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Seedling Ecology and Evolution

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Chapter 4

Specialized seedling strategies II: orchids, bromeliads, carnivorous plants, and parasites

Dennis F. Whigham, Melissa K. McCormick, and John P. O'Neill

4.1 Introduction

This chapter focuses on phylogenetically diverse groups of plants that do not have typical life history strategies as seedlings, juveniles, and mature individuals. Plants that live on other plants are classified as epiphytes, and they include both vascular and nonvascular species (Benzing, 1990). Tropical orchids and bromeliads comprise the vast majority of epiphytic flowering plants. However, orchids are global in their distribution and many are terrestrial (Dixon *et al.*, 2003). Carnivorous plants are also globally distributed, occurring in many types of ecosystems (Lloyd, 1976), as are parasitic plants (Press & Graves, 1995). The ability of seedlings to establish in habitats with extreme limiting resources is one of the few factors that links the diverse plants covered in this chapter. Epiphytes, for example, must initially become established on structures (i.e. branches) where resources are scarce. Once established, epiphytes may have to deal with combinations of stresses, including aridity, few available nutrients, and either high or low light conditions. Carnivorous plant species and many terrestrial orchids occur in habitats where nutrients or light are limiting. Many parasitic plants (e.g. mistletoes) also occur in resource-limited environments.

One of our approaches to organizing this chapter is to determine if seedlings differ in their physical or ecological characteristics in a manner similar to mature plants. The literature has few examples of investigations focusing specifically on seedlings. As an example, in the seminal book on Bromeliaceae, Benzing (2000) did not consider seedlings as a separate heading. Stems, roots, vascular cells, foliage, and trichomes were all considered separately, but information on seedlings was limited.

We organize the relatively sparse information on seedlings from these diverse groups of plants into four sections, each of which covers plants that are linked phylogenetically or functionally.

- The first section focuses on terrestrial and epiphytic orchids. All species in this family have a life history stage, the protocorm, which separates them from most other plants. We focus on the morphology and ecology of the protocorm life history stage, and also consider the ecology of seedlings that develop from protocorms. Emphasis is given to the importance of orchid–fungus interactions.
- The second section reviews epiphytic Bromeliaceae, focusing on seedling morphology and issues related to seedling ecology (e.g. seed dispersal, seedling establishment and survival, resource acquisition, mycorrhizae). Benzing (2000) provides a more comprehensive compendium on all aspects of bromeliads.
- The third section focuses on carnivorous plants, a polyphyletic group of plants functionally related by their ability to trap and consume prey as an important element of resource acquisition. Here we also cover most of the same topics presented in the section on bromeliads.
- Parasitic plants are the focus of the fourth section. This section proved the most difficult to organize as little information on seedling ecology is available. Historically, most research on parasitic plants has focused on interactions between parasites and their host plants. The format of this section differs in that it has been divided into four subsections: mistletoes, Orobanchaceae, *Cuscuta*, and mycoheterotrophic plants. In each subsection, we focus on seedling morphology and aspects of seedling ecology. The chapter concludes with a brief summary and commentary on future research needs.

4.2 Epiphytic and terrestrial orchids

The family Orchidaceae, with an estimated 20 000–35 000 species, is arguably the largest and most widespread among the monocotyledons (Cribb *et al.*, 2003) and DNA studies suggest it may be one of the oldest plant families (Chase, 2005). As diverse as the Orchidaceae is, there are likely hundreds or thousands of unidentified species left to be described (Pridgeon, 2003). Although the greatest concentration of orchid species occurs in the tropics, the family is cosmopolitan with orchids occurring on all continents except Antarctica (Stoutamire, 1974; Dressler, 1981). In tropical regions, most orchids are epiphytic and include species that are evergreen (e.g. *Epidendrum*), seasonally deciduous (e.g. *Catasetum*), and leafless (e.g. *Polyradician*), where the entire plant may be reduced to a congested system of photosynthetic roots (Benzing *et al.*, 1983). In temperate regions, orchids are restricted to the terrestrial environment but their leaf phenologies are similarly diverse. At our forested site in Maryland (USA), it is not uncommon to find evergreen (*Goodyera*), summergreen (*Galearis*), wintergreen (*Tipularia*), and leafless (*Corallorhiza*) species growing within a few meters of each other.

Despite the great diversity, several characteristics, mostly related to reproductive structures, are diagnostic for the Orchidaceae

(Dressler, 1983; Arditti, 1992), and include the abundant production of dust-like seeds that contain a simple embryo with little if any endosperm (Leroux *et al.*, 1997; Arditti & Ghani, 2000). Most plants with such limited resources begin to photosynthesize immediately after germination (Fenner, 1985). In contrast, Orchidaceae has evolved a different strategy, initially developing a protocorm, a separate life history stage that is present after germination, and eventually gives rise to the seedling (Rasmussen, 1995). Functionally, the protocorm is heterotrophic, and growth is dependent on an external source of carbohydrates, obtained *in situ* from a symbiotic fungus (Richardson *et al.*, 1992; Leake, 1994; Rasmussen, 1995; Peterson *et al.*, 1998), or from simple sugars in laboratory culture (Harrison & Arditti, 1978).

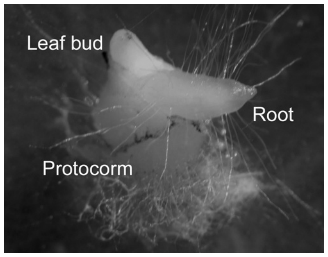

Fig. 4.1 Developing seedling of *Dactylorhiza lapponica* with the leaf bud and initial root at the apex of the protocorm. Rhizoids (epidermal hairs) are visible on the lower portion of the protocorm. Photo by J. O'Neill.

From seed to protocorm

As in all angiosperms, germination of orchid seeds is initiated by water entering the seed (Fenner, 1985). The seed coat becomes permeable to water by natural weathering processes or by chemical treatment in the laboratory and the testa splits (Yoder *et al.*, 2000). Some species can germinate without an appropriate fungus, but germination occurs faster with a fungus. Other species require a fungus (e.g. Rasmussen, 1995; McKendrick *et al.*, 2002; Whigham *et al.*, 2006). The embryo, which is morphologically undifferentiated in all but a few species, begins to swell and develops into a protocorm, which is equivalent to the radicle and hypocotyl of seedlings of other plants (Rasmussen, 1995). The protocorm forms rhizoids, which are epidermal hairs, and fungal infection occurs through either the rhizoids or the suspensor on the embryo (Rasmussen, 1995).

Protocorm to seedling

Most of our knowledge about orchid protocorms comes from *in vitro* studies, which demonstrate that most protocorms share the same basic structure (Fig. 4.1) comprising a basal part that becomes infected with an appropriate mycorrhizal fungus and an apical part that contains the meristematic cells from which a seedling develops (Fig. 4.2). Protocorms are rarely observed in nature, but when encountered, they are most often adjacent to established plants (Curtis, 1943; Willems, 1982) or have established in specialized habitats such as decomposing wood (Rasmussen & Whigham, 1998a).

