

Parasitic Plants of the World

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Chapter 2, pp. 7-27 in: J. A. López-Sáez, P. Catalán and L. Sáez [eds.], Parasitic Plants of the Iberian Peninsula and Balearic Islands

This text first written in English (as appears here) was translated into Spanish and appeared in the book whose Spanish citation is:

Nickrent, Daniel L. 2002. Plantas parásitas en el mundo. Capítulo 2, pp. 7-27 *In* J. A. López-Sáez, P. Catalán and L. Sáez [eds.], Plantas Parásitas de la Península Ibérica e Islas Baleares. Mundi-Prensa Libros, S. A., Madrid.

1. General Introduction

Just as insectivorous plants have captured the imagination of humans for many generations, parasitic plants have also been the subject of much curiosity since ancient times. What these two groups of plants have in common is that they have both evolved nutritional modes that are strikingly different than what is typically perceived to be "normal" for a green plant, i.e. photosynthetic, motionless, and oblivious to other organisms around them. One cannot help but marvel that evolution has produced insectivorous plants that "turn the tables" (specifically, the dinner tables!) on animals by actively trapping invertebrates (insects) and digesting them, thereby releasing nitrogenous compounds that are otherwise limited in the plant's environment. Similarly, parasitic plants represent another complex nutritional mode that has evolved independently in at least nine lineages (see next chapter), but in this case the parasite's alternate source of food is from another plant.

2. Nonparasitic Associations

To place parasitism into its proper context, it is useful to look at the full spectrum of trophic modes present within all flowering plants (Fig. 1). The vast majority of green plants (angiosperms) that are encountered daily are **autotrophic**, i.e. they produce all their own food via photosynthesis. In contrast, there are a significant number of plants that have adopted a **heterotrophic** mode whereby all or some of their carbohydrates are obtained from another organism. One can categorize heterotrophs into two major categories: mycotrophs and haustorial parasites (Furman and Trappe 1971) (Fig. 1). Mycotrophs, sometimes mistakenly referred to as saprophytes (only fungi are truly saprophytic), obtain carbohydrates and other nutrients by parasitizing a mycorrhizal fungus. Often the mycorrhizae are also associated with the roots of photosynthetic trees, hence the mycotroph can be thought to indirectly parasitize the tree.

Mycotrophs can be found in a number of monocot and dicot families (Fig. 1) representing over 400 species. One frequently encountered mycotroph is *Monotropa* whose ghostly white appearance suggests the fact that chlorophyll is lacking and that it receives its nutrition in a heterotrophic fashion (see Chapter 6 by L. Villar). Because of its nonphotosynthetic nature, *Monotropa* is often misinterpreted as a parasitic plant, and indeed there is some degree of penetration of the host roots by *Monotropa* (Bjorkmann 1960), hence it may be considered an epiparasite.

As discussed in the first chapter of his book "The Biology of Parasitic Flowering Plants," Kuijt (1969) describes a number of other associations between plants that have been considered parasitic. These include an *Opuntia* cactus growing from the stem of *Idria*, a *Passiflora* growing within *Euonymus*, and stem and root grafts that occur commonly among different tree species. At least for the latter examples, there is clear documentation of the movement of nutrients between the two partners, thus making the definition of parasitism an exercise in semantics. It is for this reason that the term "haustorial parasite" has been used in this chapter to restrict usage to those plants that form modified roots called haustoria that affect the morphological and physiological connection to another plant. With the possible exception of *Hyobanche* which can form secondary haustoria from scale leaves (Kuijt et al. 1978, Visser et al. 1978), essentially all haustoria are modified roots.

Hhaustorial parasitism appears to have evolved only in flowering plants (dicots), however, the case of *Parasitaxus ustus* (Viellard) de Laubenfels, a rare gymnosperm of the family Podocarpaceae, must also be considered. This shrub or small tree has fleshy, deep wine red to purple scale leaves, and is found only in New Caledonia where it occurs in remote, densely forested areas. The plant lacks roots and is always found attached to the roots of *Falcatifolium*

taxoides (Brongn. & Gris) de Laubenfels, which is also a member of Podocarpaceae. There is debate about the parasitic status of this plant because a typical haustorium is not formed but the xylem-to-xylem connections resemble a root graft (Köpke et al. 1981). More recent work (Woltz et al. 1994) indicates that the *Parasitaxus* haustorium penetrates to the cambium of the host and that both plants are infected by a mycelial endophyte that links them in a symbiotic relationship. Thus, it seems that this gymnosperm is not a haustorial parasite but a mycotroph.

