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REVIEW - FOCUS ISSUE ON PLANT HEALTH SUSTAINING MEDITERRANEAN ECOSYSTEMS

Can we breed for durable resistance to broomrapes?

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Summary. The broomrapes (*Orobanche* and *Phelipanche*) are parasitic plants that have modified biology to feed on other plants, completely losing autotrophic capability. Some broomrape species have adapted to agricultural ecosystems becoming parasitic weeds. The most damaging weedy broomrapes are *O. crenata*, *O. foetida*, *O. minor*, *O. cumana*, *O. cernua* and *P. ramosa* and *P. aegyptiaca*, which can severely constrain important dicotyledonous crops, mainly in the Mediterranean Basin. This adaptation is an active process, with recent instances of jumps from non-weedy to weedy behavior, such as for *O. cumana* adapting to infect sunflower little more than a century ago; *O. cernua* adapting to infect tomato, tobacco and eggplant; and the more recent example of *O. foetida* adapting to infect faba bean a few decades ago. This also relates to parasite speciation towards particular hosts, such as the ongoing process of *P. ramosa* populations infecting winter oilseed rape. Sunflower is a unique situation, in which highly effective monogenic resistances to broomrape have been identified and widely deployed by sunflower breeders. This was accompanied by the subsequent appearance and spread of new races of *O. cumana* overcoming the introduced host resistance genes. In contrast, only quantitative resistances were identified and exploited by breeders in other crops against other broomrapes. Achievements and prospects for broomrape resistance breeding are presented and critically discussed, along with complementary measures needed to preserve durability of resistance. Particularly important is the prevention of human-driven broomrape seed dispersal by crop seed trade, together with broomrape seed soil-bank demise.

Keywords: crop management, legume, sunflower, biotechnology.

Parasitic weeds

More than 4,500 flowering plant species, belonging to about 20 families, have adapted to parasitize other plants. They constitute a group of plants widely studied by taxonomists and ecologists. However, some parasitic plant species have evolved to become weeds and pose serious threats to agriculture. They belong to different plant families, but they can be grouped into stem or root parasites. Stem parasites of economic importance are mistletoes (*Viscum* spp. and *Arceuthobium* spp.) and dodders (*Cuscuta* spp.). However, the most damaging and difficult to control parasitic plants are the weedy root parasites, because they exert their greatest damage underground before they can be detected and their effects manifest. The most damaging root parasitic weeds are the witchweeds (*Striga* spp.) and the broomrapes (*Orobanche* spp. and *Phelipanche* spp.). The witchweeds are important in sub-Saharan Africa and parts of Asia, where *S. hermonthica* and *S. asiatica* severely affect cereals, and *S. gesnerioides* affects legumes. Broomrapes are important in North Africa, Europe and Asia, infecting a range of dicotyledonous crops (Parker, 2009; Rubiales and Heide-Jørgensen, 2011).

Being flowering plants, the biology, dispersal and management of broomrapes have been widely studied by weed scientists. Several management strategies have been attempted for these parasites, including containment, sanitation, cultural practices, and biological and chemical control (Joel *et al.*, 2007; Rubiales *et al.*, 2009b; Fernández-Aparicio *et al.*, 2011b; Goldwasser and Rodenburg, 2013). However, parasitic weeds are not just weeds, but true parasites. They cause damage to crops by competition for light and

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water and soil nutrients, as standard weeds do, but also by parasitizing host plants, altering host physiology and capturing nutrients. This fits the definition of plant disease, so parasitic weeds are also studied by plant pathologists. By causing diseases to which the plants can have defence mechanisms, parasitic weeds are also studied by plant breeders, attempting to discern host resistance and develop resistant host cultivars. Parasitic weed management by resistance breeding is the focus of the present review, which also concentrates on broomrape species of importance in Mediterranean agriculture.

The broomrapes

There are about 150 broomrape species that infect dicotyledonous plant species with Mediterranean Basin centres of diversity. They are root-holoparasites whose seeds germinate in response to chemicals released by their hosts. They attach to host roots and grow at the expense of host resources. A few broomrape species became weedy, infecting crops. These parasites include important species such as *P. ramosa* infecting many vegetable crops (e.g. tomato, potato, tobacco, cabbage, watermelon or canola); the very similar *P. aegyptiaca* with an even broader host range, damaging the previously indicated crops but also sunflower and legumes; *O. cumana* infecting sunflower only; *O. cernua* infecting solanaceous crops; *O. minor* infecting forage legumes worldwide; *O. crenata* infecting most grain and forage legumes as well as other crops including carrot or celery; and *O. foetida* infecting legumes (Joel *et al.*, 2007; Parker, 2009; Rubiales and Fernández-Aparicio, 2012).

Broomrape infection and most of the life cycle take place underground, and this hampers diagnosis and development of effective control strategies. The large amount of seeds released by each broomrape provides the parasite with genetic adaptability to environmental changes. Crop damage varies with the season and the level of parasitized plants, but can be close to 100% in early infection on susceptible crops. Different crops may have different responses to the same level of infestation (Fernández-Aparicio *et al.*, 2016a). In addition to the host effects, infection severity depends on the population density of the parasite seed bank and on different environmental factors, mainly temperature. Thermal time is a valuable tool for predicting parasite growth and establishing the developmental stage of infections (Ephrath *et al.*, 2012; Moral *et al.*, 2015; Pérez-de-Luque *et al.*, 2016).