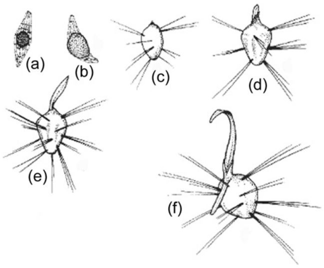

Fig. 4.2 Stages of orchid seedling development. (a) Unimbibed seed, (b) imbibed seed with cracked testa, (c) germination and production of rhizoids, (d) enlargement of protocorm and initiation of leaf primordium, (e) leaf expansion, and (f) seedling with leaf and initiation of root. Adapted from Batty *et al.* (2001b), reproduced with permission, copyright CSIRO 2001, CSIRO Publishing, Melbourne, Australia.

Protocorms of tropical epiphytic and temperate terrestrial orchids differ somewhat in shape. Protocorms of temperate terrestrial species (Fig. 4.3a) are often initially cone-shaped with a tapered end and flattened area at the apex. During growth, however, they become much more variable in shape. Older protocorms of some species resemble juvenile plants in shape and vary from sausage-shaped (e.g. Fig. 4.4a – *Goodyera pubescens*) to coralloid and branched (e.g. Fig 4.4b – *Corallorhiza odontorhiza*), but *Tipularia discolor* has bone-shaped protocorms (e.g. Fig. 4.4c) that appear very different from juvenile plants. In contrast, protocorm morphology within tropical epiphytic species varies little with the protocorm being a somewhat flattened sphere (Fig. 4.3b).

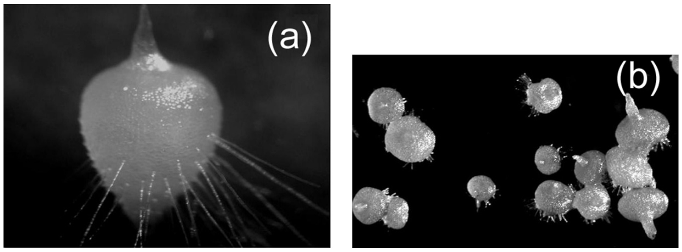

Fig. 4.3 Initial protocorm development of (a) *Dactylorhiza lapponica*, a temperate, terrestrial and (b) *Encyclia tampensis*, a tropical epiphyte. Photos by J. O'Neill.

Regardless of protocorm shape, meristematic cells at the apical end give rise to the first primordial leaf. Subsequently, the first root emerges from the same part of the protocorm (Fig. 4.1 and Fig. 4.4c). As the seedling continues to develop, protocorm tissues persist for some time before decaying and, as a result, one often finds seedlings with protocorm tissue still attached (Fig. 4.2f and Fig. 4.4c). Achlorophyllous orchids (e.g. Fig. 4.4b – *Corallorhiza*) differ from this general pattern of protocorm development by having several meristems on branched structures, each of which produces scale-like leaves at the tips.

During the protocorm stage and at least until initial leaves form, orchids are entirely dependent on fungi for the resources required for growth and development (Harvis & Hadley, 1967; Hadley & Williamson, 1971; Beyrle *et al.*, 1991, 1995). Hyphae of mycorrhizal fungi enter the protocorm, primarily through rhizoids, and grow into orchid cells where they form tight coils of hyphae called pelotons. The orchid then digests pelotons through a process that involves lysis of fungal cell walls. The obligate nature of the protocorm–fungus interaction has been demonstrated in both laboratory and field-based studies. Protocorms grown *in vivo* without an appropriate fungal partner fail to develop to the seedling stage (Anderson, 1991; Rasmussen, 1995; Batty *et al.*, 2006). Field experiments have also demonstrated the obligate nature of the mycorrhizal interaction as protocorms uninfected by fungi cease development following germination (e.g. Rasmussen, 1994; McKendrick *et al.*, 2000a, 2002). In all cases that have been examined, the fungi associated with naturally occurring protocorms represent a very specific subset of fungi in their environment (e.g. Rasmussen, 1995; McKendrick *et al.*, 2000a, 2002; Batty *et al.*, 2001a; McCormick *et al.*, 2004). However, this specificity may be less marked under laboratory conditions (e.g. Hadley, 1970; Masuhara & Katsuya, 1994). There is evidence that fungi associated with roots of adult orchids are not always the same fungi as those associated with protocorms (Rasmussen, 1995; Peterson *et al.*, 1998; McCormick *et al.*, 2004), suggesting that some orchids switch fungal symbionts during the transition from the protocorm to the seedling stage. With very few species adequately studied, the generality and ecological significance of fungal switching between these two life history stages is not clear. McCormick *et al.* (2004) found that the fungi associated with protocorms of *Tipularia discolor* belonged to a clade of fungi basal to the Sebacinaceae and differed from the fungi associated with adults. In a

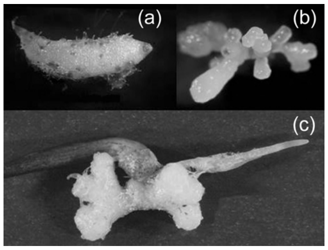

Fig. 4.4 Advanced protocorm morphology of three temperate orchids, (a) *Goodyera pubescens*, (b) *Corallorhiza odontorhiza*, and (c) *Tipularia discolor*. Photos by M. McCormick & J. O'Neill.

few instances, fungi associated with *Tipularia discolor* protocorms have also been found in adults (R. Burnett & M. McCormick, per. comm.) suggesting that this may not be a switch, but rather an accumulation of additional fungi. In contrast, both protocorms and adults of *Goodyera pubescens* and *Liparis liliifolia* have the same fungal associations.

There is no universal pattern that describes the longevity of the protocorm stage (Rasmussen, 1995). In tropical and subtropical orchids, seedlings may appear quickly following protocorm development. Field studies of temperate species using seeds sown in seed packets, have found that the protocorm stage varies, ranging from 6 months for *Goodyera pubescens* (McCormick *et al.*, 2006) to a year or more in species of *Corallorhiza* (McKendrick *et al.*, 2002). Other field studies also describe the variable length of the protocorm stage. Willems (1982) found that it took up to 3 years for *Orchis simia* seedlings to develop while, at the other extreme, protocorms of *Liparis loeselii* mature after 3–4 months (Mrkvicka, 1990).

Seedling establishment and survival

Most seedlings, juveniles, and adult orchids examined *in vivo* continue to form mycorrhizae, although the fungal relationship may no longer be obligatory. With the exception of achlorophyllous orchids, which are fully mycoheterotrophic, orchid seedlings are similar to those of other mycorrhizal monocots and growth *in vitro* is similar to that encountered in the field (Curtis, 1943; Stoutamire, 1974). Leaves of seedlings are morphologically similar to leaves of juveniles and adults, and the roots are typically fleshy with no or few secondary roots. Roots of epiphytic and terrestrial seedlings function as storage organs and roots of many epiphytic species enable the plants to remain attached to the substrate on which they occur.

Few data exist on orchid seedling survival (Batty *et al.*, 2001a), but seedlings are rarely observed in long-term population studies (Willems, 2002) and appear to have low survival rates similar to seedlings of most other plants. Curtis (1943) found that only 0.5% of the seedlings of *Cypripedium reginae*, a North American terrestrial species, survived for four years with highest mortality occurring between 1- and 2-year-old seedlings. Less than 1.0% of the seeds of a temperate Australian terrestrial species (*Caladenia arenicola*) produced a seedling that was capable of surviving the dry season (Batty *et al.*, 2001a). Mortality is also high for tropical species. Zotz (1998) estimated that out of two million seeds of the epiphytic *Dimerandra emarginata*, only one was likely to become a seedling. Additionally, among established seedlings, only 50% survived the first dry season. Ackerman *et al.* (1996) also found low survival rates of *Tolumnia variegata* with 32.8% of the seedlings surviving for 1 year and 14.5% for 2 years.

