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Genetic and agronomic approaches to control *Orobanche* and *Phelipanche* spp. parasitic weeds in vegetables and legumes

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ABSTRACT

Broomrapes (*Orobanche* and *Phelipanche* spp.) rely on the presence of a host plant for nourishment. Based on the release of specific molecules by the crop plant, their seeds germinate and eventually establish a vascular connection with host roots through a haustorium. Therefore, they deprive their hosts of water and nutrients, posing a severe threat to vegetable and legume crops worldwide. Due to their growth behaviour, amount and longevity of seeds released, and, generally, a large variety of hosts, the control of parasitic plants is rather difficult. In this review, we give an update about agronomic and genetic approaches controlling host-parasite interactions. Management of broomrapes in vegetables and legumes relies on different approaches: trap and catch crops; suicidal germination by strigolactones (SLs), analogues and mimics; SL degradation; biological and chemical control; other control methods. Further, the production of resistant cultivars is highly desirable. Some natural sources of resistance have been identified in landraces and wild relatives of vegetable and legume crops. Additional variability has been discovered by artificial mutagenesis, but it has been poorly exploited for breeding commercial cultivars. Recent genomic knowledge in parasitic and host species opens new perspectives for the comprehension of molecular bases of interaction and applied breeding, using molecular assisted breeding and biotechnological approaches aimed to modify genes controlling the various stages of parasitization. Anyway, the combination of different genetic resistance mechanisms with agronomical management practices is mandatory to develop a durable containment strategy.

Keywords*:* Broomrapes, *Orobanche*, *Phelipanche*, Strigolactones, Vegetables, Legumes.

INTRODUCTION

Hemi- and holoparasitic plants depend on a host plant for nourishment, using a haustorium that establishes a vascular connection between the two organisms. They lack a root apparatus and have lost, partially or completely, the ability to photosynthesize. Broomrapes (*Orobanche* and *Phelipanche* spp.) and witchweed (*Striga* spp.), members of *Orobanchaceae*, and dodders (*Cuscuta* spp.), belonging to *Convolvulaceae*, can determine significant yield losses (Fernández-Aparicio *et al.*, 2016; Rubiales *et al.*, 2018).

While *Cuscuta* spp. grow above-ground and attack the epigean organs of many crops, (Albert *et al.*, 2008; Runyon *et al.*, 2010; Kebede and Ayana, 2018), broomrapes and witchweed grow underground, after the perception of secondary metabolites released in the rhizosphere by host roots (Bouwmeester *et al.*, 2021). Subsequently, tubercles develop on infected roots from which new shoots will grow (Figure 1). Striga affects mainly cereals (*e.g.,* sorghum - *Sorghum bicolor L.*; rice - *Oryza sativa* L.; maize - *Zea mais* L.) and legumes (cowpea – *Vigna unguiculata* (L.) Walp.) in tropical and sub-tropical areas (Joel, 2000), whereas *Orobanche* spp. and *Phelipanche* spp. are preferentially present in agroecosystems with a Mediterranean climate (*i.e.,* southern Europe, northern Africa, and Middle East, but also some areas of California, Chile, and Australia (Casadesús and Munné-Bosch, 2021). The infestation of *Orobanche* and *Phelipanche* spp. involved about 16 million hectares in 1991 worldwide (Parker, 2009).

