

Functional biology of parasitic plants: a review

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Background – Parasitic plants are functionally specialized to acquire at least some essential resources from other plants via specialized organs called haustoria. Parasitism evolved 12 times independently in the evolution of angiosperms of which approximately 1% (4500 species) are parasitic. Not only are parasitic plants diverse in terms of evolutionary origins but also in terms of their physiological functioning and ecological behaviour.

Methods – Here, I review the importance of principal functional traits which underlie the physiology and ecology of individual parasitic plants. These include the ability to perform photosynthesis, anatomical details of the vascular connection to the host determining the quality of resources acquired from the host, location of the haustoria on the host, which is closely connected with the parasite life form, and the mode of germination (either triggered by environmental condition or induced by presence of host roots).

Results and conclusions – Based on the distribution of all these traits in parasitic plants, I introduce their functional classification into root hemiparasites, root holoparasites, stem parasites and endophytic parasites. In addition to the classification, I also present an evolutionary hypothesis explaining the evolution of advanced parasitic plant forms from root hemiparasites. This hypothesis is based on ecological constraints from which the parasites are released with increasing ability to acquire resources from the host. This evolutionary process also implies increasing host specificity which imposes new constraints on the ability to establish host connection. This explains the evolutionary stability of photosynthetic hemiparasites and their species richness which is one order of magnitude higher than that of holoparasites.

Key words – Ecology, evolution, haustorium, hemiparasite, germination, mistletoe, Orobanchaceae, parasitic plant, Santalales.

INTRODUCTION

Parasitic plants are a specialized plant functional group defined by parasitic acquisition of at least some essential resources from other plants. The parasitic resource acquisition proceeds via haustoria, specialized organs which penetrate host vascular bundles. Parasitic plants comprise approximately 4500 species which accounts for c. 1% of angiosperms (Heide-Jørgensen 2008, Nickrent 2012). Parasitism evolved several times independently during angiosperm evolution (Barkman et al. 2007, Naumann et al. 2013). Therefore, parasitic plants do not form a monophyletic group but are defined functionally by their physiology and ecological interactions, which include parasitic uptake of resources and interaction with other plant species. However, individual species differ widely in mechanisms of parasitism and other details of their biology.

A distinct functional and evolutionary difference exists between hemiparasites, which retain photosynthetic activity, and non-green holoparasites, which fully depend on their

hosts for all essential resources. Parasitic plants nevertheless display many other functional traits that are largely variable among species and underlie biological differences among them. The location of the attachment to the host defines root and stem parasites and substantial variation in growth forms exists even within these groups. Either induced by presence of the host or relying on environmental or internal germination signals, seed germination mechanisms determine the strategy of establishment on the host. Anatomical details of the connection to the host vascular bundles underpin the quality and quantity of resources acquired from the host.

Parasitism evolved twelve times during angiosperm evolution (fig. 1; Barkman et al. 2007, Nickrent et al. 2005). Individual independent lineages largely differ in size (number of species), phylogenetic age and the degree of trophic specialization (Barkman et al. 2007, Nickrent 2012, Naumann et al. 2013). Of these, Orobanchaceae and Santalales are the largest monophyletic groups of parasitic plants, both of which also contain both hemi- and holoparasites. By contrast all the other lineages are small in terms of number of species

and genera and uniform in terms of the trophic strategy of their species (table 1, fig. 1). Many of these small groups are holoparasitic and display a highly specialized morphology including extreme modifications of flowers.

In this review, I introduce the key functional traits of parasitic plants and explain their significance. On the basis of functional trait distribution among individual phylogenetic lineages or functionally defined groups within them, I propose a new functional classification of parasitic plants. This is aimed to fill a gap in current literature with the last comprehensive review on functional biology of parasitic plants published more than a decade ago (Nickrent 2002). Since then, there has been a great advancement in reconstruction of phylogenetic relations (in terms of both phylogenetic placement of parasitic plants: Nickrent et al. 2005, Barkman et al. 2007, Naumann et al. 2013, and phylogenetic relations within particular lineages, e.g. Nickrent et al. 2010, García et al. 2014, McNeal et al. 2013) and other aspects of parasitic plants, e.g. ecophysiology (Irving & Cameron 2009, Bell &

Adams 2011, Těšitel et al. 2015) or reproductive biology (Bellot & Renner 2013). In addition, a book describing biological features of many parasitic plant species of all phylogenetic lineages has been published (Heide-Jørgensen 2008). A review on key functional aspects of parasitic plants as a whole and considering the evolutionary perspective is, however, still missing.

KEY FUNCTIONAL TRAITS OF PARASITIC PLANTS

Photosynthesis and carbon nutrition

Photosynthesis is generally viewed as a principal characteristic of land plants. It uses light as the energy source for the chemical process in which carbon in CO₂ is reduced to organic substances. This makes light the principal resource for plants and competition for light the dominant interaction occurring between plant individuals. Deficiency of this principal resource also prevents photosynthetic plants from inhabiting dark habitats. Holoparasitic species that lack the

