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REVIEW ARTICLE

Innovations in parasitic weeds management in legume crops. A review

Diego Rubiales · Mónica Fernández-Aparicio

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Abstract Parasitic weeds decrease severely the production of major grain and forage legumes. The most economically damaging weeds for temperate legumes are broomrapes, in particular *Orobanche crenata*. Broomrape species such as *Orobanche foetida*, *Orobanche minor*, and *Phelipanche aegyptiaca* can also induce high local damage. Other parasitic weeds such as *Striga gesnerioides* and *Alectra vogelii* decrease yield of legume crops throughout semi-arid areas of sub-Saharan Africa. Dodders such as *Cuscuta campestris* can be damaging for some crops. Here, we review methods to control parasitic weeds. Preventing the movement of weed seeds into uninfested areas is a crucial component of control. Once a field is infested with parasitic weeds, controlling its seed production is very difficult. The only effective way to cope with parasitic weeds is to apply an integrated approach. Seedbank demise can be achieved by fumigation and solarization. However, this method is not economically feasible for low-value and low-input legume crops. A number of cultural practices including delayed sowing, hand weeding, no-tillage, nitrogen fertilization, intercropping, or rotations can contribute to seed bank demise. Other strategies such as suicidal germination, activation of systemic acquired resistance, biocontrol or target site herbicide resistance are promising solutions that are being explored but are not yet ready for direct application. The only methods currently available to farmers are the use of resistant varieties and chemical control, although both have their limitations. Chemical control with systemic herbicides such as glyphosate or imidazolinones at low rates is possible. Advances in modeling and the availability of new technologies allow the development of precision agriculture or site-specific farming. The most economical and environmentally friendly control option is the use of resistant crop varieties; however, breeding for resistance is a difficult task considering the scarce and complex nature of resistance in most crops. These strategies for parasitic weed management in legume crops will be presented and critically discussed.

Keywords Parasitic weeds · Control · Breeding · Intercropping · Germination · Biological control · Chemical control · *Alectra* · *Cuscuta* · *Orobanche* · *Striga* · Broomrape · Dodder

Contents

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1 Introduction

About 4,000 flowering plant species have adapted to parasitize other plants. Unfortunately for farmers, a small number of these species have become weeds, posing severe constraints to major crops including grain and forage legumes (Rubiales and Heide-Jørgensen 2011). The most economically damaging on legumes are the broomrapes (*Orobanche* and *Phelipanche*). Other parasitic weeds such as *Striga gesnerioides* (Willd.) Vatke, *Alectra voguelii* Benth. and the dodders (*Cuscuta* spp.) can be also damaging on some legumes (Joel et al. 2007; Parker 2009) (Fig. 1).

Orobanche crenata Forsk. (crenate broomrape) is an important pest of most grain and forage legumes being widely distributed in the Mediterranean basin and Middle East (Rubiales et al. 2009b) (Fig. 2). *Orobanche foetida* Poir. in contrast is of importance only on faba bean (*Vicia faba* L.) in Beja region of Tunisia (Kharrat et al. 1992) although it has recently also been found in Morocco infecting common vetch (*Vicia sativa* L.) (Rubiales et al. 2005b). *Orobanche minor* Sm. is widely distributed but of economic importance on clover (*Trifolium* sp.) only (Eizenberg et al. 2005). *Phelipanche aegyptiaca* (Pers.) Pomel (syn. *Orobanche aegyptiaca* Pers.) is an important pest of legumes but also of many vegetable crops in the Middle East and Asia (Parker 2009). *S. gesnerioides* and *Alectra vogelii* cause considerable yield reduction of grain legume crops, particularly cowpea (*Vigna unguiculata* (L.) Walp), throughout semi-arid areas of sub-Saharan Africa (Parker and Riches 1993). Dodders (*Cuscuta* spp.) are widely distributed, being a threat to alfalfa (*Medicago sativa* L.), chickpea (*Cicer arietinum* L.), and lentil (*Lens culinaris* Medik.) in certain locations. The most important species is *Cuscuta campestris* Yunck (Fig. 3).

There is no single technology to control these parasitic weeds (Joel et al. 2007; Parker 2009; Rubiales et al. 2009b). Large areas of new territory are at risk of invasion if care is not taken to limit the introduction of parasitic weed seeds and to educate farmers and others to be on alert for new infestations (Mohamed et al. 2006; Grenz and Sauerborn 2007). The only way to cope with parasitic weeds is through an integrated approach, employing a variety of measures in a concerted manner, starting with containment and sanitation, direct and indirect measures to prevent the damage caused by the parasites, and finally eradicating the parasite seedbank in soil.

2 Cultural practises

Preventing the movement of parasitic weed from infested into un-infested areas is a crucial component of control. Both sanitation and quarantine are required in order to prevent the dispersal of seeds. The minute seeds can easily be transferred from one field to another by cultivation, and also by water, wind, and animals. However, the most significant seed transfer agents are people, transportation vehicles, and farming machines, which easily transfer seeds and contaminated soil. Once a field is infested with parasitic weeds, controlling its seed production is very difficult. Extermination of seeds before their spread to new fields and regions is a crucial component in parasitic weed prevention program (Panetta and Lawes 2005). Quaternary ammonium salts have been found effective in seed

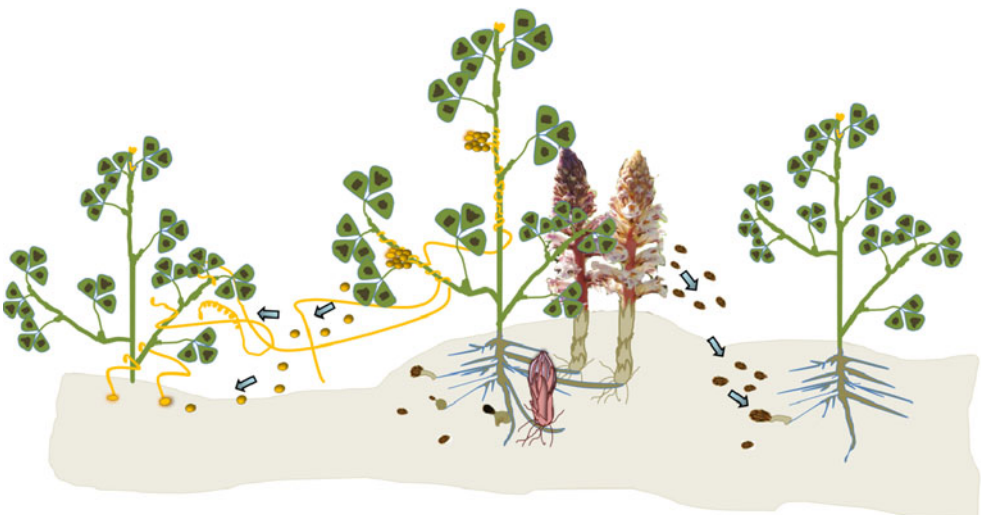

Fig. 1 Life cycle of parasitic weeds: on the *left* side, dodder seeds germinating, seedlings attaching to close-by plants, climbing and growing and infecting neighboring plants, flowering and setting seeds that replete the soil seed bank and repeat the process; on the *right* side, seeds of a weedy root parasite (either *Orobanche*, *Striga*, or *Alectra*) germinating, attaching to the roosts of host plants, emerging over the soil surface, flowering and setting seeds that replete the soil seed bank and repeat the process

