9D. Parasitic Associations

1. Introduction

We have so far mainly dealt with **autotrophic** plants that assimilate CO_2 from the atmosphere into complex organic molecules and acquire nutrients and water from the rhizosphere. There are also fascinating higher plant species that lack the capacity to assimilate sufficient CO_2 to sustain their growth and that cannot absorb nutrients and water from the rhizosphere in sufficient quantities to reproduce successfully. These plants comprise approximately 1% of all flowering plant species; they are parasitic and rely on a host plant to provide them with the materials they cannot acquire from their abiotic environment (Kuijt 1969). About 4000 plant species within 270 genera in over 20 families [predominantly angiosperms; we only have firm evidence for one gymnosperm parasite: *Parasitaxus ustus* (conifer coral tree) (Field & Brodrib 2005)] rely on a parasitic association with a host plant for their mineral nutrition, water uptake, and/or carbon supply (Table 1). They inhabit ecosystems ranging from the high Arctic to the tropics (Press & Phoenix 2005). Some of these species [e.g., *Striga* spp. (witchweed), *Orobanche* spp. (broomrape), *Cuscuta* spp. (dodder), and *Arceuthobium douglasii* (Douglas-fir dwarf mistletoe)] are economically important pests that cause large yield losses of crop or forest plants, especially in Africa and Mediterranean countries (Estabrook & Yoder 1998). Other parasitic species (*Cystanche* spp.) are grown commercially to extract traditional medicines in China, or for their fragrant wood [*Santalum album* and *Santalum spicatum* (sandalwood)]. Ecologically, parasitic plants fill a fascinating niche in their exploitation of other plants to acquire sparingly available resources.

Parasitic angiosperms are generally divided into **holoparasites** and **hemiparasites** (Table 1). Holoparasites are **obligate** parasites. That is, they depend entirely on their host for the completion of their life cycle. They do not contain appreciable amounts of chlorophyll and lack the capacity to photosynthesize; their CO_2-compensation point may be as high as 2000 μmol mol^{-1} (Dawson et al. 1994), much higher than that of autotrophic plants (Sect. 2.2.1 of Chapter 2A on photosynthesis). Holoparasites also lack the capacity to assimilate inorganic N. Hemiparasites may be either **facultative** or **obligate** parasites. They contain chlorophyll and have some photosynthetic capacity, but they depend on their host for the supply of water and nutrients. The distinction between holoparasites and hemiparasites is not sharp. For example, *Striga* species are considered hemiparasites, but they have very little chlorophyll and show only a limited photosynthetic capacity (Table 2).

Parasitic angiosperms are further subdivided into **stem parasites**, such as the holoparasitic *Cuscuta* and *Cassytha* (dodder) and the hemiparasitic *Viscum* and *Ameyema* (mistletoes), and **root parasites**, such as the holoparasitic *Orobanche* (broomrape) and the hemiparasitic *Striga* (witchweed) (Stewart & Press 1990).

Table 1. Taxonomic survey of families of parasitic vascular plants.

Subclass-Family	Type of parasitism	Representative genus
Angiospermae:		
Magnoliidae		
– Lauraceae	Hemiparasitism	*Cassytha*
Rosidae		
– Balanophoraceae	Holoparasitism	*Balanophora*
– Eremolepidaceae	Hemiparasitism	*Cynomorium*
– Hydnoraceae	Holoparasitism	*Eremolepsis*
– Krameriaceae	Hemiparasitism	*Hydnora*
– Loranthaceae	Hemiparasitism	*Krameria*
		Loranthus
		Nuytsia
		Tapinanthus
– Misodendraceae	Hemiparasitism	*Misodendrum*
– Olacaceae	Hemiparasitism	*Olax*
– Opiliaceae	Hemiparasitism	*Cansjera*
– Rafflesiaceae	Holoparasitism	*Rafflesia*
– Santalaceae	Both	*Dendrotrophe*
		Exocarpus
		Santalum
– Viscaceae	Both	*Amyema*
		Phoradendron
		Viscum
Asteridae		
– Cuscutaceae	Holoparasitism	*Cuscuta*
– Lennoaceae	Holoparasitism	*Lennoa*
– Orobanchaceae	Holoparasitism	*Conopholis*
– Scrophulariaceae	Both	*Orobanche*
		Alectra
		Melampyrum
		Odontites
		Rhinanthus
		Striga
Gymnospermae:		
– Podocarpaceae	Hemiparasitism	*Podocarpus*
		Parasitaxis

***Source*: After Kuijt (1969), Atsatt (1983).**

Table 2. Some characteristics of *Striga hermonthica* (purple witchweed), which is an obligate root hemiparasite, in comparison with *Antirrhinum majus* (snapdragon), which is a related nonparasitic species.

Trait	*Striga hermonthica*	*Antirrhinum majus*
Stomatal frequency (mm^{-2})		
Adaxial leaf surface	114	36
Abaxial leaf surface	192	132
Stem	24	28
Transpiration ($mmol\ m^{-2}\ s^{-1}$)	8.5	5.7
Chlorophyll $a+b$ content ($g\ m^{-2}$)	2.6	7.2
Soluble protein content ($g\ m^{-2}$)	12	23
Photosynthesis		
Per m^2 leaf area ($\mu mol\ s^{-1}$)	2.5	15.0
Per g chlorophyll ($\mu mol\ s^{-1}$)	1.0	2.6
Water-use efficiency [(mmol $CO_2\ mol^{-1}$ (H_2O)]	0.3	2.9

***Source*: Shah et al. (1987).**

Parasites may be small herbaceous species [e.g., *Rhinantus sclerotinus* (yellow rattle) and *Melampyrum pratense* (cow-wheat)], shrubs [e.g., *Santalum acuminatum* (quandong), or large trees [e.g., *Nuytsia floribunda* (Western Australian Christmas tree) and *Exocarpus cupressiformis* (cherry ballart)]. Most parasitic plants have a broad host range. For example, *Castilleja* (paintbrush) species parasitize over a hundred different hosts from a variety of families (Press 1998), and *Rhinanthus minor* (yellow rattle) has approximately 50 different host species from 18 families within European grasslands; a single *Rhinanthus minor* plant may parasitize up to seven different host species simultaneously. Shoot parasites tend to have a smaller host range than do root parasites, but broad host ranges still occur, such as with *Cuscuta* and *Cassytha* species (dodders) with hosts that number in the hundreds. Also, the tropical rainforest mistletoe *Dendrophthoe falcate* has nearly 400 known host species. Parasitic plants that can only utilize one or few host species are the exception; one of the most notable is the root parasite *Epifagus virginiana* (beech-drops), which only parasitizes *Fagus grandifolia* (American beech). Among shoot parasites, mistletoes provide examples of narrow host range, including the dwarf mistletoe *Arceuthobium minutissimum* (Himalayan dwarf mistletoe), which only parasitizes the pine species *Pinus griffithii* (Himalayan blue pine) and epiparasitic mistletoes, e.g., *Phoradendron scabberimum*, which only grow on other mistletoes (Estabrook & Yoder 1998, Press & Phoenix 2005).