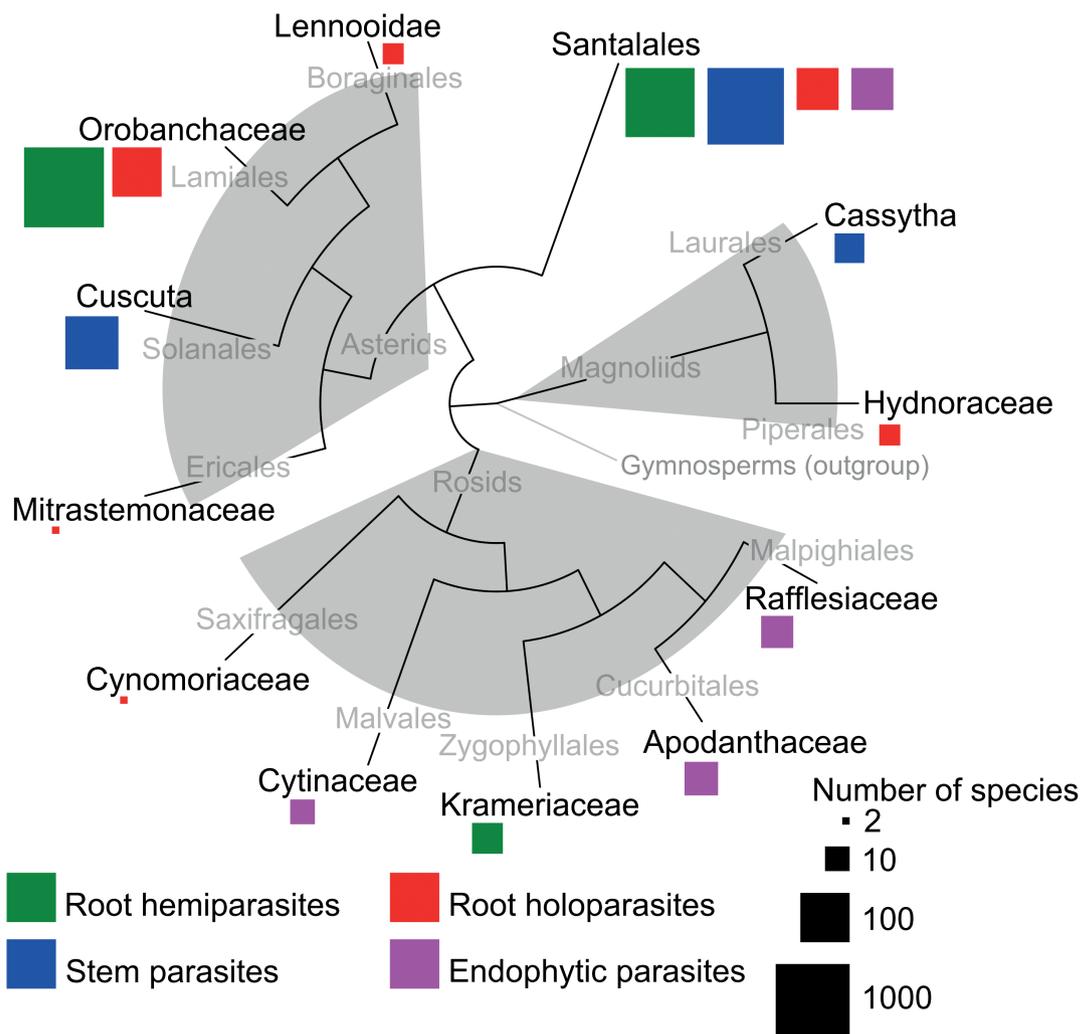


Figure 1 – Phylogenetic origins of parasitic angiosperms. The relationships among monophyletic parasitic plant lineages are based on APG III (2009). Functional classification of species of each monophyletic group (see fig. 2 for details) together with corresponding estimates of number of species (table 1) is illustrated by colour squares.

Table 1 – Summary of the current knowledge of the functional biology of parasitic plant groups defined on the basis of phylogenetic relatedness and functional similarity.

Note that the groups are not always monophyletic. - absent, + present, +/- present in some species or reduced (value 0.5 used in PCA; fig. 2); (+) present in rudimentary form/only a small fraction of species or of minor importance (value 0.25 used in PCA), +/(-) present in most species; in some species present but not fully developed (value 0.75 in PCA), ? not known (mean substitution used in PCA); * Based on Heide-Lørgensen (2008), ** typical representatives: *Arcuthobium* (most species), *Placellaria*, *Tristerix aphyllus*, *Viscum minimum*, *Phoradendron perredactum*, *** *Pediculariaceae* = Clade IV in McNeal et al. (2013); † Biology of many species/genera is not known in sufficient detail. Unequivocal classification between Orobanchaceae 1 and 2 is therefore impossible in these cases making the estimates of genus and species numbers uncertain. ‡ listed taxa indicate typical examples/largest groups, not a complete list.

Group	Number of genera / species	Location of haustoria on host				Primary haustorium	Predominant habitat *	Key references	
		Photo-synthesis	Phloem connection	Growth form	Endophytic at maturity				
Hydnoraceae	2/7	-	?	root-parasite	root	-	host-induced	? desert	Bolin et al. 2009, 2010, Tennakoon et al. 2007
<i>Cassytha</i>	1/16	+	-	parasitic vine	stem	-	autonomous	- tropical and subtropical shrublands	Cartellieri 1928, de la Harpe et al. 1980, Li et al. 2012, Pridler et al. 2009, Shen et al. 2005
Santalales	151/ c. 2000								Nickrent et al. 2010, Su et al. 2015
- root hemiparasites	60/ c. 600	+	-	root-parasite	root	-	autonomous	- subtropical shrubland, temperate grasslands, tropical forests	Radomiljac et al. 1998, 1999a, 1999b, Suetsugu et al. 2008, Tennakoon & Cameron 2006, Tennakoon & Pate 1996, Tennakoon et al. 1997, Veenendaal et al. 1996, Watson et al. 2011
- mistletoes	84/ c. 1500	+	-	mistletoe	stem	(+)	autonomous	- tropical, subtropical and temperate forests and shrublands	Calvin & Wilson 2006, Ehleringer et al. 1986, Glatzel & Geils 2009, Mathiasen et al. 2008, Shaw et al. 2004, Strong et al. 2000, Watson & Herring 2012
- endophytic mistletoes **	5/ c. 50	(+)	+	mistletoe endophytic	stem	+/(-)	autonomous	- temperate forests, deserts	Hawksworth & Wiens 1996, Hull & Leonard 1964a, 1964b, Kraus et al. 1995, Kuijt 2011, Mauseth 1990, Mauseth et al. 1984
- Balanophoraceae and Mystropetalaceae	17/50	-	+	root-parasite	root	-	host-induced	- tropical forests, subtropical shrubland	Eberwein et al. 2009, Ecroyd 1996, Gedatovich-Shedletzky & Kuijt 1990, Holzapfel 2001, Kuijt & Dong 1990, Shivamurthy et al. 1981, Su et al. 2015
Cytinaceae	3/11	-	+	endophytic	root	+	host-induced	- subtropical shrublands, tropical forests	Alvarado-Cárdenas 2009, Fernández-Alonso & Cuardos-Villalobos 2012, de Vega et al. 2007, 2010
Krameriaceae	1/18	+	-	root-parasite	root	-	autonomous	- deserts, grasslands, (forests)	Brokamp et al. 2012, Giannini et al. 2011

Table 1 (continued) – Summary of the current knowledge of the functional biology of parasitic plant groups defined on the basis of phylogenetic relatedness and functional similarity.