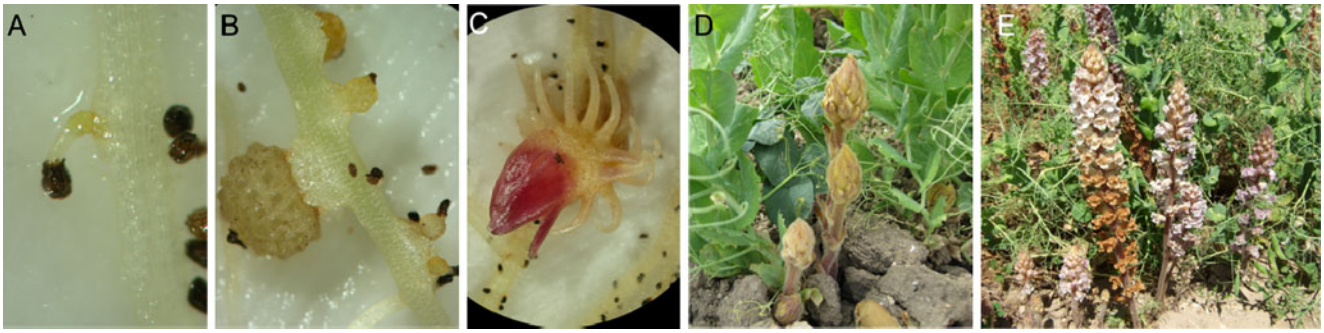

Fig. 2 Infection process of *O. crenata* on pea. **A** Germinating seedling contacting pea root; **B** haustorium formation resulting in tubercles; **C** bud formation; **D** shoots starting to emerge; **E** flowering plants

eradication with complete seed kill achieved under commercial conditions at 0.5% a.i. of the disinfectant didecyl dimethyl ammonium bromide.

Early plantings of cool season legumes are more severely infected by parasitic weeds. Delayed sowing is the best-documented traditional method for *O. crenata* avoidance (Rubiales et al. 2003b; Pérez-de-Luque et al. 2004b; Grenz et al. 2005). It also reduces *S. gesnerioides* (Touré et al. 1996) and dodder infection (Mishra et al. 2007). However, delaying sowing date implies shortening grain filling, which is detrimental for yield. Thus, options are needed that combine the yield benefit of early sowing with a decreased parasitic weed infestation.

Hand weeding can only be recommended in cases of limited infestation to prevent any further increase in the parasite population and to reduce the seed bank in the soil. However, even when hand weeding is still commonly used in some countries where no other feasible means of control are available and the wages for labor are cheap, it is only practical in preventing build-up of parasite seeds in slightly infested soils.

Solarization utilizes the sunlight in the summer to produce high temperatures under clear polyethylene mulch that covers the soil for several weeks. Mulching wet soil with transparent polyethylene sheets for a period of 4–8 weeks during the warmest season proved to be effective for a number of vegetables but also for faba beans and lentil (Sauerborn et al. 1989a; Mauromicale et al. 2001).

Cultivation of the soil can strongly affect the parasitic weed seed bank. Minimum tillage can contribute to parasitic weed control by reducing the amount of viable seeds incorporated into the soil (Ghersa and Martínez-Ghersa 2000). No tillage has been reported to considerably reduce *O. crenata* infection on faba bean (López-Bellido et al. 2009). On the other hand, deep-ploughing has been recommended to bring the seeds into a depth, where they cannot germinate due to the lack of oxygen (Van Delft et al. 2000), but expectations have not been met sufficiently perhaps due to problems with the costs and practicability.

Nitrogen compounds and manure fertilization has potential for control of broomrape species. Nitrogen in ammo-

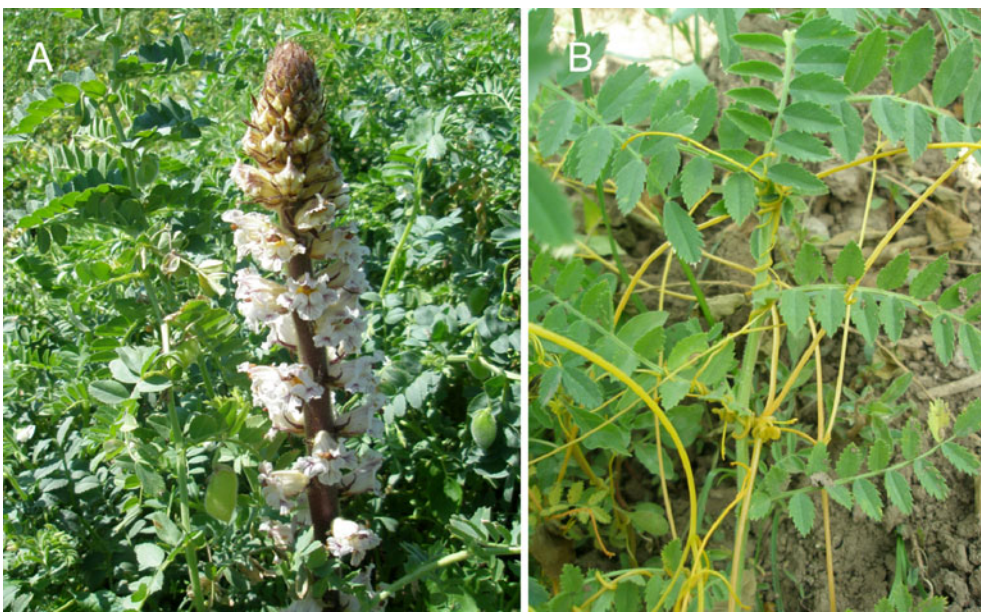

Fig. 3 Chickpea crop infected by *Orobanche crenata* (**A**); by *Cuscuta campestris* (**B**)

nium form affects negatively root parasitic weed germination (Van Hezewijk and Verkleij 1996) and/or elongation of the seedling radicle (Westwood and Foy 1999). In addition, manure fertilization augments the killing effect of solarization on *O. crenata* seeds (Haidar and Sidhamed 2000).

Intercropping is already used in Africa as a low-cost method of controlling *Striga hermonthica* on cereals (Oswald et al. 2002). It has recently been shown that intercrops with oat (*Avena sativa* L.) or with fenugreek (*Trigonella foenum-graecum* L.) or berseem clover (*Trifolium alexandrinum* L.) can reduce *O. crenata* infection on legumes being allelopathy a major component for the reduction (Fernández-Aparicio et al. 2007, 2008b, c, 2010a) (Fig. 4). The finding that germination of seeds exposed to synthetic germination stimulants is inhibited in presence of oat or fenugreek roots suggest that oat roots might be exuding substances that inhibit *O. crenata* seed germination. This has been confirmed in a subsequent work, and trigoxazonane identified from fenugreek (Evidente et al. 2007) or benzoxazolinones (Fernández-Aparicio, unpublished) from oat root exudates that might be responsible for inhibition of *O. crenata* seed germination. Considerable genetic variation in allelopathic activity has been found within crops (Baghestani et al. 1999) which may allow for selection of more allelopathic cultivars.

Rotation may have direct and indirect impacts on parasitic weed in infested areas. While trap- and catch-crops in rotation may reduce to some extent the parasite seed bank in soil, as discussed above, other rotation crops may have allelopathic effects on parasitic weed seeds. Decreasing host cropping frequency cannot, by itself, solve the parasitic weed problem. A nine-course rotation would be required to prevent *O. crenata* seedbank increases (Grenz et al. 2005).