2. Growth and Development

2.1 Seed Germination

Many parasitic angiosperms have small seeds with a hard seed coat and remain viable for many years. The seeds have very small reserves so that the seedlings run the risk of dying if they do not quickly find a host to attach to. **Germination** of the seeds of the holoparasitic stem parasite *Cuscuta* (dodder) is completely independent of its host (Dawson et al. 1994), but many species [e.g., *Alectra* (witchweed), *Orobanche* (broomrape), and *Striga* (witchweed)] require a **chemical signal** from their host to trigger germination which increases their chances to survive (Bouwmeester et al. 2007). The first naturally occurring stimulant, **strigol**, was identified from *Gossypium hirsutum* (cotton, a nonhost); it stimulates germination of *Striga*. Strigol has also been found in root exudates from plants that do act as a host for *Striga* (Siame et al. 1993). It is a sesquiterpene, active in concentrations as low as 10^{-12} M in the soil solution. A second compound has been isolated from the root exudate of *Vigna unguiculata* (cowpea), which is a host for both *Striga* and *Alectra*. A range of other germination-stimulating compounds have since been isolated from roots of a range of species. These stimulants have somewhat differing structures; they are collectively known as **strigolactones** (Fig. 1). When seeds of *Striga asiatica* are placed in agar at a distance of about 5 mm from the root surface of *Sorghum bicolor* (millet), germination takes place. No germination occurs at a distance of 10 mm or more. Germination only occurs after a minimum of 5 hours exposure to 1 mM hydroquinone.

The stimulant from *Sorghum bicolor* (millet) enhances the synthesis of the phytohormone **ethylene**, which is an absolute requirement for the germination of the *Striga* (witchweed) seeds. Inhibition of the action or synthesis of ethylene prevents the effect of the germination stimulant, whereas its action can be substituted by ethylene (Logan & Stewart 1991, Babiker et al. 1993).

The release of strigol by roots of cotton, which is not a host, has encouraged the use of this species as a "trap crop" for *Orobanche* (broomrape) and *Striga* (witchweed). [A "**trap crop**" is a "**false host**" that is used to stimulate the germination of as many seeds as possible, so that the problems for the next crop, which can act as a host, are minimized.] If strigol is abundant in the soil during seed ripening, then it does not stimulate germination in the normal concentration range. A much higher concentration of strigol is then required to allow germination. This may be a mechanism avoiding germination at the end of the season, when the concentration of root exudates may be high.

Analogues of strigol and numerous other, unrelated compounds have been synthesized and tested for their capacity to stimulate germination. Such compounds are potentially useful to reduce the economic problems that parasites cause to crops.

What might be the evolutionary advantage, if any, of the release of compounds that promote the growth and development of parasitic plants, and thus endanger their own existence? Some of the chemicals that act as triggers for germination or haustorium formation are **allelochemicals** or related to **phytoalexins**. For example, the stimulant from *Sorghum bicolor* (millet) readily oxidizes to a more stable quinone (sorgoleone) that strongly inhibits the growth of neighboring weeds (Sect. 2 of Chapter 9B on ecological biochemistry; Einhellig & Souza 1992). More importantly, plant-derived **strigolactones**, which are well known as germination stimulants for root parasitic plants, are "branching factors", involved in a critical step in host recognition by **arbuscular mycorrhizal fungi** (Sect. 2 of Chapter 9A on symbiotic associations) (Akiyama et al. 2005, Bouwmeester et al. 2007). In *Trifolium pratense* (red clover), which is a host for arbuscular mycorrhizal fungi as well as for the root holoparasitic plant *Orobanche minor* (broomrape), a reduced P_i supply promotes the release of orobanchol (a strigolactone), by clover roots. The level of orobanchol exudation is controlled by P_i availability and correlates with germination stimulation activity of the root exudates. Therefore, under **P_i deficiency**, roots not only attract symbiotic fungi, but may also promote root parasitic plants through the release of strigolactones (Yoneyama et al. 2007a). It is therefore not surprising that root exudates from **arbuscular mycorrhizal** plants of *Sorghum bicolor* (millet) induce lower germination of *Striga hermonthica* (purple witchweed) seeds than do exudates from non-mycorrhizal sorghum plants (Lendzemo et al. 2007). Field inoculation with arbuscular mycorrhizal fungi reduces the impact of *Striga hermonthica* on cereal crops and has the potential to contribute to integrated *Striga* management (Lendzemo et al. 2005).

N deficiency in *Sorghum bicolor* (millet) also promotes the production and exudation of 5-deoxystrigol, the host recognition signal for arbuscular mycorrhizal fungi (Yoneyama et al. 2007b). This would explain why germination of *Striga hermonthica* (purple witchweed) decreases with increasing root N concentrations (Ayongwa et al. 2006). Root parasitic plants have long been associated with nutrient-poor soils. This may in part be explained by their low competitive ability, but the recent findings that increased N and P availability reduce the release of strigolactones now offers an additional explanation.

2.2 Haustoria Formation

All parasitic plant species, with the exception of members of the Rafflesiaceae, have a **haustorium**, which is a specialized multifunctional organ that functions in attachment, penetration, and transfer