Seedling dormancy

In vivo studies of orchids indicate that one or more periods of dormancy are required for continued development of protocorms and seedlings (Rasmussen, 1995). Field studies of orchid populations indicate that individuals become dormant for part of the growing season (i.e. aboveground parts senesce). In temperate zones, dormancy of individual plants is triggered by periods of environmental stress such as decreasing temperatures or a combination of high temperatures associated with a prolonged dry season (Dixon, 1991). In recent years, studies have investigated another type of adult whole-plant dormancy in terrestrial orchids (Shefferson *et al.*, 2001, 2005; Tali, 2002; Kéry *et al.*, 2005). This type of dormancy is defined as a condition in which the rootstock of a perennial herbaceous plant fails to produce annual shoots during the growing season (Shefferson *et al.*, 2005). Several orchid species have been shown to exhibit this type of dormancy (see citation in Rasmussen, 1995; Shefferson *et al.*, 2005), but it also occurs in other plant families. We found no references to protocorm or seedling dormancy of this type, but it seems probable that both life history stages are capable of surviving for more than one growing season in a dormant state because similar to larger individuals are mycorrhizal.

4.3 Bromeliads

Seedling morphology

We are unaware of any systematic study of the morphology of bromeliad seedlings but descriptions found in Benzing (1980, 1990, 2000) suggest that most seedlings emerge from seeds with typical seedling structures. Seedlings of bromeliads in the Tillandsioideae, however, appear to be atypical in their morphology, especially atmospheric species that have no roots or reduced root systems (Benzing, 2000). Figure 4.5 shows examples of two bromeliad seedlings. *Canistrum lindenii* and *Pitcairnia flammea* have seedlings that are similar to many plants producing seed. The first structure to emerge from the seed is the hypocotyl, followed by the radicle and shoot axis (epicotyl). Primary and secondary roots eventually replace the radicle. In contrast, seedlings of *Vriesea scalaris* appear to be typical of atmospheric epiphytes in the Tillandsioideae in that they do not produce roots for weeks or months and the resultant roots are specialized for anchorage.

Anchorage may be the primary function of roots in the majority of epiphytes, especially bromeliads, and many species have sclerified roots that are durable and strong (Benzing & Renfrow, 1974; Benzing, 2000). Studies by Brighigna *et al.* (1990) and Fiordi *et al.* (2001) further support the generalization that roots of most epiphytic bromeliads are used primarily for anchorage. Physiological studies of nutrient and water uptake (e.g. Benzing & Renfrow, 1974) provide further evidence that roots are primarily involved in anchorage. Compared to roots, the rates of nitrate reductase induction was higher in leaves of *Vriesea hieroglyphica* that were given nitrogen in the form of calcium-nitrate (Nievola & Mercier, 1996). Laube and Zotz (2003) also provided evidence for water and nutrient uptake by leaves. They measured the growth response of *Vriesea sanguinolenta* to variations in water, nutrient, and light supply, including small individuals that had grown past the seedling stage (i.e. they had started to produce leaves that retained water). Because roots were removed when first collected and no regrowth occurred, all experimental responses resulted from uptake through leaves. The smallest plants had the greatest potential to adjust relative growth rates in response to treatment variables, providing evidence that seedlings responded to variation in resource availability, primarily by uptake of water and nutrients through leaves and not roots.

Seedling establishment and survival

For many bromeliads, aridity and low levels of nutrient availability represent the primary stresses at all life history stages (Hernández *et al.*, 1999; Benzing, 2000). Moisture stress is less important in montane tropical environments and temperate rain forests, which have abundant moisture (Madison, 1977). Aridity would be expected to influence seed germination, as most bromeliads have short-lived seeds that are nondormant and germination depends on the presence of adequate moisture. Little is known, however, about seed germination among bromeliads (Baskin & Baskin, 1998), and Benzing (2000) noted that, "seed viability and germination rank among the least-studied aspects of bromeliad reproduction." One would expect that germination rates would generally be low and highly variable in space and time because most seeds would fall on unsuitable arboreal habitats (Benzing, 1978). Additionally, short- and long-term variation in microclimatic conditions (e.g. availability of moisture) would control patterns of germination. Germination of *Tillandsia paucifolia* seeds, for example, was always less than 4.0% on several potential host trees (Benzing, 1990) and seedling survival was low (Benzing, 1981).

Many factors influence patterns of seedling survival and growth, not the least of which is the stability and surface of the substrate where the seed lodges. Bromeliad seeds, while typically smaller than most seed-bearing plants (Benzing, 2000), have a variety of structures, such as hooked coma hairs, that enable them to remain in the tree canopy (Benzing, 1990).

Seedling survival is likely highly variable in space and time. For example, Benzing (1981) found that recruitment of *Tillandsia paucifolia* occurred most frequently on trees on which maternal plants occurred. Several factors may account for the higher recruitment on trees that already support mature plants. Most seeds have leptokurotic dispersal patterns (Madison, 1979 as cited in Benzing, 1990; Baskin & Baskin, 1998), assuring that the majority of seeds will disperse within the host-tree canopy. This dispersal pattern increases the probability that seeds will be dispersed to a suitable microhabitat and results in a clumped distribution (Hietz & Hietz, 1995). In addition, host trees that support higher numbers of epiphytes grow in locations with microclimatic conditions that favor germination, seedling establishment, and growth. Zimmerman and Olmsted (1992) found that *Tillandsia* *dasylirifolia* was most abundant on trees with branches that overhang water in seasonally flooded forests of the Yucatan Peninsula (Mexico). Genetic variation within host-tree species (e.g. bark roughness) could also be important.

One would expect that seedling and juvenile establishment and survival would be low because both life history stages are vulnerable to predation as well as physical stresses associated with life in the forest canopy. Dessication is likely an especially important factor in survivorship of small individuals because of their low surface:volume ratios. We only found survivorship information for seedlings and juveniles of two bromeliads and there was no consistent pattern. Benzing (1990) reported low survival rates of seedling cohorts of *Tillandsia paucifolia*. In contrast, Schmidt and Zotz (2002) found that mortality rates averaged 16.5% for all life stages of *Vriesea sanguinolenta*, a bromeliad occurring in the outer canopy of trees in Panama. In fact, Schmidt and Zotz found that mortality was highest in medium-sized individuals, not seedlings and juveniles.

