Parasitic Plants in Agriculture: Chemical Ecology of Germination and Host-Plant Location as Targets for Sustainable Control: A Review

Justin B. Runyon, John F. Tooker, Mark C. Mescher and Consuelo M. De Moraes

Abstract Parasitic plants are among the most problematic pests of agricultural crops worldwide. Effective means of control are generally lacking, in part because of the close physiological connection between the established parasite and host plant hindering efficient control using traditional methods. Seed germination and host location are critical early-growth stages that occur prior to host attachment, and provide promising targets for ecologically sound management of parasitic weeds. Knowledge of parasite-host interactions, particularly chemical cues that induce parasite seed germination and mediate host location, should facilitate the development of novel management approaches. In parasitic plants that attach to host roots—e.g., *Striga* and *Orobanche* spp.—seed germination is known to occur only in the presence of chemical stimulants released from plant roots. The recent finding that these same chemicals promote the colonization of beneficial fungi has potentially important implications for the control of parasitic plants. Far less is known about the early stages of parasitic plants that attach above-ground to host shoots—e.g., *Cuscuta* spp. Seeds of these parasites lack germination stimulants, and it was only recently shown that foraging *C. pentagona* seedlings use airborne cues to locate and select among hosts. We review research on seed germination and host location by the major parasitic weeds that attack agricultural crops, and discuss the implications of recent findings for the development of sustainable and effective management strategies.

Keywords *Striga* · *Orobanche* · *Cuscuta* · Strigolactones · Volatiles · Plant-plant communication

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C.M. De Moraes (✉)
Department of Entomology, Pennsylvania State University, 535 ASI building,
University Park, PA, 16802, USA
e-mail: czd10@psu.edu

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1 Introduction

Approximately 4,500 species of flowering plants (more than 1% of all angiosperms) are parasitic, obtaining some or all of their water and nutrients from other plants (Kuijt, 1969; Nickrent, 2007). A small percentage of these parasitic species infest agricultural crops and cause serious problems for farmers in many parts of the world (Parker and Riches, 1993; Musselman et al., 2001). Few practical and economically sound methods are available for controlling parasitic plant species (Gressel et al., 2004; Rispail et al., 2007), in part because their physiological connection to host plants limits the usefulness of most herbicides. Parasitic weeds can also be difficult to eradicate because they often produce large numbers of long-lived seeds. For example, a single *Orobanche* sp. plant can produce over 200,000 dust-like seeds that remain viable for 8–10 years (Parker and Riches, 1993). In addition, parasitic plants that attack host roots can inflict serious damage to crop plants before the latter emerge from the soil, making it difficult to diagnose infestations before economic losses occur.

Breeding for host-plant resistance offers a potentially economical approach to controlling parasitic plants. However, with a few exceptions—e.g. resistance of cowpea to *Striga* (Lane et al., 1993)—breeding programs have not provided effective control and are challenging because plant resistance traits are often poorly characterized, genetically complex, and of low heritability (Rispail et al., 2007). Genetic engineering might help to overcome some of these difficulties (Bouwmeester et al., 2003), but societal concerns about genetically modified technology may prevent widespread adoption (Humphrey et al., 2006).

The search for improved or alternative approaches to controlling parasitic plants in agriculture will be facilitated by an increased understanding of the complex ecological and physiological interactions between parasitic plants and their hosts.

Host location is a critical part of the life cycle of the most damaging parasitic weeds, which are obligate parasites that depend on the limited reserves available in seeds to quickly locate suitable hosts. Host location thus seems a promising target for control strategies. In this paper, we review the most important plant parasites of agricultural crops, focusing on the chemical ecology of seed germination and host location, and discuss the potential for manipulating these mechanisms to control these important weeds.

