



## Invited review

# Attack on all fronts: functional relationships between aerial and root parasitic plants and their woody hosts and consequences for ecosystems

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This review discusses how understanding of functional relationships between parasitic plants and their woody hosts have benefited from a range of approaches to their study. Gross comparisons of nutrient content between infected and uninfected hosts, or parts of hosts, have been widely used to infer basic differences or similarities between hosts and parasites. Coupling of nutrient information with additional evidence of key processes such as transpiration, respiration and photosynthesis has helped elucidate host–parasite relationships and, in some cases, the anatomical nature of their connection and even the physiology of plants in general. For example, detailed analysis of xylem sap from hosts and parasites has increased our understanding of the spatial and temporal movement of solutes within plants. Tracer experiments using natural abundance or enriched application of stable isotopes (<sup>15</sup>N, <sup>13</sup>C, <sup>18</sup>O) have helped us to understand the extent and form of heterotrophy, including the effect of the parasite on growth and functioning of the host (and its converse) as well as environmental effects on the parasite. Nutritional studies of woody hosts and parasites have provided clues to the distribution of parasitic plants and their roles in ecosystems. This review also provides assessment of several corollaries to the host–parasite association.

**Keywords:** carbon assimilation, ecosystem function, hemiparasite, mistletoe, nutrient uptake, water relations.

## Introduction

According to most recent tallies, there are ~4100 species of angiosperms that are parasites on other plant species (Nickrent and Musselman 2004). Parasitic angiosperms are spread across 19 families and 227 genera and encompass a wide range of morphologies, life strategies and growth forms. In the angiosperm group, parasitism has evolved independently on a number of occasions, possibly up to 11 times (Barkman et al. 2007). For example, the mistletoe habit is thought to have arisen five times in the Order Santalales (Der and Nickrent 2008, Mathiasen et al. 2008) and holoparasitism has evolved along eight independent lineages (Barkman et al. 2007). There is even a parasitic conifer, *Parasitaxus ustus* (Field and Brodribb 2005), although it could be argued that this species is

mycoheterotrophic as a true haustorium is not formed (Köpke et al. 1981). Parasitic angiosperms can be found throughout the world in most major ecosystems, from subarctic tundra, heathlands and savanna woodlands to deserts and temperate and tropical forests. Some species are widespread agricultural pests; some are listed as rare and endangered while other species can enhance biological diversity (see reviews by Norton and Carpenter 1998, Press and Phoenix 2005).

Two broad types of parasitic angiosperm are distributed globally—those that parasitize stems (or aerial parasites, 40% of species) and those that parasitize roots (root parasites, 60% of species, Musselman and Press 1995). One exception is the genus *Tripodanthus* of which at least one species attaches to both stems and roots of hosts (Amico et al. 2007, Mathiasen

et al. 2008). Other definitions of parasitic plants are mostly function based. The most common approach is to classify parasitic angiosperms according to whether they contain chlorophyll and only require access to water and mineral nutrients from their host (hemiparasites) or lack chlorophyll and must access carbohydrates in addition to water and nutrients (holoparasites). However, some species are intermediate between hemi- and holoparasitism. A good example is the genus *Cuscuta* in which the dependence on hosts for carbon is related to the stage of growth. Hemiparasites may grow to maturity without a host (facultative parasite) or may require a host to reach maturity (obligate parasite). Parasitic plants can be further distinguished according to whether they are xylem- or phloem-feeders (e.g., Raven 1983, Irving and Cameron 2009).

Host plants of parasitic angiosperms are extraordinarily diverse and encompass much of the plant kingdom—ranging from herbaceous annuals and perennials to trees and shrubs. Some parasitic plants can parasitize many different species (e.g., >450 species in the case of *Viscum album*, Barney et al. 1998), while others are extremely host specific. A few parasitic partnerships have evolved so comprehensively that parasitic angiosperms can even parasitize other parasitic angiosperms (epiparasitism and hyperparasitism, Mathiasen et al. 2008). Trees and shrubs can have plant parasites on both their stems and roots. Mistletoes (e.g., Loranthaceae, Misodendraceae, Santalaceae) comprise the largest group of stem or aerial parasites on woody hosts, but other taxa, including the genera *Cuscuta* (Convolvulaceae) and *Cassytha* (Lauraceae) also assail aboveground parts of woody plants. Roots of trees and shrubs host a range of hemi- and holoparasitic plants in a number of taxonomic groups (e.g., hemiparasites in the Santalaceae, Olacaceae and Krameriaceae, holoparasites in the Balanophoraceae, Cytinaceae, Hydnoraceae, Lennoaceae, Mitrastemonaceae and Orobanchaceae).

This review highlights the ecophysiology of aerial and root hemiparasites on woody hosts using examples drawn from the above list of families, most of which occur in the Order Santalales.

Our focus is on trees and shrubs as hosts, and first on the water, carbon and nutrient features of the host–parasite relationship. Here we can take into account small spatial scales (e.g., leaves and branches) and the types of studies that are best suited to physiological investigations at this scale. Secondly, we include a discussion of the effects of aerial and root hemiparasitism on larger spatial scales—on whole-tree growth and ecosystem-scale impacts and how these might be measured and assessed. We restrict our discussion to woody hosts, taking advantage of the relative permanence of the host–parasitic plant relationship compared with potential constraints imposed by re-infection of annual and perennial herbaceous hosts (Marquardt and Pennings 2010). Our woody host focus is further warranted given that other recent