Management, parasitic mechanism and host defence mechanisms have been extensively reviewed (Joel *et al.*, 2007; Rispail *et al.*, 2007; Pérez-de-Luque *et al.*, 2009, 2010; Rubiales *et al.*, 2009b; Fernández-Aparicio *et al.*, 2011b, 2016c), so the focus of the present review is on implications for breeding for broomrape resistance in the various major affected crops. The durability of resistance to broomrape, as for resistance to any disease, is affected both by the evolutionary potential of the pathogen population and by the resistance breeding strategies adopted (McDonald and Linde, 2002). For design of effective and durable control strategies it is crucial to consider host factors (i.e. resistance genes and mechanisms) and those relating to the parasites (population structure, reproductive strategy and the factors affecting diversity).

Onset of parasitism and evolution of broomrape species and populations

Parasitism has evolved independently in several cases in the angiosperms, leading to varying degrees of host dependence, from facultative hemiparasitism (i.e. *Triphysaria*), obligate hemiparasitism (i.e. *Striga*), to obligate holoparasitism (i.e. *Orobanche* and *Phelipanche*). Broomrapes are therefore models of plant evolution, as they have deeply modified their biology to feed on other plants, involving many adaptations which culminate in loss of autotrophy and biological modification to identify and parasitize suitable hosts.

Some broomrapes have adapted to the selection exerted by agriculture and changes in cropping systems, driving changes in host range and speciation. These are active processes, with recent instances of jumps from non-weedy to weedy status. Examples are *O. cumana* adapting to infect sunflower more than a century ago (Velasco *et al.*, 2016), *O. cernua* adapting to infect tomato, tobacco and eggplant, and the more recent example of *O. foetida* adapting to infect faba bean a few decades ago (Vaz Patto *et al.*, 2008). This also relates to speciation towards particular hosts, such as the ongoing process of *P. ramosa* populations adapting to winter oilseed rape (Gibot-Leclerc *et al.*, 2013). These examples are discussed in more detail below.

A further level of adaptation is to the selection exerted by plant breeders. Contrary to what happens in natural habitats where hosts and parasites evolve naturally, the host plants of weedy parasitic species are crop cultivars selected by plant breeders. The strategy of deployment of these cultivars has major influence on the speed of evolution of the parasitic plants. What is known of the evolutionary potential of broomrape populations in response to host driven selection is first reviewed, and then the effects on selection of the cropping systems and breeding strategies deployed is considered.

Genetic variation and gene flow

Mutations lead to changes in the DNA sequences of individual genes, creating new alleles. The mutation rates may increase in populations with active transposable elements. A role of epigenetic re-programming of gene expression has also been suggested to explain this rapid evolution (Bruce and Gressel, 2013). Such effects are not sufficiently studied in broomrape populations, and in any case, there is likely to be little chance for breeders to reduce the creation of new alleles by reducing mutation (McDonald and Linde, 2002). However, population size may be reduced, and by doing this, probability of mutations will reduce, and in parallel with limitation of gene flow.

Mating systems affect the way that gene diversity is distributed within and among individuals, leading to genotype diversity. All broomrape species reproduce sexually, allowing generation of variants that can respond to selection pressures. The degree of autogamy varies with species, with *O. crenata* being largely allogamous, while other broomrape species are predominantly autogamous, although retaining some outcrossing that can vary with populations and environmental factors. Such (more or less complete) autogamy may play important roles in the fixation of mutations advantageous for parasitization of annual hosts. In addition to sexual reproduction, apomixis (development of seeds from unfertilized ovules) has also been documented in broomrapes (Joel, 2013), and this can contribute to fixation of mutations and reduced diversity within populations.

Broomrapes produce great numbers of long-living very small seeds, which increases the probability of finding hosts, even in nature when host plants might be temporally or spatially not separated. This may also be a key to rapid broomrape dispersal in agricultural fields, and for genetic adaptability to changes in host availability and host resistance. Broomrape seeds can be distantly dispersed by wind or animals, and remain viable in the soil for long periods (Joel, 2013). Nevertheless, most seeds are usually located close to mother plants and the distribution of broomrape populations is predictable and stable in the long term (Oveisi *et al.*, 2010). Longer distance dispersal is associated with human action, such as movement of contaminated soil with machinery, or at much greater distances by trading of contaminated crop seed lots. Dispersal of *O. cumana* seeds adhering to crop seeds, particularly to achenes of sunflower, is thought to be the main factor for long distance spread of this species (Castejón *et al.*, 1991). The risk of accidental dispersal increases with the success of the host crop, and the intensity of the seed trade. These are crop-dependent factors rather than broomrape factors. Insufficient effort is made to limit human-aided dispersal, which could have crucial effects for reducing spread of new variants. Urgent quarantine actions are needed in this respect.