2 The Major Parasitic Plants in Agriculture

Parasitism originated independently several times during angiosperm evolution, and the lifestyles of parasitic plants vary greatly across taxa (Kuijt, 1969; Nickrent et al., 1998). Some species are facultative parasites that are able to survive in the absence of hosts, while others are obligately parasitic and cannot develop independently. A distinction can be drawn between hemiparasitic plants that possess chlorophyll and are able to produce some of their required nutrients through photosynthesis and holoparasitic plants that lack chlorophyll and are completely dependent on host resources, but this distinction is not always clear-cut (Parker and Riches, 1993; Press and Graves, 1995). A more definitive division can be drawn between parasitic plants that make below-ground attachments to host-plant roots and those that attach above ground to host-plant shoots (Fig. 1). This review will focus on the most economically important groups of plant parasites: witchweeds, *Striga* spp. (Scrophulariaceae); and broomrapes, *Orobanche* spp. (Orobanchaceae), which attach to host roots; and dodders, *Cuscuta* spp. (Convolvulaceae), which make above-ground attachments to host shoots (Parker, 1991).

Striga spp. (Fig. 2) are obligate root hemiparasites and infest an estimated two-thirds of the cereals and legumes in sub-Saharan Africa, causing annual crop losses estimated at US$7 billion annually, and negatively influencing the lives of more than 300 million people (Berner et al., 1995; Musselman et al., 2001). Several species of *Striga* attack the major cereal crops in Africa (e.g., maize, sorghum, millet, and rice), but *S. hermonthica* and *S. asiatica* are the most widely distributed and destructive (Oswald, 2005). *Striga gesnerioides* parasitizes broadleaf plants and is a serious threat to cowpea production in many parts of Africa (Parker and Riches, 1993). In the 1950s, *S. asiatica* was discovered parasitizing maize in the southeastern United States, but its spread there has been halted by an intensive eradication program (Parker, 1991).

Orobanche spp. (Figs. 1 and 3) are obligate root holoparasites that constrain the production of many crops, primarily in the Mediterranean region, the Middle East, and northern Africa (Parker and Riches, 1993). Among the six *Orobanche* species considered serious pests, *O. ramosa* and *O. aegyptiaca* have the widest host ranges and heavily damage a variety of crops, including tomato, potato, eggplant, faba bean, lentil, peanut, chickpea, cucumber, cabbage, and sunflower (Parker and Riches, 1993). *Orobanche cumana* has a host range limited to Asteraceae, and it