reviews cover aspects as varied as: comparison of parasitic angiosperms with animal sap-feeders (Raven 1983), host specificity and speciation of mistletoes compared with that of animal parasites (Norton and Carpenter 1998) and comparisons of parasitic plants with herbivores (Pennings and Callaway 2002, Pennings and Simpson 2008). We provide a different view of the host–parasite relationship by reviewing the wide variety of techniques used in physiological and ecological studies of both aerial and root hemiparasitic angiosperms. Aspects of broader host–parasite physiology, including the impact of parasitic angiosperms on photosynthesis (Watling and Press 2001), nitrogen acquisition by woody hemiparasites (Hibberd and Jeschke 2001, Pate 2001) and the role of parasitic plants in nutrient cycling (Quesada 2008), have been evaluated within the last 10 years and we attempt to draw these aspects together insofar as they relate to woody plants and hemiparasitism. From time to time we are obliged to cite literature on common parasitic angiosperms such as *Striga* on herbaceous hosts, due to the wealth of biochemical and molecular research that is, by and large, lacking for woody host species. We also add holoparasites such as *Orobanche* to our discussions for the same reason and to compare obvious differences in carbon gains by parasites that are fully dependent on their hosts. The ecophysiological nature of our review complements that of Mathiasen et al. (2008), who described the changing nature of the study of the ecology of mistletoes on their woody hosts, and of Aly (2007), who evaluates conventional and biotechnological approaches to the control of parasitic weeds.

In part, the abundance of available literature in our focus area is due to the economic importance of host species. In this context, some of the more notable tree and shrub hosts of hemiparasitic plants include kapok (*Ceiba pentandra*), cacao (*Theobroma cacao*), shea butter (*Vitellaria paradoxa*) and species of *Citrus*, *Coffea*, *Hevea*, *Vitis* and important timber species in the genera *Abies*, *Eucalyptus*, *Larix*, *Pinus*, *Populus*, *Pseudotsuga* and *Tectona* (Knutson 1983, Nickrent and Musselman 2004, Mathiasen et al. 2008). However, a significant literature has developed around the relatively small number of hemiparasitic angiosperms that also have economic importance. This list includes Sandalwood (*Santalum album*), which is grown in plantations (with woody hosts) as a source of santalol for the cosmetic and pharmaceutical industries, and *V. album*, a mistletoe that is a rich source of a range of cytotoxins used to treat or alleviate symptoms of some forms of cancer (see reviews by Horneber et al. 2008, Kienle et al. 2009).

In this review, our aim is to bring attention to emerging or novel use of methods that can increase our understanding of how hemiparasitic angiosperms function and interact with their woody hosts and their environment. Our discussion includes both aerial and root hemiparasites since, in our opinion, these groups are rarely considered alongside one another.

## Water relations at a range of spatial scales

Beginning with water is logical owing to its key role in host–parasite relations—at least for the most common host–parasite combinations. There have been many demonstrations of faster rates of transpiration, reduced water potential and poorer water use efficiency of parasitic angiosperms compared with their hosts across a range of holo- and hemiparasites and the generality of these has been discussed in reviews by Ehleringer and Marshall (1995) and Press et al. (1999). Overwhelmingly, these demonstrations have been made at the leaf level (small scale) and quantified exchanges of water between leaves and the atmosphere have long been used as evidence of the probability of xylem-mediated transfer of nutrients and organic solutes from hosts to parasites (Press et al. 1988, Ehleringer and Marshall 1995).

Aerial or stem hemiparasites growing on the branches of trees and shrubs are obviously reliant on their hosts for water. A little less obvious is the partial dependence of root hemiparasites on their hosts. The latter varies strongly with the extent of the root system of the parasite. In this case, there is convincing evidence that haustorial connections can be more important for mineral nutrition than water acquisition (Ehleringer and Marshall 1995, Pate 2001). A clear example is provided by the similar water use efficiency (and several other characteristics of their water relations) of root hemiparasites *Oxalophyllanthi* and *S. album* and their woody hosts. Researchers have interpreted these results as suggesting that active uptake of mineral nutrients by the parasite via the haustorium may be more important than mass flow in water (Pate et al. 1990, Radomiljac et al. 1999b).

‘Branch-scale’ measurements have been used to elucidate various aspects of the water relations of parasitic and woody hosts. For example, Meinzer et al. (2004) determined the specific hydraulic conductivity of infected and uninfected branches of Western hemlock (Tyree et al. 1993). Whole branches were removed from adult trees and a pressure gradient imposed across 10- to 15-cm-long segments. The comparable hydraulic conductivity of similar-sized infected and uninfected branches was explained by compensatory reduction in leaf area, and increase in sapwood area of infected host trees (Meinzer et al. 2004). Radomiljac et al. (1999b) used small branches of pot-culture specimens of *S. album* grown with a number of different hosts or no host at all to determine pressure–volume curves and osmotic turgor during a 4- to 6-h period of air-drying. All measures of tissue water relations were similar regardless of the type or presence of a host. This was used to argue that fast rates of transpiration were important for protection against water stress and for nutrient gain by the hemiparasite. Bannister et al. (1999) used a similar approach and drew comparable conclusions in relation to host preference of the mistletoe, *Ileostylus micranthus*.

Leaf-based measures of pre-dawn water potential and carbon isotope ratios showed different water-use patterns for Douglas fir (*Pseudotsuga menziesii*)—an evergreen species—and Western larch (*Larix occidentalis*)—a winter-deciduous species—when parasitized by *Arceuthobium* spp. (Sala et al. 2001). These authors argued that if their data were assessed in isolation, logical conclusions relating to seasonal water stress of host trees might need to be reversed if considered in the context of whole-tree water use and changes in leaf or sapwood area. Ziegler et al. (2009) provide an example of this in that while they measured faster rates of sap flow and transpiration in the mistletoe *V. album* compared with its woody hosts, those rates lack meaning at the whole-tree scale without knowledge of sapwood or leaf area of the host or the mistletoe.