Parasite invasion into previously unoccupied areas might lead to founder effects, with reduced genetic variability of populations outside the centre of origin of a given species. The best documented example of a founder effect in parasitic weeds is the genetic uniformity of *Striga asiatica* in North Carolina (Werth *et al.*, 1984), resulting from accidental seed introduction. Similarly, this may explain the genetic uniformity of *S. gesnerioides* (Botanga and Timko, 2005) or of *O. minor* (Westwood and Fagg, 2004) in the USA. Such founder effects may also explain the differentiation found in *O. cumana* at the worldwide level. *O. cumana* was first reported on sunflower in Russia by the 1890s, and by the 1930s in neighbouring countries such as Bulgaria. By the 1950s the parasite was reported in more distant places including Spain. Today, it occurs in most of the main sunflower-producing countries in Eurasia, from Spain to China (Molinero-Ruiz *et al.*, 2015). *O. cumana* has not yet been reported in America, but may occur unless careful seed movement preventive measures are taken.

High genetic differentiation has been reported between Spanish and Bulgarian *O. cumana* populations (Gagne *et al.*, 1998), whereas low between Spanish and Romanian populations, suggesting introductions to Spain from Romania through contaminated sunflower seeds. This is further supported by the low intra-population diversity, suggesting a monophyletic origin. Spanish populations of *O. cumana* are considered to consist of two main genetic pools, one of populations from Central Spain (where the first infestations were reported on confectionary sunflower in the 1960s), and the other of populations from Southern Spain (largely oil sunflower types) (Pineda-Martos *et al.*, 2013). These populations may have derived from different introduction events. Genetic variation is low within each genetic pool, probably due to founder effects. The populations for Southern Spain are closer to populations from Hungary and Turkey than to those of Central Spain (Molinero-Ruiz *et al.*, 2014). More recently, introductions have been reported in provinces of Castilla y León (Malek *et al.*, 2017). Similarly, recent infestations in Tunisia are likely to have arisen from two independent introductions (Jebri *et al.*, 2017).

There is little genetic differentiation among *O. crenata* populations from the same country, suggesting continuous dispersal of the seeds during the many centuries of legume cultivation (Román *et al.*, 2001). However, in comparisons over long distances, some genetic differentiation has been detected (Román *et al.*, 2002a) which might be reduced in the future with increasing global exchange of crop seeds.

Host-driven selection

Parasite specialization is associated with predictable resources and generalized with unpredictable ones (Ward, 1992). In agreement with this, most non-weedy broomrape species have narrow host ranges and grow on perennial host plants in natural ecosystems, whereas most weedy species have wide host ranges and grow on annual crops (Schneeweiss, 2007). An important issue concerning within-species diversity would be host-induced selection and the possibilities of adaptation of a species of *Orobanche* to a new, possibly cultivated host, emphasizing the importance of host specificity and host-switching as a driver of evolutionary divergence (Schneider *et al.*, 2016).

The sunflower/*O. cumana* system is unique in many respects. Firstly, *O. cumana* parasitism in sunflower can be considered a recent case of the new encounter of a non-weedy parasite with a crop. *Helianthus* is a genus native to America where it is not infected by any *Orobanche* species. Originally, *O. cumana* was a non-weedy species parasitizing *Artemisia* spp. Sunflower was introduced into Europe by the 16th century, but kept only as an ornamental plant, mainly in botanic gardens and monasteries. It was utilized as an oil crop in East Europe as recently as the 19th century. This new crop became highly successful and expanded to other areas encountering native non-weedy populations of *O. cumana*. It is speculated that natural populations of the parasitic plant were able to recognize root exudates of this new crop and successfully infected it, becoming weedy. It is not documented how such encounter and recognition occurred, but *O. cumana* already infected sunflower by the end of 19th century, and with the success of sunflower crop, rapidly and concomitantly spread throughout East Europe and then throughout Mediterranean Basin and Asia (Molinero-Ruiz *et al.*, 2015).

First reports referred to sunflower broomrape as *O. cernua*, and only in recent decades was it reassigned to *O. cumana*. Though closely related to *O. cernua*, *O. cumana* is a different species (Katzir *et al.*, 1996; Pujadas-Salvá and Velasco, 2000; Román *et al.*, 2003), and did not result from adaptation of *O. cernua* to sunflower, as previously speculated. Another peculiarity of *O. cumana* is its very restricted host range, contrasting with the broad host range of most weedy broomrapes (Fernández-Aparicio *et al.*, 2009b). The sunflower/*O. cumana* encounter may have resulted from host-differentiation of natural *O. cumana* populations, because the parasite is exceptional in having a limited host range, with host preference almost exclusively on sunflower.

Non-weedy populations of *O. cernua* also parasitize perennial Asteraceae. It is not documented how or when this may have occurred, but weedy populations have adapted to various solanaceous crops, mainly tobacco, tomato and potato, and are distributed through Southern Europe, the Middle-East and Asia (Joel *et al.*, 2007; Parker, 2009).

Unlike sunflower which is a relatively new crop, faba bean is one of the longest grown crops, and has been parasitized by broomrape for centuries, being mentioned by ancient Greek and Roman authors (see Pérez-de-Luque *et al.*, 2010). For several millennia faba bean and *O. crenata* have co-evolved so that parasitism persists but the crop is able to tolerate the damage better than other legumes (Fernández-Aparicio *et al.*, 2016a). Faba bean, together with sunflower, was probably the crop in which breeding efforts were earliest initiated. However, very contrasting outcomes were achieved with these two hosts.