3. Nutritional Modes in Parasitic Plants

One can categorize parasitic plants according to their evolutionary relationships (next chapter) or according to their nutritional mode. Among the various unrelated families of parasitic plants, two basic types of parasitism exist: **hemiparasites** and **holoparasites** (Fig. 1). Hemiparasites are chlorophyllous and photosynthetic (at least during some portion of the life cycle) yet they obtain water and nutrients via haustorial connections to the host plant. Hemiparasites can be further divided into two types, facultative and obligate, depending upon their degree of dependence upon the host. Facultative hemiparasites do not require a host to complete their life cycle but are photosynthetic and, when presented with host roots, invariably form haustorial connections. When attached to host roots, these parasites extract water and dissolved minerals via direct, cell-to-cell connections to the xylem. Facultative hemiparasites can be found in several root-parasitic families, e.g. Olacaceae, Opiliaceae, Santalaceae (Santalales), Krameriaceae (Fabales), and Scrophulariaceae (Lamiales). Experimental work has documented the fact that parasitic Scrophulariaceae from Europe (e.g. *Bartsia*, *Euphrasia*, *Melampyrum*, *Odontites*, *Pedicularis* and *Rhinanthus*) and North America (*Agalinis*, *Dasistoma*, *Macranthera*, and *Seymeria*) can be grown to flowering and fruiting in the absence of host plants (Weber 1981,

Mann and Musselman 1981). Although some genera in Olacaceae are clearly facultative hemiparasites, others such as *Olex* may represent transitional states between facultative and obligate. For example, seedlings of *O. phyllanthi* first exist in a preparasitic state without developing haustoria but will succumb after six months if they do not attach to a host (Pate et al. 1990a, Pate et al. 1990b). To distinguish between the facultative and obligate conditions, it must be determined if the parasite is able to flower and fruit during the preparasitic stage. Plants grown from seed of *Osyris alba* (Sanalaceae) survived and flowered for several years in pots without hosts (Nickrent, pers. obs.), however, the cause of the eventual death of these potted plants was not determined.

Obligate hemiparasitism represents a further advancement in a continuum of parasitism types. In contrast to facultative hemiparasites, obligate hemiparasites must attach to a host plant to complete their life cycle. Among the obligate hemiparasites, one can differentiate two types, primitive and advanced (Fig. 1). The primitive type includes stem parasites of Loranthaceae, Misodendraceae and some Viscaceae. These plants are photosynthetic xylem feeders, but, being stem parasites, they cannot exist independent of the host plant. Possible exceptions to this may be the root parasites found in Loranthaceae (*Atkinsonia*, *Gaiadendron*, and *Nuytsia*) which, unlike other members of the family, do not form primary but only secondary (lateral) haustoria. For *Atkinsonia* (Menzies 1959), *Gaiadendron* (Kuijt 1963) and *Nuytsia* (Main 1947) seedlings can exist independent of a host plant for many months to at least a year. For *Nuytsia*, this phase is transitory, for seedlings will die within six to nine months if not provided a host plant (Main 1947). Interestingly, their life can be extended to at least three years with fertilization and hormone treatment (Grieve 1975). It is unlikely that any of these mistletoes are capable of independent existence for the long term because all lack root hairs that are essential for nutrient

uptake (Hocking 1983). Six of the seven genera of Viscaceae can be categorized as primitive obligate hemiparasites, the exception being *Arceuthobium* whose adult shoots fix only about 30% of the carbon needed for growth (Hull and Leonard 1964). The advanced obligate hemiparasites attach not only to host xylem but also obtain host carbon via phloem connections. Concomitant with this nutritional mode is the loss of photosynthetic function, at least to some degree or during some stage of the life cycle. Examples of this nutritional mode include most species of *Cuscuta* (Cuscutaceae), *Cassytha* (Lauraceae), *Phacellaria* (Santalaceae), *Striga gesnerioides* (Scrophulariaceae), and *Arceuthobium* (Viscaceae).

The most extreme manifestation of the parasitic mode can be found among the holoparasites. These plants are totally achlorophyllous (or nearly so), nonphotosynthetic, and obtain all their water and nutrients from host xylem and phloem. Most holoparasites occur on host roots, however, some species of *Cuscuta* (e.g. *C. europaea*) are stem holoparasites that have lost RUBISCO, thylakoids, chlorophyll and light-dependent CO₂ fixation (Machado and Zetsche 1990). Some members of Rafflesiales also occur as stem parasites (e.g. *Apodanthes*, *Pilostyles*, *Rafflesia*), but it is likely that these first become established on host roots and continued growth of the endophyte results in relocation to the stem (see Kuijt 1969, p. 207). Holoparasitism has evolved independently in at least seven lineages: Balanophoraceae, Cynomoriaceae, Hydnoraceae, Rafflesiales, Cuscutaceae, Lennoaceae and Orobanchaceae (Fig. 1); however, the taxonomic circumscription and phylogenetic positions of these plants is currently undergoing intensive re-evaluation (see next chapter). Two families, Cuscutaceae and Scrophulariaceae (the latter in the broad sense, including Orobanchaceae) serve as models for studying the evolution of holoparasitism from hemiparasitism because both modes (and transitional forms) exist among particular species.