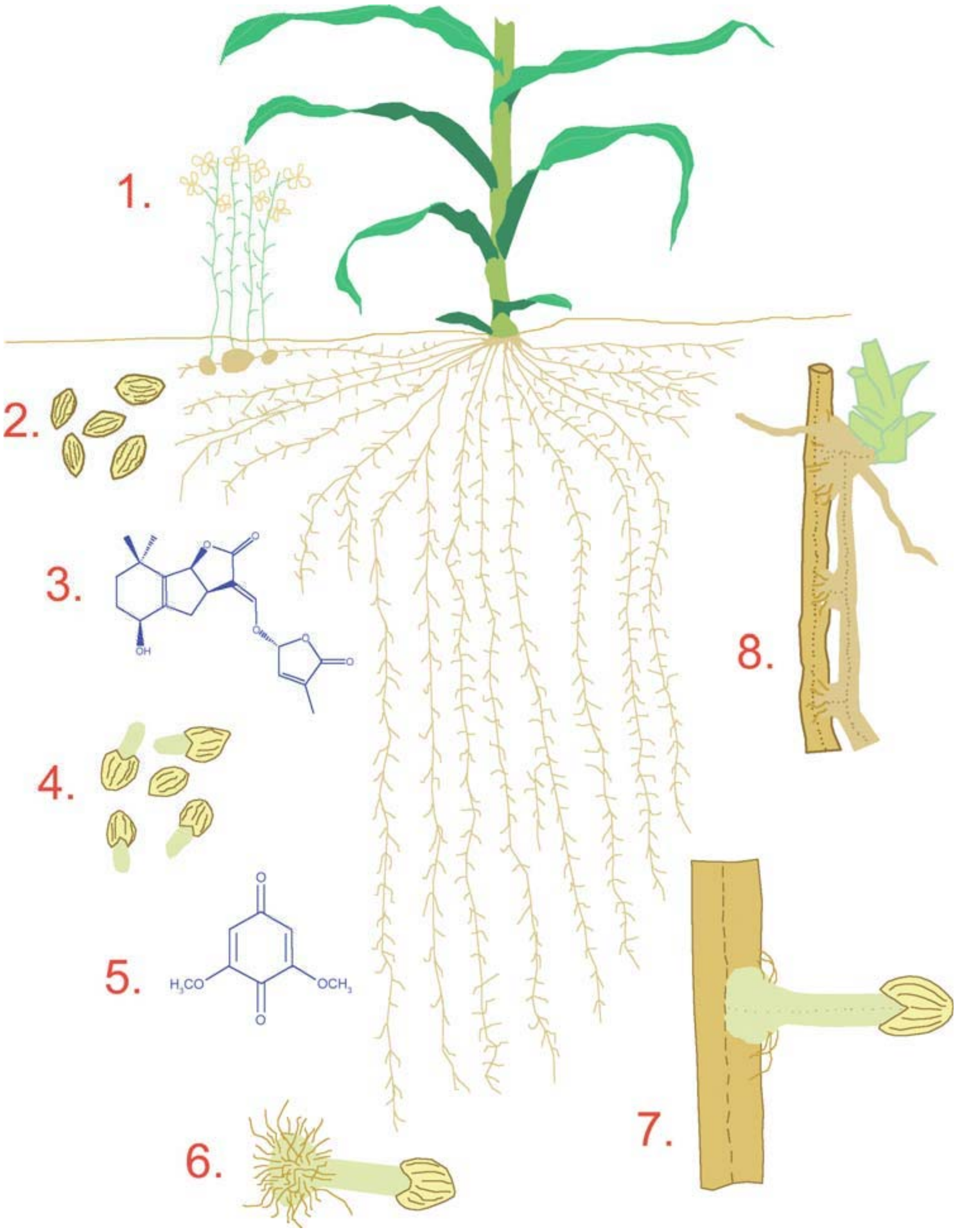

FIGURE 1. Life cycle of *Striga* (witchweed), an obligate root hemiparasite that can only complete its life cycle when attached to a host (1). Germination of the very small seeds (2) is stimulated by signal molecules (strigolactones) released from the roots of a host plant (3). Attachment via a haustorium (4) requires an additional signal molecule (5). Upon penetration of the root via its haustorium, inorganic nutrients are imported from the host's xylem (7). Once the parasite starts growing, more haustoria are produced (8).

of water and solutes. Most parasitic plants will only develop a functional haustorium in the presence of a **chemical signal** from the host, which differs from the signal that triggers germination. For example, haustorium formation in *Striga* (witchweed) species proceeds only when a signal molecule is released from host roots. An example of such a signal molecule is 2,6-dimethoxy-*p*-benzoquinone, which is produced by the host roots, in response to an enzyme from the parasite (Smith et al. 1990, Yoder

1999). Seeds of *Zea mays* (corn) are a rich source of a range of anthocyanins, other flavonoids, and simple phenolics that induce haustoria formation in *Triphysaria versicolor* (yellow owl's clover) (Albrecht et al. 1999). The chemical signals are often bound tightly to cell walls and are not released into the root environment. They are classified into four groups: flavonoids, *p*-hydroxy acids, quinones, and cytokinins; they are biologically active in the concentration range of 10^{-5}–10^{-7} M (Estabrook & Yoder 1998). The holoparasitic stem parasite *Cuscuta pentagona* (dodder) uses volatile cues from *Solanum lycopersicum* (tomato), *Impatiens walerana* (patient Lucy), and *Triticum aestivum* (wheat) to direct its growth toward nearby plants. Seedlings of the parasite can distinguish volatiles from different hosts and preferentially grow toward *Solanum lycopersicum* plants. Several individual compounds from *Solanum lycopersicum* and *Triticum aestivum* elicit directed growth by *Cuscuta pentagona*, whereas one compound from *Triticum aestivum* is repellent (Runyon et al. 2006).

Signals that are involved in preventing haustoria formation and subsequent attachment of the parasite to its host may explain **resistance** of some species to parasites (Rispail et al. 2007). Complete resistance to *Striga hermonthica* (purple witchweed) infection has not been identified in *Zea mays* (corn). A valuable source of resistance may be present in the genetic potential of wild germplasm, especially a wild relative of corn, *Tripsacum dactyloides* (gamma grass). *Striga hermonthica* development is arrested after attachment to *Tripsacum dactyloides*. Vascular continuity is established between parasite and host, but there is poor primary haustorial tissue differentiation on *Tripsacum dactyloides* compared with that on *Zea mays*. Partial resistance is inherited in a hybrid between the two species. *Tripsacum dactyloides* produces a signal that inhibits haustorial development: this signal may be mobile within the parasite haustorial root system (Gurney et al. 2003). Two distinct defense responses against *Rhinanthus minor* (yellow rattle) occur in the nonhost forbs *Leucanthemum vulgare* (field daisy) and *Plantago lanceolata* (snake plantain). *Leucanthemum vulgare* encapsulates the parasite's invading structures, thus preventing it from gaining access to the stele. In *Plantago lanceolata* host cell fragmentation occurs at the interface between the parasite and host. Grasses and a legume that are good hosts for *Rhinanthus minor* show no evidence of defense at the host/parasite interface (Cameron et al. 2006).

Elaborate work has been done on the ultrastructure of haustoria formation in a range of root parasites [e.g., in the Australian root hemiparasite *Olax phyllanthi* (Kuo et al. 1989)]. Walls of parasitic cells that contact host xylem are thickened with polysaccharides rather than with lignin. Host xylem pits are a major pathway for water and solute transport from the host to the haustorium, whereas direct connections between xylem-conducting elements of host and parasite are extremely rare. Symplasmic connections between the two partners are absent. Cells of the parasite that are adjacent to host cells often have an appearance similar to that of **transfer cells**.

The completely encircling haustorium of the root hemiparasite *Nuytsia floribunda* (Western Australian Christmas tree) is unique in cutting the host root transversely by means of a sclerenchymatic sickle-like sclerenchymatous cutting device (Fig. 2). Electron micrographs suggest that the developing haustorium acts as "scissors", which effectively cut off the distal part of the host from the rest of the plant. Parenchymatous tissue of the parasite then develops tube-like apical extensions into the cut host xylem vessels, thereby facilitating absorption of xylem solutes from host xylem sap. Conducting xylem tissue in the haustorium terminates some distance from the interface, so absorbed substances must traverse several layers of parenchyma before gaining access to the xylem stream of the parasite. When grown in pots with a range of hosts, as well as in the field, *Nuytsia floribunda* has a more negative water potential than its host, causing water movement to the parasite (Calladine & Pate 2000).

After germination in the soil, the seedlings of the obligate stem parasite *Cuscuta* (dodder) start to grow up and circumnutate. Under favorable conditions many stems may grow from a twined seedling after attachment to the host. Enzymes from the parasite soften the surface tissue of the host, and the haustorium penetrates the host tissue. Vascular cells of the parasite contact vascular cells of the host, and the contents of the host's sieve tubes and xylem conduits are diverted into the parasite. As the dodder continues to grow, it maintains its support by continually reattaching to host plants (Fig. 3; Dawson et al. 1994).

Transfer of solutes via the haustorium may be partly passive, via the apoplast. The presence of parenchyma cells with many mitochondria, dictyosomes, ribosomes, and a well-developed ER, however, suggests that active processes play a role as well. Indeed, compounds absorbed by the haustoria may be processed before entering the shoot. As a result, the carbohydrates, amino acids, and organic acids in the xylem sap of *Striga hermonthica* (purple witchweed) and *Olax phyllanthi* differ from those in their hosts. The major compound in *Striga hermonthica* is mannitol, which does not occur in the

Figure 2. Haustoria of root hemiparasites on host roots. (A) *Santalum acuminatum* (quandong) and (B) *Nuytsia floribunda* (Western Australian Christmas tree) (courtesy M.W. Shane, School of Plant Biology, the University of Western Australia, Perth, Australia).

Figure 3. Haustoria of the stem holoparasite *Cassytha* sp. parasitizing on a leaf of *Banksia elderiana* (photo H. Lambers).

host *Sorghum bicolor* (millet). Similarly, in xylem sap of *Sorghum bicolor* asparagine predominates as a nitrogenous compound, and malate and citrate as organic acids, whereas the major nitrogenous compound of *Striga hermonthica* is citrulline, and shikimic acid is the main organic acid. The carbohydrate concentrations in the parasite xylem sap may be five times higher than those in the host (Pate 2001).