Orobanche crenata is the most damaging and widespread broomrape species affecting faba bean; however, other species, such as *O. foetida* and *P. aegyptiaca*, can also infect the crop locally. Host-differentiation has not been reported in *O. crenata*, nor in *P. aegyptiaca*

(Paran *et al.*, 1997). Only recently, some weak levels of host specificity have been suggested in *O. crenata* populations growing on lentil (Ennami *et al.*, 2017). In contrast, *O. foetida* is another instance of recent host-differentiation. Non-weedy populations of *O. foetida* are widely distributed in the western Mediterranean, infecting only wild legumes (Pujadas-Salvá *et al.*, 2003). However, relatively recently *O. foetida* populations became weedy on faba bean in the Beja region of Tunisia (Kharrat *et al.*, 1992). Contrasting with the sunflower case explained above, which was a new encounter of a newly introduced crop with non-weedy populations of *O. cumana*, faba bean and other major legume crops have been in contact with natural non-weedy populations of *O. foetida* for centuries, without being infected. This sudden adaptation *O. foetida* to infect crops grown in the same area over very long periods is not sufficiently documented or understood. The Tunisian weedy populations infesting crops have not been compared with the non-weedy ones infecting wild legumes in the area. The only available study compared weedy populations infecting faba bean and chickpea, collected from one farm, and showed significant divergence among populations. This suggested the ability of *O. foetida* to evolve in response to host selection pressures (Román *et al.*, 2007b). *O foetida* has later been found in Morocco infecting common vetch (*Vicia sativa*) (Rubiales *et al.*, 2005b). A study of weedy and non-weedy Moroccan populations of *O. foetida* showed a level of host-differentiation, suggesting that the vetch-infecting population was not a new introduction but an evolution in the populations previously infecting *Scorpiorus muricatus* (Vaz Patto *et al.*, 2008).

Phelipanche ramosa has been known for many centuries as a parasite of hemp in Europe. Hemp was widely cultivated for fibre production. The parasite later became an emerging threat to vegetable crops, especially in the Mediterranean region (Parker, 2009). With the expansion of winter oilseed rape cultivation, *P. ramosa* is becoming increasingly important in Western France and more recently in other European countries. Genetic diversity studies have shown some geographic differentiation (Vaz Patto *et al.*, 2009), but particularly some host-differentiation in *P. ramosa* populations. The populations infecting oilseed rape show some preference for rape compared with the populations collected from hemp or tobacco (Buschmann *et al.*, 2005; Benharrat *et al.*, 2005; Brault *et al.*, 2007; Gibot-Leclerc *et al.*, 2013).

Host driven selection leading to speciation has also been suggested for *O. minor* (Thorogood *et al.*, 2008, 2009), and for other non-weedy *Orobanche* species (Román *et al.*, 2007a; Schneider *et al.*, 2016). There is also evidence of host driven selection occurring in parasitic plant species belonging to other genera, such as *Viscum*, *Cytinus* and among others (Zuber and Widmer, 2000; de Vega *et al.*, 2008).

Mechanisms contributing to host-specificity

Specialization and evolutionary divergence, following host-switching, are expected outcomes given the complexities of host detection and invasion for parasitic plants. Multiple layers of incompatibility may contribute to host-specificity. A first mechanism of host-driven selection is exerted by recognition systems. The seeds of broomrapes germinate only in response to specific chemicals that are released by plant roots. By germinating only when a root of a potential host is available in their immediate vicinity, the young seedlings increase their chances of survival. There must be strong selection in favour of the stimulant-dependence trait, because any germination occurring away from a host root would lead to the death of the germinated seedling. Such chemical signalling between host and parasite can determine host specificity and thus host range (Yoder, 2001; Fernández-Aparicio *et al.*, 2009b).

Several chemical compounds have been identified as germination inducing compounds. The most active are host-derived strigolactones, which have been characterized as plant hormones involved in regulation of shoot branching and root morphology (Gomez-Roldan *et al.*, 2008). Strigolactones are also involved in symbiotic interactions through induction of hyphal branching in arbuscular mycorrhizal fungi (Akiyama *et al.*, 2005), and by interacting with other beneficial and detrimental organisms (López-Raez *et al.*, 2017). These compounds are also likely to have long played roles in evolution since they are also signaling molecules in mosses, suggesting that they may have contributed to the colonization of land by plants (Proust *et al.*, 2011). There has been convergent evolution towards strigolactone perception in parasitic plants (Conn *et al.*, 2015), with a greater range of strigolactone receptors and an accelerated evolution in parasitic plants compared with non-parasitic relatives.