4. Numbers and Distributions of parasitic plants

Parasitic plants are never the dominant life form in an ecosystem, yet what can be said about their relative diversity? As shown in Table 1, there exists approximately 4200 species of haustorial parasitic plants, that is, just over 1% of all flowering plants. The total number of parasite species is not distributed evenly among the 18 families or 274 genera. Almost half the total can be attributed to Scrophulariaceae s. lat. and within this family, the genera *Castilleja* (200 spp.), *Euphrasia* (170 spp.), and *Pedicularis* (350 spp.) account for over 700 species. Other large genera (ca. 100 species or more) include *Cuscuta* (Cuscutaceae), *Amyema* (Loranthaceae), and *Viscum* and *Phoradendron* (Viscaceae). Thus, 30% of all parasite species can be attributed to the above seven genera. These figures are of course dependent upon current taxonomic concepts. For example, the circumscription of *Tapinanthus* in the recent "Mistletoes of Africa" (Polhill and Wiens 1998) indicates the genus is composed of 30 species, reduced from previous estimates of nearly 250 species by broader species concepts and taxonomic transfers to other genera.

One can encounter parasitic plants in nearly every habitat type found throughout the world. For example, *Pedicularis dasyantha* occurs on the Svalbard archipelago at latitudes of more than 80° N (Musselman and Press 1995). At the opposite pole, *Nanodea muscosa* occurs in Tierra del Fuego Argentina at 55° S. Families such as Balanophoraceae, Rafflesiaceae, Mitrastemonaceae, Loranthaceae, and Olacaceae have significant numbers of genera and species in moist tropical habitats. Grassland and savannah ecosystems that receive less precipitation also harbor diverse parasite floras, particularly in the families Scrophulariaceae and Loranthaceae. Even in xeric habitats such as deserts, parasitic plants such as Hydnoraceae, Cynomoriaceae, Lennoaceae and

Apodanthaceae can be found. It should be remembered that parasitic plants must have lower water potentials than their host plants to ensure the flow of water and nutrients moving through the haustorial connection. For many parasites, this is accomplished by maintaining higher transpiration rates than that of their host plants. This may be the reason that one does not encounter large numbers of stem parasitic Loranthaceae and Viscaceae in dense (hence dark) tropical rainforest conditions. Savannas, with their high solar incidence and numerous host trees, provide ideal situations for these mistletoes, and significant adaptive radiations in these families have taken place in such dry ecosystems in Central and South America, Africa and Australia.

In terms of overall numbers, the majority of parasitic plant species occur in ecosystems undisturbed by humans. In the minority are those parasite species that have adaptations to human disturbance and thereby increase in population size. In the case of *Phoradendron leucarpum* (= *P. serotinum*) in the Eastern United States, the patchy distribution of host trees in urban and park settings appears ideal for the spread and proliferation of this parasite. The heaviest concentration of this mistletoe was in residential areas of middle Tennessee, USA (McKinney and Hemmerly 1977) and this is likely the case throughout much of the distribution of this parasite. A patchy distribution of host trees (instead of dense forest stands) appears to limit and concentrate the movements of seed-dispersing birds such as waxwings (Skeate 1987), thus allowing the development of large parasite populations. Even-aged stands of coniferous species derived from large-scale replantings can support explosive increases in populations of *Arceuthobium*, particularly when these plantations are adjacent to infected old-growth trees (Hawksworth and Wiens 1996 p. 136). Fragmentation of *Acacia* woodlands in the Northern Territory of Australia and the movements of the mistletoe bird *Dicaeum hirundinaceum* apparently increases the incidences of parasitism by *Amyema preissii* (Lavorel et al. 1999).

Striga and *Orobancha* each have species highly adapted to agricultural habitats. Indeed, it has been hypothesized that *Striga hermonthica* coevolved with wild relatives of *Sorghum* (Mohamed et al. 1996) and the current pathogenic strain of the species has only emerged following domestication of this crop (Kuiper 1997). The reproductive potential of these plants is high (given their numerous tiny seeds), hence large populations of susceptible crop species offer numerous opportunities for parasitism (Musselman 1980, Wegmann et al. 1998).

5. Host Relationships

It is often stated that a good parasite does not kill its host. That said, variation in the degree of pathogenicity exhibited by various parasitic plants is great, from those that exert little impact on their hosts (e.g. *Epifagus* on *Fagus*) to those that dramatically affect the host physiology and fecundity (e.g. *Striga* and *Orobancha* on various crop plants). Pathogenicity depends upon many factors, such as the biomass ratio of parasite to host, the number of parasites attached to an individual host plant, the length of time required for the parasite to complete its life cycle, and possibly the degree of coevolutionary "tuning" that has occurred over time between the two species. Complicating factors include examples such as *Striga* on cereals. Here the size of the parasite does not appear to be concordant with the degree that the host physiology is perturbed (Press et al. 1996) and is likely related to changes in host growth regulating (Drennan and El-Hiweris 1979). Reduction in host biomass is not explained simply by source-sink relationships, but by phytotoxic effects that change the partitioning of host photosynthate from shoot to root and an overall reduction in photosynthetic rate (Ransom et al. 1996). Despite variations in pathogenicity and life cycle dynamics, all parasitic plant species have evolved under the constraint that they do not kill their hosts prior to successful reproduction.