2.3 Effects of the Parasite on Host Development

Although some hemiparasitic plants can grow in the absence of a host, their productivity is greatly enhanced when they are attached to a host (Fig. 4). At the same time, the growth of the host is reduced when a parasite is attached to it. The reduction in growth and grain yield of *Sorghum bicolor* (millet)

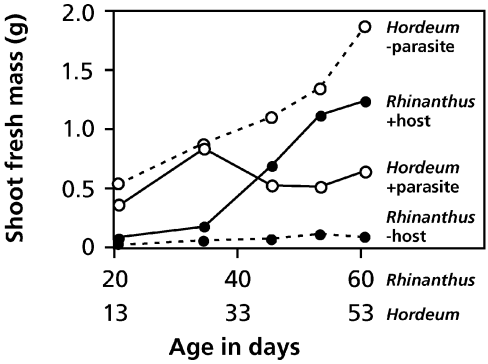

Figure 4. The increment of shoot fresh mass of *Hordeum vulgare* (barley), either grown alone or with a hemiparasite attached to its roots, and of *Rhinanthus serotinus* (late-flowering yellow rattle), a hemiparasite, either grown alone or attached to its host (Klaren 1975). Reproduced with the author's permission.

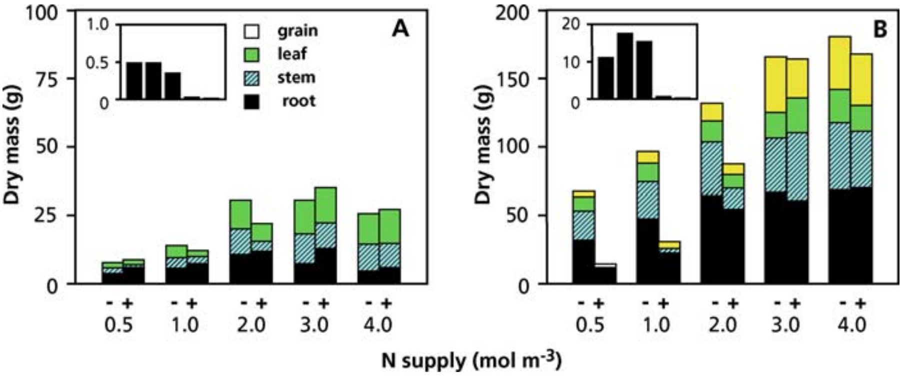

Figure 5. Partitioning of dry mass in *Sorghum bicolor* (millet) grown at a range of N-supply rates in the absence (–) and presence (+) of *Striga hermonthica* (purple witchweed). Dry masses of the parasite are shown in the insets; (A) and (B) refer to 50 and 140 days after planting. Different shades in the columns, from bottom to top, refer to roots, stems, leaves, and seeds (after Cechin & Press 1993).

infected by the parasitic *Striga hermonthica* (purple witchweed) is strongest at low N supply and may disappear completely at optimum N supply. The parasite is also affected by the low N supply, with considerably reduced seed germination, reduced attachment, and poor growth of *Striga hermonthica* plants (Fig. 5).

Even though the root growth of *Ricinus communis* (castor bean) is inhibited when parasitized by *Cuscuta reflexa* (dodder), which is an obligate stem holoparasite, the rate of **NO_3^- uptake** per unit root mass is stimulated by 40 and 80% at high and low NO_3^- supply, respectively (Jeschke & Hilpert 1997). The rate of NO_3^- uptake in the host plant obviously increases with increasing N demand of the parasite–host association (Sect. 2.2.3 of Chapter 6 on mineral nutrition). When parasitized by holoparasites, host plants may transiently show a higher rate of **photosynthesis**, greater stomatal conductance, and higher rates of transpiration, despite their smaller root system (Watling & Press 2001). Enhanced photosynthesis may be due to a higher N concentration in the leaves (Sect. 6.1 of Chapter 2A on photosynthesis), a higher sink demand (Sect. 4.2 of Chapter 2A on photosynthesis), or delayed leaf senescence (Jeschke & Hilpert 1997, Hibberd et al. 1998, 1999). Hemiparasites tend to have a negative effect on host photosynthesis (Watling & Press 2001).

Xylem-tapping stem hemiparasites (mistletoes), such as *Phoradendron juniperinum* (juniper mistletoe) and *Amyema preissii* (wire-leaf mistletoe), have no phloem connection with their host and they tend to kill the host shoot beyond the point of infection. In this way, the mistletoe is the only green tissue to be supplied via the xylem by a particular branch. Despite the absence of phloem connections, the growth of the mistletoe and that of xylem of the host are closely correlated. Just like the correlation between leaf area and sapwood area in trees (Sect. 5.3.5 of Chapter 3 on plant water relations), there is also a close correlation between the leaf area of the mistletoe and the sapwood area of the host branch proximal to the point of attachment (Fig. 6). This indicates that enlargement of the host stem must

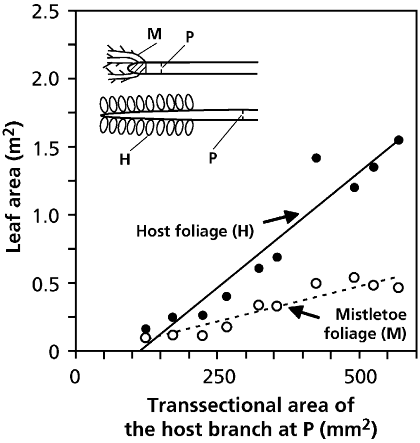

Figure 6. Correlations between the area of the foliage of a nonparasitized branch of *Acacia acuminata* (raspberry jam) or the foliage of the xylem-tapping stem hemiparasite *Amyema preissii* (mistletoe), parasitizing on *Acacia acuminate*, and the transectional area of the branch of the host. Note that a similar transectional branch area supports substantially more foliage of the host than of the parasite (after Tennakoon & Pate 1996a).

proceed, despite the impossibility of transport of any signals from the parasites' leaves via the phloem. For a similar area of foliage, the mistletoe appears to require a substantially greater sapwood area than does the host plant itself. This is probably related to a relatively high rate of transpiration of the hemiparasite (Sect. 4).

3. Water Relations and Mineral Nutrition

Most herbaceous root and stem hemiparasites have high **stomatal frequencies**, high rates of **transpiration,** and lower **water-use efficiency** than their host (Schulze & Ehleringer 1984, Davidson & Pate 1992). The stomata of the herbaceous hemiparasites do respond to water stress, but stomatal closure is induced at much lower relative water contents (Fig. 7). Thus, the gradient in **water potential** between leaves and roots is steeper for the parasite than it is for its host, facilitating the flux of solutes imported via the xylem (Klaren & Van de Dijk 1976, Davidson et al. 1989). This reflects a lower sensitivity of the stomata to ABA, the hormone associated with stomatal closure during water stress (Sect. 5.4.2 of Chapter 3 on plant water relations), in the parasitic species [*Striga hermonthica* (purple witchweed)] than in related nonparasites (*Antirrhinum majus*) (Shah et al. 1987). Leaves of *Zea mays* (corn) plants that are parasitized by *Striga hermonthica* have higher levels of ABA than leaves of control plants, and the concentration of this phytohormone is an order of magnitude higher again in the leaves of the parasite (Taylor et al. 1996). The stomates of *Striga hermonthica* do not close, however, even when the relative water content of its leaves declines to 70% or less.