Other metabolites have been reported to contribute to host specificity, selectively stimulating *Orobanche* seed germination. These include sesquiterpene lactones in sunflower (Macías *et al.*, 2009; Joel *et al.*, 2011), glucosinolate breakdown products in oilseed (Auger *et al.*, 2012), peagol, peagoldione and peapolyphenols in pea (Evidente *et al.*, 2009; 2010) and soyasapogenol B and trans-22-dehydrocampesterol in common vetch (Evidente *et al.*, 2011). Taken together, this shows the significant role that host-derived germination stimulants may play in host specificity (Fernández-Aparicio *et al.*, 2011c). Non-weedy species, typically with narrow host ranges, have probably more specific germination requirements, requiring unique combinations and concentrations of signaling chemicals (Fernández-Aparicio *et al.*, 2009b, 2011b). Adaptation to more or different germination stimulants may play key roles in host-switching. Although *O. cumana* is responsive to strigolactones, dehydrocostus lactone is the active germination stimulant exuded by sunflower roots (Joel *et al.*, 2011). Similarly, although *P. ramosa* is also sensitive to strigolactones, the main germination stimulants for *P. ramosa* in oilseed rape root exudates are isothiocyanates, which are breakdown products of glucosinolates (Auger *et al.*, 2012). Also, the host specialization for *O. foetida* that is still progressing may be related to sensitivity to non-strigolactone compounds such as peagol and a polyphenol (Evidente *et al.*, 2009, 2010).

Spontaneous germination occurs in some natural seed populations, although this is a lethal trait leading to suicidal germination. Nevertheless, there is genetic variation for this trait in broomrape species (Plakhine *et al.*, 2012). This suggests that if the selection pressure against spontaneous germination were reduced by the repeated monoculture of the host, such as tomato or sunflower in certain regions, regulation of germination might not be needed to ensure successful contact with a susceptible host.

Changes in recognition systems may be a first key step driving speciation. However, many plant species may induce germination of various broomrape species without being infected (Fernández-Aparicio *et al.*, 2009b). For instance, pea is known to induce high levels of germination of *O. foetida* and *P. aegyptiaca*, without being infected by these parasites (Fernández-Aparicio and Rubiales, 2012).

A second step in host recognition, widely studied in other parasitic weeds, is haustorium initiation. Haustorium formation in most members of the Orobanchaceae is initiated by host-derived metabolites, mostly phenols, flavonoids and quinones (Banderanayake and Yoder, 2013). Broomrapes were thought to not require such signals, until the role of sphaeropsione derivatives (Fernández-Aparicio *et al.*, 2016b) and cytokinins (Goyet *et al.*, 2017) were documented. Haustorium-inducing mechanisms might also be exploited as host resistance factors by plant breeding. As an example, low haustorial initiation activity has been identified in sorghum against *S. hermonthica*, and has been combined in sorghum varieties for improved *Striga* resistance (Ejeta, 2007).

Once an haustorium is differentiated in contact with a host root, a variety of defence mechanisms, occurring at pre- or post-attachment stages, can also provide the physiological basis for host specificity (Pérez-de-Luque *et al.*, 2005b; Thorogood and Hiscock, 2010; Westwood *et al.*, 2010). Several mechanisms can prevent root penetration through host root cortices and into the central root tissues. These include reinforcement of cortical host cell walls by protein cross-linking, suberization or callose deposition, and lignification of endodermal cells (Goldwasser *et al.*, 1999; Echevarría-Zomeño *et al.*, 2006; Pérez-de-Luque *et al.*, 2006a, 2007, 2008). Additional resistance mechanisms may operate at later stages, preventing or retarding further development of broomrape shoots, which can result in darkening and necrosis of the formed tubercles (Goldwasser *et al.*, 1997; Labrousse *et al.*, 2001; Rubiales *et al.*, 2003c, 2004; Fernández-Aparicio *et al.*, 2008a; Louarn *et al.*, 2016). This may be caused by accumulation of substances inside host xylem vessels that block the flux of water and nutrients, or that are toxic such as cumarins or defensins (Serghini *et al.*, 2001; Pérez-de-Luque *et al.*, 2005b, 2006b; Letousey *et al.*, 2007; Lozano-Baena *et al.*, 2007; de Zélicourt *et al.*, 2007).

Selection exerted by plant breeders

As stated above, the host plants of weedy parasitic species are cultivars selected by breeders, and the outcome of such selection can have major impacts on parasite evolution. This has led to contrasting situations regarding the different weedy broomrapes. Due to this complexity, the different scenarios of selection of cultivars with resistance to broomrapes are considered below.

Breeding sunflower for resistance to *Orobanche cumana*

Orobanche cumana is to date the only broomrape species in which races have been described. This began soon after the development of sunflower as a crop (see Molinero-Ruiz *et al.*, 2015; Velasco *et al.*, 2016). Race differentiation in *O. cumana* is unique, as all other broomrape resistances identified in other crops are quantitative. Russian and East European sunflower breeders identified resistance to this new parasite at the very beginning of the 20th century, and developed resistant cultivars that were successfully grown on large scales. Race-specific dominant genes have been considered to be the ideal sources of resistance for single-cross hybrid breeding, because they only need to be incorporated into one of the respective parents (see Fernández-Martínez *et al.*, 2015; Kaya, 2016). As a drawback of this wide exploitation of these monogenic resistances, a continuous stepwise development of new physiological races of *O. cumana* has occurred, from the early race A through to the novel race H.