Before discussing host specificity, it is important to highlight two concepts: host range and host preference. The host preference of a parasite refers to those hosts that are parasitized in nature. When these parasites are presented with additional hosts under artificial conditions, parasitism may occur, thus indicating a broader host range. An example of this is *Cuscuta epilinum* which occurs naturally only on *Linum*, but will colonize *Impatiens* when given the opportunity (Kuijt 1969). In terms of host specificity, the full range from generalists to specialists can be found, sometimes among species of the same genus. For example, among the 45 species of *Arceuthobium* (dwarf mistletoes, Viscaceae), some parasitize only a single host species, such as *A. apacheum* on *Pinus strobiformis*, whereas others, such as *A. globosum* ssp. *grandicaule*, infects at least 12 host species (Hawksworth and Wiens 1996). A similar broad host range can be cited for various species of *Cuscuta*. Some Loranthaceae have especially wide host ranges, as exemplified by *Dendrophthoe falcata* which has been recorded from over 350 species and additional reports continue to increase this number (Joshi 1985, Narayanasamy 1981). Note that, however, recent work has shown that this widespread and polymorphic taxon is actually composed of several morphologically and geographically discrete species (Barlow 1995). The pantropical *Cassytha filiformis* (Lauraceae) appears to be totally indiscriminate in host choice, often covering and parasitizing dozens of host species simultaneously (Werth, 1979). Moreover, the parasite as often forms attachments to itself (autoparasitism) as it does to its host.

Parasite groups in which host specialization is the norm include Misodendraceae (*Misodendrum* occurs exclusively on *Nothofagus*), some Scrophulariaceae (Orobanchaceae, i.e. *Conopholis* on *Quercus*, *Epifagus* on *Fagus*, etc.) and Rafflesiaceae. For the latter order, all three genera of Rafflesiaceae s. str. (*Rafflesia*, *Rhizanthus* and *Sapria*) are known only from

Tetrastigma (Vitaceae). Similar host specializations have evolved in the other segregate families of this order, e.g. *Apodanthes* on *Flacourtiaceae*, *Pilostyles* (including *Berlinianche*) on legumes, and *Mitrastema* on Fagaceae. One might predict that, like Rafflesiales, Balanophoraceae and Hydnoraceae would be similarly specialized along host lines, but such is not the case. One factor that may promote selection of host specificity is the occurrence of a parasite within a more homogeneous community (e.g. temperate vs. tropical forests), thus increasing the density of potential hosts (Kuijt 1969). Such an explanation does not apply to Rafflesiales, the majority of whose members occur in tropical forests with extremely high host diversity. Canalization along host lines, i.e. the “specialist strategy,” likely has advantages when hosts are common, but from an evolutionary perspective, generalists likely persist longer in geologic time. This may explain why the majority of parasitic flowering plants are not host specialists.

6. Coevolutionary Relationships

One of the most remarkable coevolutionary relationships that exists is the presence of one parasitic angiosperm upon another. Two forms of association can be distinguished, facultative and obligate. As suggested by Wiens and Calvin (1987) the term hyperparasite should be used to describe a facultative association between different parasite species. Probably the most frequent and generalized examples of hyperparasitism involve *Cuscuta* and *Cassytha*. These genera parasitize a variety of plants which, by chance, may include woody root hemiparasites such as *Ximenia* (Olacaceae), *Santalum* (Santalaceae), etc. *Cuscuta* and *Cassytha* have also been reported as hyperparasites of mistletoes such as *Phoradendron* and *Struthanthus* (Kuijt 1964).

In contrast, the obligate situation called epiparasitism is known from mistletoes of both Loranthaceae, Viscaceae and Santalaceae in both the Paleotropics and Neotropics. The sole