A novel branch-scale technique was described in Davidson et al. (1989). A single branch of the host tree *Casuarina obesa* bearing two individuals of the mistletoe *Amyema linophyllum* was detached and the transpiration stream re-established. One of the mistletoes was bagged and kept cool and dark while the other remained exposed to light and ambient temperature. Leaf water potentials of the bagged parasite remained higher than those of the host over the course of a day, while the unbagged mistletoe maintained leaf water potentials lower than those of the host. An obvious inference is that the *C. obesa*–*A. linophyllum* association has evolved to the point where the parasite has lost its ability to regulate water loss. Similar leaf- and branch-scale measurements of water use by parasitic plants and their woody hosts are beginning to be coupled with whole-tree measurements of water use (Meinzer et al. 2004, Shaw et al. 2004). An example of the power of this approach is provided by Meinzer et al. (2004). Maximum water use by Western hemlock (*Tsuga heterophylla*) was 40% less for trees heavily infected with a dwarf mistletoe (*Arceuthobium tsugense*) than for uninfected trees. When considered in conjunction with analysis of leaf and sapwood area, rates of transpiration were far less for infected trees than uninfected, and the authors estimated that rates of carbon accumulation were up to 60% slower in infected trees. Whole-plant water-use measurements need to be expanded to a wider range of host–parasitic angiosperm combinations to elucidate broad patterns of forest growth, particularly where infestation is heavy and assessment of timber production is warranted.

## Mineral nutrient and organic solute transfer

There is large variation in rates of nutrient uptake by parasitic angiosperms from their hosts and their physical environment and this corresponds to variable reliance on the host. Some parasites show a high degree of autonomy (i.e., root hemiparasites with functional roots) while others show complete dependence on the host (i.e., aerial parasites). Similarly, reliance of parasites on hosts for carbon-based nutrition varies widely and

depends in part on the photosynthetic capacity of the parasite (Press 1995).

Given that mineral nutrients and organic solutes are transported in solution, the nutrition of host–parasite systems is usually closely linked to their water relations (see above). Even so, only a few species form the basis of our knowledge of nutritional aspects of host–parasite systems (Pate 1995, Hibberd and Jeschke 2001) and of the host plants, by far the majority are herbaceous. Early anatomical studies using tracers (e.g., lanthanum nitrate), histological stains (e.g., uranyl acetate) and fluorescent dyes (e.g., Calcofluor white, Coetzee and Fineran 1987, Kuo et al. 1989) revealed some of the functioning of haustorium structure and showed varying degrees of vascular contact between parasite and host within the haustorium (see reviews by Riopel and Timko 1995, Pate 2001). Tracers are still used intermittently, although stable and radioactive isotopes including  $^{14}\text{C}$ ,  $^{15}\text{N}$ ,  $^{18}\text{O}$ ,  $^{32}\text{P}$  and deuterium-labelled water (e.g., Tennakoon et al. 1997b, Calladine and Pate 2000, Hibberd and Jeschke 2001, Cameron and Seel 2007) and unusual marker compounds (e.g., djenkolic acid, Calladine et al. 2000; green fluorescent protein, Haupt et al. 2001) have in recent years become the tools of choice.

The use of such techniques is highlighted by studies such as those of *S. album* (Tennakoon and Cameron 2006), *V. album* (Khan et al. 2009) and several others (e.g., Luna and Guidice 2007, Khan et al. 2009). Together, they emphasize congruity between physical and physiological properties. Interestingly, studies of haustorial anatomy of common parasitic angiosperms with herbaceous hosts are still being published despite the wealth of information that has already been compiled. For example, the anatomy of the common root hemiparasitic species *Rhinanthus minor* has recently been revisited (Cameron and Seel 2007) with a view to determining its role in solute transport.

As an example of the congruity between physical and physiological characteristics, we might consider the nature of vascular tissues. The range extends from direct lumen-to-lumen contact between xylem or phloem of parasite and host, such as that found in many holoparasites, to indirect contact with xylem or phloem vessels of the parasite lying adjacent to an interface of parenchymatous tissue surrounding host vessels (Riopel and Timko 1995, Hibberd and Jeschke 2001, Pate 2001). Transfer of solutes and water is typically via apoplastic flow in both mistletoes and root hemiparasites, but the possibility of symplastic transfer cannot yet be ruled out (Pate 1995, Hibberd and Jeschke 2001), despite refinement of techniques and use of fluorescent probes, isotopic labelling and viral transport (Birschwilks et al. 2006). Greater amounts of host xylem tissue support the flow of solutes from host to parasite. For example, analysis of the woody host *Acacia acuminata* showed infected branches to have two to three times more sapwood xylem per unit foliage area than uninfected branches when

parasitized by the mistletoe *Amyema preissii* (Tennakoon and Pate 1996). Similarly, ratios of sapwood area to foliage area of *T. heterophylla* were smaller for branches infected by the dwarf mistletoe *A. tsugense*, than for uninfected branches (Meinzer et al. 2004).

Most modern studies couple 'mass balance' approaches (Irving and Cameron 2009) with more sophisticated or extensive nutrient analyses (e.g., Bannister et al. 2002, Bowie and Ward 2004, Reblin et al. 2006). One approach used with success with woody hosts and their hemiparasites is extraction of xylem sap under a mild vacuum (Pate 1995). It has been hypothesized that if there is lumen-to-lumen continuity between xylem of the host and parasite, compounds would be essentially unchanged in form and quantity and would move by mass flow into the transpiring parasite. The composition and concentration of compounds in the xylem sap of the parasite should then match that of the host. In contrast, symplastic transfer would allow the possibility of selective uptake by the parasite with modification of the amount and type of transferred compounds. Once the composition of solutes in the xylem and phloem is known, fluxes of carbon and nitrogen within whole plants can be modelled empirically (see reviews by Pate 1995, Hibberd and Jeschke 2001, Irving and Cameron 2009).