Several major (*Or*) resistance genes controlling the resistance to specific *O. cumana* races have been used in breeding programmes (Fernández-Martínez *et al.*, 2015). This resistance was first identified in landraces and in wild species, first in *H. tuberosus* and later in other wild annual and perennial *Helianthus* species (Fernández-Martínez *et al.*, 2008; Seiler and Jan, 2014; Velasco *et al.*, 2016). Although exotic germplasm can serve as a good reservoir of genes, being exotic is not a guarantee of durability of resistance traits. The use of wild relatives in resistance breeding may have implications for the durability of resistance, as parasite populations may have already been exposed to the resistance gene and have evolved towards new virulence (Leroy *et al.*, 2014). The pre-existence of virulence in the parasite population, even at low frequency, can change the durability of the resistance gene in the crop plant populations (Lof *et al.*, 2017). However, this may not be the case for sunflower, as *O. cumana* is not present in the area of origin of wild *Helianthus* spp.

Although introgression of major resistance genes is an easy and quick solution for plant breeding, more sustainable resistance must be developed. Because of this, there has been increasing interest in breeding methods that integrate quantitative resistance and/or combine different resistance mechanisms (Pérez-Vich *et al.*, 2004; Akhtouch *et al.*, 2016; Louarn *et al.*, 2016). However, for the success of any breeding strategy, increased knowledge is required of the genetic basis of resistance, resistance mechanisms, and the diversity of parasite populations.

Apart from the resistance to *O. cumana* in sunflower, resistance to *S. gesnerioides* in cowpea is the only other instance known of monogenic dominant resistance. This acts in a race-specific gene-for-gene manner, similar to effector-triggered immunity described in some host–pathogen interactions. A race-specific R gene from cowpea has been cloned and characterized encoding a CC-NBS-LRR type R-protein (Timko *et al.*, 2012). Homologues of some of the involved NBS-LRR proteins have also been identified in quantitative trait loci (QTL) controlling resistance in sunflower (Louarn *et al.*, 2016).

Breeding legumes for resistance to *Orobanche crenata*, *O. foetida* and *Phelipanche aegyptiaca*

Contrary to sunflower, in which strong and singly inherited resistance was soon identified and used, little resistance is available against *O. crenata* in legumes, and this shows complex inheritance. Nonetheless, progress has been made by accumulating the available quantitative resistances through host breeding, and this has resulted in the release of moderately resistant faba bean cultivars in several countries (Kharrat *et al.*, 2010; Maalouf *et al.*, 2011; Rubiales *et al.*, 2014) and more recently also resistant pea cultivars (Rubiales *et al.*, 2009a; Fondevilla *et al.*, 2017).

Faba bean breeding for resistance against *O. crenata* mainly relied on the use of resistance from the Egyptian line F402. This was developed as Giza 402, derived mainly from resistant breeding lines developed by the International Centre of Agricultural Research in Dry Areas (ICARDA), and selected across different Mediterranean countries (Rubiales *et al.*, 2006; Sillero *et al.*, 2010). This multi-location field selection has contributed to the stability of the resistance across different environments. Resistance in faba bean to *O. foetida* has been an additional target in Tunisia, approached by selecting within host lines resistant to *O. crenata*, and crossing them mainly with local germplasm. This programme succeeded in the selection of lines showing resistance to *O. foetida* (Abbes *et al.*, 2007).

Resistance identified in faba bean appears to be polygenic, as shown by all genetic analyses performed that resulted in the identification of QTLs both for *O. crenata* or *O. foetida* resistance (Román *et al.*, 2002b; Díaz-Ruíz *et al.*, 2010). Many of these QTLs were not stable across environments and explained little phenotypic variation, and are therefore of little value in Marker Assisted Selection (MAS). However, recent studies have highlighted QTL *Oc7* as a more suitable candidate for MAS, being located within a narrow genomic region in chromosome VI of faba bean. This explains a substantial part of the variation for resistance to *O. crenata*, and was consistently detected over three seasons (Gutiérrez *et al.*, 2013).

Several resistance mechanisms to various broomrape species has been described in different faba bean accessions (Rubiales *et al.*, 2016). Particularly relevant is the resistance based on low induction of broomrape seed germination (Fernández-Aparicio *et al.*, 2012), that is probably associated with low root exudation of strigolactones (Fernández-Aparicio *et al.*, 2014; Trabelsi *et al.*, 2017), being operative also against *O. foetida* and *P. aegyptiaca*. Low induction of seed germination probably plays a major role in the non-host resistance of faba bean against the low infectivity species (Rubiales *et al.*, 2016). Nevertheless, it is desirable to have cultivars exuding some strigolactones, as these are beneficial for mychorrization and for normal plant architecture and branching. The positive aspect of the identified accessions is that they were selected among good performers in field trials, and therefore did not have detrimental effects associated with lack of strigolactones. It is now understood that there is high specificity in strigolactone/broomrape species recognition (Fernández-Aparicio *et al.*, 2011b). Therefore, these accessions may produce other strigolactones different from those stimulating broomrape germination. Increased understanding of the profile of strigolactones exuded by host plants, and of their specific effects on each broomrape species will assist the design of crops producing the strigolactones required to regulate plant architecture and favour mychorrization, but not those that stimulate broomrape germination.