epiparasitic genus in the latter family is *Phacellaria* of southeast Asia which is an obligate parasite of Loranthaceae (Danser 1939). All possible host-parasite combinations have been reported (e.g. loranth on loranth, viscid on viscid, viscid on loranth, and loranth on viscid), although certain combinations are more common in particular regions. For example, Viscaceae have rarely been reported on Loranthaceae in the New World, a rare exception being *Phoradendron iltisii* on *Cladocolea pringlei* (Kuijt 1990). Approximately ten species of *Phoradendron* have been reported to be epiparasites, and indeed the entire 'Amplectens' group may be so (Kuijt 1987). At least ten species of hyperparasitic and epiparasitic *Viscum* have been documented from Australia and Asia (examples include *V. articulatum* and *V. loranthi*) and Africa (e.g. *V. loranthicola*) with Loranthaceae being the most frequent hosts. In Africa, Loranthaceae such as *Agelanthus pungu* are frequently found parasitizing other members of both Loranthaceae and Viscaceae (Polhill and Wiens 1998). New World loranth-loranth combinations can be found in *Ixocactus*, *Notanthera*, *Phthirusa*, and *Tristerix*, however, only one report of the inverse exists, i.e. *Oryctanthus occidentalis* on *Phoradendron crassifolium* (Kuijt 1964). Even more remarkable are tripartite epi- or hyperparasitic associations, such as *Scurrula ferrugineus* on *Viscum articulatum* on *Elytranthe barnesii* which was itself parasitic on *Durio* (Sands, 1924). Similarly, in South Africa, the following association has been reported: *Viscum verrucosum* on *Tapinanthus quequensis* (= *T. leendertziae*) on *Agelanthus natalitius* (= *T. natalitius*) upon *Combretum apiculatum* (Visser 1982). Field studies have shown that mistletoes maintain a water potential difference ca. 1000 kPa less than their nonparasitic hosts when both species are transpiring maximally. When an epiparasitic mistletoe is measured, its water potential is 1000 kPa less than its host mistletoe (Visser 1982). Water potential measurements

have never been made on the component species in involved a three-way association, but the question can be asked "how great can water potential differences become?"

In addition to their relationships with their hosts, parasitic plants often develop complex associations with other organisms they encounter throughout their life cycle. Pollination and fruit/seed dispersal have been extensively reviewed elsewhere, hence only an overview will be presented here. A recent review of floral biology and reproductive ecology of parasitic plants can be found in (Molau 1995). Pollination involves the full spectrum of syndromes including: 1) beetles, e.g. Hydnoraceae (Musselman 1991) and *Lophophytum* (Balanophoraceae) (Borshenius and Olesen, 1990); 2) bees, e.g. *Pedicularis* (Scrophulariaceae) (Macior 1986), *Krameria* (Simpson, 1989), and *Balanophora* (Govindapa and Shivamurthy 1975) and *Mystroptalon* (Visser 1981); 3) flies, e.g. *Rafflesia* (Beaman et al. 1988), *Rhizanthus* (Bänziger 1996), *Sarcophyte* (Visser 1981); 4) birds, e.g. many Loranthaceae (Reid 1990), *Arjona*, *Quinchamalium* (Santalaceae), *Castilleja* (Scrophulariaceae), and *Mitrastema* (Beehler 1994); and 5) bats, e.g. *Dactylanthus* (Ecroyd 1995).

As with pollination, seed dispersal syndromes are various. Among mistletoes, birds are important dispersal agents in most species of Loranthaceae and Viscaceae. Indeed, for the former family, the mistletoe birds (Dicaeidae) have highly specialized digestive tracts and behaviors that aid in dispersing loranth seeds (Docters van Leeuwen 1954, Reid 1990). Mammals are also involved in dispersing fruits and seeds of some parasitic plants, e.g. possums for *Prosopanche* (Cocucci and Cocucci 1996) and treeshrews (*Tupaia*) or plantain squirrels (*Callosciurus*) for *Rafflesia* (Emmons et al. 1991).

A significant yet poorly known aspect of parasitic plant biology is their association with microorganisms (fungi and bacteria). Atsatt (1973) suggested that haustoria were first produced

in response to microbial parasitism and subsequently were modified for water and nutrient uptake. As mentioned in the Introduction, the gymnosperm *Parasitaxus* and its host root are both infected by a fungus that acts as a bridge between host and "parasite." This type of symbiotic association is almost certainly not homologous with (or ancestral to) haustorial parasitism in angiosperms, but it may represent an independent evolutionary experiment that approaches parasitism. Field observations have shown that seedlings of the holoparasite *Conopholis americana* (Scrophulariaceae) are only found attached to mycorrhizal roots of their oak host (Baird and Riopel 1980). Because essentially all oak roots found in nature are mycorrhizal, it is difficult to determine whether this association is obligate. Experimental studies using exudates from intact oak mycorrhizal roots yielded a 3% germination rate, comparable to rates seen from soil samples (Baird and Riopel 1986). Hemiparasitic Scrophulariaceae (e.g. *Melampyrum*) may also show a preference for mycorrhizal roots (Heinricher 1917). It has also been observed that *Cuscuta* preferentially parasitizes host plants that have mycorrhizal associations (Sanders et al. 1993). A number of fungi are associated with mistletoes, usually as facultative hyperparasites but obligate associations are also known such as *Wallrothiella arceuthobii* on *Arceuthobium* (see review in (Gill 1961).

7. Parasitic Plants and Human Activities

As discussed under "Host Relationships" above, it is useful to distinguish between a plant that is a parasite and one that is also a pathogen (i.e., causing disease). Such a distinction is a difficult one to make, for disease implies a condition where the normal host functions disrupted (Holliday 1989). Exactly how much functional alteration is required before a parasite can be called a pathogen is open to question and may require measurements of many parameters to determine

the degree of deviation from the "normal" condition. In point of fact, parasitic plants occupy all possible positions along the symbiotic pathway from parasitism to commensalism.