Modelling of nitrogen fluxes, pioneered with  $\text{N}_2$ -fixing legumes (Pate et al. 1979), was eventually adopted for use with parasitic angiosperms. Host–parasite systems examined in this way are overwhelmingly agricultural and herbaceous (e.g., *Cuscuta reflexa*, Jeschke et al. 1994a, 1994b; *Orobancha cernua*, Hibberd et al. 1999; *R. minor*, Seel and Press 1996, Seel and Jeschke 1999, Jiang et al. 2004), with fewer studies of hemiparasites and their woody hosts (*O. phyllanthi*, Pate et al. 1990, Tennakoon et al. 1997a). A key assumption of modelling carbon and nitrogen fluxes of hemiparasites is that there is an unimpeded mass flow of mineral nutrients and organic solutes from host to parasite. This approach must be modified for holoparasites such as *Cuscuta* which gain some of their solutes from phloem (Jeschke et al. 1994b). Instead, solute flux can be calculated on the basis of the immobility of calcium in phloem and the assumption that any intake of calcium is via the xylem. Ratios of Ca:N and Ca:C in xylem sap can then be used to estimate the movement of carbon and nitrogen by difference (Jeschke et al. 1994b). Studies of root hemiparasites must also be modified by assessing xylem sap from roots of both the host and the parasite, particularly as hemiparasites have the ability to access water and mineral nutrients directly from the soil (Hibberd and Jeschke 2001). Nutrient transfer from woody hosts to aerial hemiparasites is obviously more straightforward in this respect.

Only rarely have researchers attempted to quantify host–parasite nitrogen transfer. We found in the literature only one association involving a woody host. Nevertheless, we have included this information to illustrate the assortment of approaches that have been used (Table 1). Two studies involve



Table 1. Proportion (%) of nitrogen gained by parasitic angiosperms from their herbaceous (unless otherwise indicated) hosts.

Host–parasitic angiosperm relationship	Nitrogen gain (%)	Method used	Reference
Root hemiparasite ( <i>R. minor</i> ) on a grass ( <i>Cynosurus cristatus</i> ) and forbs ( <i>Leucanthemum vulgare</i> and <i>Plantago lanceolata</i> )	0.2–2.5 (forbs) 17 (grass)	Pot-culture, histological characterization and <sup>15</sup> N tracer	Cameron and Seel (2007)
Root hemiparasite ( <i>R. minor</i> ) on a grass ( <i>Hordeum vulgare</i> )	18	Pot-culture, C and N concentration in xylem sap and dry matter	Jiang et al. (2004)
Root hemiparasite ( <i>O. phyllanthi</i> ) on woody host ( <i>Acacia littorea</i> )	56	Pot-culture, C and N concentration in xylem sap and dry matter of <i>Olex</i> and parasitized and unparasitized <i>Acacia</i>	Tennakoon et al. (1997a)
Root holoparasite ( <i>O. cernua</i> ) on herbaceous host ( <i>Nicotiana tabacum</i> )	100 (5–15 in xylem)	Pot-culture, C and N concentration in xylem sap, gas exchange, parasitic transpiration rates	Hibberd et al. (1999)
Holoparasite ( <i>C. reflexa</i> ) on N <sub>2</sub> -fixing herbaceous host ( <i>Lupinus albus</i> )	223 (6 in xylem)	Pot-culture, C and N concentration in xylem sap, gas exchange, parasitic transpiration rates, Ca:N and Ca:C ratios	Jeschke et al. (1994b)

holoparasites that, by definition, should derive all of their nitrogen from their host. Of these, one showed heavy reliance of the parasite on uptake of mineral nutrients and organic solutes from the phloem of the host, with low fluxes of nitrogen in the xylem (Hibberd et al. 1999). The other showed that the holoparasite appropriated almost all of its nitrogen from its N<sub>2</sub>-fixing host (Jeschke et al. 1994b). Of the studies involving root hemiparasites, the proportion of nitrogen derived from the host ranged widely—from low proportions for host grasses and forbs to a very large proportion for a N<sub>2</sub>-fixing plant (Table 1). An important point here is the very limited amount of available data on which to base models.

Movement of organic solutes from hosts to parasites also facilitates transfer of carbon (see review by Press 1995). Quantification of carbon gain from hosts or ‘heterotrophic carbon gain’ has advanced over the last 20 years from posing hypotheses (Raven 1983) to estimations of gain (Press et al. 1990, Stewart and Press 1990) to more precise calculation of carbon gain using a number of techniques (Table 2). A first point is that, unlike the studies of nitrogen transfer referred to above, there is a richer field of information relating to carbon exchange between woody hosts and both above- and below-ground parasitic plants. Initially, heterotrophic carbon gain was estimated by measuring concentrations of carbon in the xylem sap of the host and, using rates of transpiration and photosynthesis, calculating how much carbon would be transferred from the host and how much carbon would be fixed by the parasite. This has been called the ‘the carbon budget method’ (Marshall and Ehleringer 1990). The ‘ $\delta^{13}\text{C}$  difference method’ involves measurement of carbon isotopes in the xylem sap or leaves of the parasite and the host and combining these data with measurements of gas exchange (Press et al. 1987). Many studies have now compared both methods (e.g., Pate et al. 1991b, Richter and Popp 1992, Richter et al. 1995, Tennakoon and Pate 1996), and just as many studies have used either one or the other technique (e.g., Pate et al. 1991b, Marshall et al. 1994a, Wang et al. 2008). We have included in Table 2 data

for the root holoparasite, *O. cernua*, as there are no published estimates of heterotrophic carbon gain by holoparasites from woody hosts. This host–parasite system has amongst the greatest values of heterotrophic carbon gain—unsurprisingly, given the total dependence of the holoparasite on the host for water, mineral nutrients and carbon. Clearly, much of the transfer of carbon for *Orobanch* is via the phloem (Hibberd et al. 1999), whereas it is via the xylem in mistletoes and root hemiparasites.

We might expect that heterotrophic carbon gain by root hemiparasites (*Striga* and *Olex*) should be comparable to the range estimated for aerial hemiparasites (Table 2). The nature of the host (herbaceous or woody) seems to have little effect, yet, according to fertilizer experiments, nitrogen supply to the host does have an effect on heterotrophic carbon gain by parasitic plants (Table 2; Cechin and Press 1993, Marshall et al. 1994a), as is also indicated by the N<sub>2</sub>-fixing capacity of the host (Pate et al. 1991b). A greater understanding of heterotrophic gain by a wider range of parasitic angiosperms on both herbaceous and woody hosts is needed to clarify these patterns. Cernusak et al. (2009) have recently posed a number of hypotheses to explain <sup>13</sup>C enrichment in heterotrophic tissues, some of which could be used as a basis for further study using woody host–parasitic angiosperm relationships.