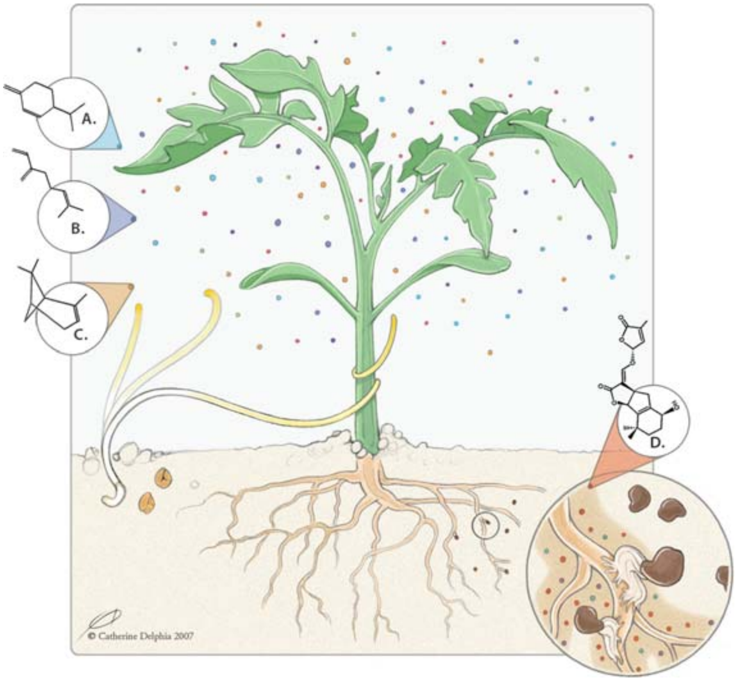

Fig. 1 Plant-derived chemical cues are used by both shoot and root parasitic weeds to locate hosts. Upon germination, the growth of *Cuscuta* seedlings is directed toward volatile compounds released from nearby tomato plants (*above-ground at left*). The entire blend of tomato volatiles (at least seven compounds) is most attractive, but three compounds from this blend individually elicit directed growth of *Cuscuta*: (**A**) β-phellandrene, (**B**) β-myrcene, and (**C**) α-pinene (Runyon et al., 2006). Seeds of the root parasites *Striga* and *Orobanche* will only germinate in response to specific chemicals released by plant roots (*below-ground at right*). These germination stimulants, called strigolactones, are active only within several millimeters of the host root. *Orobanche* seedlings are shown with haustoria attaching to the tomato (inset, lower right). Strigol (**D**) was the first germination stimulant identified. Strigol has not been isolated from tomato roots, but similar strigolactones are produced. The chemical ecology of host location by parasitic weeds provides early developmental points that could be exploited and manipulated for sustainable control

is an important pest of cultivated sunflowers (Parker and Riches, 1993; Press and Graves, 1995). Infestation by *Orobanche* spp. can result in total crop loss (Bernhard et al., 1998).

Cuscuta spp. have yellow-to-orange, rootless, leafless vines that attach to the shoots of host plants (Fig. 4). They are obligate holoparasites, typically exhibiting broad host ranges, and inflict serious damage to many crops, including forage legumes (alfalfa, clover, lespedeza), potato, carrot, sugar beets, chickpea, onion, cranberry, blueberry, and citrus (Dawson et al. 1994). Seeds of *Cuscuta* spp. have been transported worldwide in contaminated shipments of crop plant seeds. *Cuscuta pentagona* is a major weed of tomatoes in California, causing yield losses of

Fig. 2 A sorghum field infested with *Striga hermonthica* (*pink flowers*) in Ethiopia. *Striga* spp. attach to host-plant roots and produce green, flowering shoots that emerge 1–2 months later. Credit: Lytton J. Musselman

Fig. 3 *Orobanche ramosa* parasitizing cabbage in Sudan. *Orobanche* spp. attach to host-plant roots, and their flowering shoots, which lack chlorophyll, emerge several months later. Credit: Lytton J. Musselman

50–75% (Goldwasser et al., 2001). In China, several *Cuscuta* species inflict severe damage on soybeans (Dawson et al., 1994).

3 Parasitic Plants Use Chemical Cues to Locate Hosts

The seeds of most parasitic plants contain a few energy reserves that allow limited growth. Consequently, seedlings can survive only a few days after germination before attaching to a host. The imperative of finding hosts quickly presumably imposes strong evolutionary selection pressure favoring the development of efficient

Fig. 4 *Cuscuta pentagona* parasitizing tomato plants in California. *Cuscuta* spp. lack chlorophyll and attach above-ground to host-plant shoots. Credit: Jack Kelly Clark, courtesy UC Statewide IPM Program

host-location mechanisms. Both root and shoot parasitic plants utilize chemical cues released by host plants for this purpose (Fig. 1).