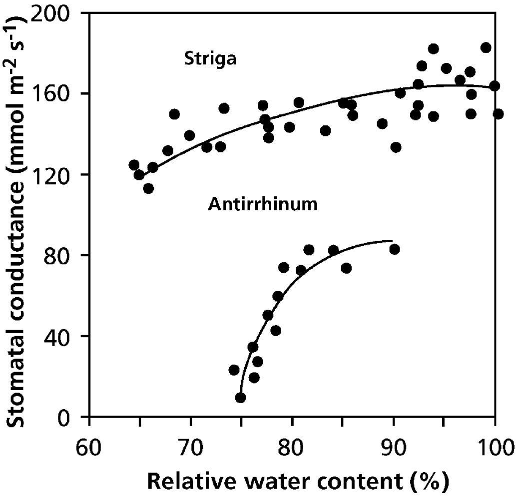

Figure 7. The relationship between stomatal conductance and the relative water content of the leaves for the hemiparasite *Striga hermonthica* (purple witchweed) and the closely related nonparasitic plant *Antirrhinum majus* (snapdragon) (Shah et al. 1987). Copyright Physiologia Plantarum.

Rapid rates of transpiration are one of the reasons for a more negative **water potential** of the shoots of the hemiparasites compared with that of their hosts. This low shoot water potential of hemiparasites requires accumulation of solutes to maintain turgor. In *Santalum acuminatum* (quandong) a significant proportion of the osmotic potential is accounted for by mannitol, Na^+, K^+, and Cl^-. A water potential difference of 1–2 MPa is maintained between this hemiparasitic shrub and its host. Xylem sap and leaves of *Santalum acuminatum* contain considerable concentration (0.1–0.4 mol kg^{-1} tissue water) of mannitol (Loveys et al. 2001b). A favorable water-potential gradient toward the *Striga hermonthica* (purple witchweed) is maintained even when rates of transpiration are severely reduced. This is due to the haustorial resistance to water flow, which is 1.5–4.5 times greater than that offered by the parasite shoot (Ackroyd & Graves 1997). Both the high rate of transpiration and the increased resistance across the haustoria facilitate the diversion of host resources to the parasite. These host resources may also include **secondary metabolites** (naturally occurring insecticides) that increase the parasite's resistance against insects, e.g., in *Santalum acuminatum* (quandong) attached to *Melia azedarach* (cape lilac) (Loveys et al. 2001a).

The high rates of transpiration of hemiparasitic plants have major consequences for the **leaf temperature** of the parasitic plants. The leaf temperature of *Striga hermonthica* (purple witchweed) may be as much as 7°C below air temperature (Sect. 2.1 of Chapter 4A on leaf energy budgets). The use of **antitranspirants**, which reduce transpirational water loss, may enhance the leaf temperature of parasites to an extent that the leaves blacken and die. These compounds have been suggested as tools to control parasitic pests (Press et al. 1989).

The high stomatal conductance and high rate of transpiration of parasites allows rapid import of solutes via the xylem. As expected, the C_i of hemiparasites is relatively high and the **carbon-isotope fractionation** is stronger in mistletoes than it is in their host, because of the high stomatal conductance of the parasite (Sect. 6 of Chapter 3 on plant water

Table 3. Carbon-isotope fractionation values for mistletoe–host pairs (number of pairs in brackets) from different continents; mean values and standard errors in brackets.

Region	Carbon-isotope composition (‰) Host	Carbon-isotope composition (‰) Mistletoe	Difference between host and mistletoe (‰)
		Nitrogen-fixing hosts	
United States (7)	–26.3 (0.5)	–26.5 (0.2)	0.2
Australia (28)	–26.9 (0.2)	–28.3 (0.3)	1.4
South Africa (4)	–24.7 (0.3)	–25.7 (1.0)	1.1
		Nonfixing hosts	
United States (8)	–23.4 (0.1)	–26.6 (0.1)	3.2
Australia (19)	–26.5 (0.3)	–28.8 (0.2)	2.3
South Africa (11)	–24.7 (0.4)	–26.9 (0.6)	2.2

***Source*: Ehleringer et al. (1985).**

relations). It is interesting that the difference in fractionation between host and parasite is less when the host is an N_2-fixing tree than when it is a nonfixing one. It has been suggested that more nitrogenous compounds are imported when the host is fixing N_2 which then reduces the transpiration and increases the parasite's water-use efficiency (Schulze & Ehleringer 1984). The smaller difference in the case of the N_2-fixing hosts, however, also reflects a high isotopic fractionation by the rapidly transpiring hosts (Table 3). The decline in carbon-isotope fractionation with increasing N concentration is, in fact, due to **enhanced carbon import** from the host; a substantial part of the carbon in mistletoes originates from the host via the xylem as organic acids and amino acids (Sect. 4).

Holoparasites, which predominantly import compounds from the sieve tubes of the host, have distinctly lower **Ca:K ratios** than do parasites that only tap the xylem (Ziegler 1975). This is due to the fact that Ca is only present in very low concentrations in phloem sap, whereas most other minerals occur in higher concentrations in phloem sap than in xylem fluid (Sect. 2 of Chapter 2C on long-distance transport). To acquire sufficient Ca for their growth, some additional xylem connections are required. Whereas *Cuscuta reflexa* (dodder) acquires 94% of its N and 74% of its K from the phloem of the host *Lupinus albus* (white lupin), virtually none of its Ca arrives via the phloem (Jeschke et al. 1995).

Because most xylem-tapping mistletoes, with the notable exception of *Olax phyllanthi* (Tennakoon & Pate 1996b), have no mechanism to selectively import specific ions that arrive via the xylem or to export ions that have arrived in excess of their requirement, mistletoes often accumulate vast amounts of inorganic ions. Increased succulence with increasing leaf age and sequestration of Na in older leaves appear to be mechanisms to maintain inorganic solute concentrations at a tolerable level (Popp et al. 1995). A consequence of the accumulation of vast amounts of inorganic ions is the need for compatible solutes in the cytoplasm (Sect. 4.1 of Chapter 3 on plant water relations). This may well account for the high concentrations of polyols in xylem-tapping mistletoes (Richter & Popp 1992, Popp et al. 1995). Some of the accumulated ions may be excreted via leaf glands [e.g., in *Odontites verna* (red bartsia) and *Rhinanthus serotinus* (late-flowering yellow rattle) (Govier et al. 1968, Klaren & Van de Dijk 1976)].

Rapid import of N may lead to higher concentrations of organic N in the leaves of the parasite than in those of the host. This often coincides with a similarity in leaf shape and appearance: **cryptic mimicry** (Bannister 1989). The N concentration of the parasite's leaves, however, is sometimes lower than that of the host, which may coincide with differences in leaf shape and appearance between host and parasite: **visual advertisement**. Because many herbivores prefer leaves with a high organic N concentration, it has been suggested that both "cryptic mimicry" and "visual advertisement" **reduce herbivory** (Ehleringer et al. 1986).

High leaf nutrient concentrations in combination with a low nutrient-resorption proficiency (Sect. 4.3 of Chapter 6 on mineral nutrition) in hemiparasitic plants give rise to litter with high nutrient concentrations (Quested et al. 2002, 2003). Since most hemiparasites also produce less **quantitative secondary metabolites** (Sect. 3.2 of Chapter 9B on ecological biochemistry) than their hosts, their leaf litter tends to decompose readily. As a consequence, hemiparasites can accelerate nutrient cycling in nutrient-poor communities, as found for *Bartsia alpina* (velvetbells) in a European subarctic community (Bardgett et al. 2006, Quested et al. 2005). In the nutrient-impoverished environment of Western Australia, introduced weeds often thrive under hemiparasitic trees and shrubs, when they show very poor growth away from these plants.