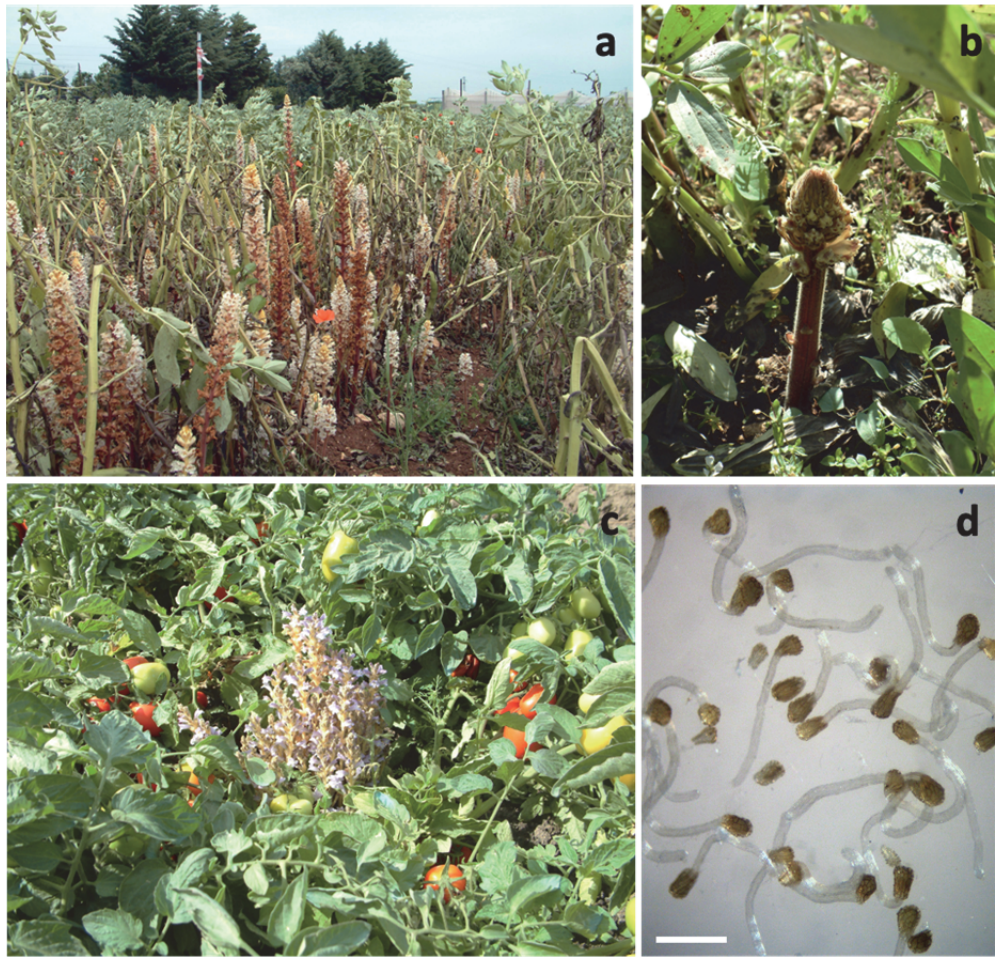

Figure 1. Infestations of *Orobanche crenata* (a,b) and *Phelipanche ramosa* (c) in broad bean and tomato fields, respectively. In (d) germinating seeds of *P. ramosa.* Bar in panel d is about 1 mm.

Out of ten broomrape species relevant to agriculture, five (P. ramosa (L.) Pomel., P. *aegyptiaca* (Pers.) Pomel., *O. crenata* Forssk., *O. foetida* Poir. and *O. cernua* Loefl.) affect vegetables and legumes (Kebede and Ayana, 2018) (Figure 2). *O. crenata*, and to a lesser extent *O. foetida*, preferentially colonize carrot (*Daucus carota* L.) and legumes, especially faba bean (*Vicia faba* L.), chickpea, pea (*Pisum* spp.), lentil (*Lens esculenta* Moench.), with about 4 million Ha of legumes at risk in the Mediterranean region (Parker, 2009). *O. cernua*

constitutes a severe risk in *Solanaceae* crops, including tomato, pepper (*Capsicum annuum* L.) and eggplant (*S. melongena* L.). Tomato and potatoes can be parasitized also by *P. ramosa* (L.) Pomel., with up to 80% of losses in tomato production (Casadesús and Munné-Bosch, 2021). *P. aegyptiaca* affects the same hosts as *P. ramosa* plus cucurbits (*Cucurbitaceae*) and legumes (Parker, 2009; Fernández-Aparicio *et al.*, 2012; Rubiales *et al.*, 2016; Casadesús and Munné-Bosch, 2021).
Agronomic and genetic approaches to combat *Orobanche* spp. and *Phelipanche* spp. attacking vegetable and legume crops are discussed in the present review.

