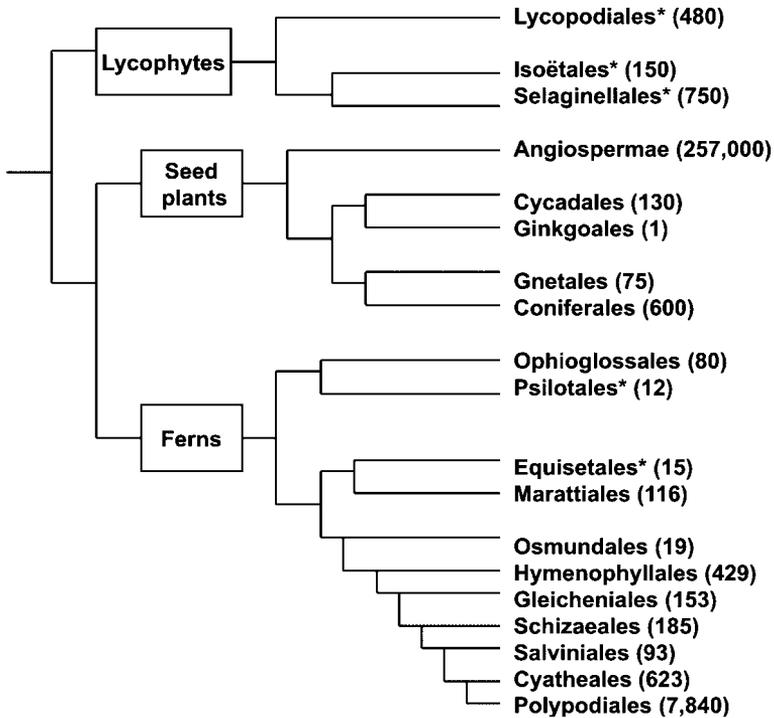


Fig. 1.1 Diagram of the vascular plant lineages (Schuettpelz and Pryer, 2008), including species counts, of the orders of lycophytes and ferns (Appendix A; Smith *et al.*, 2008) as well as seed plants (Judd *et al.*, 2008). Note that all flowering plant orders are included in Angiospermae, whereas the four gymnosperm orders are shown. Plant groups formerly called “fern allies” are denoted by an asterisk (\*).

a gametophyte and (2) that the gametophyte reproduces sexually (see Box 1.2 for details) to develop into a sporophyte. The differences between the fern and seed plant life cycles are discussed in detail in Box 1.1. Here we focus on a comparison of ferns and seed plants with respect to (1) the more conspicuous, usually leafy green sporophyte generation and (2) dispersal units (sperm cells and spores for ferns and pollen and seeds for seed plants). Characteristics of both of these elements of the life cycle have profound ecological consequences.

### *Sporophytes*

There are several obvious morphological characteristics that differentiate fern sporophytes from seed plant sporophytes such as the angiosperms (Table 1.1). Ferns and lycophytes do not produce secondary woody tissue as do woody seed plants. Fern sporophytes do not have long-lived primary roots as do most seed plants. Instead, the root system of most ferns consists of thin adventitious secondary roots that are fibrous and surface foraging, although in the Marattiales and

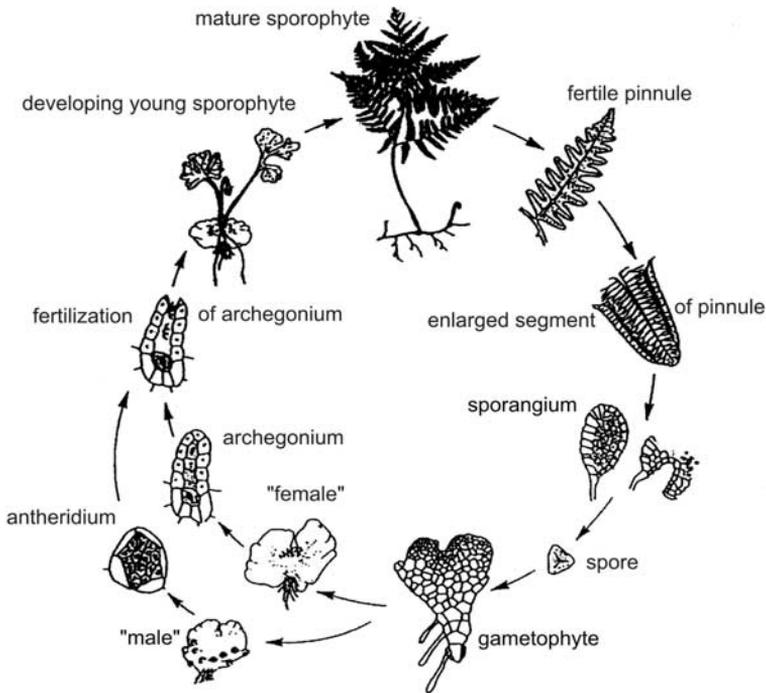


Fig. 1.2 General life cycle for homosporous ferns. Note the separate drawing of male and female gametophytes to imply outcrossing, which is more common than self-fertilization that is usually shown in life cycle diagrams for ferns. (Adapted with permission from Sheffield, 2008.)