Xylem sap analysis has led to a number of interpretations of the functional relationship between host plants and their parasites (see recent review by Irving and Cameron 2009). These patterns can be explored for hemiparasites with woody hosts, as more data are compiled. For example, the mistletoe *V. album*, growing on *Populus* and *Abies*, shows selective uptake of compounds containing sulphur (S) from xylem. This generalization holds across differing types of S-containing compounds, host species and thiol status of the leaves of the mistletoe in different seasons (Escher et al. 2003). Similarly, specific amino acids are accumulated by *V. album* via selective uptake from xylem of *Populus* and *Abies* (Escher et al. 2004b). Selective uptake of nitrogen as nitrate by *V. album* has also been

Table 2. Proportion (%) of heterotrophic carbon (C) derived from woody hosts (unless otherwise indicated<sup>a</sup>) by parasitic angiosperms.

Host–parasitic angiosperm relationship	Heterotrophic gain of C (%)	Method used	Reference
Range of Australian mistletoes on woody hosts	5–21	Field study, stable C isotopes	Marshall et al. (1994b)
Mistletoe ( <i>Amyema linophyllum</i> ) on woody host ( <i>Casuarina obesa</i> )	24	Field study, C and N concentration in xylem sap	Pate et al. (1991b)
Root hemiparasite ( <i>S. hermonthica</i> ) on herbaceous host ( <i>Sorghum bicolor</i> ) <sup>a</sup>	30–35 (6–27) <sup>a</sup>	Pot-culture, fertilizer trials, stable C isotopes, gas exchange	Press et al. (1987) and Cechin and Press (1993)
Root hemiparasite ( <i>O. phyllanthi</i> ) on herbaceous and woody hosts <sup>a</sup>	12–20, 19–30	Field study, stable C isotopes, gas exchange, parasitic transpiration rates, C and N concentration in xylem sap	Tennakoon and Pate (1996)
Mistletoe ( <i>V. album</i> ) on woody host ( <i>Malus domestica</i> )	23–43	Field study, parasitic transpiration rates, C concentration in xylem sap	Richter and Popp (1992)
Root hemiparasites ( <i>Castilleja linariifolia</i> and <i>Orthocarpus tolmiei</i> ) on a woody host ( <i>Artemisia tridentata</i> )	40	Field study, stable C isotopes, gas exchange, parasitic transpiration rates	Ducharme and Ehleringer (1996)
Mistletoe ( <i>Tapinanthus oleifolius</i> ) on a range of woody hosts	55	Field study, stable C isotopes, gas exchange, parasitic transpiration rates, C concentration in xylem sap	Richter et al. (1995)
Mistletoe <i>P. juniperinum</i> on woody host ( <i>Juniperus osteosperma</i> )	58 (47–64) <sup>b</sup>	Field study, fertilizer trials, stable C isotopes, gas exchange, parasitic transpiration rates, C concentration in xylem sap	Marshall et al. (1994a)
Mistletoe ( <i>Tapinanthus oleifolius</i> ) on woody C <sub>3</sub> and CAM hosts	47–67	Field study, stable C isotopes	Schulze et al. (1991)
Mistletoe <i>P. juniperinum</i> on woody host ( <i>J. osteosperma</i> )	62	Field study, stable C isotopes, gas exchange, parasitic transpiration rates, C concentration in xylem sap	Marshall and Ehleringer (1990)
Mistletoe ( <i>T. oleifolius</i> ) on a range of woody hosts	35–78	Field study, stable C isotopes	Wang et al. (2008)
Root holoparasite ( <i>O. cernua</i> ) on herbaceous host ( <i>N. tabacum</i> ) <sup>a</sup>	73	Pot-culture, C and N concentration in xylem sap, gas exchange, parasitic transpiration rates	Hibberd et al. (1999)

<sup>a</sup>Varying heterotrophy depending on addition of N fertilizer.

suggested after feeding experiments using <sup>15</sup>N- and <sup>13</sup>C-labelled inorganic and organic nitrogen compounds, albeit dependent on the availability of glutamine (Escher et al. 2004c). In contrast, some root hemiparasites on herbaceous hosts show non-selective uptake of nitrogen compounds, based on studies using natural abundance of <sup>15</sup>N (Pate and Bell 2000) and analysis of xylem and phloem sap collected from parasite and parasitized and unparasitized hosts (Jiang et al. 2004).

Seasonal patterns of carbohydrate flux in xylem sap of the mistletoe *V. album* suggested leaf development- or leaf senescence-dictated patterns of uptake from the host (Escher et al. 2004a). Similarly, <sup>13</sup>C and <sup>15</sup>N natural abundance analysis of mistletoes in New Zealand showed non-selective uptake of nitrogenous and organic solutes (Bannister and Strong 2001). The available evidence seems to suggest a degree of selective uptake (or exclusion) of organic solutes by parasitic angiosperms, especially when these compounds have osmotic significance for the parasite. Parasitic angiosperms generally maintain osmotic potentials below that of their hosts by accumulating amino acids (e.g., proline, arginine), organic acids, carbohydrates (e.g., pinitol, chiro-inositol, mannitol) and xylem-mobile cations (e.g., Na<sup>+</sup>, K<sup>+</sup>) (see reviews by Pate 1995, Press et al. 1999). The type of osmotica depends on the species of

parasitic plant and host involved. Investigation of carbon movement within related taxa with differing capacities for photosynthesis may be useful for further examination of functional relationships between woody hosts and their parasites. A good example may be comparison of organic and inorganic solutes of species in the Viscaceae—we would expect significant differences in solute uptake (both composition and rates of exchange) for *Phoradendron* and *Viscum* with relatively high capacities for photosynthesis, compared with *Arceuthobium* with lower photosynthetic rates.