3.1 Root Parasitic Plants: Germination Stimulants

Seeds of *Striga* and *Orobanche* spp. germinate only in the presence of chemical compounds exuded from host roots (Fig. 1; Bouwmeester et al., 2007). Because these germination stimulants, collectively called strigolactones, are unstable and degrade rapidly in the soil, they occur at concentrations sufficient to induce germination only within a few millimeters of host roots (Fate et al., 1990). Concentration gradients of strigolactones may also facilitate directed growth of the parasite radicle toward the host root (Dubé and Olivier, 2001). The sensitivity of parasite seeds to these germination stimulants depends upon a conditioning period under warm and humid conditions and concomitant synthesis of gibberellins in seed tissues (Matusova et al., 2004). To date, several germination stimulants have been isolated and identified from root exudates of both host and non-host plants. In work with *Striga lutea*, the first germination stimulant (strigol) was isolated from the root exudates of the non-host cotton (Cook et al., 1966). Strigol has since been found to be released by the roots of true hosts, including maize and millet (Siame et al., 1993). Additional strigolactone germination stimulants that have been identified include sorgolactone from sorghum, orobanchol and alectrol from red clover, and 5-deoxy-strigol from *Lotus japonicus* (Hauck et al., 1992; Yokota et al., 1998; Akiyama et al., 2005). Recently, strigolactones have been shown to be apocarotenoids produced by plants via the carotenoid pathway, rather than sesquiterpenoids as had previously been assumed (Matusova et al., 2005). The details of germination induction by strigolactones are not understood (Bouwmeester et al., 2007), though possible mechanisms have been proposed (Mangnus and Zwanenburg, 1992). Application of ethylene can trigger seeds of *Striga* and *Orobanche* spp. to germinate, indicating that strigolactones may act by stimulating ethylene biosynthesis (Logan and Stewart, 1991). The recent discovery that strigolactones serve as important cues for plant-beneficial arbuscular mycorrhizal fungi (AMF; Akiyama et al., 2005; Besserer et al., 2006) suggests that parasitic plants may have co-opted these signals to recognize and locate host roots.

3.2 Shoot Parasitic Plants: Plant Volatiles

In contrast to root parasitic plants, germination of *Cuscuta* spp. seeds is not dependent on stimulants derived from a host plant (Dawson et al., 1994). Instead, seedlings must forage to locate potential hosts nearby. We recently reported that seedlings of *C. pentagona* use host-plant volatiles to guide host location and selection (Fig. 1; Runyon et al., 2006). It had previously been suggested that *Cuscuta* spp. seedlings forage randomly (Dawson et al., 1994), or orient their growth to various light cues associated with the presence of host plants (Benvenuti et al., 2005). While light cues may play a role in host location, we found that *C. pentagona* seedlings exhibited directed growth toward tomato volatiles experimentally released in the absence of any other plant-derived cues. Moreover, seedlings used volatile cues to “choose” tomatoes, a preferred host, over nonhost wheat. Several individual compounds from the tomato volatile blend were attractive to *C. pentagona* seedlings, including α-pinene, β-myrcene, and β-phellandrene, while one compound from the wheat blend, (*Z*)-3-hexenyl acetate, had a repellent effect. We subsequently confirmed that C. pentagona seedlings respond to volatiles from a range of host plants, including *Impatiens*, wheat (Runyon et al., 2006), and alfalfa (Mescher et al., 2006). These findings provide a plausible mechanism to explain previous reports of selective foraging by *Cuscuta* spp. (Kelly, 1990, 1992; Sanders et al., 1993; Koch et al., 2004). It is tempting to speculate that the remarkably similar but unrelated shoot-parasitic plants in the genus *Cassytha* (Lauraceae), and perhaps climbing vines in general, might also use volatile cues to locate their hosts, but this possibility has yet to be examined empirically.

4 Control Strategies Targeting Germination/Host Location

Considerable research has examined the possibility of exploiting germination stimulants for control of *Striga* and *Orobanche*. Control strategies include: (1) inducing "suicidal germination," (2) inhibiting germination, and (3) reducing the production of germination stimulants by crop plants. In addition, the newly discovered role of strigolactones in the recruitment of symbiotic AMF (Akiyama et al., 2005) has opened new possibilities for modifying the production of germination stimulants by host plants. We are not aware of any studies exploring the possibility of disrupting host location by using *Cuscuta* spp., which have no germination stimulants. However, the recently documented role of volatiles in host location by *C. pentagona*, and the identification of several attractive and repellant compounds (Runyon et al., 2006), suggests that such strategies might be plausible.