Preliminary observations suggest that the inheritance of this non-germination trait in faba bean may be simple, which would facilitate resistance breeding and its pyramiding with other resistance mechanisms. The relevance of low germination induction was previously demonstrated by its successful use in sorghum breeding for resistance to *S. hermonthica* (Ejeta, 2007). The genetic basis of this trait in sorghum is simple, being controlled by a single recessive gene (Vogler *et al.*, 1996). The trait has also been induced by mutation in pea (Rameau *et al.*, 2002), in *Arabidopsis thaliana* (Goldwasser and Yoder, 2001) and in tomato (Dor *et al.*, 2010). This indicates monogenic inheritance of the trait. Since the tomato and *Arabidopsis* genomes are published, it may be useful to isolate the responsible gene. This will facilitate the *in silico* isolation of genes with similar functions in other crop species for which the genomes are available, and by PCR analysis from other crops not yet sequenced.

Efforts on pea breeding for resistance to broomrape are relatively recent, in contrast to the long term programmes for sunflower and faba bean. The first comprehensive screenings showed little resistance to *O. crenata* in pea cultivars (Rubiales *et al.*, 2003b). However, several sources of resistance were identified in pea landraces and in wild relatives (Rubiales *et al.*, 2005a). The resistance was incomplete in all cases, but was based on several resistance mechanisms acting at different stages of the infection processes. Resistant wild relatives were successfully hybridised with cultivated pea and submitted to selection, resulting in the development of the first resistant cultivars (Rubiales *et al.*, 2009a; Fondevilla *et al.*, 2017). Pea accessions with reduced induction of broomrape seed germination were also identified from the early screenings (Pérez-de-Luque *et al.*, 2005a; Pavan *et al.*, 2016), and were later reinforced with strigolactone deficient mutants (Rameau *et al.*, 2002).

In these quantitative resistances, the accuracy of phenotypic evaluation is of utmost importance for the study of the genetic basis of resistance. Phenotyping in the field, complementing *in vitro* screenings in minirhizotrons, enabled identification of QTLs governing specific mechanisms of resistance (Fondevilla *et al.*, 2010). The integration of information obtained from QTL analyses with the gene and protein expression analyses performed in pea or in the model plant *Medicago truncatula*, in response to *O. crenata* infection (Castillejo *et al.*, 2009, 2012; Die *et al.*, 2007; Dita *et al.*, 2009), can shortcut selection.

Only moderate levels of resistance to *O. crenata* have been reported in lentil (Fernández-Aparicio *et al.*, 2008b, 2009b), and resistance is also very limited in *Lathyrus sativus* and *L. cicera* (Fernández-Aparicio *et al.*, 2009a, 2011a; Fernández-Aparicio and Rubiales, 2010). However, resistance *O. crenata* is frequently identified in vetch and chickpea germplasm and cultivars (Gil *et al.*, 1987; Goldwasser *et al.*, 1997; Rubiales *et al.*, 2003a; c, 2004; Sillero *et al.*, 2005; Fernández-

Aparicio *et al.*, 2008c), making resistance breeding also feasible for these crops.

Breakdown of resistance

The first resistant sunflower cultivars based on the Or_1 gene were developed in Russia in the 1920s, soon after the onset of the first infections by race A of *O. cumana*. Race B of the parasite appeared by the 1930s and the resistance gene Or_2 was introduced into sunflower cultivars between the 1930s and 1950s. A new race (C) appeared in the 1960s and the resistance gene Or_3 was soon identified and new resistant cultivars released by the 1970s. However, these were effective only until the 1990s, when race D appeared and later races E, F, G and H of the parasite have developed (Molinero-Ruiz *et al.*, 2015). Such continuous emergence and spread of new races of *O. cumana* every 1-2 decades is important, and should force a change in sunflower breeding strategies.

In spite of the importance of the issue, the actual race situation in broomrape in the main infested areas remains unclear, and there is concern that specific reported races in different countries may differ in virulence (Molinero-Ruiz *et al.*, 2014; Martín-Sanz *et al.*, 2016). Therefore, actions are needed on standardization of race identification protocols.

In contrast with *O. cumana*, there is no clear evidence for the existence of races in *O. crenata* or in any other broomrape species. Although variations among *O. crenata* populations in the ability to parasitize different faba bean accessions have been suggested (Maalouf *et al.*, 2011; Rubiales *et al.*, 2016), no physiological races have been undoubtedly reported so far. It is well known that the breakdown of resistance is not equally common in all plant-pathosystems. First, a prerequisite for the development of new virulent pathogen strains is a wide-scale exposure of the crop containing the resistance gene to inoculum of that pathogen. Therefore, breakdown of resistance is a much bigger problem in major than in minor crops. Sunflower is thus somehow paying a price for its success as a major crop. Second, the risk of breakdown of resistance is especially high in crops against airborne pathogens with long-range dispersal of spores, that have both sexual (allowing new recombination) and asexual (allowing fixation of virulent recombination) cycles of reproduction. Thus, the risk of development of new races of *O. cumana* is indeed lower that shown by other pathogens such as rusts and powdery mildews where new races arise every few years (McDonald and Linde, 2002). The emergence of new races of *O. cumana* might be ascribed to recombination and mutation leading to an increase of genetic diversity, and to selection within specific gene pools, or gene flow between wild and weedy *O. cumana* populations (Pineda-Martos *et al.*, 2013, 2014). The predominantly self-pollinating nature of *O. cumana* compared to other *Orobanche* species (Satovic *et al.*, 2009) leads to low intra-population and large inter-population genetic variation facilitating differentiation of separated gene pools (Pineda-Martos *et al.*, 2013). However, *O. cumana* is not strictly self-pollinating and some degree of crosspollination can occur (Rodríguez-Ojeda *et al.*, 2013) contributing also to new genetic diversity.