### Carbon assimilation and growth at a range of spatial scales

In their review, Watling and Press (2001) argued that parasites provide a sink for photosynthates produced by hosts and that some host plants can compensate by increasing rates of photosynthesis or the capacity for photosynthesis. Compensatory mechanisms can include increases in leaf area, delayed leaf senescence, increased Rubisco content and general reallocation of carbon. However, a more common generalization is that compensation is insufficient to maintain overall rates of carbon gain of the host–parasite system.

Rates of photosynthesis of hosts and parasites are usually measured directly using well-established gas analysis systems (e.g., LICOR Portable Photosynthesis System) and indirectly through isotopic tracers (Cernusak et al. 2004) or by determining growth increments (see Table 2 for examples). Glasshouse and field-based studies are widely used to determine the effects of different tree and shrub hosts on parasite growth (e.g., Barrett and Fox 1994, Tennakoon and Pate 1996, Radomiljac et al. 1998, 1999a, Calladine et al. 2000, Loveys et al. 2002, Brand et al. 2003, Brand 2009) and the effects of parasitic angiosperms on woody host plants (e.g., Reid et al. 1992, 1994, Shaw et al. 2008). Not surprisingly, improvement in growth of the parasite is the focus of attention in studies of economically important parasitic plants such as *Santalum* sp. (e.g., Barrett and Fox 1994, Loveys et al. 2002, Brand 2009) while growth and nutrition of the host is of greater interest when the host is of economic importance (e.g., Bickford et al. 2005, Reblin et al. 2006, Stanton 2006).

Relationships between growth and performance of parasitic angiosperms, on the one hand, and those of their woody host plants, on the other, vary widely (see reviews by Graves 1995, Pennings and Callaway 2002, Glatzel and Geils 2009). Parasitic angiosperms rarely kill their host, but under most circumstances, the host, both woody and herbaceous species, suffers reduced growth and reproductive performance (Nickrent and Musselman 2004). This accords with physiological responses that have been detailed earlier and, in turn, reduces the competitive ability of the host and affects broader community dynamics (Press and Phoenix 2005, Watson 2009; and see Ecosystem-scale studies section).

Turning the host–parasite relationship around, we understand far less well how the ‘health’ or ‘condition’ of the host affects the growth and performance of the parasite. There are some reports of improved host condition imposing stress on the parasite, but this hypothesis needs to be explored more fully. Perhaps the most logical example is shading of the parasite as a result of improved growth of the host (Glatzel and Geils 2009). In comparison, and equally logical, Bickford et al. (2005) noted that increased growth of Ponderosa pine (*Pinus ponderosa*) showed concomitant increases in growth, water use and nutrient content of the dwarf mistletoe *Arceuthobium vaginatum*. A similar, perhaps inadvertent example of the effect of host condition on parasite functioning comes from Marshall et al. (1994a). Nitrogen fertilizer added to stands of Utah juniper (*Juniperus osteospermum*) resulted in increased foliar nitrogen concentrations, net assimilation rates and water-use efficiency of the mistletoe *Phoradendron juniperinum*. To add to the uncertainty of emerging patterns, a study involving the same host–parasite combination showed no correlation of distribution of female plants with hosts of better condition (Marshall et al. 1993). Clearly, further basic physiological

research is required to elucidate the impact of host condition on parasitic plant response.

Of particular topical interest is the response of parasitic plants and their hosts to future climate change and greenhouse gas emission scenarios. Several studies have investigated the effects of elevated CO<sub>2</sub> on parasitic plants and their hosts, but all involve herbaceous hosts. Hwangbo et al. (2003) exposed the root hemiparasite *R. minor* and its herbaceous host *Poa pratensis* to elevated CO<sub>2</sub>. Both host and the parasite increased rates of photosynthesis under elevated atmospheric [CO<sub>2</sub>], but while the parasite increased in biomass and nitrogen content, the host did not. *Striga hermonthica* and *Striga asiatica*, two root invasive hemiparasites that parasitize a variety of herbaceous hosts, also increased rates of photosynthesis but did not accumulate biomass when atmospheric [CO<sub>2</sub>] was increased. It can be speculated that increased growth and nutrient content of parasitic plants may translate to an improvement in reproductive effort and success and, quite plausibly, an increase in population size, distribution and competitive ability. Regardless of host type—and we hypothesize that there would be no overall difference in patterns of response to elevated CO<sub>2</sub> for woody hosts and their parasites compared with herbaceous hosts and their parasites—this accords with common responses to increased host photosynthesis (Watling and Press 2001).

### Ecosystem-scale studies

A theme developed in previous sections is that parasitic angiosperms directly modify the physiological functioning of their hosts (i.e., small scale) and therefore, directly and indirectly affect the environment in which they occur (ecosystem scale). Parasites are often themselves an important resource for animals, particularly birds (see reviews by Press et al. 1999, Watson 2001, 2009, Shaw et al. 2004, Press and Phoenix 2005, Mathiasen et al. 2008), providing an obvious influence on their surroundings. Indirectly, parasitic plants influence herbivores, pollinators and seed vectors of their hosts and their impacts may be particularly manifest in low nutrient ecosystems (Press 1998). The role of parasitic angiosperms beyond that of immediate effects on host plants has been investigated most thoroughly in the past decade (see review by Press et al. 1999) but, once again, mostly for herbaceous rather than woody hosts. As a consequence of this body of research, land managers are becoming increasingly aware of the importance of monitoring parasite populations and their environmental effects, particularly in situations that involve potential risk to assets including timber production and biodiversity (e.g., Norton and Reid 1997, Shaw et al. 2004, Mathiasen et al. 2008, Carnegie et al. 2009).