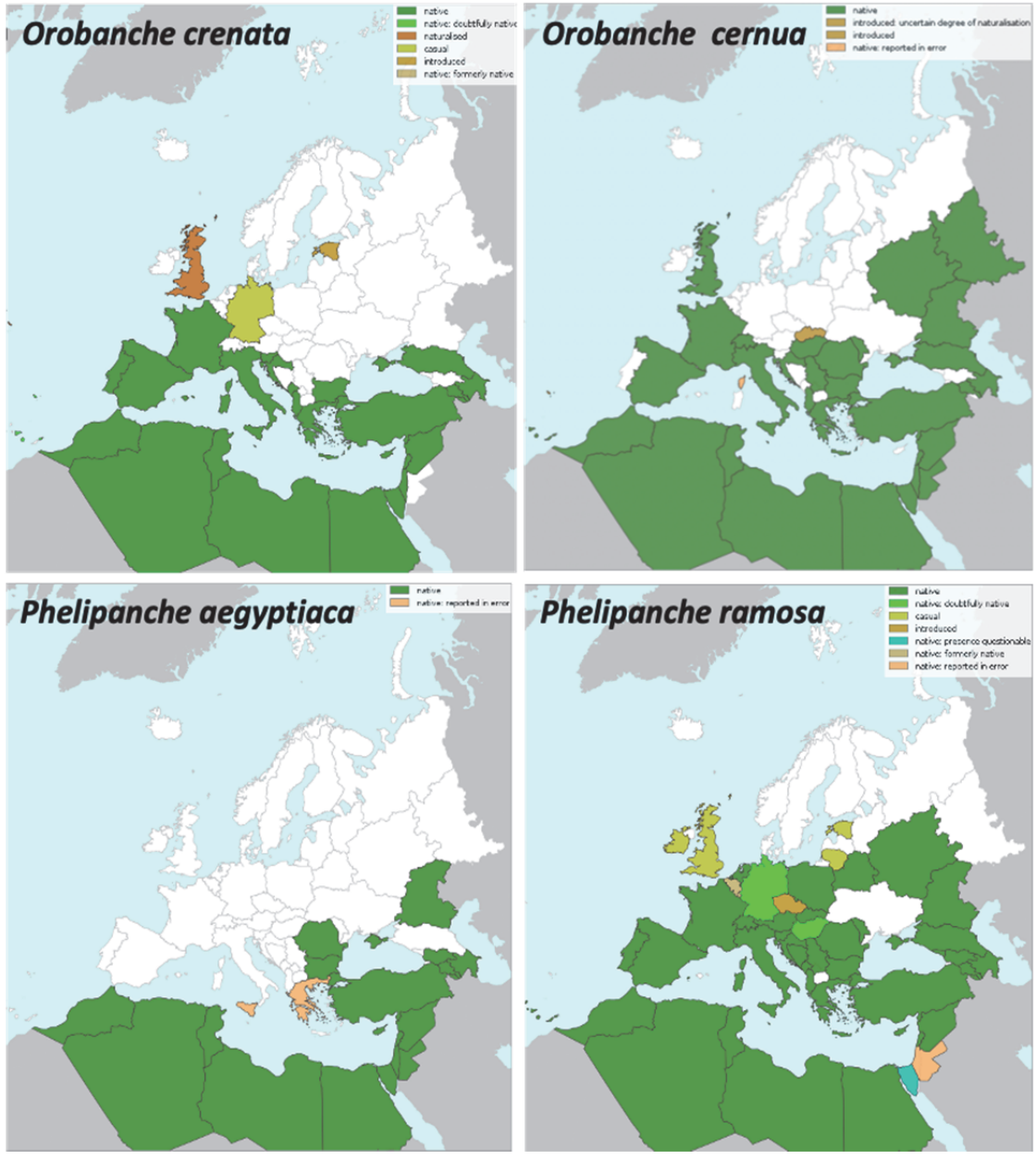

Figure 2. Distribution of *Orobanche crenata, O. cernua*, *Phelipanche aegyptiaca* and P. *ramosa* in Europe and the Mediterranean Basin. Extracted from The Euro+Med PlantBase (https://europlusmed.org/).