Pathogenicity also carries an antropocentric connotation in that one is more likely to call a parasitic plant a pathogen when it negatively impacts a host that has some economic importance.

How many genera of parasitic plants are pathogens of plants utilized by humans? As shown in Table 2, approximately 30 genera of parasitic angiosperms have been reported to negatively impact a host plant that is cultivated or harvested by humans. Given that there exists 274 genera, only about 11% of all genera have members that could be considered pathogens. This number is actually inflated, for indeed most of the damage inflicted upon economically valuable hosts is caused by just four genera: *Cuscuta*, *Arceuthobium*, *Orobanche*, and *Striga*. *Arceuthobium* represent an unusual case where a native pathogen inflicts a significant impact upon a natural forest community that is harvested for timber (Hawksworth and Wiens 1996). Although the other three genera do exist on native hosts, populations can explosively increase on monocultures of herbaceous crop plants. Despite the fact that only a tiny fraction of the total number of parasitic plants are pathogens on host plants used by humans, it must also be stated that the economic impact of the above four genera is enormous. For *Arceuthobium*, it is estimated that about 11.3 million cubic meters of wood are lost annually in the western U.S. and Canada valued at several billion dollars (Hawksworth and Wiens 1996). The witchweeds (particularly *Striga asiatica*, *S. aspera*, *S. gesnerioides*, and *S. hermonthica*) are the most significant parasitic weeds in the world, particularly in semi-arid regions of Africa and Asia (Riches and Parker 1995). Both the extent of infestation by *Striga* and the annual dollar amount lost are difficult to determine. One estimate indicates that of 67% of the 73 million ha placed in cereal production in sub-Saharan Africa is infested with *Striga* (Lagoke et al. 1991). In Northern Ghana alone, the

economic loss from *Striga* on maize, millet and sorghum amounted to 25 million dollars in 1988 (Sauerborn 1991). As pointed out in this report, the focus on monetary terms presents an incomplete picture because the people operating these small farms rely directly on such grain crops for survival. The genus *Orobanche* includes four damaging pathogens: *O. crenata*, *O. cernua*, *O. ramosa*, and *O. aegyptiaca*. Several hundred thousand hectares are infested with *Orobanche* from Europe to the Middle East, Russia and China as well as Cuba and California (Riches and Parker 1995). Broomrape species are particular problems on crop plants in Apiaceae, Asteraceae, Brassicaceae, Cucurbitaceae, Fabaceae, and Solanaceae, hence they impact directly food destined for human consumption.

Conventional methods for controlling *Striga* and *Orobanche*, such as the use of herbicides, have not generally proven successful. For small-scale subsistence farmers in Africa, herbicides are not a financially practical solution to *Striga* control, hence they often resort to hand weeding, crop rotations, or fallow rotations. Alternatives involve varying agronomic methods (integrated control), the development of resistant crops (Kuiper et al. 1998), and biological control agents such as *Fusarium oxysporium* (Ciotola et al. 1995). More recently, it has been suggested that genetic engineering can be used to debilitate *Striga* by incorporating deleterious genes (Gressel 1999, Joel et al. 1995). Similar approaches are also being explored for *Orobanche* (Cubero et al. 1999, Lu et al. 1999, Thomas et al. 1999) and it has even been suggested (Rubiales 1999) that eating broomrape might be considered as part of the integrated control package! Ultimately, development of effective and low-cost control measures for *Striga* and *Orobanche* remains the "holy grail" for plant pathologists, agronomists, and biotechnologists.

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Table 1. Parasitic Angiosperms