Group	Number of genera / species	Location of haustoria on host				Primary haustorium	Predominant habitat *	Key references
		Photo-synthesis	Pholem connection	Growth form	Endophytic at maturity			
Cynomoriaceae	1/2	-	?	root-parasite	root	?	salty grasslands	Heide-Jørgensen 2008, Zhang et al. 2009, Nickrent et al. 2005
Rafflesiaceae	3/20	-	+	endophytic	root	?	tropical forests	Bellot & Renner 2013, Davis et al. 2007, Fernandes et al. 1998, Filipowicz & Renner 2010, Hidayati et al. 2000, Nickrent et al. 2004, Nikolov et al. 2014, Patiño et al. 2002
Apodanthaceae	2/23	-	?	endophytic	stem	?	tropical forests, deserts	
<i>Cuscuta</i>	1/145	(+)	+	parasitic vine	stem	-	open vegetation from tropics to temperate	Birschwilks et al. 2006, Clayson et al. 2014, Garcia et al. 2014, Hibberd et al. 1998a, Jeschke et al. 1997, Koch et al. 2004, Lee & Jernstedt 2013, McNeal et al. 2007, Meulebrouck et al. 2009, Švubová et al. 2013
Lennoiodae	3/7	-	+	root-parasite	root	+	desert, dry forests	Kuijt 1966, Kuijt 1967, Yatskievych 1982
Mitrasomonaceae	1/2	-	-	root-parasite	root	?	tropical and subtropical forests	Heide-Jørgensen 2008
Orobanchaceae	96/ c. 2000	-	-	root-parasite	root	-		Bennett & Mathews 2006, Joel et al. 2013, McNeal et al. 2013, Westwood et al. 2010
- 1: <i>Rhinanthus</i> , <i>Melampyrum</i> , <i>Euphrasia</i> , <i>Odonites</i> , <i>Bartisia</i> , <i>Pediculariaceae</i> ***, <i>Cymbartiae</i> ‡	c. 70†/ c. 1650†	+	-	root-parasite	root	-	mostly grasslands, forest understory	Cameron et al. 2005, Cameron & Seel 2007, Fisher et al. 2013, Govier et al. 1967, 1968, Jiang et al. 2010, Klaren & Janssen 1978, Li et al. 2013, Mann & Musselmann 1981, Matthies 1995, 1997, Mudrák & Lepš 2010, Světlíková et al. 2015, Těšitel et al. 2015, Těšitel & Tesatová 2013, Weber 1981
- 2: <i>Striga</i> , <i>Alectra</i> , <i>Cyrenium</i> , <i>Tozzia</i> , perennial <i>Rhynchosorys</i> ‡	c. 15†/ c. 100†	+/(-)	-	root-parasite	root	-	mostly grasslands, stream edges	Cardoso et al. 2011, Dörr 1997, Gomez-Roldan et al. 2008, Graves et al. 1992, de la Harpe et al. 1980, Jamil et al. 2012, Kubat & Weber 1987, Simier et al. 2006, Weber 1973

Table 1 (continued) – Summary of the current knowledge of the functional biology of parasitic plant groups defined on the basis of phylogenetic relatedness and functional similarity.

Group	Number of genera / species	Location of haustoria on host				Primary haustorium	Predominant habitat *	Key references		
		Photo-synthesis	Phloem connection	Growth form	Endophytic at maturity					
- 3: <i>Orobanchae</i> , <i>Cistanche</i> , <i>Harveya</i> , <i>Hyobanche</i> , <i>Epifagus</i> ‡	15/ c. 250	-	+	root-parasite	root	-	host-induced	+	grasslands, deserts, forest understorey	Hibberd et al. 1998b, 1999, Schneeweiss 2007, Thorogood & Hiscock 2010
- 4: <i>Lathraea</i> , <i>Boschniakia</i>	2/11	-	-	root-parasite	root	-	host-induced	-	temperate forest understorey	Fay 2010, Heinricher 1894, Kujit & Toth 1985, Renaudin & Larher 1981, Světlíková et al. 2015, Těšitel & Tesatová 2013, Ziegler 1955

photosynthetic ability and essentially acquire all organic carbon from the host represent an exception of this rule (together with fully mycoheterotrophic plants; Selosse & Roy 2009).

Most parasitic species are hemiparasites with functional photosynthesis (table 1, fig. 1). The efficiency of their photosynthetic activity can vary largely, not only between species but also within species depending on host quality and environmental conditions (Cechin & Press 1993, Seel & Press 1994, Radomiljac et al. 1999a, Strong et al. 2000, Těšitel et al. 2015). In general, hemiparasite photosynthesis can vary from levels hardly exceeding the compensation point to levels comparable to those of non-parasitic plants. Despite possibly efficient photosynthesis, hemiparasites uptake organic carbon from the host in the form of xylem-mobile organic elements (Těšitel et al. 2010a, Bell & Adams 2011). This host-derived carbon can substantially contribute to hemiparasite biomass. Nevertheless, the importance of host-derived carbon as an energy resource seems highest when the hemiparasite's own photosynthesis is limited, either because of competition for light or inefficient photochemistry caused by stress such as mineral nutrient deficiency (Těšitel et al. 2015). The host-derived carbon can thus be viewed as a backup resource for hemiparasites.

Some hemiparasitic species are non-green and thus completely dependent on their host during the initial period of their life. Such a strategy evolved at least three times independently in the Orobanchaceae. It is typical of closely related *Striga* and *Alectra* species, which evolved dust seeds with minimal reserves, thus requiring immediate contact with host roots after germination (Dörr 1997, Irving & Cameron 2009, Westwood et al. 2010). By contrast, the life cycles of *Tozzia* and perennial species of *Rhynchosorys* include a long-term underground holoparasitic stage (which evolved independently in these two genera) and they produce green photosynthetic shoots only for the purpose of sexual reproduction (Těšitel et al. 2010b). In all of these cases, the holoparasite stage occurs early in the ontogeny and this ability to acquire all necessary resources is likely to substantially increase establishment success in communities with intense competition for light. Seedling establishment of related hemiparasitic species not displaying such holoparasite stages tends to be the most significant factor limiting their occurrence in competitive environments (Těšitel et al. 2011, 2013).