The use of trap crops offers the advantage of stimulating parasitic weed seed germination without being parasitized, contributing to seed bank depletion. However, given the high amount of seeds in infested soils, it cannot be expected that the application of trap crops or germination stimulants will eliminate the seed bank in the soil immediately. It is a feature of parasitic weeds that their numerous tiny seeds stay viable for a long time and never do germinate all at the same time. The application of trap crops therefore should be included in the regularly rotation and fallow management for the infested fields. For each species, suitable trap crops need to be identified, as they show host specificity (Fernández-Aparicio et al. 2009a). For instance, pea is only infected by *O. crenata* but pea root exudates stimulate germination of *P. aegyptiaca*, *O. foetida*, and *O. minor* (Fernández-Aparicio et al. 2008d) that are known to infect other legumes. Pea could be efficiently used as trap crop for these species inducing suicidal broomrape germination. Other examples of potential trap crops are cereals such as durum wheat (*Triticum turgidum* L.) and oat that stimulated high germination of *O. minor* and *P. aegyptiaca* (Lins et al. 2006; Fernández-Aparicio et al. 2009a) or sorghum (*Sorghum bicolor* (L.) Moench) that strongly stimulated *S. gesnerioides* (Berner and Williams 1998). The use of cereals could be a suitable solution due to the high frequency in which they are cultivated and its importance for human consumption. For that reason, breeding on cereal germplasm for the maximum inductor effect on broomrape seeds could be of great interest. In fact clear genotypic effects have been reported in sorghum in induction of *S. gesnerioides* germination (Berner and Williams 1998). Growing the selected varieties with high inductor potential for suicidal broomrape germination in rotations introduced in infected soils could shorten the time necessary between host crops.

Catch crops in contrast to trap crops are plants which are heavily parasitized. Harvesting or destroying them after the

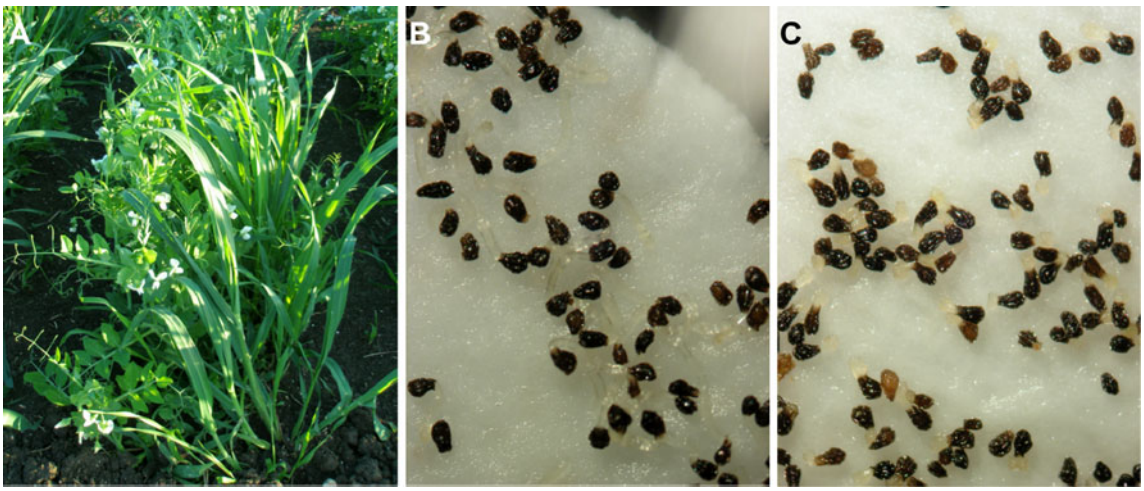

Fig. 4 Pea:oat intercrop reducing *Orobanche crenata* infectation in pea (**A**); detail of well-developed *O. crenata* seedlings when stimulated by pea root exudates (**B**); restricted *O. crenata* seedling elongation by addition of L-tryptophan (**C**)

appearance of the parasite would dramatically reduce the seed potential in the soil. The ideal solution would be a catch crop of agronomical interest by itself.

There are claims of reduction in infestation in rotations with rice due to water flooding (Sauerborn and Saxena 1986); however, this has not been substantiated. It has also been evidenced that soil irrigation during summer does not change broomrape seed germination (López-Granados and García-Torres 1996) what is in agreement with the high levels of infection in faba bean in irrigated areas such as the Nile Valley, quite often in rotations with rice.

3 Chemical control

3.1 Herbicides

The intimate connection between host and parasite also hinders efficient control by herbicides. Volatile compounds such as methyl bromide, ethylene dibromide, metham-sodium, or formalin are effective for the control of broomrape (Foy et al. 1989), but the high cost seldom justifies their use in legumes. The herbicides that are currently in use for parasitic weed control are glyphosate, imidazolinones, or sulfonylureas (Joel et al. 2007). Glyphosate disrupts the biosynthesis of aromatic amino acids inhibiting the key enzyme 5-enolpyruvylshikimate-3-phosphate synthase (EPSPS), whereas imidazolinones and sulfonylurea herbicides inhibit acetolectate synthase (ALS) (Schloss 1995). All of them are systemic herbicides absorbed through foliage and roots of plants with rapid translocation to the attached parasite, which acts as a strong sink (Colquhoun et al. 2006).

Chemical control of broomrape by foliar applications of glyphosate at low rates is recommended for faba bean and vetches (Jacobsohn and Kelman 1980; Mesa-García and García-Torres 1985; Sauerborn et al. 1989b), but problems of lack of effectiveness or phytotoxicity can arise when it is not applied properly. Selective control has also been reported in lentils (Arjona-Berral and García-Torres 1983) at lower rates, but not in peas that are very sensitive to glyphosate. However, tolerance to glyphosate exists in pea germplasms that could be exploited in breeding (Sillero et al. 2001). Further, pea and other legumes could be genetically engineered with the glyphosate-resistance gene.

Pea and lentil tolerate better pre- and post-emergence treatment of other herbicides suitable for broomrape control such as imidazolinones (Jurado-Expósito et al. 1986). However, no complete control is provided, and treatment is less effective in the earlier sowing dates (Rubiales et al. 2003c) probably due to the dissipation of the herbicide from the sowing date till the time of broomrape establishment. Faba bean tolerates pre-emergence treatments of imazapyr (12.5–25 g/ha) and imazethapyr (75–100 g/ha) and post-emergence treatments of imazapyr (2.5–5 g/ha), imazethapyr (20–40 g/ha), and imazaquin (40–60 g/ha) (García-Torres and López-Granados 1991). Lentil tolerates pre-emergence treatments of imazapyr (25 g/ha) and imazethapyr (75 g/ha) and post-emergence treatments of imazaquin (7.5 ml/ha) (Arjona-Berral et al. 1988; Jurado-Expósito et al. 1997) and imazapic (3 g/ha) (Bayaa et al. 2000). Two post-emergence applications of imazapic are recommended, with the first application recommended when lentil has 5 to 7 true leaves, when broomrape usually starts to develop attachments on lentil roots, followed by a second application 2 to 3 weeks later. Lentil may need a third application of 2 g/ha when late rain comes and extends the growth period, or when lentil is supplementary irrigated (Bayaa et al. 2000). Phytotoxicity might be higher in the presence of water, low temperature, and heat stresses and vary with the lentil cultivar used (Hanson and Hill 2001). An additional problem of these imidazolinone herbicides for broomrape control is that they are not registered in every country, and that doses and timing for application need to be adjusted case by case. Also, traditional imidazolinones are being replaced in some countries by imazamox that has less residual in the soil, so doses and timing of application need re-adjustment.