4.1 Suicidal Germination

Inducing the germination of *Striga* and *Orobanche* spp. seeds in the absence of a suitable host plant results in "suicidal germination," and subsequent reduction in numbers of parasitic-plant seeds in soil. Both man-made and natural compounds have been investigated for their ability to induce germination. Analogs of strigol have been synthesized (e.g., GR 24 and Nijmegen 1) and are potent elicitors of germination in both *Striga* and *Orobanche* spp. (Wigchert et al., 1999); however, their instability in soil (Barbiker et al., 1987), and the high cost of producing large quantities of these compounds, have so far prohibited their use in agriculture (Humphrey et al., 2006). Ethylene has been a valuable component of the eradication program targeting *Striga asiatica* in the United States, where it induces about 90% germination when injected into the soil (Parker 1991). However, fumigating soil with ethylene is likely to negatively influence AMF and other nontarget soil microorganisms (Lendzemo et al., 2005). It has been proposed that ethylene-producing nonpathogenic bacteria could be used to induce suicidal germination of *Striga* (Berner et al., 1999), but a better understanding of bacteria/ethylene/crop interactions is needed before this method can be used in agriculture. Other natural compounds, including fungal toxins (Evidente et al., 2006) and methyl jasmonate (Yoneyama et al., 1998) have been shown to induce germination of *Striga* and *Orobanche* spp. seeds, but their potential uses in agriculture remain largely unexplored.

Planting nonhost trap crops that induce suicidal germination is perhaps the most effective strategy currently available for *Striga* control (Oswald, 2005). Recent studies in this area have focused on identifying and assessing the effectiveness of potential trap crops (Gbèhounou and Adango, 2003; Lins et al., 2006; Fenández-Aparicio et al., 2007; Khan et al., 2007) and the possibility of breeding for increased production of germination stimulants (Botanga et al., 2003). Use of nitrogen-fixing legumes as trap crops has the added benefit of increasing soil fertility, which can further assist in *Striga* control because *Striga* thrive in poor soils (Parker and Riches, 1993). The efficacy of legume rotations could potentially even be improved by inoculating crops with supplemental nitrogen-fixing rhizobia, in combination with ethylene-producing bacteria, to simultaneously increase suicidal germination and soil fertility (Ahonsi et al., 2003; Babalola et al., 2007).

Legumes have also proven useful as part of a novel "push-pull" (stimulo-deterrent) pest management approach that illustrates the utility of increased plant diversity, simultaneously reducing *Striga* and lepidopteran stemborer infestations (Khan et al., 2000). Intercropping maize or sorghum with the leguminous trap crop *Desmodium* spp. decreases parasitism by *Striga* spp. and repels ovipositing stemborers, which subsequently move toward grasses bordering the field. *Desmodium* suppress *Striga*, not only by producing a germination stimulant, but also by producing chemicals that interfere with the development of haustoria (Khan et al., 2002).

4.2 Inhibiting Germination of Parasitic Plants

The sensitivity of *Orobanche* spp. seeds to germination stimulants is positively correlated with the production of gibberellin during seed conditioning; therefore, their germination can be inhibited by gibberellin biosynthesis inhibitors (Joel, 2000). Applying the gibberellin inhibitor uniconazole to soil near sunflowers significantly decreased broomrape parasitism and increased sunflower performance (Joel, 2000). Sunflower varieties that are resistant to *O. cernua* exude coumarins that inhibit germination and are toxic to newly germinated seedlings (Serghini et al., 2001). More recently, unidentified allelochemicals from oats appeared to inhibit seed germination of *O. crenata* and reduced parasitism when intercropped with legumes (Fenández-Aparicio et al., 2007). Seed germination can also be influenced by some amino acids, which have been shown recently to have profound effects on the development of *O. ramosa*. For instance, applying exogenous methionone almost completely inhibited seed germination and reduced the number of developing *Orobanche* spp. tubercles on tomato roots, possibly indicating that soil applications of amino acids or amino acid-producing microbes might be used to manage parasitic weeds (Vurro et al., 2006).