Physiological studies of parasitic angiosperms and their woody hosts that have been conducted in natural settings provide a good opportunity for broader interpretation of their

biology and ecology. For example, Dawson and Ehleringer (1991) deduced that larger seed from older individuals of the mistletoe *P. juniperinum* would ensure that greater resources were available and help to ensure seed survival, germination success and subsequent growth of the parasite. Similarly, the mistletoe *Struthanthus flexicaulis* that parasitizes an endemic legume shrub, *Mimosa calodendron*, showed predictable patterns of infestation (up to 65% of the host population) and growth in proportion to the size of its woody host (Mourao et al. 2009). When coupled with limited host distribution (i.e., only in rupestrian fields on ironstone outcrops), this knowledge had significant implications for host populations and their demographic structure (Press and Phoenix 2005). In both cases, the physiological advantage of greater supply of nutrients, water and/or carbon from hosts can be hypothesized and tested using the range of techniques described in previous sections of this review. Medel (2000) used a statistical approach to determine the potential for two co-occurring columnar cacti to evolve defensive traits against infection by the holoparasite *Tristerix aphyllus*. Spine length was important in preventing individuals from being parasitized, but it was unclear whether this characteristic mediated parasite infection (e.g., preventing seed-dispersing birds perching on columns) or had some other physiological function (e.g., protection from solar radiation, reduction in water loss). This is an indubitably emerging research field that will require combination of basic plant biology and physiology (using well-established ecophysiological measurement techniques) and population ecology to be coupled with new modelling techniques to gain greater understanding of host–parasite functional relationships.

The general distribution of parasitic angiosperms is tightly linked with that of their hosts and their dispersal agents. Using a classic example from Europe, the distribution of the mistletoe *V. album* has been linked with the migratory routes of birds, the spread of apple tree cultivation and increased planting of host trees in public spaces (Zuber 2004). In South Africa, distribution of mistletoes correlates well with overall nutrient status of an ecosystem, whereby nutrient-rich mesic savanna has greater mistletoe biodiversity than nutrient-poor shrublands and evergreen forests (Dean et al. 1994). Elsewhere in Africa, the abundance of the mistletoe *Phragmanthera dschallensis* depends on host tree size and age and, ultimately, on perching preferences of the three bird species involved in its seed dispersal (Roxburgh and Nicolson 2008). The physiological link that can be made between nutrient/water supply from the host and parasitic growth and success is obvious in all of these examples. Overton (1994) described one of the few manipulative experiments published to determine dispersal patterns and abundance of the mistletoe *Phrygilanthus sonorae* (n.b. the proper name for this species is *Psittacanthus sonorae* (Barlow and Weins 1973)) growing on woody hosts *Bursera microphylla* and *Bursera hindsiana*. Again, host tree size and age can be

used as a physiological explanation for the dispersal pattern and abundance of the mistletoe, but, in this case, establishment success and mortality of the mistletoe and host turnover could not. Watson et al. (2007) combined physical mapping and measurement of height of individuals of the root hemiparasite *Santalum lanceolatum* associated with its host *Acacia tetragonophylla* to model spatial patterning of both partners. Host plants were strongly associated with the creek-line while the parasite was clustered more tightly, indicating the importance of water availability and the quality of the host for successful parasitic infection.

Teasing apart interactions of parasitic plants with their wider environment currently relies heavily on manipulative experiments applied to parasitic plants with herbaceous hosts. Marvier (1996, 1998) grew the root hemiparasite *Castilleja wightii* on herbaceous N<sub>2</sub>- and non-N<sub>2</sub>-fixing host plants and examined the performance of aphids feeding on different combinations of host plants. Growth and reproductive performance of the root hemiparasite was better when it was grown with a mixture of N<sub>2</sub>- and non-N<sub>2</sub>-fixing host plants, but nitrogen content was greater when it was grown with N<sub>2</sub>-fixing hosts. Aphids survived and reproduced better when feeding on parasitic plants with higher nitrogen content. Similarly, Adler (2000) found that uptake of alkaloids by the root hemiparasite *Castilleja indivisa* from an N<sub>2</sub>-fixing host directly reduced herbivory and indirectly increased visitation by pollinators (which ultimately increased seed production). Schädler et al. (2005) noted the possibility of anti-herbivore defences conferred by host plants on the root hemiparasite, *Melampyrum arvense*. Clearly, knowledge of the physiology of host–parasite interactions has increased our understanding of the ecological roles that parasitic angiosperms have in their environmental setting.

Likewise, in a study of competition between two root hemiparasites, *Odontites rubra* and *Rhinanthus serotinus*, and their herbaceous host, *Medicago sativa*, both parasites impaired host growth, while the host reduced growth of the parasites through competition for light (Matthies 1995). The same pattern was found when *Rhinanthus alectorolophus* was grown in isolation or in competition with two herbaceous hosts, the grass *Lolium perenne* and the legume *M. sativa* under elevated CO<sub>2</sub> conditions (Matthies and Egli 1999). In a third study, the presence of arbuscular mycorrhizal fungi enhanced not only the biomass production of the herbaceous host plant, red clover (*Trifolium pratense*), but also the biomass and fruit production of the root hemiparasite, *Rhinanthus serotinus*. In contrast, the root hemiparasite *Odontites vulgaris* had little effect on the growth of a host grass, *Poa annua* (Salonen et al. 2001), while the presence of ectomycorrhizal fungi on roots of Scots pine, *Pinus sylvestris*, enhanced the growth of biomass and flower production of the root hemiparasite *Melampyrum pratense*, most likely due to greater nutrient availability conferred on the host by the mycorrhizal association (Salonen et al. 2000).



Together, these studies point to complex ecophysiological interactions that need considerable further research.