Knowledge of the phenology of parasitic weeds is essential for their effective chemical control. Application must be repeated in time interval of 2 to 4 weeks, because *Orobanche* seeds may germinate throughout the season and may therefore re-establish on newly developed hosts roots. Models for broomrape development can be helpful for precise chemical control. Such models, which exist for *O. minor* infecting red clover (Eizenberg et al. 2005) and as a subroutine of the Manschadi et al. (2001) model, can help to anticipate the occurrence of parasite development stages susceptible to, e.g., herbicide application. Advances in modeling and the availability of new technologies are allowing the development of precision agriculture or site-specific farming. Parasitic weeds are usually distributed in patches within the field (González-Andújar et al. 2001), so precision agriculture techniques like discrimination by near-infrared reflectance spectroscopy (Jurado-Expósito et al. 2003) could be adapted to detect broomrape-infected areas of the crop, for example, attending to differences in transpiration within infected and no infected plants.

Soil applications of sulfonylurea herbicides have proven effective to control broomrape in tomato (*Solanum lycopersicum* L.) and in potato (*Solanum tuberosum* L.), but the herbicide should be incorporated with irrigation. However, most cool season legume fields are not equipped with irrigation systems, because they are low input crops. Furthermore, legumes are not tolerant to sulfonylurea herbicides and probably will be injured when applied. For

such reasons, the only alternative should be pre-planting application or post-planting incorporated with rainfall.

Seed treatments with imidazolinones have proven to be effective controlling *O. crenata* in faba bean and lentil (Jurado-Expósito et al. 1997) and *S. gesnerioides* and *A. vogelii* in cowpea (Berner et al. 1994). The herbicide is incorporated as a coating on the seeds and distributed with them at planting. This replaces a pre-emergence treatment and saves mechanical application costs. In addition, it reduces the herbicide rate required by two- to threefolds, being more environmental friendly. However, under favorable environmental conditions for broomrape attack, the treatment must be supplemented to obtain high broomrape control.

The efficient management of dodders starts with the use of dodder-free seed and the spraying of the first affected patches with a contact herbicide to prevent spread. Infested equipment should be cleaned before and after use, and the movement of domestic animals from infested to dodder-free areas should be limited. The application of pendimethalin at 0.7–1.0 kg/ha as pre-emergence or early post-emergence is effective against *Cuscuta* in lentil. In chickpea, *Cuscuta* is selectively controlled by pre-emergence application of propyzamide (0.5–0.75 kg/ha), pronamide (2.5 kg/ha), or pendimethalin (1.0 kg/ha) or by pre-sowing application of Weedazol (Aminotriazol + ammonium thiocyanate) at 1.2–2.5 kg/ha. In faba bean, *Cuscuta* can be controlled with imazethapyr at 75 g/ha when applied pre-emergence or 20 g/ha post-emergence (Khallida et al. 1993). In alfalfa, *Cuscuta* can be controlled by pre-emergence application of imazethapyr at 0.1–0.15 kg/ha (Cudney and Lanini 2000) or pendimethalin (1.0 kg/ha) (Dawson 1990; Orloff et al. 1989) or by post-emergence treatment with low doses of glyphosate (0.075–0.15 kg/ha) (Dawson 1989).

Nanotechnology applications are already being explored and used in medicine and pharmacology, but interest for use in crop protection is just starting. Nanoparticles can be used as smart delivery systems for targeting and uploading substances at specific areas within whole plants (González-Melendi et al. 2008; Corredor et al. 2009). The development of nanocapsules for controlled release and systemic application of herbicides will greatly increase the possibilities of their utilization against parasitic weed, for example, by allowing the use of herbicides with different modes of action such as contact herbicides. The nanoparticles would carry the active substance and specific property and/or external modification of these nanoparticles would allow their accumulation and/or guidance into broomrape-specific areas in which the chemical charge would be unloaded. Nano-encapsulation of herbicides could be used to solve problems regarding phytotoxicity on the crop. Lower doses of herbicides would be needed because they will not be degraded by the crop, and they will accumulate preferentially in the parasitic weed due to the sink effect (Pérez-de-Luque and Rubiales 2009).

3.2 Suicidal germination

Orobanche, *Phelipanche*, *Striga*, and *Alectra* seeds require chemical stimulation from the host root to germinate. This suggests that the artificial use of suitable chemicals may reduce the parasitic weed seed bank by stimulating seeds germination in the absence of a suitable host, which should lead to their demise due to their inability to survive without nutritional supply by a host. Attempts have been made with the application to the soil of synthetic strigolactones, such as GR24 (Johnson et al. 1976) or Nijmegen-1 (Zwanenburg and Thuring 1997). However, the application in the field has not yet been successful, due to the instability of the compound, particularly in alkaline soil, and probably also to the lack of proper field application formulation for these compounds.

Several classes of plant secondary metabolites are known to induce seed germination of root parasitic weeds (Yoneyama et al. 2008). More than ten strigol-related compounds, collectively called strigolactones, have been identified as germination stimulants for root parasitic weeds (Yoneyama et al. 2009). Orobanchol, orobanchyl acetate, and 5-deoxystrigol are widely distributed in the Fabaceae (Yoneyama et al. 2008). Fabacyl acetate has recently been identified from root exudates of pea (Xie et al. 2009). Strigolactones play a major role in host specificity (Fernández-Aparicio et al. 2011). In addition to these, two new compounds (peagol and peagoldione) have been indentified in pea root exudates showing a selective stimulation of *Orobanche* seed germination (Evidente et al. 2009). Successively, three polyphenols, named peapolyphenols A–C, together with a polyphenol and a chalcone were isolated from same root exudates. Interestingly, only peapolyphenol A, 1,3,3-substituted propanone and 1,3-disubstituted propenone had specific stimulatory activity on *O. foetida*, not stimulating any other *Orobanche* or *Phelipanche* species tested (Evidente et al. 2010). Also, a triterpene and a sterol, identified as syasapogenol B and *trans*-22-dehydrocampesterol, have recently been isolated from common vetch root exudates. Soyasapogenol B was very specific stimulating germination of *O. minor* seeds only, whereas *trans*-22-dehydrocampesterol stimulated *P. aegyptiaca*, *O. crenata*, *O. foetida*, and *O. minor* (Evidente et al. 2011). Stimulatory activity of these metabolites on parasitic weed germination could be exploited in suicidal germination control strategies by synthesizing and directly applying them to the field. Also, their production in plants could be increased by breeding or by genetic transformation. Soyasapogenol B increased has already been achieved in transgenic *Medicago truncatula* Gaertn. (Confalonieri et al. 2009).

Ethylene stimulates the germination of *Striga* and *Orobanche* seeds (Berner et al. 1999; Zehar et al. 2002). Other compounds of natural origin, such as fungal metabolites (Fernández-Aparicio et al. 2008a), fungal phytotoxins, natural amino acids (Vurro et al. 2009), or plant or algae extracts (Economou et al. 2007) have also been suggested for use in parasitic weed management, being able to inhibit seed germination or seedling elongation, or, conversely, stimulate suicidal seed germination in the absence of the host.