LIFE CYCLE

Seeds of *Orobanche* spp. and *Phelipanche* spp. can persist in the soil for many years. They germinate only in appropriate moist and temperature conditions, and in the presence of the proper stimulus (Bouwmeester *et al.*, 2021).
The latter is exuded in the rhizosphere by host roots (Waters *et al.*, 2017) and is represented mainly by strigolactones (SLs), phytohormones involved also in the inhibition of secondary shoot branching, thus in plant architecture, and interactions with arbuscular mycorrhizal fungi (AMF) (López-Ráez *et al.*, 2008a; Casadesús and Munné-Bosch, 2021). Parasites can discriminate against hosts based on the identity of exudated SLs (Clarke *et al.*, 2019). Indeed, plant species/ecotypes produce more than 25 SL types and combinations (Brun *et al.*, 2021). They derive from carotenoids and several key genes of their biosynthetic pathway have been characterized in past years (Seto *et al.*, 2014; Jia *et al.*, 2018). Other molecules (*e.g.*, sesquiterpene lactones, polyphenols, and isothiocyanates) can be also involved in the germination of some parasitic species, such as *O. cumana* (Raupp and Spring, 2013), *O. foetida* (Evidente *et al.*, 2010), and *P. 66ramose* (Auger *et al.*, 2012).
Upon germination, pseudo-roots of the parasitic plant move towards host roots sensing an SL gradient. Thereafter, a haustorium is differentiated thanks to specific haustorium-inducing factors (HIF) (*i.e.*, flavonoids, phenolic acids, quinones, cyclohexene oxides, and cytokinins). The parasite's endogenous levels of auxins and cytokinins allow for the correct growth and development of haustorium, until it reaches and invades the host root (Goyet *et al.*, 2017, 2019; Clarke *et al.*, 2019; Casadesús and Munné-Bosch, 2021).
Auxins and cytokinins are fundamental, respectively, also for the correct formation of the vascular continuum between the two organisms (Aloni, 2015), and for the maintenance of the source-sink connection (Roitsch and Ehneß, 2000). Jasmonic acid, salicylic acid and abscisic acid (ABA) are also involved in the initial stages of holoparasitic plant–host communication (Gutjahr and Paszkowski, 2009; Torres-Vera *et al.*, 2016).
After the attachment to the host root vasculature, tubercles develop on the root surface. These structures contain a reserve of hexoses, amino acids, and starch necessary to support the emergence of above-ground shoots carrying flowers and seeds (Draie *et al.*, 2011; Abbes *et al.*, 2009). Seeds, very small and numerous, facilitate the dispersion and formation of a persistent seed bank in the soil (Delavault, 2015).
Parasite plants withdraw water, nitrogen, and carbohydrates from the host (Péron *et al.*, 2017), exchanging, at the same time, micro-RNAs that interfere with host mRNAs connected to several functions (auxin receptors, development regulators, pathogen defense, and phloem function) that increase the parasite fitness (Clarke *et al.*, 2019).
The management of *Orobanche* spp. and *Phelipanche* spp. is not an easy task, due to interactions with multiple hosts, the underground mechanism of parasitism, the ability to synchronize the life cycle with that of the host, and the high reproductive potential (Fernández-Aparicio *et al.*, 2016).

MANAGEMENT

The main difficulties in controlling parasitic *Orobanchaceae* weeds are due to the characteristics of the parasitism and the properties of their seeds. The physical and physiological connection between host and parasite hamper most of the direct control methods (e.g., mechanical, physical, and chemical) attempting to control the weed without damaging the host.
The enormous seed production by each plant, the minute size of the seeds, their longevity, and easy dispersal cause a rapid increase in the soil seed bank, even when the original infested area is minimal, or when only a few plants are left after effective management

practices, making of an infested field, a field permanently infested. Thus, the 'indirect' control, i.e., the containment of infested areas and prevention of seed dispersal should be a major objective of parasitic weed management strategies, besides direct control interventions against the parasites.

Table 1. Examples of control strategies for the management of *Orobanche* and *Phelipanche* spp. in vegetables and legumes[a].