Several intermediate strategies between hemi- and holoparasitism can be distinguished in parasitic plants. Species of the genus *Cuscuta* are functionally holoparasitic and acquire all saccharides from the host via phloem connections, but most of them display rudimentary photosynthetic activity (Hibberd et al. 1998a, Clayton et al. 2014) and their plastid genome evolution is functionally constrained (McNeal et al. 2007). Despite its low intensity and efficiency (Hibberd et al. 1998a), photosynthetic activity plays an important role in the biosynthesis of lipids which serve as energy reserves. These are stored in *Cuscuta* seeds and used by seedlings actively searching for suitable host stems in their surroundings (McNeal et al. 2007, Švubová et al. 2013). Similarly, in mistletoe species of the genus *Arceuthobium* (Viscaceae), the limited photosynthesis produces assimilates supplementing host-derived carbon in nutrition of exophytic shoots bearing

flowers and fruits (Miller & Tocher 1975), while extensive endophytic structures are completely dependent on host carbon (Hull & Leonard 1964a, 1964b). In summary, a parasite's own photosynthetic activity plays an important role in providing resources for sexual reproduction in all species on the edge between hemi- and holoparasitism. That is likely to be the cause why maintaining even a rudimentary and inefficient photosynthetic activity is evolutionarily stable despite efficient carbon uptake from the host, which generally meets the requirements for vegetative growth of the adult parasite.

Interestingly, all hemiparasitic mistletoes (e.g. *Viscum album*) have evolved photosynthesis in the endosperm (Heide-Jørgensen 2008, Nickrent & Garcia 2009), which is highly unusual within the angiosperms. This adaptation helps the seedling to penetrate through possibly thick host bark, which requires a large amount of energy. This unusual location of photosynthesis thus facilitates the establishment of a parasite with a free pre-attachment stage, which is quite similar to the situation in *Cuscuta*.

Anatomy of haustorial connections and resource uptake from the host

The details of the anatomical connection to host vascular bundles hidden in the haustorium are as important to parasitic plant biology as the ability to photosynthesize. All parasitic plant species have access to host xylem, but only some of them have the ability to also withdraw nutrients from the phloem (table 1; Hibberd & Jeschke 2001, Irving & Cameron 2009). The anatomy of the vascular connection to the host underlies not only the quality and quantity of resources acquired, but is also associated with host specificity. The importance of this trait led to a suggestion of a functional classification of parasitic plants into xylem- and phloem-feeders instead of hemi- and holoparasites (Irving & Cameron 2009).

Haustorial anatomy is indeed largely correlated with the ability to photosynthesize or with photosynthetic efficiency. Typical hemiparasites with efficient photosynthesis (hemiparasitic Santalales, Orobanchaceae, Krameriaceae) access host xylem only (table 1). This provides parasitic uptake of mineral nutrients and water but only a limited amount of organic carbon available as xylem-mobile organic elements (Bell & Adams 2011, Těšitel et al. 2010a). Thus, photosynthesis appears to be a requirement for an efficient xylem-feeding strategy. This is however not true for the holoparasites of the genera *Lathraea* and *Boschniakia*, which display a holoparasitic xylem-only feeding strategy (Kuijt & Toth 1985, Ziegler 1955). In *Lathraea*, this is underpinned by acquisition of xylem-mobile organic elements and the ability to actively secrete excess water using hydathode trichomes located on underground leaf scales (Renaudin & Garrigues 1967, Světlíková et al. 2015, Těšitel & Tesařová 2013, Weber 1975). Although providing only a limited spectrum of resources, the xylem parasitism has a largely mechanical nature; i.e. penetrating a host vessel can be viewed as a simple penetration of a dead tube in which resources are transported. Establishment of a xylem connection usually imposes little constraint on the host ranges of xylem-feeding parasites (Gibson & Watkinson 1989, Radomiljac et al. 1999b, Suet-sugu et al. 2008), although host defence reactions based on

root tissue lignification were identified as a cause of distinct host preferences in some hemiparasitic species (Cameron et al. 2006).

In holoparasites, parasitic uptake of phloem sap rich in assimilates can cover the demand for carbohydrates not provided by autonomous photosynthesis. Such independence from photosynthesis presents the main advantage of phloem parasitism, releasing the parasites from competition for light. In contrast to xylem, phloem is a living tissue. Its parasitism thus requires biochemical compatibility between host and parasite (Thorogood & Hiscock 2010). Therefore, phloem-feeders tend to be more host-specific (Heide-Jørgensen 2008, Thorogood et al. 2009). Their occurrence is consequently limited by their ability to find a compatible host. Although phloem connections are closely associated with holoparasitism, their presence in haustoria of some holoparasitic lineages (Apodanthaceae, Hydnoraceae, Cynomoriaceae, Mitrastemonaceae) remains to be confirmed (table 1). The existence of the holoparasitic xylem-feeding *Lathraea* and *Boschniakia* species (see above) prevents extrapolating phloem parasitism to other lineages based just on the lack of photosynthesis.

Growth habit and location of the haustoria on the host

Parasitic plants display a variety of growth habits (table 1). Root-parasites attach to the host below ground and seem to grow independently of the host from the above-ground perspective. Stem parasites that attach to the host above ground can be further divided into mistletoes and parasitic vines. Mistletoes are parasitic epiphytic shrubs, which attach to the host stem immediately after germination. Parasitic vines are herbs which germinate on the ground and their seedling attaches to the host stems after a certain period of independent growth, which can last from a few days up to several months (Heide-Jørgensen 2008). The most extreme modification is represented by parasitic plants which are completely endophytic at maturity except for their reproductive organs (endophytic parasites; table 1). These parasites produce haustoria only after germination when entering the host.