3.3 Activators of systemic acquired resistance

Systemic acquired resistance (SAR) has been reported in a number of crops against different broomrape species by application of chemical agents (Sauerborn et al. 2002; Gonsior et al. 2004; Pérez-de-Luque et al. 2004a; Kusumoto et al. 2007). A significant reduction of *O. crenata* infection in faba bean and pea was achieved under field conditions by foliar application of BTH (1,2,3-benzothiadiazole-7-carbothioic acid *S*-methyl ester) (Pérez-de-Luque et al. 2004c). *O. minor* control has also been reported on red clover grown in plastic chambers after application of salicylic acid and BTH by inhibition elongation of *O. minor* radicles and the activation of defense responses in the host root including lignification of the endodermis (Kusumoto et al. 2007). Pérez-de-Luque et al. (2004a) described highly varying success on broomrape control after different BTH and salicylic acid modes of application on pea in growth chamber experiments. This shows that more host–parasite specific application techniques or perhaps other resistance inducing products are necessary to increase efficacy and reduce negative effects.

4 Biological control

Numerous microorganisms that might be useful for biocontrol of parasitic weeds have been isolated and reported (Amsellem et al. 2001; Boari and Vurro 2004; Sauerborn et al. 2007; Zermane et al. 2007). The fungal isolates reported to be pathogenic to parasitic weeds are for the most part *Fusarium* spp., prevailing especially strains of *Fusarium oxysporum* Schlecht.: Fr.. Advantages of *Fusarium* spp. relate to their host specificity and longevity in soil. However, to date, only *F. oxysporum* f. sp. *orthoceras* (Müller-Stöver et al. 2004) and *F. solani* (Mart.) Sacc. (Dor and Hershenhorn 2009) are under investigation as potential candidates for broomrape control. *Ulocladium atrum* (Preuss) Sacc. and *Ulocladium botrytis* Preuss have been found pathogenic towards *O. crenata* (Linke et al. 1992; Müller-Stöver and Kroschel 2005). *Myrothecium verrucaria* (Alb. & Schwein.) Ditmar isolated from faba bean roots has been found to inhibit germination of *O. crenata* seeds due to the production of the macrocyclic trichothecene, verrucarin A (El-Kassas et al. 2005). Preliminary results demonstrated control of infection of faba bean by *O. crenata* by the addition of spores of *M. verrucaria* to soil, raising the possibility that this approach might be applicable in the field. Andolfi et al. (2005) isolated seven macrocyclic trichothecenes, namely, verrucarins A, B, M, and L acetate, roridin A, isotrichoverrin B, and trichoverrol B from *M. verrucaria* and neosoloaniol monoacetate from *Fusarium compactum* was, a trichothecene, all being potent inhibitors of *Pinguicula ramosa* seed germination. Roridin A was considered the metabolite with highest potential as herbicide, as at 1 μmol concentration, it preserves a high phytototoxic activity lacking zootoxicity (Andolfi et al. 2005).

Some compatible *Rhizobium* strains have been reported to decrease *O. crenata* infections in pea by activation of oxidative process, LOX pathway, and production of possible toxic compounds, including phenolics and pisatin, inhibiting germination of *O. crenata* seeds, and causing a browning reaction in germinated seeds (Mabrouk et al. 2007). Colonization by the nitrogen-fixing bacterium *Azospirillum brasilense* has also been reported to inhibit germination and radicle growth of *P. aegyptiaca* (Dadon et al. 2004). Also colonization by arbuscular mycorrhizal fungi can provide protection against parasitic weeds as reported in cowpea reducing germination of *S. gesnerioides* (Lendzemo et al. 2009) or in pea reducing germination of various *Orobanche* and *Phelipanche* species (Fernández-Aparicio et al. 2010b).

Most of the insects reported to occur on root parasitic weed species are polyphagous without any host specificity and thus, damage to these parasitic weeds is limited (Klein and Kroschel 2002). However, for biological control, only oligo- and mono-phagous herbivorous insects are of interest. *Smicronyx* spp. has potential for *Striga* seed reduction (Kroschel et al. 1999). *Phytomyza orobanchia* Kalt. is a fly monophagous on broomrape. The feeding of the larvae within the capsules markedly diminishes seed multiplication of the parasite (Klein and Kroschel 2002). *P. orobanchia* is widely distributed in the broomrape infected area, eating a substantial number of seeds (Rubiales et al. 2001). This natural infestation is however insufficient to reduce broomrape in areas with heavy broomrape infestations. Nevertheless, bio-control with *P. orobanchia* can be helpful to slow down further dissemination and infestation in weakly infested areas and can be part of an integrated control approach to reduce the seed bank in heavily infested soils. This effect could be substantially increased by massive propagation and inundative release of this insect (Klein and Kroschel 2002).

Further success of mycoherbicides in agricultural applications will depend largely on the development of an

appropriate formulation which allows storage, handling, and a successful application of the fungal propagules (Shabana et al. 2003; Sauerborn et al. 2007). Effectiveness of biological control could be increased by the combination of two or more pathogens (Charudattan 2001). For instance, *F. oxysporum* f. sp. *orthoceras* and *F. solani* gave a low control *Orobanche cumana* in sunflower (*Helianthus annuus* L.) when used individually, but when applied as a mixture control improved (Dor et al. 2003). Integration of SAR inducers with *F. oxysporum* f. sp. *orthoceras* also resulted in highly reliable control of *O. cumana* (Müller-Stöver et al. 2005). The engineering of hypervirulence genes into weed-specific pathogens is receiving increasing attention (Gressel et al. 2004).

Another potential strategy would be to change the end uses, so that broomrape would be a desirable product in its own right. In the Puglia region of Italy, *O. crenata* is considered a tasty vegetable very appreciated by consumers. There are several recipes for cooking broomrape that are offered in restaurants (Rubiales 1999). Alternative uses might include the pharmaceutical and cosmetic industries (Andary 1993).

5 Resistance breeding

5.1 Breeding for resistance to the parasites

Breeding for disease resistance is straight-forward when a good source of resistance is available and an efficient, easily controlled, and practical screening procedure exists to provide good selection pressure. Unfortunately, this is not the case in legumes against broomrape (Rubiales 2003; Rubiales et al. 2006). The only instance in which broomrape resistance of simple inheritance has been identified and widely exploited in breeding is in sunflower against *O. cumana* Wallr. This has been particularly important allowing a rapid progress in sunflower breeding against *O. cumana* (Fernández-Martínez et al. 2008). *O. crenata* resistance identified in legumes so far is of polygenic nature (Román et al. 2002a; Valderrama et al. 2004; Fondevilla et al. 2010). Faba bean breeding for *O. crenata* resistance was founded using the Egyptian line F402 as source of resistance (Nassib et al. 1982). Similarly, resistance against *O. foetida* has also been identified in faba bean germplasm. Some lines selected against *O. crenata* have also shown a high level of resistance to *O. foetida*, with a high yield potential (Abbes et al. 2007).