4. Carbon Relations

Hemiparasites are assumed to rely on their hosts only for water and mineral nutrients, but to fix their own CO_2. Their photosynthetic capacity, however, is often very low (0.5–5.0 μmol m^{-2} s^{-1}), and in many species there is substantial carbon import from the host. *Striga gesnerioides* (witchweed), which is an obligate root hemiparasite, has a very low photosynthetic capacity coupled with a very high rate of respiration. There is no net CO_2 fixation even at light saturation (Graves et al. 1992), so it imports carbohydrates from its host. In *Striga hermonthica* (purple witchweed) approximately 27% of the carbon is derived from its host [*Sorghum bicolor* (millet)] at a low N supply; this value declines to approximately 6% at a high N supply and higher rates of host photosynthesis (Cechin & Press 1993). Xylem-tapping mistletoes also import a large fraction of all their carbon from the host (Schulze et al. 1991) [e.g., 23–43% in *Viscum album* (European mistletoe) (Richter & Popp 1992)]. Two methods have been used to assess heterotrophic carbon gain in the African xylem-tapping mistletoe, *Tapinanthus oleifolius* (lighting match). One method is based on an analysis of xylem sap and transpiration rate (Sect. 3.4 of Chapter 8 on life cycles; Pate et al. 1991); the other is based on an analysis of carbon-isotope composition and gas exchange (Sect. 5.3 of Chapter 2A on photosynthesis, Box 2A.2; Marshall & Ehleringer 1990). Both methods agree and yield values in the range of 55–80%, with the higher values pertaining to older leaves that have high transpiration rates (Table 4).

The presence of a parasite like *Cuscuta europaea* (dodder) on the stem of a host plant greatly enhances the release of amino acids and other solutes from the **phloem** of the host (Fig. 8). In *Cuscuta* parasitizing on *Genista acantholada*, *Lupinus albus* (white lupin), or *Digitalis* sp. (foxglove) alkaloids and glycosides synthesized in the host are transported to the parasite (Rothe et al. 1999). These results suggest an open symplastic connection between the phloem of host and parasite. This is confirmed by translocation experiments using fluorescent dyes, which are translocated together with the assimilates in the phloem and unloaded symplastically into the sinks. In all investigated host–parasite systems with *Cuscuta* species 3 hours after application the dyes are detectable in the parasite. In both the host and the parasite the

TABLE 4. Heterotrophic carbon gain of the xylem-tapping mistletoe *Tapinanthus oleifolius* (lighting match) on *Euphorbia virosa* (milkbush) and *Acacia nebrownii* (water acacia).*

	Tapinanthus oleifolius* on *Euphorbia virosa		
	Young leaves	**Old leaves**	***Tapinanthus oleifolius* on *Acacia nebrownii***
Carbon-budget method			
Carbon concentration of xylem sap (mmol C l^{-1} xylem sap)	121	121	116
Transpiration [l H_2O m^{-2} (10 hour)$^{-1}$]	1.3	3.9	1.6
Carbon import via the xylem (C_x) [mmol C m^{-2} (10 hour)$^{-1}$]	157	470	188
CO_2 assimilation in photosynthesis [mmol CO_2 m^{-2} (10 hour)$^{-1}$]	126	108	144
Total carbon gain [mmol C m^{-2} (10 hour)$^{-1}$]	283	578	332
Heterotrophic carbon gain (%)	55	81	57
δ^{13}C-difference method			
δ^{13}C xylem sap (‰)	–16.92	–16.92	–21.05
δ^{13}C parasite leaves (‰, measured)	–23.73	–18.99	–26.81
δ^{13}C parasite leaves (‰, predicted from measured C_i/C_a)	–29.60	–33.20	–32.88
Heterotrophic carbon gain (%)	46	87	51

***Source*: Richter et al. (1995).**

[*] The host-derived part of the mistletoe's carbon was calculated from the carbon flux from the host xylem sap (i.e., carbon concentration in the xylem sap multiplied by the transpiration rate; "carbon-budget method") or from the difference between the predicted and the actual carbon isotope ratios of the parasite ("δ^{13}C-difference method").

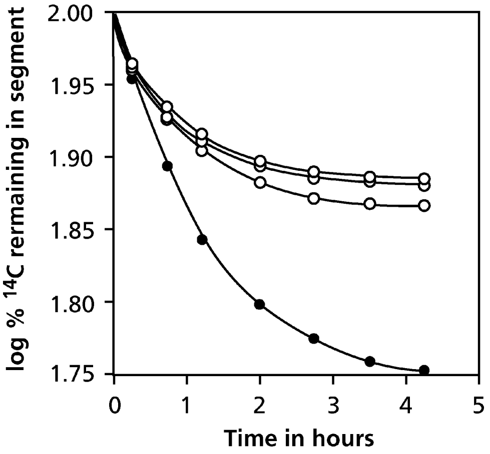

Figure 8. The effect of *Cuscuta europaea* (dodder), a stem parasite, on the release of ^{14}C-labeled valine from the sieve tubes in the stem of its host, *Vicia faba* (broad bean). The values represent the fraction of the labeled amino acid originally present in the stem segment that was not released from the sieve tubes to the apoplast. Open symbols refer to nonparasitized segments of the stem; filled symbols refer to the release in the apoplast of the segment where the parasite had formed a haustorium (after Wolswinkel et al. 1984). Copyright American Society of Plant Biologists.

fluorescence is restricted to the phloem (Birschwilks et al. 2006).

A parasite like *Striga gesnerioides* (witchweed) may use up to 70% of all the imported carbohydrates for its respiration; the use of carbon from the host may be even more important for the yield reduction of its host, *Vigna unguiculata* (cowpea), than the reduction in host photosynthesis (Graves et al. 1992). It is not clear why such a large fraction of imported carbon is used in respiration; in the holoparasite *Cuscuta reflexa* (dodder), when it grows on the stem of *Lupinus albus* (white lupin), only 29% of all the incorporated carbon is respired (Jeschke et al. 1994). This value is in the same range as that of heterotrophic plant parts of nonparasitic plants (Sect. 5 of Chapter 2B on plant respiration).

The reduction in photosynthesis of the host *Sorghum bicolor* (millet) by *Striga hermonthica* (purple witchweed) is strongest at a low N supply and high infection rate (approximately 40%). This may be associated with reduced N concentrations in the host leaves or reduced stomatal conductance which is due to the high demand for N and water of the parasite. At a very low infection rate and high N supply, there may be some enhancement of photosynthesis in the presence of the parasite, which is due to the stimulation of photosynthesis by enhanced sink strength (Cechin & Press 1993).

5. What Can We Extract from This Chapter?

The 4000 or so species of parasitic angiosperms of the world flora collectively represent an extraordinarily broad assemblage of taxa from distantly related families of dicotyledonous species and an equally profuse range of woody forms, morphologies, and life strategies. **Hemiparasites** tend to have high rates of transpiration and a low shoot water potential which ensures rapid intake **of xylem solutes**. Hemiparasites also import carbon (amino acids, organic acids) via the transpiration stream which supports their carbon requirement to a varying extent: from almost none to virtually completely.

Holoparasites tap the host's phloem and depend entirely on their host for their carbon requirements. Because the phloem contains very little Ca, holoparasites have distinctly lower Ca:K ratios than do hemiparasites.

Some parasitic plants are notorious **pests**, reducing crop yield in many areas of the world. A thorough understanding of host factors that affect seed germination of some parasitic plants may help to control these pests, either by employing trap crops or by using analogues that stimulate seed germination of the parasite. The possibility of using intercrops to reduce the impact of parasitic weeds on crops is further explored in Sect. 6.3 of Chapter 9E on interactions among plants.

References

Ackroyd, R.D. & Graves, J.D. 1997. The regulation of the water potential gradient in the host and parasite relationship between *Sorghum bicolor* and *Striga hermonthica*. *Ann. Bot.* **80:** 649–656.

Akiyama, K., Matsuzaki, K., & Hayashi, H. 2005. Plant sesquiterpenes induce hyphal branching in arbuscular mycorrhizal fungi. *Nature* **435:** 824–827.