Some bromeliad seedlings store water in cotyledons, hypocotyls, and the first roots (Benzing, 1990), but most deal with aridity through adaptations that absorb water from the atmosphere or protect them from desiccation. Seedlings of some tank-forming bromeliads do not form tanks for 1–5 years, but a dense layer of trichomes covers juvenile foliage. Juveniles of *Vriesea geniculata* had at least twice the density of trichomes on leaves and the percent of the leaf surface covered by trichome shields was 30–40 times greater on juveniles (Benzing, 2000). As a result, they respond physiologically more like atmospheric bromeliads (Benzing, 1980), which are able to photosynthesize at a higher rate than adults and use water more efficiently under conditions of drought stress (Adams & Martin, 1986). Laube and Zotz (2003) found similar results for *Vriesea sanguinolenta*. In fact, seedlings of some bromeliads may be so well-adapted to aridity that they die when exposed to too much moisture. *Tillandsia circinnata*, exhibits this adaptation and mortality occurs when plants are not able to dry out (Benzing, 1978).

Seedlings and mycorrhizae

Similar to orchids, other epiphytes benefit from mycorrhizal interactions through increased resource acquisition. However, because many bromeliads have reduced root systems or roots that are not the primary organ involved in water and nutrient uptake, interactions with mycorrhizal fungi may not occur or be limited in extent. There are no reports of mycorrhizal colonization of seedlings in non-orchid epiphytes, although there is also no record that seedlings have been examined. Lesica and Antibus (1990) examined 50 taxa in 14 families of epiphytes on fallen trees and tree branches in two Costa Rican forests. Most adult orchids and species of Ericaceae and Gesneriaceae had colonized roots but only one genus (*Pitcairnia*) in the Bromeliaceae had colonized roots. The standard deviation for the measured metric (% colonization) was similar to the mean, indicating that colonization was highly variable. No colonization or low levels of colonization have been reported for bromeliads in Mexico and Malaysia (Allen *et al.*, 1993; Nadarajah & Nawawi, 1993). In contrast, Rabatin *et al.* (1993) found that roots in 16 of 19 bromeliads in a Venezuelan cloud forest had arbuscular mycorrhizae fungi, with infection occurring at higher levels in more mesic sites. Rains *et al.* (2003) also found high levels of infection in epiphytic Araceae, Clusiaceae, Ericaceae, and Piperaceae in a lower montane cloud forest in Costa Rica. None of these studies, however, reported on infection in seedlings. Thus, the relationship between bromeliad seedlings and mycorrhizal fungi requires study.

4.4 Carnivorous plants

Rice (2006) reported that there are about 650 described species that can be categorized as carnivorous. They occur in all regions of the world from the Arctic to the tropics, and grow over a wide range of habitats from tree canopies to wetlands, in nutrient-poor to nutrient-rich habitats. The species are distributed, however, among a relatively small number of families (12) and genera (19). Carnivorous plants are polyphyletic, having multiple origins but also demonstrating a high degree of convergent evolution (Albert *et al.*, 1992; Ellison & Gotelli, 2001). Well known examples are species of *Darlingtonia* (Sarraceniaceae), *Sarracenia* (Sarraceniaceae), and *Nepenthes* (Nepenthaceae) that trap prey passively in pitcher traps (Juniper *et al.*, 1989). Carnivorous plants that use glandular secretions to capture prey are species of *Drosera* (Droseraceae) (e.g. Crowder *et al.*, 1990) and *Pinguicula* (Lentibulariaceae) (e.g. Lüttge, 1983). The monotypic genera *Dionaea* (Droseraceae) and *Aldrovanda* (Droseraceae) have the most active prey-capturing mechanisms with leaves that function as snap-traps. The genus *Utricularia* (Lentibulariaceae) uses a trapdoor mechanism (suctioning bladders) to capture small prey (Schnell, 1976; Forterre *et al.*, 2005).

Seedling morphology

Few references, mostly in older publications, described the seedling morphology of carnivorous plants. A general pattern emerges among a wide range of species in this functional group of plants. The first leaves of seedlings of most species are already capable of trapping prey. Small seedlings of *Dionaea muscipula* (Smith, 1931; Schnell, 1976), *Sarracenia purpurea* (Shreve, 1906), *Cephalotus follicularis* (Cephalotaceae) (Boon, 2006) and species of *Nepenthes* (Geddes, 1893) and *Drosera* (Crowder *et al.*, 1990) have insect-trapping leaves. Seedlings of *Utricularia* spp. quickly form prey-trapping bladders (Kondo *et al.*, 1978). The early formation of functional leaves in the seedling stage indicates the importance of prey-capturing as an ecologically adaptive strategy among carnivorous plants.

The second general characteristic of carnivorous plant seedlings is that most have weakly developed root systems or no roots at all

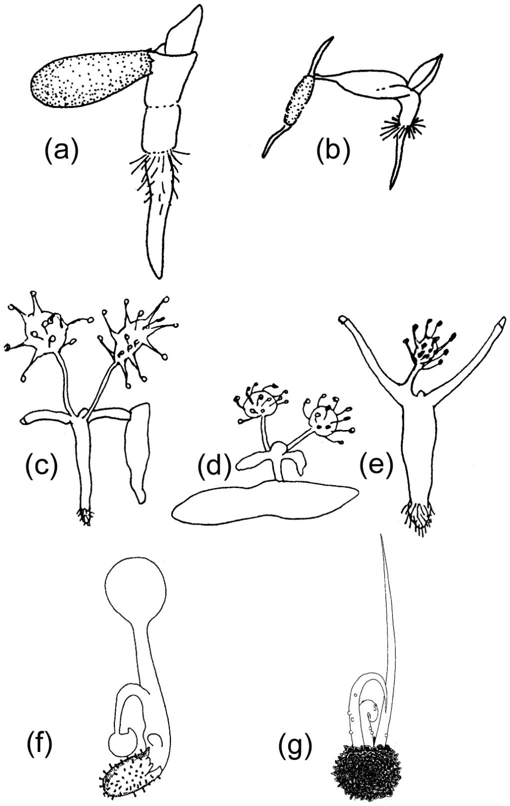

Fig. 4.5 Seedlings of bromeliads (a) *Canistrum lindenii* and (b) *Pitcairnia flammea*, and of carnivorous plants (c) *Drosera anglica*, (d) *D. rotundifolia*, (e) *D. intermedia*, (f) *Utricularia striatula*, and (g) *U. radiata*. From Benzing (2000) (a & b); Crowder *et al.* (1990) (c – e) and Kondo *et al.* (1978) (f & g). Reproduced with permission (f & g) from New York Botanical Garden, Bronx, NY.

(Emerson, 1921; Baskin & Baskin, 1998). Seedlings of *Cephalotus follicularis* produce a single, small tap root (Boon, 2006) and *Dionaea muscipula* seedlings have a tap root from which arise numerous root hairs (Smith, 1931). *Drosera* seedlings also have poorly developed root systems (Fig. 4.5), and the tap root is replaced by relatively few adventitious roots with few root hairs and persists for less than a year (Crowder *et al.*, 1990). Seedlings and mature plants of *Utricularia* spp. do not produce roots (Fig. 4.5; Shannon, 1953; Adamec, 2000) and roots of *Aldrovanda vesiculosa* stop growing when they are less than 1 mm long (Kondo *et al.*, 1978).