Little resistance is available within pea germplasm against *O. crenata* (Rubiales et al. 2003c), but promising sources of resistance have been identified in wild relatives within the genus *Pisum* (Rubiales et al. 2005a; Pérez-de-Luque et al. 2005a), which have successfully been hybridized with cultivated pea (Rubiales et al. 2009a). Resistance is also very limited in grass pea (*Lathyrus sativus* L.) and chickling vetch (*Lathyrus cicera* L.) (Fernández-Aparicio et al. 2009b; Fernández-Aparicio and Rubiales 2010), but is available in related *Lathyrus* species (Sillero et al. 2005a). Resistance in lentils has only recently been reported (Fernández-Aparicio et al. 2008e, 2009c). However, resistance is frequent in common vetch and chickpea germplasm and cultivars (Gil et al. 1987; Rubiales et al. 2003a; Fernández-Aparicio et al. 2008f) as well as in their wild relatives (Rubiales et al. 2004, 2005a; Sillero et al. 2005b). Resistance to *P. aegyptiaca* has been found in purple vetch (*Vicia atropurpurea* Desf.) (Goldwasser et al. 1997) (Fig. 7).

Cowpea breeding for resistance to *S. gesnerioides* in West Africa was founded using the Botswana landrace B301 as a source of resistance. Following extensive field evaluation, a number of new resistant cultivars have been released. Different dominant genes for resistance have been identified in lines resistant to different *S. gesnerioides* strains identified in West Africa so these have been used as complimentary parents when breeding for all strains (Singh 2002; Timko et al. 2007). Resistance to *Alectra* was discovered after screening more than 650 cowpea accessions. Landraces B301 and B359 appeared to be particularly useful (Riches 1987, 1989). It is important to notice that landrace B301 is resistant to both *S. gesnerioides* and *A. voguelii*, being resistance to each weed conferred by independent non-allelic genes (Atokple et al. 1993).

5.2 Pathogenic variation

Knowledge on the existence of host specialization and parasite races is vital for any breeding program. There is no clear evidence for the existence of races of *O. crenata*. Molecular analysis suggest that most of the intraspecific variation in *O. crenata* is among individuals and not among hosts nor between regions (Román et al. 2002a) what supports the lack of physiological races and the high flow among broomrape populations. Only several levels of host-driven differentiation have been described in *O. minor* growing on *Trifolium pratense* and *Daucus carota* ssp. *gumminfer* (Thorogood et al. 2009) or *O. foetida* on chickpea and faba bean (Román et al. 2007). Races have not been described in any of these species and the lack of selection pressure by the host due to the lack of highly resistant cultivars to any of these species. It would appear at least possible that new parasitic biotypes could originate, however, as *O. crenata* populations are very heterogeneous (Román et al. 2001, 2002b). There is the risk that diverse *O. crenata* populations could be selected for virulence when challenged by the widespread use of highly resistant cultivars. In fact, a new race of *O. crenata* has been

suggested in Israel attacking resistant vetches (Joel 2000). This putative race seems to have been selected by the frequent culture of the resistant vetch cultivar in the area.

There is considerable variation in host specificity between isolates of *S. gesnerioides*, and different host species vary in their susceptibility to different parasite isolates. Mohamed et al. (2001) described eight *Striga* host-specific strains called *Euphorbia*, *Ipomoea, Indigofera*, *Jaquemontia*, *Merremia*, *Nicotiana*, *Tephrosia*, and *Vigna* strains. The *Vigna* strain is by far the most important, causing considerable damage to cowpea. It was initially proposed that there are five distinct races of *S. gesnerioides* in West and Central Africa, based on their ability to differentially parasitize different cowpea lines (Lane et al. 1997). At least seven distinct races were recognized in a later study with genome profiling with molecular markers and host differential resistance response (Botanga and Timko 2006). Because of the autogamous nature of *S. gesnerioides*, variations among isolates become genetically fixed, and geographic distributions of morpho-types, strains, and races frequently overlap (Parker and Riches 1993).

Although less systematic research has been completed with *A. vogelii*, it is clear that there is also variability in the virulence of populations of this parasite in different areas of Africa (Riches et al. 1992). *A. vogelii* also has distinct races that differentially parasitize cowpea (Polniaszek et al. 1991).

5.3 Resistance mechanisms

Resistance against root parasitic weeds is a multicomponent event, being the result of a battery of avoidance factors and/or resistance mechanisms acting at different levels of the infection process (Joel et al. 2007; Pérez-de-Luque et al. 2008, 2009; Rubiales et al. 2009a). Avoidance due to precocity is known in some legumes, early flowering genotypes having an advantage limiting *O. crenata* infection (Rubiales et al. 2005a; Fernández-Aparicio et al. 2009b) (Fig. 5) what can be explained by an earlier pod-setting and maturity, which would restrict the dry-matter partitioning into parasites (Grenz et al. 2005).

Some pre-attachment mechanisms of resistance could be acting prior to parasite contact with the host root. One of them is low induction of seed germination. It has been successfully used in sorghum breeding for resistance to *S. hermonthica* (Ejeta 2007) but has not been identified in legumes against *S. gesnerioides*. Resistance to *O. crenata* associated to low induction of parasite seeds germination has been reported in several legumes (Pérez-de-Luque et al. 2005a; Rubiales et al. 2003a, 2004; Sillero et al. 2005). Another pre-attachment mechanism could be related to the chemotropism responsible for the correct guidance of the broomrape seedling towards the host root. A wrong orientation of germinated *O. crenata* seeds within the potentially infective distance has been observed in pea (Pérez-de-Luque et al. 2005a) (Fig. 6) probably due to changes in the concentration of compounds exuded from host roots that are responsible for the chemotropic response of the seedlings (Whitney and Carsten 1981). Pre-haustorial mechanisms of resistance consisting in physical barriers such as protein crosslinking, callose depositions, and suberization reinforcing cortical cell walls (Pérez-de-Luque et al. 2006a, 2007) or in lignification of endodermal cells (Pérez-de-Luque et al. 2005b, 2007) have also been identified in legumes. In addition, chemical barriers in the form of accumulation and excretion of phytoalexins into the apoplast have been identified in the central cylinder of *M. truncatula* (Lozano-Baena et al. 2007).

Post-haustorial resistance mechanims, where attached parasites fail to develop, have also been described in legumes. These can be physical response consisting on sealing of host vessels by gel or gum-like substances and blocking the flux of water and nutrients from the host to the parasite (Pérez-de-Luque et al. 2005b, 2006b) or chemical, consisting on delivery of toxic compounds such as phenolics into the host vascular system causing death of *O. crenata* tubercles on chickpea (Pérez-de-Luque et al. 2006c) and *M. truncatula* (Lozano-Baena et al. 2007) or of *P. aegyptiaca* in purple vetch (Goldwasser et al. 1999) (Fig. 7).

A rapid necrosis of the host cells around the point of infection, leading to the death of the parasite, has also been identified in cowpea against *S. gesnerioides* (Lane et al.