Albrecht, H., Yoder, J.I., & Phillips, D.A. 1999. Flavonoids promore haustoria formation in the root parasite *Triphysaria versicolor. Plant Physiol.* **119:** 585–591.

Atsatt, P.R. 1983. Host-parasite interactions in higher plants. In: Encyclopedia of plant physiology, N.S. Vol. 12C, O.L. Lange, P.S. Nobel, C.B. Osmond, & H. Ziegler (eds). Springer-Verlag, Berlin, pp. 519–535.

Ayongwa, G.C., Stomph, T.J., Emechebe, A.M., & Kuyper, T.W. 2006. Root nitrogen concentration of sorghum above 2% produces least *Striga hermonthica* seed stimulation. *Ann. Appl. Biol.* **149:** 255–262.

Babiker, A.G.T., Ejeta, G., Butler, L.G., & Woodson, W.R. 1993. Ethylene biosynthesis and strigol-induced germination of *Striga asiatica*. *Physiol. Plant.* **88:** 359–365.

Bannister, P. 1989. Nitrogen concentration and mimicry in some New Zealand mistletoes. *Oecologia* **79:** 128–132.

Bardgett, R.D., Smith, R.S., Shiel, R.S., Peacock, S., Simkin, J.M., Quirk, H., & Hobbs, P.J. 2006. Parasitic plants indirectly regulate below-ground properties in grassland ecosystems. *Nature* **439:** 969–972.

Birschwilks, M., Haupt, S., Hofius, D., & Neumann, S. 2006. Transfer of phloem-mobile substances from the host plants to the holoparasite *Cuscuta* sp. *J. Exp. Bot.* **57:** 911–921.

Bouwmeester, H.J., Roux, C., Lopez-Raez, J.A., & Becard, G. 2007. Rhizosphere communication of plants, parasitic plants and AM fungi. *Trends Plant Sci.* **12:** 224–230.

Calladine, A. & Pate, J.S. 2000. Haustorial structure and functioning of the root hemiparasitic tree *Nuytsia floribunda* (Labill.) R.Br. and water relationships with its hosts. *Ann. Bot.* **85:** 723–731.

Cameron, D.D., Coats, A.M., & Seel, W.E. 2006. Differential resistance among host and non-host species underlies the variable success of the hemi-parasitic plant *Rhinanthus minor*. *Ann. Bot.* **98:** 1289–1299.

Cechin, I. & Press, M.C. 1993. Nitrogen relations of the sorghum-*Striga hermonthica* host-parasite association: growth and photosynthesis. *Plant Cell Environ.* **16:** 237–247.

Davidson, N.J. & Pate, J.S. 1992. Water relations of the mistletoe *Amyema fitzgeraldii* and its host *Acacia acuminata*. *J. Exp. Bot.* **43:** 1459–1555.

Davidson, N.J., True, K.C., & Pate, J.S. 1989. Water relations of the parasite: host relationship between the mistletoe *Amyema linophyllum* (Fenzl) Tieghem and *Casuarina obesa* Miq. *Oecologia* **80:** 321–330.

Dawson, J.H., Musselman, L.J., Wolswinkel, P., & Dörr, I. 1994. Biology and control of *Cuscuta*. In: Reviews of weed science, Vol. 6, S.O. Duke (ed). Imperial Printing Company, Champaign, pp. 265–317.

Ehleringer, J.R., Schulze, E.D., Ziegler, H., Lange, O.L., Farquhar, G.D., & Cowan, I.R. 1985. Xylem-tapping mistletoes: water or nutrient parasites? *Science* **227:** 1479–1481.

Ehleringer, J.R., Ullmann, I., Lange, O.L., Farquhar, G.D., Cowan, G.D., & Schulze, E.-D. 1986. Mistletoes: a hypothesis concerning morphological and chemical avoidance of herbivory. *Oecologia* **70:** 234–237.

Einhellig, F.A. & Souza, I.F. 1992. Phytotoxicity of sorgoleone found in grain sorghum root exudates. *J. Chem. Ecol.* **18:** 1–11.

Estabrook, E.M. & Yoder, J.I. 1998. Plant-plant communication: Rhizosphere signaling between parasitic angiosperms and their hosts. *Plant Physiol.* **116:** 1–7.

Field, T.S. & Brodrib, T.J. 2005. A unique mode of parasitism in the conifer coral tree *Parasitaxus ustus* (Podocarpaceae). *Plant Cell Environ.* **28:** 1316–1325.

Govier, R.N., Brown, J.G.S., & Pate, J.S. 1968. Hemiparasitic nutrition in angiosperms. II. Root haustoria and leaf glands of *Odontites verna* (Bell.) Dum. and their relevance to the abstraction of solutes from the host. *New Phytol.* **67:** 863–972.

Graves, J.D., Press, M.C., Smith, S., & Stewart, G.R. 1992. The carbon canopy economy of the association between cowpea and the parasitic angiosperm *Striga gesnerioides*. *Plant Cell Environ.* **15:** 283–288.

Gurney, A.L., Grimanelli, D., Kananpiu, F., Hoisington, D., Scholes, J.D., & Press, M.C.. 2003. Novel sources of resistance to *Striga hermonthica* in *Tripsacum dactyloides*, a wild relative of maize. *New Phytol.* **160:** 557–568.

Hibberd, J.M., Quick, W.P., Press, M.C., & Scholes, J.D. 1998. Can source-sink relations explain responses of tobacco to infection by the root holoparasitic angiosperm *Orobanche cernua*? *Plant Cell Environ.* **21:** 333–340.

Hibberd, J.M., Quick, W.P., Press, M.C., Scholes, J.D., & Jeschke, W.D. 1999. Solute flux from tobacco to the parasitic angiosperm *Orobanche cernua* and the influence of infection on host carbon and nitrogen relations. *Plant Cell Environ.* **22:** 937–947.

Jeschke, W.D. & Hilpert, A. 1997. Sink-stimulated photosynthesis and sink-dependent increase in nitrate uptake: nitrogen and carbon relations of the parasitic association *Cuscuta reflexa-Ricinus communis*. *Plant Cell Environ.* **20:** 47–56.

Jeschke, W.D., Bäumel, P., Räth, N., Czygan, F.-C., & Proksch, P. 1994. Modelling of the flows and partitioning of carbon and nitrogen in the holoparasite *Cuscuta reflexa* Roxb. and its host *Lupinus albus*. L. II. Flows between host and parasite and within parasitized host. *J. Exp. Bot.* **45:** 801–812.

Jeschke, W.D., Bäumel, P., & Räth, N. 1995. Partitioning of nutrients in the system *Cuscuta reflexa-Lupinus albus*. *Asp. Appl. Biol.* **42:** 71–79.

Klaren, C.H. 1975. Physiological aspects of the hemiparasite *Rhinanthus serotinus*. PhD Thesis, University of Groningen, the Netherlands.

Klaren, C.H. & Van de Dijk, S.J. 1976. Water relations of the hemiparasite *Rhinanthus serotinus* before and after attachment. *Physiol. Plant.* **38:** 121–125.

Kuijt, J. 1969. The biology of parasitic flowering plants. University of California Press, Berkeley.

Kuo, J., Pate, J.S., & Davidson, N.J. 1989. Ultrastructure of the haustorial interface and apoplastic continuum between host and the root hemiparasite *Olax phyllanthi* (Labill.) R. Br. (Olacaceae). *Protoplasma* **150:** 27–39.

Lendzemo, V.W., Kuyper, T.W., Kropff, M.J., Van Ast, A. 2005. Field inoculation with arbuscular mycorrhizal fungi reduces *Striga hermonthica* performance on cereal crops and has the potential to contribute to integrated *Striga* management. *Field Crops Res.* **91:** 51–61.