The location of the haustoria on the host is an important trait which has been used to classify parasitic plants into the functional groups of root and stem parasites (Nickrent 2002). It is really important for photosynthetic hemiparasites, which, if established from an epiphytic seedling, acquire not only the resources from xylem but also a position in the canopy with much more favourable light conditions compared to the understory. In contrast, the position of haustoria makes little difference to non-photosynthetic parasites that do not use light as a resource. Moreover, the endophytic parasites might enter host roots or stems during their establishment and then spread throughout the host body (e.g. in *Rafflesia*; Heide-Jørgensen 2008). Considering the whole diversity of growth habits of parasitic plants might be more ecologically meaningful than just using the location of the haustoria. Nevertheless, the location of haustoria is a simple binary trait more suitable when multiple traits are analysed, which is why I retain it in a multitrait analysis (fig. 2).

The evolution of parasitic plant growth form started from perennial hemiparasitic woody plants (shrubs or trees) in

Santalales (Nickrent et al. 2010) and Krameriaceae (Carlquist 2005). The Orobanchaceae contain few woody taxa (shrubs: *Brandisia*, *Asepalum*, *Cyclocheilon*, *Pterygiella suffruticosa*; woody herbs or subshrubs: *Hedbergia*, *Nothobartsia*, *Sopubia*, *Graderia*; Morawetz et al. 2010, Těšitel et al. 2010b, Dong et al. 2013, McNeal et al. 2013). These are mostly phylogenetically unrelated and many of them form either isolated lineages within the family (*Brandisia*; McNeal et al. 2013) or sister groups to the major clades within the family (*Cyclocheilon*, *Asepalum*, *Sopubia*, *Graderia*; Morawetz et al. 2010; in part also *Pterygiella*; Dong et al. 2013). Such an evolutionary pattern together with the woody habit of the Paulowniaceae, the sister family to Orobanchaceae (APG III 2009), may suggest a possibility of a hemiparasitic woody ancestor also in Orobanchaceae. Given the current knowledge, it difficult to conclude whether the first plant which evolved hemiparasitism in this family was a shrub or an herbaceous plant. By contrast, it is certain that the parasitic vines of the genus *Cuscuta* evolved from non-woody Convolvulaceae vines (García et al. 2014). Other groups of parasitic plants are too distant from their non-parasitic relatives

and their vegetative morphology is strongly modified, which prevents drawing conclusions on their growth form evolution.

Germination and establishment

Seed germination and establishment of the connection to the host represent critical points of the parasitic plant life cycle. Individual parasitic plant species have adopted one of two distinct germination strategies. Germination can be either autonomous or induced by chemical signals released by the host.

The autonomous germination might be started just by conditions favourable for seedling survival (e.g. sufficient humidity) or might require specific environmental germination clues to break seed dormancy. This is well-documented for some temperate hemiparasitic Orobanchaceae (e.g. *Rhinanthus*, *Melampyrum*, *Odontites*, *Euphrasia*, *Cordylanthus*, *Orthocarpus*, some species of *Castilleja* or *Agalinis*) which require variable periods of low temperature to initiate germination (Royal Botanical Gardens Kew 2015). This ensures

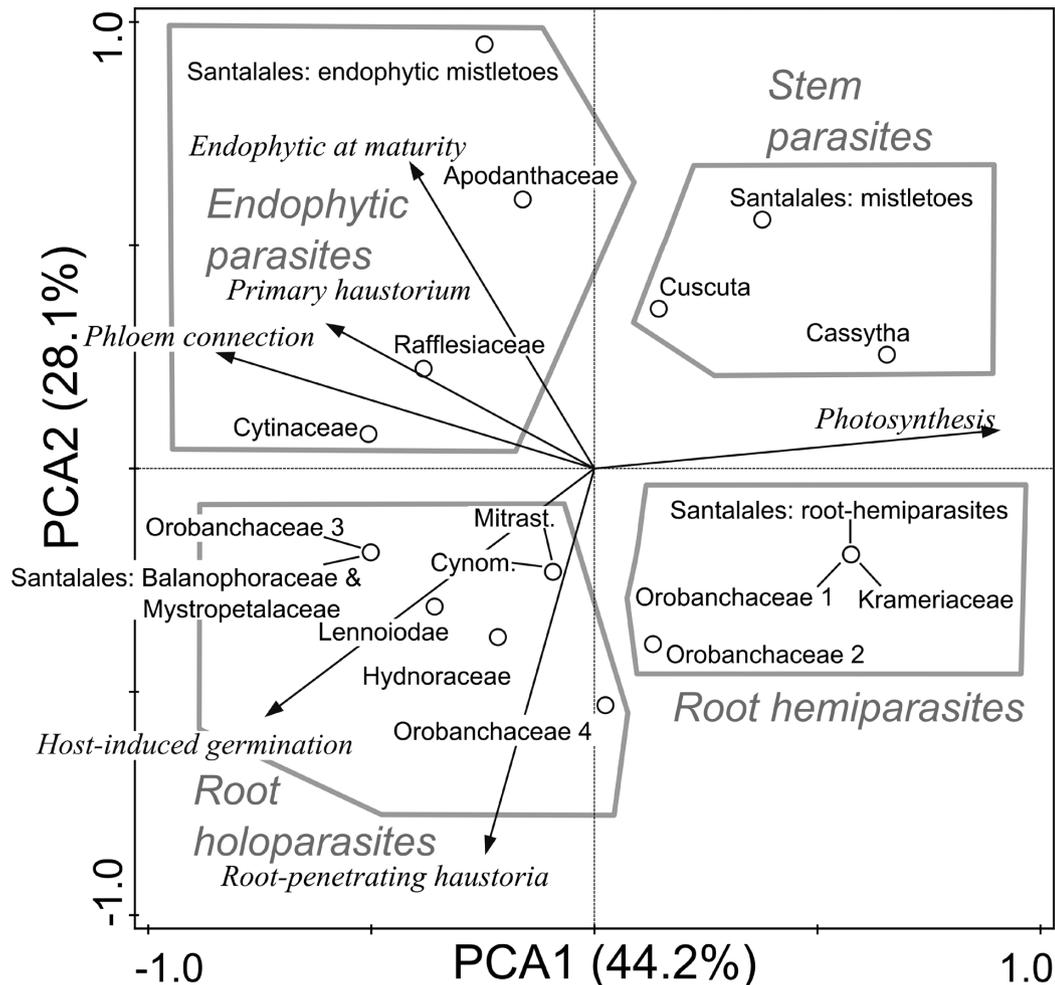


Figure 2 – Principal component analysis plot displaying the functional similarities among individual parasitic angiosperm lineages. The analysis is based on the functional trait values summarized in table 1, which are also displayed in the ordination space. Four principal functional groups of parasitic plants are defined on the plot by grey envelopes. The PCA was computed in Canoco 5 (ter Braak & Šmilauer 2012). Mean substitution was applied in case of missing data. See electronic appendix for exact data table which served as the basis for the PCA.