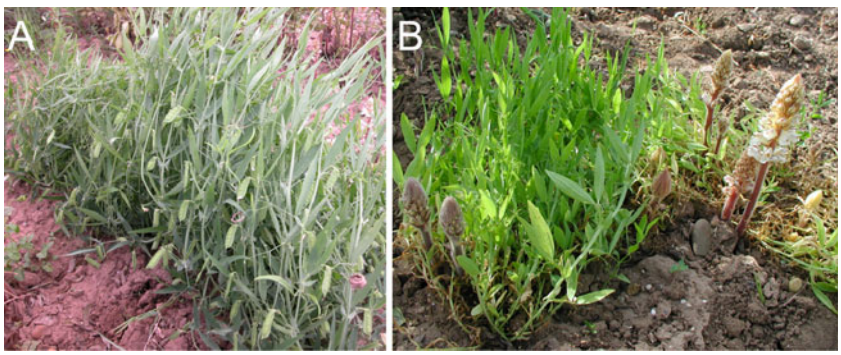

Fig. 5 Effects of earliness on *Orobanche crenata* infection: **A** very early *Lathyrus* accession filling pods and escaping from *O. crenata* infection; **B** late accession heavily infected

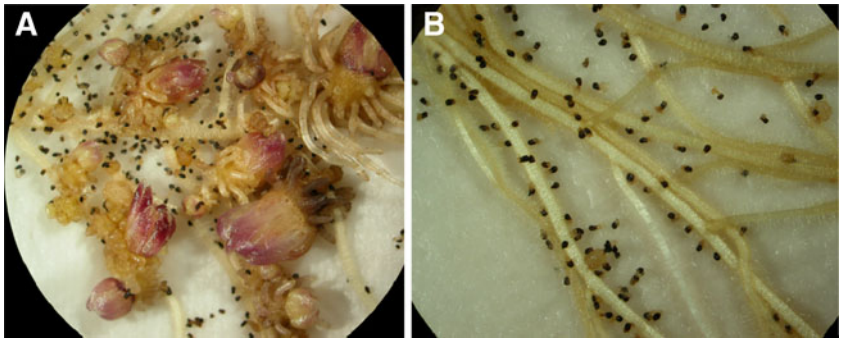

Fig. 6 Successful *Orobanche crenata* infection on pea in mini-rhizotrons (**A**) versus failed *Phelipanche aegyptiaca* attemps (**B**): seeds germinated, but failed to infect due to a combination of wrong orientation of radicles and arrested root penetration

1993). Another resistance mechanism was observed in other cowpea cultivars consisting in growth arrest of *S. gesnerioides* tubercles. Although tubercles began to develop on the host root surface, they did not enlarge, remaining less than 0.5 mm in diameter or their cotyledons failed to expand (Lane and Bailey 1992; Lane et al. 1993).

Resistance to *Cuscuta* has only recently been reported in chickpea characterized by the failure of the prehaustorium to penetrate the chickpea stem (Goldwasser et al. 2009).

5.4 Potential use of molecular markers and biotechnologies in resistance breeding

The development of marker-assisted selection (MAS) techniques for broad-based polygenic resistance is a particularly promising approach since parasitic weed resistance tests are difficult, expensive, and sometimes unreliable.

In pea, quantitative trait loci (QTLs) conferring resistance to *O. crenata* have been identified (Valderrama et al. 2004; Fondevilla et al. 2010). However, QTLs identified explained a low portion of the observed variation (altogether 21%). An in vitro screening method assaying different phases of the parasite cycle using a Petri dish technique, enabled identification of QTLs governing specific mechanisms of resistance, explaining a higher proportion of the variation (38–59%, depending on the trait) (Fondevilla et al. 2010).

In faba bean, three QTLs linked to resistance were identified in a map developed using an F2 population segregating for the trait (Román et al. 2002b). The QTLs explained a high percentage of the phenotypic variation of the trait (74%), mainly because of one of the QTL *Oc1*, which explained more than 37% of the character. Unfortunately, when a RIL population derived from this same cross was evaluated in other seasons and locations, this QTL vanished (Díaz-Ruiz et al. 2010), showing that it was not a stable QTL and should therefore be excluded for MAS. Two additional QTLs for resistance against *O. foetida* were identified using the same RIL, but both instable across environments and explained very little phenotypic variation (7–9%) (Díaz-Ruiz et al. 2009). The accuracy of phenotypic evaluation is of the utmost importance for the accuracy of QTL mapping. These screenings for broomrape resistance were performed under field conditions with not sufficient control of crucial environmental factors and of homogeneity of inoculum in the soil. Also, assessments were based on final number of emerged broomrapes per plant in the infested fields, what is likely to be influence by many confounding factors (Fernández-Aparicio et al. 2009b) such as earliness or plant vigor (Fondevilla et al. 2010). These can be avoidance to the contact by reduced root biomass or root architecture, low induction of broomrape seed germination, resistance to penetration, and/or hampered

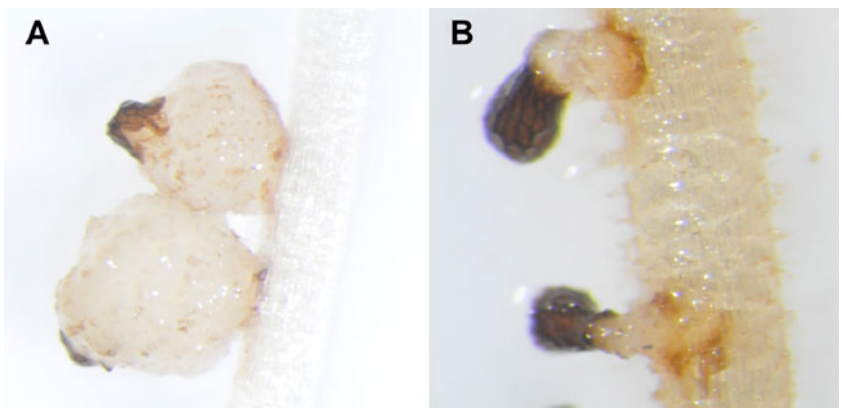

Fig. 7 Successful (**A**) versus failed (**B**) penetration of *Phelipanche aegyptiaca* in roots of two different vetch genotypes (Mezquita vs. Popany). Pictures taken 11 days after parasitic radicle contacted with the host root

development of established tubercles (Rubiales et al. 2006; Pérez-de-Luque et al. 2010). To overcome the disadvantages of screenings under field conditions, phenotyping should be performed using mini-rhizotrons, allowing the dissection of the resistance into specific mechanisms acting in different stages of the infection process, increasing the accuracy of the assessment, as done in pea (Fondevilla et al. 2010).

The genetic basis of resistance to *S. gesnerioides* and *A. vogelii* parasitism has been examined by a few laboratories. Single genes conferring resistance to *S. gesnerioides* (named *Rsg* genes: Touré et al. 1997; Ouédraogo et al. 2001; Li et al. 2009) or to *A. vogelii* (named *Rav* genes: Atokple et al. 1993, 1995) have been reported. Molecular markers linked to *Rsg1-1*, *Rsg2-1*, *Rsg3-1*, *Rsg4-3*, and *Rsg994-1* genes for *S. gesnerioides* resistance have been identified, and several sequence-confirmed amplified regions have been developed for use in marker-assisted selection (Ouédraogo et al. 2002; Li et al. 2009). Markers linked to *A. vogelii* resistances are being sought (Kouakou et al. 2009).

Although QTLs for resistance to *O. crenata* have been identified in pea and faba bean, they cannot yet be used in MAS. Saturation of genomic regions associated with broomrape resistance is needed to facilitate the identification of the most tightly linked markers that could be used to transfer the genes/QTLs responsible to the broomrape. The distances between the flanking markers and QTLs are still high and numerous recombinants between the QTL flanking markers and resistance are expected. Therefore, before using the available QTLs in MAS, the genomic regions containing the QTLs should be further saturated in order to refine the position of the QTLs and to identify molecular markers more closely linked to the resistance genes. The identification of the genes governing resistance included in the QTLs would allow the development of primers for these genes. These primers would be really useful for MAS, as they would be specific and recombination between the markers and resistance would be absent.