The success of highly resistant sunflower hybrids widely deployed over large areas with resistance based on single genes is therefore imposing a high selection pressure on the *O. cumana* populations. In contrast, the selection pressure imposed on *O. crenata* populations may be low as there is little resistance among commercial cultivars of most legume crops, and even when some resistance is available; these cultivars are not widely cultivated in large acreages (Rubiales et al., 2006). However, *O. crenata* populations are known to be very heterogeneous (Román *et al.*, 2001, 2002a) and it might well be possible that more virulent *O. crenata* biotypes could be selected when challenged by the widespread use of newly deployed highly resistant cultivars. This deserves constant monitoring.

Conclusions

Broomrapes can evolve by enlarging their host ranges to new crops, or by overcoming resistance genes introduced by plant breeding. Better informed and integrated breeding strategies are required that lead to durable host resistance to these parasitic plants. It is generally agreed that the use of cultivars in which resistance depends on single genes for race-specific hypersensitivity should be avoided. However, there are still several options for managing these resistance genes, including the use of multilines or cultivar mixtures, gene rotations, gene pyramids, and regional gene deployment. The deployment of these genes should be complemented with other management strategies that reduce parasite populations and that limit the expansion of newly developed virulence (Mundt, 2014). To achieve this, increased knowledge is required, on host resistance genes, on the broomrape populations, and on factors affecting their diversity and the development of broomrape infection epidemics.

The key to the development of cultivars with long-lasting resistance is diversity (Rubiales and Niks, 2000). A first strategy could be pyramiding more than one gene or by combining monogenic and polygenic resistance with the help of reliable molecular markers for efficient selection. The durability of pyramids is reduced when cultivars with single genes are used concurrently with the pyramided cultivar (Lof *et al.*, 2017), particularly when variability of virulence exists in the parasite populations. There is still a range of mechanisms of resistance not exploited in broomrape resistance programmes. Rather than pyramiding several genes acting at the same level, combining different resistance mechanisms providing multiple barriers not easily overcome by simple race-type parasite changes may provide more durable outcomes (Niks and Rubiales, 2002). Durability is not solely an issue of the number of genes, but also depends on the mechanism of action of the genes. It is widely acknowledged that complex resistance is likely to be more durable than monogenic resistance. However, the fact is often neglected that we have excellent examples of durable resistances conferred by single genes. Examples are *mlo* genes conferring durable resistance to powdery mildew in barley (Lyngkjær *et al.*, 2000), *er1* to powdery mildew in pea (Iglesias-García *et al.*, 2015), or *Lr34* to rust in wheat (Rubiales and Niks, 1995). Thus, the "low germination induction" resistance, likely to be singly inherited, could be most relevant for providing durable outcome, particularly when used in combination with other mechanisms.

Durability of resistance genes used singly or in pyramids depends largely on pathogen population size and gene flow, and it is recommended that this strategy be complemented with other parasite management practices to reduce populations, such as chemical control (Stam and McDonald, 2018). Major efforts are required to better understand broomrape population dynamics and to carefully design spatial and temporal deployment of resistance genes with the aid of information on virulence distribution, which presently is clearly insufficient. Efforts are needed to define sanitation and quarantine strategies to limit the spread of broomrape seeds to areas free of infestations, and to prevent expansion of new races.

Novel biotechnology approaches will accelerate and improve the process (Gressel, 2013). The complete genome sequence of hosts (e.g. Badouin *et al.*, 2017) and the parasitic plant species (Westwood *et al.*, 2012) will also help in understanding parasite virulence and host resistance mechanisms. This will allow direct screening for molecular diversity in specific genome regions associated with resistance. New genome editing technologies such as CRISPR/Cas9 will impact on resistance breeding. In these ways increased efforts to deliver parasite resistant cultivars can be effective, using the tools of modern plant breeding (Dita *et al.*, 2006; Rispail *et al.*, 2007; Yoder *et al.*, 2009). Strategies to build host resistance have been approached by engineering crops with broomrape-inducible expression of toxins specifically targeting the penetrating broomrape seedlings (Aly *et al.*, 2007), or by trans-specific gene-silencing of key metabolic genes critical to broomrape life cycles (Dubey *et al.*, 2017).

As evolution of broomrape populations is particularly affected by selection pressure exerted by resistant cultivars, careful adoption of these approaches will contribute to delaying development of new races which defeat existing resistances. However, the investment required in these new technologies should not reduce the use of well-established approaches to control parasite population size, and to prevent human-driven long distance spread of parasite seed (Rubiales *et al.*, 2009b; Goldwasser and Rodenburg, 2013). These strategies will reduce the chances of appearance, fixation and spread on new genetic parasite variants.

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