that germination occurs in periods when most plant species are dormant and thus the seedlings at least in part avoid above-ground competitive pressure from the surrounding vegetation (Těšitel et al. 2011). Germination dynamics in response to temperature can be largely variable among closely related species and to a lesser extent also among populations of a single species, as documented for *Rhinanthus* by ter Borg (2005). Attachment to the host occurs after an independent seedling stage which can last up to many weeks. This germination strategy is typical of many root hemiparasites and stem parasites, seedlings of which can support their growth by own photosynthesis and/or abundant seed reserves. Despite limited development of the root-hemiparasitic seedling root system, it still allows foraging for a suitable host in a sizeable volume of soil. Combined with low host specificity, this strategy provides a good chance to find a suitable host. In mistletoes, the chance of establishing a host connection is increased by specialized dispersal mechanisms (mostly endozoochory by birds, but also explosive seed dispersal in *Arceuthobium*) and sticky seeds. Seedlings of parasitic vines use all their energy to forage for a host above-ground across a distance of tens of centimetres. Active foraging based on volatiles produced by the host has been demonstrated in *Cuscuta* (Koch et al. 2004) together with selection of hosts with higher nutritional status (Kelly 1992).

Host induction of germination combined with long-term seed dormancy can be expected in all host-specific parasitic plants as a trait reducing wasteful seed germination in the absence of a suitable host. Still, it has only been documented in a few species. The best-known examples include dust-seeded Orobanchaceae such as *Striga*, *Alectra*, *Orobanche* and *Phelipanche*. Their germination is induced by strigolactones, plant hormones responsible for signalling with arbuscular mycorrhizal fungi (Akiyama et al. 2005, Cardoso et al. 2011), but also affecting plant architecture (Gomez-Roldan et al. 2008, Cardoso et al. 2011). In the Orobanchaceae, host-induced germination was also reported in *Lathraea* and *Epifagus* (Heinricher 1894, Williams & Zuck 1986 reviewed in Bolin et al. 2009). Bolin et al. (2009) experimentally demonstrated host-induced germination in *Hydnora* (Hydnoraceae) and reviewed this phenomenon in *Bdallophytum* (Cytinaceae), *Dactylanthus* (Mystropetalaceae; formerly Balanophoraceae; Su et al. 2015) and *Pholisma* (Boraginaceae - Lenooideae). Despite the great importance for understanding biology of parasitic plants, data on germination of many holoparasites and in particular endophytic holoparasites are still largely missing (table 1).

Another important establishment trait is the ability to form a primary (terminal) haustorium. Haustoria of this type are produced by seedlings of mistletoes and some Orobanchaceae (*Striga*, *Orobanche*) to establish the first contact with the host. By contrast, most parasitic plant species produce only secondary (lateral) haustoria, which is typical of species with self-sustained seedling including root-hemiparasitic Santalales, parasitic vines and most Orobanchaceae (table 1). It has been suggested that the ability to form a primary haustorium is closely related to host-induced germination, as is the case in some Orobanchaceae such as *Striga* and *Orobanche* (Westwood et al. 2010). However, this is not true in mistletoes, which produce a primary haustorium

but their seedlings germinate autonomously (table 1), nor in root-parasitic *Lathraea*, which requires host germination cues but does not produce a primary haustorium (Ziegler 1955). Functional roles and evolutionary pathways of these establishment traits can thus be diverse, making such generalizations difficult. Unfortunately, the difficulty in observing germination and initial life stages of many parasitic plants results in a large data deficiency for this trait (table 1).

FUNCTIONAL CLASSIFICATION OF PARASITIC PLANTS

A principal component analysis (PCA) was performed to summarize functional trait distribution across parasitic plant lineages and establish a new functional classification of parasitic plants (fig. 2). On the basis of the PCA results, it is possible to define four functional groups, located in the quadrants of the first two principal components: root hemiparasites, root holoparasites, stem parasites and endophytic parasites. The major advantage of this classification is that it is based on variability of all key functional traits across all parasitic angiosperms. Every parasitic plant species can thus be assigned to one of the functional groups based on current knowledge of their biology. The functional groups are not homogeneous (i.e. a certain variability in functional traits is present within the group) but that is always the case in such categories comprising species of different evolutionary lineages.

Probably the largest heterogeneity is present in stem parasites including both mistletoes and parasitic vines. There are however substantial differences even between functionally similar *Cuscuta* and *Cassytha* (presence/absence of phloem connections in haustoria, differential degree of photosynthetic ability) which justifies the concept of a single heterogeneous functional group of stem parasites.

Endophytic parasites are newly distinguished here as a functional group of parasitic plants. They are defined by the dominance of an endophytic stage in their life cycle. Typically, these species form a haustorium immediately after germination to penetrate the host. They then form extensive endophytic structures and produce exophytes only for flowering and seed production. The exophytes may be just flowers or inflorescences (Rafflesiaceae, Apodanthaceae, Cytinaceae), or larger shoots (most endophytic mistletoes). There is an entire gradient of parasitic strategies and host dependence in mistletoes. A majority of the species attach to their host by haustoria, each of which forms a single connection to host vascular bundles (species with epicortical roots, clasping unions, and wood roses; Calvin & Wilson 2006, Mathiasen et al. 2008). These can be clearly classified as stem parasites. Other species produce endophytic bark strands with multiple connections to the host vasculature. The extent of the endophytic system is rather limited and smaller in size compared to the exophytic shoots in many species (e.g. *Viscum album*; Zuber 2004). These species are considered stem-parasitic mistletoes here. By contrast, other species may cause systemic infections and the endophyte of some of them is even isophasic, i.e. it proliferates into the apical buds of the hosts and displays growth synchrony with the host (Calvin & Wilson 1996, Kuijt 2011, Lye 2006). Photosynthesis tends to be