Novel strategies for the control of plant pathogens include selective silencing of target genes by small interfering RNAs (siRNA) (Prins et al. 2008). A key component to success with RNAi technology is identifying the best parasite genes to silence (Yoder et al. 2009). Sequence information obtained from different parasite species can be used to clone the homologous gene from a particular pest or can be directly transformed into crop plants.

5.5 Lessons to learn from model legumes

The use of model plants is valuable to identify new resistance genes that can be directly transferred or reintroduced under the control of a more active promoter via genetic transformation to improve resistance in crops. Following the example of other plant pathogen–interaction, the use of model plants such as *Arabidopsis thaliana* (L.) Heynh., *M. truncatula*, *Lotus japonicus* L., and rice (*Oryza sativa* L.), may improve our understanding of the plant–parasitic plant interaction. *A. thaliana* and *M. truncatula* are suitable hosts of some *Orobanche* species (Westwood 2000; Rodríguez-Conde et al. 2004; Fernández-Aparicio et al. 2008d), while rice may be used to study *Striga* (Gurney et al. 2006). *L. japonicus* can be infected by *P. aegyptiaca* but shows incompatible interaction against *O. minor* and *S. gesnerioides* (Kubo et al. 2009). Further studies should thus take advantage of these models to get insight more rapidly into the molecular bases of plant resistance, which should improve the efficiency of both MAS and transgenic approaches for crop improvement toward resistance to parasitic plants. The powerful "omics" tools implemented for *M. truncatula* makes this species highly suitable as a model for these studies (Dita et al. 2006, 2009; Die et al. 2007; Rispail et al. 2007, 2010; Castillejo et al. 2009).

M. truncatula is resistant to *O. crenata*, with rather insufficient variation in resistance among accessions hampering its use for genetic studies and presenting a non-host rather than host resistance response (Fernández-Aparicio et al. 2008d; Lozano-Baena et al. 2007). However, other *Orobanche* species different from *O. crenata*, might infect *M. truncatula*. Significant variation in the level of resistance/susceptibility to *O. aegyptiaca*, *O. foetida*, *P. nana* (Reut.) Soják and *P. ramosa* (L.) Pomel is available in *M. truncatula* germplasm (Fernández-Aparicio et al. 2008d). Genomic resources developed in *M. truncatula* (Young and Udvardi 2009) have the potential to accelerate practical advances in crop legumes.

Gene expression studies provide another source of candidate genes for parasitic weed resistance. They allow increasing the knowledge on the molecular basis of the resistance and the mechanisms underlying the host–parasite interaction. To improve our understanding of the *M. truncatula–O. crenata*, a suppression subtractive hybridization (SSH) library was created allowing the identification of candidate genes for *O. crenata* defense (Die et al. 2007). In addition, a microarray analysis of the *M. truncatula* genes regulated in response to *O. crenata* has been performed on a M16kOLI1 microarray platform (Dita et al. 2009). These analyses revealed the activation of both the salicylic acid (SA) and jasmonate defense pathways. Hybridization of *M. truncatula* microarray chips with RNA from related species such as pea is possible (Fondevilla et al. 2011). Thus, the same microarray platform may eventually be used directly with RNA from pea, allowing a more comprehensive understanding of pea molecular response to broomrape.

Differential expression studies in cowpea suggested that *PR5* expression may be a useful marker of *S. gesneroides* infection, and that salicylic acid signaling appears to play a

role in the cowpea–*S. gesnerioides* interaction (Li et al. 2009). Resistance to *S. gesnerioides* has been knocked down by virus-induced gene silencing (Li and Timko 2009). The differential display approach has also been applied to *Cuscuta*-infected alfalfa, showing the induction of PR genes such as PPRG2, a PR-10 homolog (Borsics and Lados 2002), and a calmodulin-related protein, PPRG1, indicating that defense signaling pathways to dodder is linked to calcium (Borsics and Lados 2001).

A proteomic approach was also applied to compare the proteome of two pea genotypes differing in their sensitivity to *O. crenata* at different stages of the infection (Castillejo et al. 2004). However, only 25% of the proteins differentially regulated were identified by mass spectrometry, hampered by the low number of pea sequences available in databases. The use of *M. truncatula* allowed the identification of more proteins involved (Castillejo et al. 2009).

5.6 Breeding for resistance to the herbicides

Herbicide-treated crops with target-site resistances would allow control of parasitic weeds (Gressel 2009). The herbicide would pass through the plant and flow into the hidden parasite; it is essential for this mode of action that the host plant does not metabolize the herbicide. In target site resistance, the parasite takes the herbicide together with the nutrients from the protected host and thereby accumulates toxic levels. This hypothesis has been already borne out by using transgenic crops with target-site resistance for the acetolactate synthase (ALS), enolphosphate shikimate phosphate (EPSP) synthase, and dihydropteroate synthase-inhibiting herbicides allowing control of *Striga* or *Orobanche* (Gressel 2009). This is therefore, a promising solution for controlling parasitic weeds in legumes. Resistance could be transferred into legumes following existing protocols, allowing an efficient broomrape control. However, apart from the difficulties of transforming legume plants, other drawbacks such as high cost, lengthy development time, and high economic risk, limit the use of this solution (Duke and Cerdeira 2005).

Imidazolinone-tolerant plants with altered ALS genes and enzymes have been discovered in many crops through mutagenesis and selection. This allowed developing by conventional breeding methods of imidazolinone-tolerant maize, wheat, sorghum, rice, oilseed (*Brassica napus* L.), and sunflower (Tan et al. 2004). Imidazolinone-tolerant mutations have also been discovered in other crops, and it is technically possible to identify them in legume crops and develop imidazolinone-tolerant cultivars by breeding. A number of lentil cultivars are being introduced to the market under the trademark "CLEARFIELD® lentils" (BASF Agsolutions 2008) that are not genetically modified and that tolerate higher doses of imidazolinone herbicides.

However, ALS-inhibitor resistance can rapidly evolve in weeds as a consequence of repeated application of herbicides with this site of action. In fact, resistance to ALS inhibitor herbicides such as chlorsulfuron and sulfometuron-methyl has already been reported in *C. campestris* (Rubin 1994). Herbicide mixtures are recommended to manage herbicide resistance.

6 Conclusions

In this review, we discuss the most advanced methods for parasitic weed control in legumes. Some of these methods are ready for commercial use by farmers (chemical control), some are in the final stages of development toward commercialization (resistant varieties and sanitation), and some need further development and improvement before commercial implementation (biological control).

Altogether, the available control methods have not proven to be as effective, economical, and applicable as desired. Although several potential control measures were developed in the past decades for some crops, any approach applied alone is often only partially effective and sometimes inconsistent and affected by environmental conditions.

The only way to cope with the parasitic weeds is through an integrated approach, employing a variety of measures in a concerted manner, starting with containment and sanitation, direct and indirect measures to prevent the damage caused by the parasites, and finally eradicating the parasite seedbank in soil. Much research is needed in order to develop new means for parasitic weed control. Basic research should provide new targets for control within the life cycle of the parasites and among their metabolic activities. The genomic research of parasitic weeds, which has already started, is likely to help in an overall understanding of some key aspects of parasitism.

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