Lendzemo, V.W., Kuyper, T.W., Matusova, R., Bouwmeester, H.J., & Van Ast, A. 2007. Colonization by arbuscular mycorrhizal fungi of sorghum leads to reduced germination and subsequent attachment and emergence of *Striga hermonthica*. *Plant Signal. Behav.* **2:** 58–62.

Logan, D.C. & Stewart, G.R. 1991. Role of ethylene in the germination of the hemiparasite *Striga hermonthica*. *Plant Physiol.* **97:** 1435–1438.

Loveys, B.R., Tyerman, S.D., & Loveys, B.R. 2001a. Transfer of photosynthate and naturally occurring insecticidal compounds from host plants to the root hemiparasite *Santalum acuminatum* (Santalaceae). *Aust. J. Bot.* **49:** 9–16.

Loveys, B.R., Loveys, B.R., & Tyerman, S.D. 2001b. Water relations and gas exchange of the root hemiparasite *Santalum acuminatum* (quandong). *Aust. J. Bot.* **49:** 479–486.

Marshall, J.D. & Ehleringer, J.R. 1990. Are xylem-tapping mistletoes partially heterotrophic? *Oecologia* **84:** 244–248.

Pate, J.S. 2001. Haustoria in action: case studies of nitrogen acquisition by woody xylem-tapping hemiparasites from their hosts. *Protoplasma* **215:** 204–217.

Pate, J.S., True, K.C., & Rasins, E. 1991. Xylem transport and storage of amino acids by S.W. Australian mistletoe and their hosts. *J. Exp. Bot.* **42:** 441–451.

Popp, M., Mensen, R., Richter, A., Buschmann, H., & Von Willert, D.J. 1995. Solutes and succulence in southern African mistletoes. *Trees* **9:** 303–310.

Press, M.C. & Phoenix, G.K. 2005. Impacts of parasitic plants on natural communities. *New Phytol.* **166:** 737–751.

Press, M.C., Nour, J.J, Bebawi, F.F., Stewart, G.R. 1989. Antitranspirant-induced heat stress in the parasitic plant *Striga hermonthica*—a novel method of control. *J. Exp. Bot.* **40:** 585–591.

Quested, H.M., Press, M.C., Callaghan, T.V., & Cornelissen, H.J. 2002. The hemiparasitic angiosperm *Bartsia alpina* has the potential to accelerate decomposition in sub-arctic communities. *Oecologia* **130:** 88–95.

Quested, H.M., Press, M.C., & Callaghan, T.V. 2003. Litter of the hemiparasite *Bartsia alpina* enhances plant growth: evidence for a functional role in nutrient cycling. *Oecologia* **135:** 606–614.

Quested, H.M., Callaghan, T.V., Cornelissen, J.H.C., & Press, M.C. 2005. The impact of hemiparasitic plant litter on decomposition: direct, seasonal and litter mixing effects. *J. Ecol.* **93:** 87–98.

Richter, A. & Popp, M. 1992. The physiological importance of accumulation of cyclitols in *Viscum album* L. *New Phytol.* **121:** 431–438.

Richter, A., Popp, M., Mensen, R., Stewart, G.R., & Von Willert, D.J. 1995. Heterotrophic carbon gain of the parasitic angiosperm *Tapinanthus oleifolius*. *Aust. J. Plant Physiol.* **22:** 537–544.

Rispail, N., Dita, M.-A., Gonzalez-Verdejo, C., Perez-de-Luque, A., Castillejo, M.-A., Prats, E., Roman, B., Jorrin, J., & Rubiales, D. 2007. Plant resistance to parasitic plants: molecular approaches to an old foe. *New Phytol.* **173:** 703–712.

Rothe, K., Diettrich, B., Rahfeld, B., & Luckner, M. 1999. Uptake of phloem-specific cardenolides by *Cuscuta* sp. growing on *Digitalis lanata* and *Digitalis purpurea*. *Phytochemistry* **51:** 357–361.

Runyon, J.B., Mescher, M.C., De Moraes, C..M. 2006. Volatile chemical cues guide host location and host selection by parasitic plants. *Science* **313:** 1964–1967.

Schulze, E.-D. & Ehleringer, J.R. 1984. The effect of nitrogen supply on growth and water-use efficiency of xylem-tapping mistletoes. *Planta* **162:** 268–275.

Schulze, E.-D., Lange, O.L., Ziegler, H. Gebauer, G. 1991. Carbon and nitrogen isotope ratios of mistletoes growing on nitrogen and non-nitrogen fixing hosts and on CAM plants in the Namib desert confirm partial heterotrophy. *Oecologia* **88:** 457–462.

Shah, N., Smirnoff, N., & Stewart, G.R. 1987. Photosynthesis and stomatal characteristics of *Striga hermonthica* in relation to its parasitic habit. *Physiol. Plant.* **69:** 699–703.

Siame, B.P., Weerasuriya, Y., Wood, K., Ejeta, G., & Butler, L.G. 1993. Isolation of strigol, a germination stimulant for *Striga asiatica*, from host plants. *J. Agric. Food Chem.* **41:** 1486–1491.

Smith, C.E., Dudley, M.W., & Lynn, D.G. 1990. Vegetative/parasitic transition: Control and plasticity in *Striga* development. *Plant Physiol.* **93:** 208–215.

Stewart, G.R. & Press, M.C. 1990. The physiology and biochemistry of parasitic angiosperms. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* **41:** 127–151.

Taylor, A., Martin, J., & Seel, W.E. 1996. Physiology of the parasitic association between maize and witchweed (*Striga hermonthica*): is ABA involved? *J. Exp. Bot.* **47:** 1057–1065.

Tennakoon, K.U. & Pate, J.S. 1996a. Effects of parasitism by a mistletoe on the structure and functioning of branches of its host. *Plant Cell Environ.* **19:** 517–528.

Tennakoon, K.U. & Pate, J.S. 1996b. Heterotrophic gain of carbon from hosts by the xylem-tapping root hemiparasite *Olax phyllanthi* (Olacaceae). *Oecologia* **105:** 369–376.

Watling, J.R. & Press, M.C. 2001. Impacts of infection by parasitic angiosperms on host photosynthesis. *Plant Biol.* **3:** 244–250.

Wolswinkel, P., Ammerlaan, A., & Peters, H.F.C. 1984. Phloem unloading of amino acids at the site of *Cuscuta europaea*. *Plant Physiol.* **75:** 13–20.

Yoder, J.I. 1999. Parasitic plant responses to host plant signals: a model for subterranean plant–plant interactions. *Curr. Opin. Plant Biol.* **2:** 65–70.

Yoneyama K., Yoneyama K., Takeuchi Y., & Sekimoto, H. 2007a. Phosphorus deficiency in red clover promotes exudation of orobanchol, the signal for mycorrhizal symbionts and germination stimulant for root parasites. *Planta* **225:** 1031–1038.

Yoneyama, K., Xie, X., Kusumoto, D., Sekimoto, H., Sugimoto, Y., Takeuchi, Y., Yoneyama, K. 2007b. Nitrogen deficiency as well as phosphorus deficiency in sorghum promotes the production and exudation of 5-deoxystrigol, the host recognition signal for arbuscular mycorrhizal fungi and root parasites. *Planta* **227:** 125–132.

Ziegler, H. 1975. Nature of transported substances. In: Encyclopedia of plant physiology, N.S. Vol. 1, M.H. Zimmermann & J.A. Milburn (eds). Springer-Verlag, Berlin, pp. 59–100.