reduced in these species and they acquire most of the organic carbon from the host (Hull & Leonard 1964a, 1964b). Such species are considered as endophytic mistletoes here. Typical representatives include most *Arceuthobium* species (e.g. *A. americanum*, *A. pusillum*, *A. douglasi*; Lye 2006), *Phoradendron perredactum* (Kuijt 2011), *Viscum minimum* of Viscaceae (Engler & Krause 1908), *Phacellaria* (Amphorogynaceae; Nickrent et al. 2010) and *Tristerix aphyllus* (Loranthaceae; Mauseth et al. 1984, Kraus et al. 1995, Mauseth 1990). Most *Arceuthobium* species that do not show isophasic growth still have a large endophyte and a low photosynthetic capacity and can be assigned to this group. *Arceuthobium oxycedri*, which is seemingly the most photosynthetic species of the genus acquiring c. 50% of its carbon by its own photosynthesis (Hawksworth & Wiens 1996, Rey et al. 1991), is difficult to classify and should be probably considered a transitional case between stem and endophytic parasites.

Root hemiparasites are considered a single group here without further classification to facultative and obligate as suggested by Nickrent (2002). Facultative parasitism, which, in a strict ecological sense, means the ability to keep per-capita population growth rate $r > 0$ in the absence of a host, is very rare in parasitic plants and difficult to demonstrate. It probably exists e.g. in *Triphysaria* (Westwood et al. 2010) and *Odontites vernus* (Weber 1981, Geppert 2012). Most of the species suggested as facultative hemiparasites (Nickrent 2002) are nevertheless unable to survive, produce flowers or their growth is largely reduced and flower production is minute in host-free cultivation (Mann & Musselmann 1981, Matthies 1997, Weber 1981) unless high doses of mineral nutrients are applied (Mann & Musselmann 1981). In addition, no hemiparasite has been reported to grow without a host under natural conditions (Heide-Jørgensen 2013). By contrast, even *Striga asiatica*, member of a genus comprising typical “obligate root-hemiparasites” (Westwood et al. 2010) can grow and flower without host in an axenic culture if provided with nutrients and germination stimulants (Yoshida & Shirasu 2012). The cultivation studies hence demonstrated that both “facultative” and “obligate” root-hemiparasites can grow and reproduce under artificial conditions, although the latter require a higher level of condition control. In summary, there is apparently a large variability in host-dependence among hemiparasitic species. *Triphysaria* and *Odontites* discussed above represent one extreme root-hemiparasitism while species with holoparasitic seedlings, like *Striga*, *Alectra*, *Tozzia* and the perennial species of *Rhynchospora* represent the other. Most of the other root-hemiparasitic species lie between these extremes and it is difficult to make a clear border line between “facultative” and “obligate” root hemiparasites. Therefore, I suggest viewing root hemiparasites as a single, yet variable functional group, members of which are dependent on their hosts to various extents.

COMMUNITY ECOLOGY AND HABITAT PREFERENCES OF PARASITIC PLANTS

Parasitic plants occur in all terrestrial ecosystems ranging from tropical rainforests and hot deserts to temperate grasslands and arctic tundra (Heide-Jørgensen 2008). Numerous species are known to act as keystone species in the ecosys-

tems they inhabit. This is based on their specialized nutritional or reproductive strategies interacting with organisms in many different ways (Press & Phoenix 2005). The most important mechanisms of the ecosystem effects include: (1) harm inflicted to the host species by parasitism, which can modify competitive relations in plant communities (Cameron et al. 2005, Li et al. 2012, Prider et al. 2009, Shen et al. 2005); (2) effects on nutrient cycling via modifications of soil microbial community structure (Bardgett et al. 2006, Quedstedt et al. 2003, Spasojevic & Suding 2011) and (3) provision of important resources for animals, such as birds or insects (Watson 2001, Watson et al. 2011, Watson & Herring 2012).

Despite the general omnipresence of parasitic plants in terrestrial habitats, individual species, parasitic plant lineages and functional groups often show contrasting habitat preferences (table 1). The low number of independent evolutionary origins of parasitic plants does not allow a formal testing of these differences and relating them to functional traits or groups. Still, some patterns are clear and can be interpreted using the knowledge of ecology and physiology of individual parasitic plant groups.

The greatest benefit of parasitism for root hemiparasites lies in the uptake of mineral nutrients, although they also acquire water and organic carbon from the host (Těšitel et al. 2015). Hemiparasites require light to transform this benefit into fitness by photoassimilation. This implies that root hemiparasitism should be most advantageous in habitats where mineral nutrients are limiting and light is available in abundance (Matthies 1995, Těšitel et al. 2011). It is not so straightforward, since the hemiparasites' growth can be increased by abundant mineral nutrients to an extent similar to non-parasitic plants and light deficiency may be in part compensated by heterotrophic carbon acquisition (Těšitel et al. 2015). Still, root-hemiparasitism provides only limited advantages in habitats such as closed canopy forest where competition for light is the major ecological constraint restricting recruitment ability (e.g. Whitmore 1990). That is why open habitats host the greatest diversity of root hemiparasites.