The notion of parasitic angiosperms influencing their surroundings as 'ecosystem engineers' (Press and Phoenix 2005) has recently been investigated in a number of ways. Parasitic plants contain large concentrations of certain mineral nutrients, and their influence by producing nutrient-rich, rapidly decomposing litter, litterfall and its subsequent decomposition should contribute to nutrient cycling (Quested et al. 2003). This is likely for the mistletoe *Amyema miquelii* growing on *Eucalyptus* spp. hosts, based on high rates of mistletoe leaf turnover and greater understorey biomass beneath heavily infected trees (March and Watson 2007), and little evidence of pre-senescence retrieval of nutrients from leaves of other species of *Amyema* (Pate et al. 1991a). The resulting pattern of nutrient patches will reflect distribution patterns of the mistletoes themselves (Press and Phoenix 2005). In certain cases, an increase in productivity of host plants may eventually translate to increased fuel accumulation and potential for fire. Crown fires are generally thought to be useful to 'sanitize' an area of shoot parasitic plants but ground fires may have mixed effects on hosts and parasites alike (Shaw et al. 2004).

Ecosystem analysis of the effects of parasitic angiosperms often involves some form of qualitative assessment of the level of infestation and reduction in host growth (Mathiasen et al. 2008). In the USA, the Hawkesworth 6-class system is commonly used for infestation of dwarf mistletoes (Hawkesworth 1977) and in Australia the Mistletoe Infestation Level (MIL) is used (Reid et al. 1994). Using physiologically relevant examples, Carnegie et al. (2009) used MIL classes in conjunction with a simulated growth analysis to show that mistletoe infection could reduce stand basal area of *Corymbia* (eucalypt) plantations by 10% and stand volume by 13%. In another, Mathiasen (2009) used the Hawkesworth system to compare susceptibility of a variety of conifers to infestation of knobcone pine dwarf mistletoe. While use of a common assessment system for mistletoe infestation is largely accepted in the USA (e.g., Shaw et al. 2000, Howell and Mathiasen 2004), its adoption elsewhere is much less sure.

### New (and old) areas of research

One of the promising areas of research involving parasitic angiosperms is the broad field of molecular biology and genetics. The majority of this research to date has understandably focussed on management of agricultural weed species on their herbaceous hosts; particularly mechanisms of host resistance and tolerance (see reviews by Shen et al. 2006, Irving and Cameron 2009). Genetic research has ranged from selective breeding of agricultural host species for resistance to parasitic infection (e.g., Haussmann et al. 2001) to transgenic expression of genes to show transfer of specific proteins in phloem

pathways (e.g., Birschwilks et al. 2007). As a result, it is now known that a number of defence and resistance mechanisms are heritable and work is underway to identify the genes responsible. The potential for use of tissue culture for physiological and biochemical study of parasitic plants has been suggested by Deeks et al. (1999). At least 23 species of parasites in the Santalales have reportedly been cultured *in vitro* and this list has representatives of both aerial and root hemiparasites.

As stated previously, there are many reviews available that summarize growth and functioning of parasitic angiosperms and their hosts. Without exception, each one concludes that we do not know enough about host-parasite systems regardless of whether they are in natural, agricultural or laboratory settings. For example, Pennings and Callaway (2002) recognized that many fundamental aspects of the ecology of parasitic plants are poorly studied. This is not only the case for their ecology but also for their anatomy, basic biology and physiology (Irving and Cameron 2009). The effects of the parasitic plant on their host are also poorly understood. Research to date has been dominated by laboratory or glasshouse investigations of crop weeds or field studies of silvicultural pests rather than studies in natural communities (Watling and Press 2001). From the discussions presented in recent reviews and studies, we suggest some of the more innovative topics for current and future research of host-parasitic plant interactions: (i) identification of pathways and cell types involved in solute transfer using markers and a parasitic angiosperm-*Arabidopsis* system (Hibberd and Jeschke 2001, Birschwilks et al. 2007); (ii) mutant or transgene expression in *Arabidopsis* may be used to determine host transporters and solutes important in the establishment and development of the host-parasite association (Hibberd and Jeschke 2001); (iii) regulation of the interaction between the parasitic angiosperm xylem-feeder and host plant, including a deeper understanding of the role of the transpiration stream and use of xylem- and phloem-feeding animals as model systems (Press and Whittaker 1993); (iv) along with natural abundance and enrichment of stable isotopes of carbon, nitrogen and oxygen (Cernusak et al. 2004, 2009), short-lived isotopic tracers and positron-emitting imaging systems may be used to study fluxes and pathways of mineral nutrients and organic solutes (see Irving and Cameron 2009). The first two research areas necessarily rely on herbaceous hosts and may be modified to include woody hosts in due course; the second two can be immediately tailored to suit woody hosts and their parasites.

### Conclusions

There are a large number of parasitic angiosperms and many parasitize woody plants. Xylem-feeders outnumber phloem-feeders several fold. Increasing economic importance of several parasitic angiosperms is quickly increasing our knowledge of

the host–parasite association. Studies of the water relations of host–parasite associations have advanced from comparisons of isolated parameters (e.g., xylem water potential) to analysis of net water fluxes, with an accompanying increase in functional understanding. Foremost amongst the advantages of the latter, more modern approach has been the ability to more properly consider the effects of parasites on their hosts. Mostly, those effects are negative and most hemiparasites seem likely to have relatively poor ability to regulate their water loss. Processes that govern nutrient and carbon transfers from hosts to parasite are closely linked to anatomy. While there are relatively few studies that fully detail the anatomical features of host and parasite, especially the features of the haustorium, those that provide a full analysis show close congruence between anatomy and physiology. There is increasing evidence of selective uptake of carbon and nutrients across haustoria and more studies of this type are needed, especially if models are to be used to quantify effects at whole-plant and ecosystem scales. Growth of hemiparasites is clearly linked to the growth and health of their hosts. Hosts are generally adversely affected by parasites, but the reverse is not necessarily the case. In conjunction with their direct effects on their hosts and their indirect effects on carbon and nutrient turnover, many parasites have significant roles in ecosystems, least of all through their roles in supporting birds and other pollination vectors. Monitoring of parasite populations and their effects is increasingly becoming a part of management frameworks and requirements.

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