Seedling establishment and survival

Most carnivorous species for which seedling information is available occur in low nutrient and relatively open wetland habitats, typically bogs, where moisture is adequate and competition is low. In addition, little information is available on patterns of seedling distribution in relation to patterns of seed dispersal. Ellison and Parker (2002) found that most seedlings of *Sarracenia purpurea* occurred near parent plants, but suggested that long-distance dispersal of seeds likely also occurred, accounting for the broad dispersal of *Sarracenia purpurea* following the end of the last ice age. Similar rare long-distance dispersal, perhaps by animals or water, must have occurred in other carnivorous genera species (e.g. *Drosera*, *Utricularia*) that are broadly distributed across much of the boreal zone. We found no quantitative dispersal data for seeds of other species of carnivorous plants. The review of *Drosera* for the *Biological Flora of the British Isles* (Crowder *et al.*, 1990), for example, contained no information on seed dispersal and only suggests that wind, the feet of birds, and water were likely dispersal agents. Schnell (1976) suggested that seeds of *Sarracenia* species are water dispersed because of their relatively large size, but provided no supporting evidence. Longer-distance seed dispersal may occur in species of *Nepenthes* that are wind dispersed (Schatz, 1996).

Seedling survival is probably low in most habitats, but similar to data on patterns of seed dispersal, there have been few studies of seedling survival. Ellison and Parker (2002) found that only 5% of the observed seedlings of *Sarracenia purpurea* survived an entire growing season. Only 5–7% of the *Dionaea muscipula* seed sown by Luken (2005a) survived as seedlings compared to between 72–85% survival for transplanted adults.

Seedlings of *Drosera intermedia* had the highest rates of survival in cut-over bogs with more available nitrogen (N) and low phosphorous (P) (Sansen & Koedam, 1996). Seedlings of *Drosera capillaris* and *Dionaea muscipula* were most abundant in hollows in a bog system, a habitat that is consistently wet and largely devoid of litter and competing vegetation (Luken, 2005a). In a separate study, Luken (2005b) found that removal of vegetation by mowing in a low-nutrient Carolina Bay (NC, USA) resulted in greater survival of already established *Dionaea muscipula* plants and that establishment of *Dionaea*, *Drosera capillaris*, and *Utricularia subulata* seedlings increased. Seedling densities of species of *Drosera* and *Sarracenia alata* have also been shown to increase significantly following burning of pine-savanna wetland ecosystems in southeastern USA (Barker & Williamson, 1988; Brewer, 1999a,b) although fire exhibited little effect on seedling survival of *Sarracenia alata* (Brewer, 2001).

Nutrient acquisition

Carnivorous plants obtain varying degrees of nitrogen from captured prey (see Table 1 in Ellison & Gotelli, 2001). Ellison and Gotelli concluded that the amount of N obtained from prey increases with increasing complexity of the carnivorous structures. Species with sticky leaves obtain less N from prey compared to species with pitchers. Carnivorous plants also obtain a significant amount of nutrients other than N from captured prey (e.g. Jaffe *et al.*, 1992; Schulze *et al.*, 2001; Adamec, 2002). Additionally, root uptake provides significant resources (Karlsson *et al.*, 1987). In a few instances, the process of capturing prey resulted in increased root uptake of nutrients. Hanslin and Karlsson (1996) found that root uptake of N increased following prey capture by *Pinguicula alpina*, *P. villosa, P. vulgaris*, and *Drosera rotundifolia* in a subarctic ecosystem. Adamec (2002) found similar results working with three species of *Drosera* and suggested that, "the main physiological effect of leaf nutrient absorption from prey is a stimulation of root nutrient uptake."

While most studies of nutrient uptake in carnivorous plants have been based on mature plants (e.g. Adamec 1997, 2002; Schulze *et al.*, 1997; Thorén & Karlsson, 1998; Ellison & Gotelli, 2001), two studies examined nutrient acquisition in smaller individuals, including seedlings. Schulze *et al.* (2001) found that seedling survival of *Dionaea muscipula* increased after plants had reached the six-leaf stage, a size that facilitates the capture of prey. Seedlings and small plants had less N in leaves but their δ^{15}N signature suggested that insect capture continued to be an important source of N. Adamec (2002) applied mineral nutrients to leaves of seedlings of three species of *Drosera* and found that they were able to assimilate nutrients at rates that were similar to those obtained from prey. Except for P, the roots were responsible for most of the nutrient uptake in fertilized plants, primarily through increased root biomass rather than increased root uptake.

Seedlings and mycorrhizae

Carnivorous plants appear to be nonmycorrhizal, although few species have been examined, and we found no studies that focused on seedlings. *Dionaea muscipula* (Roberts & Oosting, 1958), *Pinguicula* spp. (Harley & Harley, 1987) and *Drosera* spp. (Crowder *et al.*, 1990), have all been reported to be nonmycorrhizal. Efficient uptake of nutrients from captured prey and from root systems that assimilate nutrients more efficiently following prey capture in leaves, may have precluded the benefits of mycorrhizal interactions that are common in flowering plants.

4.5 Parasitic plants

There are 3 000–4 000 species of direct plant parasites, making up somewhat less than 1% of all angiosperms (Musselman & Press, 1995; Nickrent, 2003; Press & Phoenix, 2005). Parasitic species occur in most plant communities worldwide and include members of 22 plant families, including trees, shrubs, vines, and herbs (Musselman & Press, 1995; Nickrent *et al.*, 1998; Phoenix & Press, 2005). Roughly 60% of parasitic plants are root parasites and 40% are shoot parasites. A few are important crop pests, but many others can have dramatic impacts on the composition of plant communities (Riches & Parker, 1995; Pywell *et al.*, 2004; Phoenix & Press, 2005; Press & Phoenix, 2005). Approximately 20% of parasitic plants lack chlorophyll and are holoparasitic, with the rest being hemiparasitic (Musselman & Press, 1995).

In addition to these direct plant parasites, which are united by their ability to form haustoria, there are also more than 400 species of mycoheterotrophic plants in 11 families that parasitize other plants through specialized mycorrhizal connections (Leake, 1994).

The seedling stage is clearly critical for parasitic plants because that is the stage at which a host connection must be established (Musselman & Press, 1995). The morphology and ecology of seedlings has only been studied in a few groups, primarily the mistletoes, members of Orobanchaceae, and *Cuscuta* (Convolvulaceae). These have focused on a few economically important crop pests within each group. Of the mycoheterotrophic plants, we will focus on the most extensively studied group, the Monotropaceae. Obviously, there are many groups not addressed, but we hope that those presented give an indication of the range of seedling stages present. For additional information on some of these groups, we refer the reader to *Biology of Parasitic Flowering Plants* by Kuijt (1969) and *Parasitic Plants* edited by Press and Graves (1995).

Mistletoes

The mistletoes are a phylogenetically diverse group of plants, primarily belonging to the families Loranthaceae and Viscaceae, with a few members of the Misodendraceae, Eremolepidaceae, and Santalaceae (Restrepo *et al.*, 2002) represented. The best studied are the Loranthaceae and Viscaceae (Reid *et al.*, 1995). Primitive mistletoes (*Atkinsonia*, *Nuytsia*, and *Gaiadendron*) are terrestrial root parasites or facultatively epiphytic shoot parasites, whose early development is typical of nonparasitic flowering plants. The radicle, with a typical radicular cap, grows out of the seed to penetrate the soil, soon after which the hypocotyl elongates and lifts the seed from the ground. The cotyledons dissociate themselves from the endosperm, the shoot begins to elongate, and the root begins to branch. After a root forms, it may form a haustorium (discussed in detail below), but always as a lateral organ (Kuijt, 1969).