4.3 Reducing the Production of Germination Stimulants by Crop Plants

Decreased production of germination stimulants is the best characterized mechanism of crop resistance to parasitic plants (Rispail et al., 2007). This strategy has been exploited successfully in sorghum breeding to confer resistance of certain sorghum varieties to *Striga* (Haussmann et al., 2000). Resistance is apparently absent in some crop plants, including cowpea and maize (Rubiales, 2003), although considerable variation has been reported among genotypes of tomato and *Arabidopsis* (Goldwasser and Yoder, 2001; El-Halmouch et al., 2006). Recent findings suggest that selecting for reduced production of germination stimulants might negatively influence crop interactions with beneficial AMF (Akiyama et al., 2005). Recognition that strigolactones that induce parasitic plant seeds to germinate also recruit nutrient-supplying AMF suggests that manipulating mycorrhizal colonization could be used to manage parasitic plants (Akiyama et al., 2005). Recent reports show that nutrient deficiency, which in some cases is mitigated by AMF, can increase strigolactone production by potential host plants (Yoneyama et al., 2007). Moreover, colonization of host plants by AMF can down-regulate the production of germination stimulants (Lendzemo et al., 2007; Bouwmeester et al., 2007), suggesting that enhancing AMF colonization of crop seedlings in fields could reduce strigolactone production, and possibly reduce the numbers of parasitic plant seeds that germinate.

4.4 Disruption of Volatile Host Location by **Cuscuta** *spp.*

The discovery that *Cuscuta* spp., like root-parasitic plants, use chemical cues to find hosts, may lead to control strategies aimed at disrupting host location analogous to those described for root-parasitic plants. Plant volatiles, even more so than strigolactones, are sensitive to environmental variables (De Moraes et al., 1998, 2001; Tooker and De Moraes, 2007; Tooker et al., 2008) and could potentially be manipulated (cf. Turlings and Ton, 2006) to reduce the attraction of *Cuscuta* spp. seedlings. In addition, the production of plant volatiles is a heritable trait (Degen et al., 2004) that could potentially be incorporated into a plant-breeding program for *Cuscuta* resistance. Moreover, because at least one repellent compound ([*Z*]-3-hexenyl acetate) has been identified, a “push-pull” approach for control of *Cuscuta* spp. can be envisioned similar to that used for African stemborers. However, little to no work to date has examined the feasibility of such approaches, and further work is needed to elucidate how *Cuscuta* spp. perceive and respond to plant volatiles.

5 Conclusion

In spite of intensive research, adequate strategies for controlling parasitic plants remain elusive, and these weeds continue to threaten agricultural crops worldwide. Chemically mediated interactions between early-stage parasitic plants and their hosts play a key role in infestation and may be exploited for control. Recent advances in this area suggest a number of potentially fruitful approaches, including the prospect of simultaneously managing beneficial symbionts and parasitic weeds. For example, implementing cultural practices that favor AMF, such as reducing tillage and fungicide application, could improve growth and increase drought tolerance in crops (Plenchette et al., 2005), and potentially reduce *Striga* infestations

(Lendzemo et al., 2007). Additional research is needed to understand the mechanisms underlying strigolactone perception and responses in both parasitic plants and AMF. Intercropping with nonhost plants that induce "suicidal germination" and/or are allelopathic to root parasites (e.g., Khan et al., 2002) is another promising approach that warrants continued efforts to identify potential trap crops and improve their efficacy. Recent work on the role of volatiles in host location by *C. pentagona* suggests that control strategies aimed at disrupting host location might be used against parasites that make above-ground attachments, but more work is needed in this area. It seems unlikely that any single method alone will provide long-term control of parasitic weeds. An integrative approach incorporating one or several methods targeting the chemistry used in host location by parasitic weeds is more likely to provide sustainable strategies that will minimize crop losses.

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