Ophioglossales (Fig. 1.1) they can be thick and fleshy. Fern leaves exhibit three distinctive characteristics. First, with few exceptions (e.g., Ophioglossales, adder's tongues; Psilotales, whisk-ferns) emergent fern leaves unroll as they develop from a coiled, or occasionally hooked, leaf structure called a crozier or fiddlehead. The crozier exhibits circinate vernation in that the leaf is rolled from apex to base (Fig. 3.9a), a feature lacking in lycophytes and very rare in seed plants (e.g., the Cycadales and a few angiosperms, Fig. 1.1). Second, mature fern leaves can bear sporangia aggregated into sori that are often arrayed in various patterns, mostly on the lower leaf surface (Plate 5B) or the leaf margin or on specialized fertile, spore-bearing leaves (Plate 5C). In contrast, lycophytes bear one or more sporangia on the upper leaf surface. Third, free leaf venation (i.e., branched but not netted veins) for minor veins or partly netted (i.e., aerolate) venation occurs in many ferns (Plate 5B), whereas completely netted or parallel venation is characteristic of leaves of most seed plants. When fully expanded, mature leaves of ferns take on a variety of simple to highly dissected complex shapes (Plates 4–6). Fern leaves are mostly 10–200 cm in length, but can range from <1 cm to >10 m long. Croziers and leaves (also called

**Box 1.1 Alternation of generations: ferns and seed plants**

The reproductive life cycles of ferns and seed plants are similar, because in both groups the most common pattern is for a large usually diploid ( $2n$ ) sporophyte generation to produce usually haploid ( $1n$ ) spores. These spores develop into small haploid gametophytes (in ferns, sometimes called a prothallus) that produce gametes which are joined by fertilization to produce a diploid ( $2n$ ) sporophyte. We describe the details of a general fern life cycle of using the more common homosporous ferns as an example (Fig. 1.4a) and its important differences from the seed plant life cycle using angiosperms as an example (Fig. 1.4b). We start with the diploid sporophyte. Sporophytes of both ferns and angiosperms may reproduce asexually (off the right side of the diagrams, Fig. 1.4a, b) by vegetative growth processes such as budding, rhizome division or by producing runners. During the sexual life cycle (bold circle of diagrams, Fig. 1.4a, b) the number of sets of chromosomes changes twice from one generation to another, first through meiosis and then through fertilization. In homosporous ferns meiosis occurs in sporangia on the fertile leaves of a diploid fern sporophyte and results in haploid spores. Meiosis in angiosperms occurs in flowers where haploid male microspores are produced in the anthers and haploid female megaspores are produced in the ovary, making them heterosporous. Fern spores are released from the sporangia, usually dispersed by wind, and then develop into independent haploid gametophytic plants (see Box 1.2), while the alternate generation in seed plants is completely dependent on the sporophyte. In some fern species, the fern gametophytes are capable of vegetative propagation by producing gemmae that are multicellular propagules which break off, disperse and grow into mature gametophytes (left portion of the diagram, Fig. 1.4a).

In our angiosperm example (Fig. 1.4b) the microspore develops into a male haploid gametophyte (pollen grain) that is released and dispersed (by wind, water or animals) to the stigma of a flower while the female megaspore remains attached to the mother plant where it develops in the ovary of the flower into a haploid female gametophyte (embryo sac). Fern gametophytes mostly produce either motile sperm or immobile egg cells although some produce both types of gametes at the same time. Fertilization occurs on the gametophyte (in its habitat, e.g., the forest floor, rock crevice or tree bark) and the diploid zygote then develops directly into a new diploid sporophyte plant. In contrast, the angiosperm gametophyte is located within the flower where the egg cell is fertilized by a sperm nucleus that is delivered by a pollen grain that is dispersed to a stigma, germinates and forms a pollen tube that grows down the style to the ovule. After fertilization, the diploid zygote develops into a diploid embryo that together with the nutritive tissue (endosperm) and a protective wall (testa) constitute a seed. The mature seed is released from the parent seed plant and after dispersal (by wind, water or animals) to suitable habitat, germinates into a new diploid sporophyte plant (Fig. 1.4b). Some ferns may have an asexual apogamic cycle (inner central life cycle, Fig. 1.4a) in which all stages (sporophytes, spores and gametophytes) have the same set of chromosomes (usually two, but sometimes three or more). In the apogamic life cycle, the sporophyte is produced from vegetative cells of the gametophyte and the gametophyte germinates from a diplospore (i.e., spores that develop without undergoing meiosis; Fig. 1.3e).