Some primitive mistletoes persist independently for up to a year before contacting a host (Kuijt, 1982). In contrast, more advanced and typical mistletoes have only a brief free-living phase. Often only a few days occur between germination and infection after which the seedling is dependent on the host. Growth during this free-living period involves primarily the radicle, which emerges from the seed and grows in search of a host (Fig. 4.6a). Radicle growth precedes cotyledon emergence (if they emerge), and is physiologically dependent on mobilization of the endosperm, except *Aetanthus* (Loranthaceae), *Psittacanthus* (Loranthaceae), and *Lepidoceras* (Eremolepidaceae), where the cotyledons function as storage organs (Kuijt, 1982). In these typical mistletoes, the radicle lacks a root cap and develops into the primary haustorium. Radicle growth depends on temperature and moisture, with growth being higher in moderate temperatures and high humidity (Reid *et al.*, 1995). In many species, radicle growth is negatively phototropic and geotropic, allowing it to grow

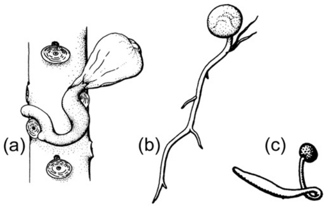

Fig. 4.6 Seedlings of parasites. (a) *Phorodendron densum* (Viscaceae) seedling with radicular lobes, (b) young seedling of *Lathraea clandestina* (Scrophulariaceae) showing branching of the emerging radicle, and (c) young seedling of *Cuscuta gronovii* showing coiling growth pattern of foraging radicle. (From Kuijt, 1969, reproduced with permission.

toward the host from the underside of a branch on which they are often deposited (Kuijt, 1969). Radicle growth may be very limited in some species, especially tropical ones. In other species, radicles can be extremely long. When the tip of the radicle contacts a solid surface, it flattens against the surface and begins to develop into a haustorium (Dobbins & Kuijt, 1974a).

Seedling morphology

The haustorium is a defining character in direct plant parasites and its formation is critical for seedling survival. With the exception of the primitive genera, mistletoes that are independent of a host cannot persist for long. Haustoria in the mistletoes come in a range of types but all are similar in some respects (Kuijt, 1969). The tip of the radicle appears to be thigmotropically sensitive. Once the radicle contacts a host branch, its tip thickens to form a club-shaped or hemispherical disk (Kuijt, 1969). The radicle tip is made up of several layers of tissue, including an epidermis and a hypodermis, each one-cell-layer thick, that surrounds an inner core of parenchyma (Dobbins & Kuijt, 1974a). At the point of contact with the host, the epidermal cells sometimes disintegrate with surrounding epidermal cells forming finger-like projections reaching toward the host surface and becoming an interwoven network. Both the radicle tip and developing haustorium contain chloroplasts and appear green (Dobbins & Kuijt, 1974a).

Host penetration is carried out in a structurally complex contact zone. The network of epidermal cell projections develops very dense cytoplasm in thin-walled tips that terminate at the host surface. Although this association is not yet fully described, the tips may then lyse with their cellular contents aiding in adhesion to the host (Dobbins & Kuijt, 1974a). A defining characteristic of mistletoe haustoria is the formation of the gland. This lens-shaped mass of dense cells forms in the center of the haustorium near the contact zone and is filled with fibrillar material that is secreted onto the host surface (Dobbins & Kuijt, 1974b). Tissue from the haustorium is thought to penetrate host tissue using a combination of enzymatic digestion and mechanical pressure (Thoday, 1951). After formation of the gland, a layer of dense parenchyma cells in the center of the haustorium contiguous with the gland region begins to differentiate into xylem vessels (Dobbins & Kuijt, 1974b). If initial host penetration is unsuccessful, a second contact zone forms with the expanding cells displacing the previous contact zone laterally (Dobbins & Kuijt, 1974b).

Once the haustorium reaches the host vascular cambium, direct xylem-to-xylem contact is quickly established and the mistletoe xylem is subsequently embedded in the host wood. Further mistletoe growth occurs by an intercalary meristem that allows correlation between host and mistletoe growth (Kuijt, 1969). The point at which the mistletoe begins to draw on host plant resources defines the end of the seedling stage in mistletoes (Kuijt, 1982).

Cotyledon emergence, if it occurs, happens somewhat after initiation of haustorium formation. In most advanced mistletoes, the epicotyl and cotyledons remain within the seed until a host connection is established (Kuijt, 1969). Cotyledon morphology varies markedly among mistletoes. Cotyledons are free and leaf-like in the primitive genus *Gaiadendron*. More advanced genera have varying combinations of cotyledon fusion (gamocotyly) and cotyledons that do not emerge from the seed (cryptocotyly). In some cases, cotyledons remain within the seed as a fused absorptive organ and never become photosynthetic (Kuijt, 1969). Small-flowered Loranthaceae generally have two large, green, spreading cotyledons that appear to function as storage organs (Kuijt, 1982). The large-flowered groups of Loranthaceae are somewhat more variable. In this group, seedlings of *Aetanthus* and *Psittacanthus* have large, fleshy cotyledons that appear to have replaced the endosperm of the seed as seeds are large but almost lacking in endosperm. Seedlings in the genus *Psittacanthus* have a variable number of cotyledons, ranging from 2 to as many as 14 that vary in shape and size (Kuijt 1982). Cotyledons in the genus *Tristerix* (Loranthaceae) are cryptocotylar and range from being fused only at the tips to complete fusion. The fused portions are often shed with the endosperm when the shoot emerges from the seed.

Seedling establishment and survival

Much of mistletoe seedling establishment depends on host suitability. Mistletoe seeds are dispersed by birds and deposition on appropriate hosts depends on which trees the birds encounter (Aukema, 2003). Viscin, which coats the seeds, adheres them to branches until they germinate and form haustorial connections. Not all trees are suitable hosts (Roxburgh & Nicolson, 2005). Host preference in mistletoes can range from specialists with only one appropriate host species, to generalists that can use most of the tree species in a forest (Barlow, 1981; Reid *et al.*, 1995; Norton & Carpenter, 1998). In general, temperate mistletoes are more host-specific than tropical mistletoes, perhaps because specificity is disadvantageous in very diverse tropical forests (Norton & Carpenter, 1998). Among mistletoes with more specific host requirements, host range tends to include several closely related hosts. Similarly, mistletoes that are closely related also tend to infect closely related hosts. The compatibility of a host is determined by a combination of host attachment and attempts at host penetration (Lopez De Buen & Ornelas, 2002). Hosts can resist mistletoe colonization by having bark that is impenetrable or exfoliating, forming wound periderm that prevents penetration, or by resisting xylem growth once penetration has occurred (Yan, 1993).