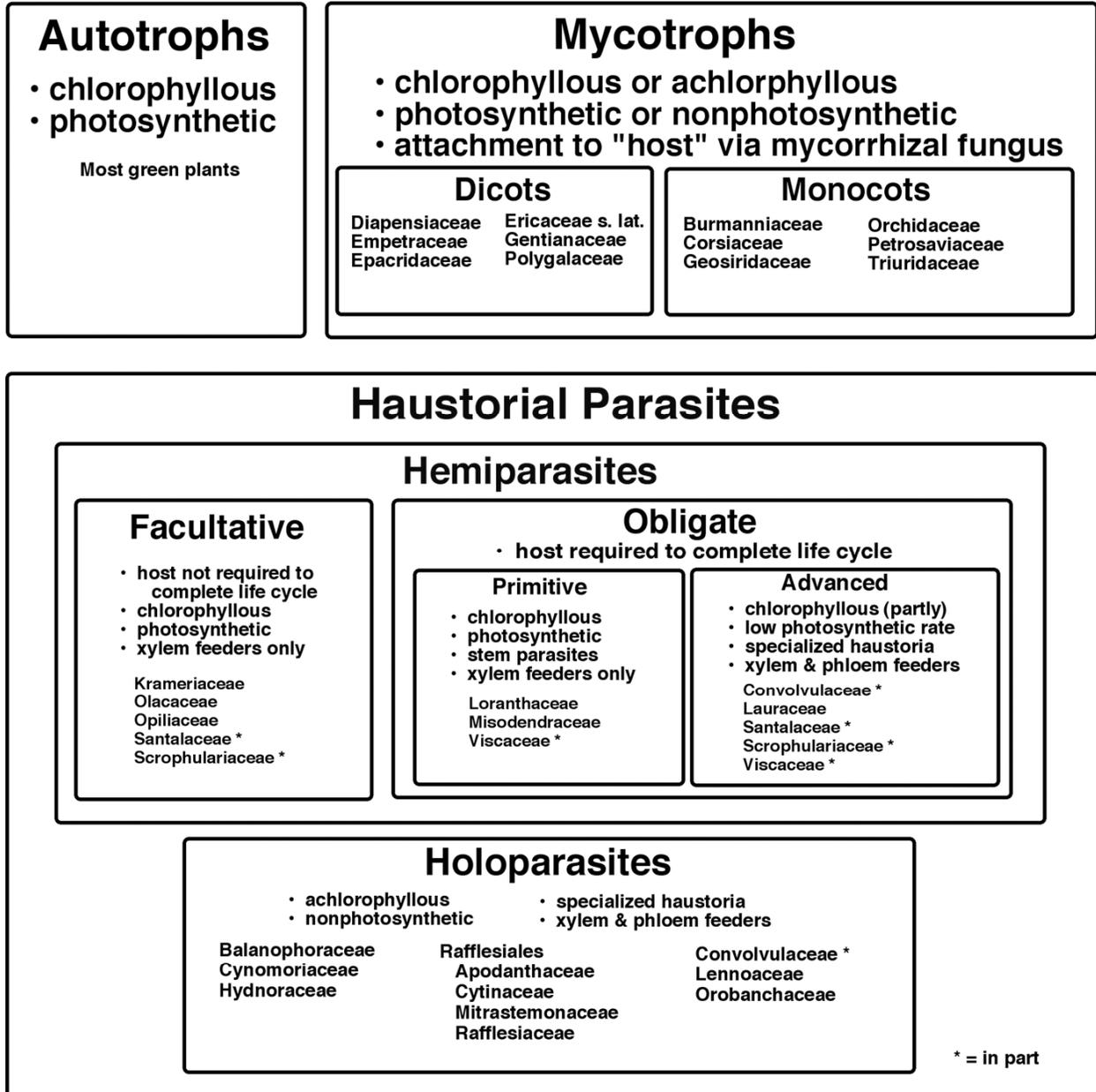
Family/Order	Number Genera	Number Species	Parasitism Type	Example Genera	Distribution
Balanophoraceae	17	43	root, holo.	<i>Balanophora, Corynaea, Scybalium, Thonningia</i>	Pantropical
Convolvulaceae	1	160	stem, hemi. & holo.	<i>Cuscuta</i>	Worldwide
Cynomoriaceae	1	1-2	root, holo.	<i>Cynomorium</i>	S. Europe, N. Africa, C. Asia
Hydnoraceae	2	ca. 15	root, holo.	<i>Hydnora, Prosopanche</i>	S. Amer., Africa, Madagascar
Krameriaceae	1	17	root, hemi.	<i>Krameria</i>	N. & S. America
Lauraceae	1	20	stem, hemi.	<i>Cassytha</i>	Pantropical
Lennoaceae	2	5	root, holo.	<i>Lennoa, Pholisma</i>	N. & S. America
Santalales					
• Loranthaceae	74	910	stem & root, hemi.	<i>Amyema, Phthirusa, Psittacanthus, Tapinanthus</i>	Pantropical
• Misodendraceae	1	8	stem, hemi.	<i>Misodendrum</i>	S. America
• Olacaceae	29	193	root, hemi.	<i>Schoepfia, Ximenia</i>	Pantropical
• Opiliaceae	10	32	root, hemi.	<i>Agonandra, Opilia</i>	Pantropical
• Santalaceae	38	490	stem & root, hemi.	<i>Comandra, Santalum, Thesium</i>	Worldwide
• Viscaceae	7	ca. 350	stem, hemi.	<i>Arceuthobium, Phoradendron, Viscum</i>	Worldwide
Scrophulariaceae s.lat.	85	ca. 1600	root, hemi. & holo.	<i>Agalinis, Buchnera, Castilleja, Epifagus, Euphrasia, Pedicularis, Orobanche, Rhinanthus, Striga</i>	Worldwide
Rafflesiales					
• Rafflesiaceae	3	19	stem & root, holo.	<i>Rafflesia, Rhizanthus, Sapria</i>	Malaya
• Cytinaceae	2	7-11	stem & root, holo.	<i>Bdallophyton, Cytinus</i>	Africa, Madagascar, Mexico, C. America
• Apodanthaceae	2-3	23	stem, holo.	<i>Apodanthes, Pilostyles</i>	Africa, N., C. S. America, Middle East, Australia
• Mitrastemonaceae	1	2	root, holo.	<i>Mitrastema</i>	C. America, Malaya to Japan
Totals	278	ca. 3900			