This association of root hemiparasites with open habitats is clear in Orobanchaceae root-hemiparasitic species of which occur mostly in grasslands and only a tiny fraction them (such as some species of *Melampyrum*) grow in closed-canopy forests. Similarly, most *Krameria* species are restricted to open habitats (though e.g. *K. lappacea* and *K. lanceolata* occur also in forests; Giannini et al. 2011). In Santalales, root-hemiparasitism has probably evolved in tropical trees (Nickrent et al. 2010). Apart from the major clades (see below), extant root-hemiparasitic Santalales comprise multiple mostly small phylogenetic lineages whose species grow in tropical forests. Of these, the family Aptandraceae is probably the largest group containing 34 predominantly forest species; Nickrent et al. 2010). Another example includes the genus *Okoubaka* (Cervantesiaceae) occurring in tropical forests of Africa. *Okoubaka aubrevillei*, the largest hemiparasitic tree, is known to reduce the competitive pressure from the surrounding vegetation by strong reduction of growth or even killing the trees it parasitizes (Veenendaal et al. 1996). Nevertheless, the major radiation events in root-hemiparasitic Santalales are associated with lineages of open habitats

(*Thesium* with c. 350 species is the largest genus of Santalales, *Olax* with forty species; Nickrent et al. 2010). Such evolutionary pattern implies that the fact that the root-hemiparasitic strategy *per se* provides the largest benefits in habitats where light is available in abundance may apply also to Santalales. Why Santalean root hemiparasitism evolved in tree species growing in tropical forests, i.e. a habitat where light deficiency is a limiting factor (Whitmore 1990), remains a question. This might be answered by a detailed analysis of habitat preferences and ecological niches of the forest species of the small basal clades of Santalales.

The limitation by competition for light is largely overcome in stem parasites which grow epiphytically. This is clear in mistletoes which start their life as seedlings attached to host branches and many species of which indeed grow in forest canopy. By contrast, parasitic vines have a ground-based, at least partially photosynthetic seedling, which probably underlies their occurrence in open habitats.

Root holoparasites and endophytic parasites occur mostly in forest understory and arid habitats. Only a few of them (e.g. some *Orobanche* species) grow in grasslands and other open habitats inhabited by root hemiparasites. The non-photosynthetic parasites can thus be viewed as ecological vicariants of root-hemiparasites at least in non-arid habitats and the evolution of holoparasitism as a strategy to colonize habitats not accessible to hemiparasites.

EVOLUTIONARY TRENDS IN FUNCTIONAL TRAITS

The evolution of parasitism in the angiosperms must have started from a non-parasitic ancestor in all parasitic plant lineages. It is now largely accepted that except in parasitic vines the first parasitic stage was a root-hemiparasitic species (Westwood et al. 2010, Naumann et al. 2013). This is also supported by the evolutionary trends in Orobanchaceae and Santalales, the only two extant monophyletic parasitic plant lineages that comprise species of multiple functional groups (table 1, fig. 2). It is likely that further evolution towards more specialized forms was triggered by their ability to colonize habitats unsuitable for their root-hemiparasitic ancestors. This resulted in the repeated evolution of epiphytic mistletoes in Santalales (Nickrent et al. 2010) and of root-holoparasitism in both Santalales (Su et al. 2015) and Orobanchaceae (Bennett & Mathews 2006, McNeal et al. 2013).

Root hemiparasitism and stem parasitism are very successful strategies measured by both the number of species and their profound impact on plant communities and ecosystems. Ecosystem effects are based on the primary consequences of parasitism, but also on secondary effects such as enrichment of ecosystems by nutrient-rich litter and consequent enhancement of nutrient cycling (Phoenix & Press 2005, Cameron et al. 2005, Press & Phoenix 2005, Quedstedt et al. 2005, Prider et al. 2009, Watson 2009, Shen et al. 2010, Li et al. 2012, Watson & Herring 2012, Demey et al. 2013, Fisher et al. 2013). This contrasts with generally low species richness recorded in lineages of root holoparasites and endophytic parasites. Profound ecosystem effects of species of these functional groups are also rather exceptional (well

documented only in the case of *Arceuthobium* dwarf mistletoes; Shaw et al. 2004).

Such evolutionary patterns suggest that the greatest benefits causing evolutionary radiations were associated with the evolution of haustoria and connection to host xylem. These evolutionary innovations, defining the initial phase of the evolution of parasitism in land plants, released the hemiparasitic plants from nutrient limitation, which is likely to be the major cause of their radiation and spread across the Earth. Further constraints based on competition for light and seedling establishment were addressed at least to some extent by the evolution of stem parasitism and especially epiphytic seedlings. This caused the great evolutionary success of mistletoes as indicated by multiple origins of this growth form and intense radiation in some mistletoe lineages. The evolution of host-induced germination, phloem connection, loss of photosynthesis and tendency to grow endophytically is likely also a reaction to establishment-related constraints. Although these advanced evolutionary innovations allowed parasitic plants to colonize habitats inaccessible to root hemiparasites, they produced highly specialized forms (often host-specific) with a limited evolutionary potential. Such multistep evolution associated with changes in ecology is also likely to trigger the evolution of extreme morphological modifications typical of many extant root-holoparasitic and endophytic lineages.

CONCLUSION

This paper summarizes current knowledge on functional biology of parasitic plants. Identification of key functional traits and an analysis of their distribution in parasitic plant lineages underpin a new functional classification of parasitic plants into four principal groups: root hemiparasites, stem parasites, root holoparasites and endophytic parasites. These categories have been used in literature on parasitic plants, but have never been combined in a comprehensive functional classification. Despite being heterogeneous, these functional groups allow each parasitic plant species to be classified into one of them, which is the key advantage over previous concepts based on model species biology. This functional classification is particularly useful in the global view on biology of parasitic plants. Focussing on just one of the key traits underlying biological differences within individual lineages or genera might, however, be a more pragmatic approach on a finer taxonomic scale.

I also attempted to relate the functional biology and classification of parasitic plants with their habitat preferences and community ecology. In addition, an evolutionary scenario is presented to explain diversity and functional trait patterns observed in parasitic plants. Still, the ecological and evolutionary hypotheses presented in this paper are only of an informal nature. Although some formal modelling approaches might seem available, the low number of independent origins of parasitism in the angiosperms largely disqualifies their use at the global perspective adopted in this review. Still, they might be perfectly useful for detailed analyses within a particular parasitic plant lineage.

Parasitic plants are often considered a fascinating group of organisms. That is, however, based on many fascinat-

ing stories on individual parasitic plant lineages displaying unique biological features or evolutionary patterns rather than on any general trends typical of the biology of parasitic plants. This is why studying a particular parasitic plant species is always important and might reveal unexpected natural processes.

SUPPLEMENTARY DATA

Supplementary data are available at *Plant Ecology and Evolution*, Supplementary Data Site (<http://www.ingentaconnect.com/content/botbel/plecevo/supp-data>), and consist of the data table that served as the basis for the principal component analysis (Excel spreadsheet).

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