For most mistletoes, the uptake of host-derived water and nutrients occurs through open tracheids and vessels that offer little flow resistance. In many cases however, specialized parenchyma cells form the primary link between host and parasite xylem. Many holoparasitic species even link to host phloem elements (Riopel & Timko, 1995). Mistletoes are often divided into heterotrophic and autotrophic groups: dwarf mistletoes, which contain little chlorophyll and tap into both host xylem and phloem, and other mistletoes (all

Loranthaceae and most Viscaceae), which have substantial chlorophyll and generally access only host xylem. Still, even photosynthetic mistletoes are at least partially heterotrophic (Room, 1971; Raven, 1983; Marshall & Ehleringer, 1990; Pate *et al.*, 1991; Schulze *et al.*, 1991; Pate, 1995; Press, 1995).

Adult parasite transpiration is generally much greater than host transpiration and 5–68% of parasite carbon, and essentially all nitrogen and water (except in root parasitic species) is derived from the host. Less is known about transpiration in seedlings. It is clear that, except for primitive species, mistletoe seedlings do not survive long without connecting to a host. It is reasonable, therefore, to suppose that once seed reserves are exhausted, the great majority of seedling water, nitrogen, and, especially in species without foliar cotyledons, carbon is derived from host sources at least until the first true leaves are produced. For holoparasitic species, most, if not all, seedling nutrients are likely host derived. Parasite concentrations of most mineral nutrients are substantially higher than their hosts. Although it is not certain, this may be a reflection of greater parasite transpiration rates, which allows concentration of nutrients. It is likely that seedlings also transpire at the high rates seen in adult mistletoes (Press, 1995).

Once established, the growth rates of mistletoes are host dependent, growing very quickly on one host and slowly on another (Reid *et al.*, 1995). Seedlings are recruited episodically in some species, while in others, tropical species in particular, recruitment is continuous (Reid *et al.*, 1995).

Orobanchaceae

Unlike the mistletoes, which reach their greatest diversity in the tropics, members of the Orobanchaceae are primarily temperate (Musselman & Press, 1995). Members of this family include some of the most obvious root parasitic plants in temperate forests. With a few exceptions, *Striga* among them, these plants are largely absent in the tropics (Kuijt, 1969). While many species were previously classified as Scrophulariaceae (e.g. Musselman & Press, 1995), all parasitic and hemiparasitic species have been reclassified as Orobanchaceae (Olmstead *et al.*, 2001; Bennett & Mathews, 2006). However, in much referenced literature, the species are still separated into two families. We consider them together here under the Orobanchaceae, which includes holoparasites and both obligate and facultative hemiparasites.

Seedling morphology

Germination of most species is epigeous, with the hypocotyl growing down into the soil (Kuijt, 1969; Westbury, 2004). In many Orobanchaceae, host-root exudates stimulate seed germination and also attract the emerging radicle. As in advanced mistletoes, the seedling radicle is generally capless (Kuijt, 1969). Less than 24 hours after contact with a host plant, it swells, produces a ring of haustorial hairs, and quickly forms many branches (Kuijt, 1969; Fig. 4.6b). Haustoria formation in *Striga asiatica* seedlings begins with a redirection of cellular expansion at the root meristem from longitudinal to radial, starting roughly eight hours subsequent to exposure to the host-derived chemical 2,6-dimethoxy-*p*-benzoquinone (DMBQ; Smith *et al.*, 1990). This cell expansion resulted in a swollen radicle tip followed by the formation of prominent haustorial hairs (Musselman & Dickison, 1975 and references therein; Riopel & Timko, 1995; Tomilov *et al.*, 2005). These haustorial hairs had surface papillae of hemicellulose, which bond the parasite to the host tissue (Riopel & Timko, 1995). A similar sequence of events occurs in *Triphysaria versicolor* (Tomilov *et al.*, 2005).

Haustoria formation differs somewhat between holo- and hemiparasitic plants. In hemiparasites, which make up the majority of the family, haustorium development occurs laterally, just behind the radicle meristem. Normal growth resumes after haustorium development and additional haustoria may be formed (Tomilov *et al.*, 2005). In holoparasites, a primary haustorium forms at the meristematic tip and halts further growth (Okonkwo & Nwoke, 1978). Additional lateral haustoria, similar to those of hemiparasites, may form after the primary haustorium has established a connection with the host (Tomilov *et al.*, 2005).

Differentiation of vascular tissues within the haustorium is variable and influenced by host roots. Following the penetration of host tissues by either release or induction of cellulases, pectinases (Reddy *et al.*, 1980, 1981), and/or acid phosphatases (Toth & Kuijt, 1977), elongated haustorial tip cells divide longitudinally, pushing aside host tissues (Stephens, 1912; Maiti *et al.*, 1984). Once the host endodermis is penetrated, haustorial cells enter the host vessel lumen through pits in the side wall or dissolution of the vessel wall with hydrolytic enzymes. Cells in the haustorial tip differentiate into xylem elements, and quickly establish a connection between host and parasite xylem (Riopel & Timko, 1995; Bouwmeester *et al.*, 2003). Musselman and Dickison (1975) found that phloem elements were generally lacking in the haustorium, though specialized parenchyma cells may connect host and parasite phloem, as in *Striga*.

Seedling establishment and survival

After haustorium penetration, the holoparasite seedling is entirely dependent on the host and can trigger root proliferation by altering host hormone balances (Musselman & Press, 1995). Most holoparasites are cryptocotylar and cotyledons never emerge from the seed. In many hemiparasitic species, the cotyledons emerge from the seed shortly after germination as in typical nonparasitic plants. Some species, such as *Tozzia*, live entirely belowground for several years as parasites, only producing a green shoot when flowering (Kuijt, 1969).

Host specificity varies dramatically in the Orobanchaceae, from species that associate with hundreds of hosts to those that associate with only a single species, such as *Epifagus virginiana* (Musselman & Press, 1995). Most species exhibit some level of host preference (Musselman & Press, 1995). Seeds are thought to be primarily dispersed by a combination of wind and water, which washes seeds into soil crevices, but ants have also been shown to aid in dispersal (Kuijt, 1969).

Cuscuta

In addition to the families mentioned above, which consist mostly or entirely of parasitic species, there are also several small parasitic families, including the holoparasitic Lennoaceae (e.g. *Lennoa* and *Pholisma*), and hemiparasitic Krameriaceae (e.g. *Krameria*). Other parasitic species occur in largely autotrophic families. These include *Cuscuta* in the Convolvulaceae and *Cassytha* in the Lauraceae. Dodders of the genus *Cuscuta* are the best known of these groups, with more than 150 species (Kuijt, 1969). Little or nothing appears to be known about the seedling stages of *Cassytha*, Lennoaceae, and Krameriaceae. Members of the genus *Cuscuta* occur on all continents except Antarctica, and are important agricultural pests in many areas (Runyon *et al.*, 2006).

Seedling morphology

Largely or completely lacking chlorophyll, dodders are entirely parasitic. Seedlings are rootless and must forage for host plant tissues. The shoot that emerges from the seed exhibits directed growth toward volatile compounds produced by potential host plants (Runyon *et al.*, 2006; Fig. 4.6c). Soon after initial contact with a host, thigmotropic responses produce a narrow coil that bears multiple haustoria. After establishment of initial haustoria, the radicle dies and subsequent growth is in the form of wide coils that can contact the host in another location or contact a new host (Kuijt, 1969). Haustoria in dodder are structurally similar to those in the mistletoes and Orobanchaceae, but dodder haustoria also include a bridge of parenchymatous cells that link host and parasite phloem elements (Dörr, 1990). Embryos of dodders lack cotyledons but have two laterally arranged scale leaves.