Table 2. Pathogenic* Parasitic Angiosperms

Parasite	Hosts	Distribution
Balanophoraceae		
<i>Thonningia sanguinea</i>	<i>Hevea</i>	Nigeria
<i>Balanophora indica</i>	<i>Coffea</i>	India
Cuscutaceae		
<i>Cuscuta</i> spp.	Various crops	Worldwide
Hydnoraceae		
<i>Prosopanche bonacinae</i>	<i>Gossypium</i>	Argentina
Lauraceae		
<i>Cassytha filiformis</i>	Various ornamentals	Pantropical
Santalaceae		
<i>Acanthosyris pauloalvimii</i>	<i>Theobroma</i>	Brazil
<i>Exocarpos</i> spp.	<i>Eucalyptus</i>	Australia
<i>Osyris alba</i>	<i>Vitis</i>	Yugoslavia
<i>Pyrularia pubera</i>	<i>Abies fraseri</i>	West Virginia, USA
<i>Thesium</i> spp.	<i>Saccharum, Hordeum, etc.</i>	Australia, USA, Spain, Libya, S. Africa
Viscaceae		
<i>Arceuthobium</i> spp.	Pinaceae (New World) & Cupressaceae (Old World)	USA, Europe, Asia, Africa
<i>Dendrophthora poeppigii</i>	<i>Hevea</i>	Brazil
<i>Phoradendron</i> spp.	various trees	North, Central and South America
<i>Viscum</i> spp.	various trees	Europe, Africa, Australia, Asia
Loranthaceae		
<i>Amyema</i> spp.	<i>Eucalyptus</i>	Australia
<i>Tapinanthus bangwensis</i>	various trees	Africa
<i>Dendrophthoe falcata</i>	various trees	India
<i>Phthirusa brasiliensis</i>	<i>Hevea</i>	Brazil
<i>Psittacanthus calyculatus</i>	<i>Citrus</i>	Mexico
<i>Struthanthus</i> spp.	<i>Coffea, Citrus, etc.</i>	Central & South America
Scrophulariaceae		
<i>Aeginetia indica</i>	<i>Saccharum</i>	India
<i>Alectra</i> spp.	<i>Arachis, Vigna, Helianthus</i>	Africa
<i>Bartsia odontites</i>	<i>Medicago</i>	Wisconsin, USA
<i>Christisonia wightii</i>	<i>Saccharum</i>	Philippines
<i>Orobancha</i> spp.	Various crops,	Worldwide
<i>Rhamphicarpa fistulosa</i>	<i>Arachis, Oryza</i>	Africa
<i>Rhinanthus serotinus.</i>	forage crops	Europe
<i>Seymeria cassioides</i>	<i>Pinus</i>	Southern USA
<i>Striga</i> spp.	Various crops, esp. Poaceae	Africa, Asia, Australia, USA

* Pathogenic defined as negatively impacting a host plant that is cultivated or harvested by humans. Data compiled from: Musselman (1980), Gill, and Hawksworth (1961), Hawksworth, and Wiens (1996), Riches and Parker (1995).

Figure 1. Summary of trophic modes seen in flowering plants.



Photos for Chapter 2



Photo 2. *Monotropa uniflora*, a mycotrophic species that frequently has been incorrectly considered a parasitic plant because of its ghostly appearance. North Carolina (USA).

Photo 3. *Hyobanche sanguinea* (Scrophulariaceae). This south African parasitic plant is one of the few that form secondary haustoria from scale leaves.



Photo 4. *Parasitaxus ustus* (Podocarpaceae), the only possibly parasitic gymnosperm. New Caledonia.



Photo 5. *Agalinis purpurea* (Scrophulariaceae): a facultative hemiparasite of the eastern USA.

Photo 6. *Phoradendron scabberinum* (Viscaceae), epiparasitic on a related species, *P. longifolium*, in Sinaloa (Mexico).



Photo 7. *Pilostyles thurberi* (Apodanthaceae), stem parasite of *Dalea formosa*, Texas (USA).

Photo 8. *Macrosolen crassus* (Loranthaceae). The flowers are 10 cm long and are pollinated by birds. Sarawak (Malaysia).





Photo 9. *Prosopanche americana* (Hydnoraceae). This species, parasitic on many other hosts, is on the roots of Prosopis (a tree in the legume family), belongs to a genus whose seeds are usually dispersed by possums. Argentina.



Photo 10. *Striga asiatica* (Scrophulariaceae), a parasitic plant considered a pathogen because it causes damage to agriculture. Here it appears parasitizing maize in North Carolina (USA), where it is known as "witch weed".



Photo 11. *Alectra vogellii* (Scrophulariaceae). The image perfectly shows the parasite-host union in an African zone.