Seedling establishment and survival

Some dodder species have minute quantities of chlorophyll and are capable of fixing limited amounts of CO_2, but most depend on host-derived carbon in addition to water, nitrogen, and other nutrients (Pate, 1995; Press, 1995). Adult dodder haustoria can divert substantial quantities of host carbon, resulting in crop yield reductions of 23–57% or more (Riches & Parker, 1995). As with many other parasitic plants, it is clear that the seedling stage, during which dodder must locate a host and establish haustorial connections, is the critical point in its life history. Recognizing this, most agricultural control methods focus on the seedling stage (Runyon *et al.*, 2006). The seedling stage also likely determines population dynamics in natural environments. Dodder can parasitize a wide range of plants, but is capable of exploiting a narrower range (Musselman & Press, 1995) and shows distinct host preferences in its foraging behavior (Runyon *et al.*, 2006).

Mycoheterotrophic plants

Mycoheterotrophism has apparently evolved independently many times in the plant kingdom. These plants are often considered epiparasites because they exploit a fungus involved in an ectomycorrhizal relationship with woody plants. Mycoheterotrophism is especially common in the Orchidaceae and several families within the Ericales (Leake, 1994; Bidartondo, 2005). Mycoheterotrophism here is defined as applying only to nonphotosynthetic plants, not the many plants that supplement their photosynthetic carbon with carbon from mycorrhizal fungi or those that are only initially mycoheterotrophic. Some Orchidaceae and Gentianaceae and all Monotropoideae and Triuridacae are mycoheterotrophic (Bidartondo, 2005). As orchids are covered in section 4.2, we will limit the discussion here to the most extensively studied group of mycoheterotrophic plants, the Monotropes (Ericaceae).

Seedling morphology

After germination triggered by molecules released by specific fungi, monotrope seedlings are morphologically quite different from nonparasitic plants (Bidartondo, 2005; Bidartondo & Bruns, 2005). They do not form haustoria as the other parasitic groups mentioned here, but rather resemble seedlings of mycoheterotrophic orchids, perhaps due to their minute seeds with undifferentiated embryos that lack cotyledons or nutrient resources.

Prior to fungal infection, but likely stimulated by fungal chemical signals, the embryo/hypocotyl emerges from the cracked seed coat (Bidartondo & Bruns, 2005). Once an embryo is successfully colonized by an appropriate mycorrhizal fungus, it quickly begins to branch, coming to resemble the dense aggregation of mycorrhizal roots which can adventitiously produce inflorescences. Colonization by an appropriate mycorrhizal fungus takes place immediately after germination such that, unlike direct plant parasites, connection to a host is present throughout the seedling stage and cannot be said to define the end of this stage. Although a few individuals of *Monotropa uniflora* (Monotropoideae) start to flower after two years, it is clear that most plants remain entirely belowground for several years before producing an inflorescence that is devoid of chlorophyll and has only minute scale leaves.

Seedling establishment and survival

Monotrope seedlings obtain all nutrients from their mycorrhizal fungi and all monotropoid mycorrhizal fungi form ectomycorrhizae with trees. Thus, the monotropes are effectively epiparasites on the tree hosts of this three-way interaction. Mycorrhizal associations involving a mycoheterotrophic plant are also very specific. Each mycoheterotroph studied only associated with a narrow range of fungi. Each monotrope lineage required fungi from a single clade of obligate ectomycorrhizal fungi (Bidartondo & Bruns, 2005). The transfer of nutrients between fungus and monotrope may occur by lysing hyphal ingrowths and absorbing their nutrients, in a process similar to hyphal digestion in orchids (section 4.2). However, in monotropes where there is little intracellular fungal colonization, it seems likely that more transfer of nutrients occurs by a disruption of plant and fungal cell membranes or by source-sink dynamics across a permeable membrane (Bidartondo, 2005).

It is clear, given the large numbers of dust seeds produced by mycoheterotrophs compared to the small number of emerging inflorescences, that the life history stages that experience the greatest mortality are those that occur underground (Rasmussen & Whigham, 1993; Bidartondo & Bruns, 2005). For monotropes, which emerge only to flower, the underground phase includes the seed, seedling, and a vegetative stage of unknown duration. Bidartondo and Bruns (2005) found that the fungal specificity in monotropes begins at the time of germination and seedlings associated exclusively with the same fungi that formed successful mycorrhizae with adult plants. This suggests that germination and the seedling stage are critically important to monotrope population dynamics.

4.6 Summary and future needs

This chapter focuses on phylogenetically diverse groups of organisms that demonstrate a high degree of convergent evolution in several life history characteristics, apparently associated with their occurrence in habitats with severe environmental constraints. Most species in the groups of plants considered have small seeds (Baskin & Baskin, 1998) and many have simple or undifferentiated embryos. Following germination, embryos take divergent paths as they grow and develop into seedlings. Seedlings of carnivorous species assume adult structures and are capable of capturing prey (Fig. 4.5c–g). Embryos of orchids and mycoheterotrophic parasitic plants develop into a life history stage that is very different from juveniles and adults, and is completely dependent on mycorrhizae for nutrient acquisition. Seedlings of most epiphytic bromeliads and parasitic plants are similar in that they do not have mycorrhizal associations, but differ in how seedlings become established. Most bromeliads allocate resources to aboveground tissues through which most resources are acquired; roots are often highly reduced and primarily provide anchorage. In contrast, seedlings of parasitic species allocate most of their resources to haustoria, an adaptation that is important because seedlings must quickly become morphologically and physiologically attached to their host plant.

There are, of course, exceptions to these general descriptions but it is important to note that knowledge about seedlings of any of the groups described in this chapter is minimal. Seedlings of species in each of these groups acquire resources through nontraditional pathways. Seedlings of parasitic plants obtain resources directly from their hosts. Protocorms and seedlings of mycoheterotrophic plants including achlorophyllous orchids that interact with ectomycorrhizal fungi also obtain all of their resources from host plants, but rather than being connected directly to the host, they use host resources that have first been obtained by fungi. Seedlings of carnivorous plants obtain resources from prey and in the process of trapping prey, nutrient uptake through roots is enhanced. Seedlings of epiphytic bromeliads allocate most of their resources to nonroot structures and a variety of leaf modifications allow resources to be captured in tanks and other modified leaves.

As very few species in any of the groups of plants covered in this chapter have had extensive studies performed on seedlings, further research should focus on seedling morphology, physiology, and ecology. Particular attention, however, should be given to quantitative studies of seedling establishment and survival. This information must be obtained if we are to fully understand the ecology of these groups, and so that we may apply that knowledge to conservation and restoration issues. Perhaps the best example of this need is seen in the orchids where there is a paucity of information on the fungal requirements of protocorms, including the identification of fungal species that are essential for their growth and survival. There is even less information on the distribution and substrate requirements for nonectomycorrhizal fungi that protocorms and seedlings of many species, especially epiphytes, require.

The main conclusion is that we still know very little about the seedling ecology of these interesting groups of plants. An unlimited number of themes and challenges await our attention as we seek to integrate knowledge about the seedling ecology into our understanding of population ecology.

4.7 Acknowledgments

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