Approach	Aim	Parasitic plant	Remarks	References
Trap crops	Reduce the seed bank in the soil through stimulation of parasitic seed germination.	*O. minor, P. aegyptiaca, O. cumana*	Examples of trap crops: sorghum; flax; soybean; wheat; radish; fennel; cumin; maize. Could be effective only in the long term	Al-Menoufi, 1989; Parker and Riches, 1993; Saxena *et al*., 1994; Kleifeld *et al*., 1994; Acharya, 2014; Aksoy *et al*., 2016
Catch crops	Reduce the seed bank in the soil through stimulation of parasitic seed germination.	*Orobanche and Phelipanche spp.*	Examples of catch crops: faba bean; field mustard; white mustard; lentil; berseem clover; fenugreek.	Sauerborn and Saxena, 1986; Parker and Riches, 1993; Kleifeld *et al*., 1994; Dhanapal *et al*., 1996; Acharya *et al*., 2002; Fernández-Aparicio *et al*., 2008,
			All plants must be removed from the field before flowering and seed dispersal of the parasitic plants	
Suicidal germination by SLs, Analogues and Mimics	Reduce the seed bank in the soil through stimulation of parasitic seed germination in the absence of a host	*O. cumana, P. aegyptiaca,*	Synthesis of natural SLs for effective field applications is not feasible yet due to their complex structure.	Chang *et al*., 1986; Evidente *et al*., 2009; Joel *et al*., 2011; Evidente *et al*., 2011
			Natural compounds (e.g., from sunflower; pea; common vetch) proved to have a modest stimulatory activity only under lab conditions	
SL Degradation	Prevent parasitic weed germination by degrading the stimulatory signal.	-	To achieve degradation of SLs soon after they are released into the soil, both chemical and biological approaches can be used. Far from the practical use	Kannan and Zwanenburg, 2014; Boari et al., 2016
Biological control	Suppress or reduce parasitic weed growth and diffusion	*O. cumana; O. cernua; P. ramosa; P. aegyptiaca*	Biological control agents include various organisms, among them: insects (e.g., *Phytomyza orobanchia*). plant pathogenic fungi (e.g., *Fusarium sp.*), bacteria (e.g. *Pseudomonas aeruginosa*)	Parker and Riches, 1993; Thomas, 1998; Amsellem *et al*., 2001; Klein and Kroschel, 2002; Boari and Vurro, 2004; Zermane et al., 2007; Bouwmeester *et al*., 2007; Barghouthi and Salman, 2010; Watson, 2013
Chemical control	(Selectively) eliminate parasitic species	*Orobanche and Phelipanche spp.*	It includes three approaches: (a) soil fumigation; (b) application of the herbicide through the soil; (c) translocation from host plant foliage into root-attached	Foy *et al*., 1989; Hershenhorn *et al*., 1998a; Hershenhorn *et al*, 1998b; Goldwasser *et al*., 2001; Eizenberg *et al*., 2004; Gressel, 2009; Ephrath and Eizenberg, 2010
			Monitoring of underground parasite development facilitates the development of modelling approaches for precise parasite control.	
			Target-site herbicide resistant hosts increase selectivity of systemic herbicides. The risk of developing herbicide resistance in the parasites is an issue.	
Other control methods	Reduce the contact between host and parasite; increase the capability of the host plant to 'tolerate' the parasite's attack; remove the parasite or reduce seed viability	*Orobanche* and *Phelipanche* spp.	They include cultural, mechanical, and physical practices: crop rotation, fallowing, transplanting, hand-pulling, nitrogen fertilization, time and method of planting, intercropping, and solarization.	Sauerborn *et al*., 1989; Parker and Riches, 1993; Verkleij and Kuiper, 2000; Mauromicale *et al*., 2005

[a] *For a more comprehensive list of control strategies, see Fernández-Aparicio et al. (2016)*

Considering the importance of SLs in the life cycle of these parasites, some management strategies act at this level, e.g., trying to prevent the stimulation of seed germination, or conversely to favor it, in the absence of a host (Table 1).

Trap and Catch Crops

Trap crops are non (false)-host crops, the roots of which release strigolactones, thus stimulating parasitic plant seed germination. Since they are not a host, the viable connection of the haustorium to the host root is prevented, and thus any further development of the parasite (Parker and Riches, 1993).
Catch crops are host plants that also produce strigolactones but do allow attachment by the parasite. In this case, the crop is simply removed from the field after the parasite seeds have germinated (and possibly attached), but before flowering and seed dispersal of the parasite are initiated. Thus, any susceptible crop can be a potential catch crop. What makes a species more suitable as a catch crop is thus the structure of the root system and the capability to release SLs.
The aim of using trap and catch crops is not to directly control the parasitic weeds, but rather to reduce the infestation over time, by reducing the seed bank in the soil. This effect is also defined as "suicidal" germination. Trap crops can be used both for intercropping, i.e., by growing it in between the main crop, and as the main crop on itself.
Besides its main effect, the induction of seed germination, a non-host crop can potentially also contribute to parasitic weed control by providing shade and reducing soil temperature (as a cover crop).
Several trap crops have been reported to reduce broomrape seed banks (even if some of them were effective only under controlled conditions), such as sorghum (*S. bicolor*), flax (*Linum usitatissimum* L.) and soybean (*Glycine max* L.) (Al-Menoufi, 1989; Kleifeld *et al.*, 1994; Saxena *et al.*, 1994). Other examples of effective broomrape trap crops include different wheat cultivars against *O. minor*, radish, linseed, fennel, and cumin against *P. aegyptiaca*; and hybrid maize against *O. cumana* (Acharya, 2014; Aksoy *et al.*, 2016).
Important crops reported as potential catch crops for broomrape control are faba bean, field mustard (*Brassica campestris* L.), white mustard (*Sinapis alba* L), lentil (*Lens culinaris* Medik.), berseem clover (*Trifolium alexandrinum* L.) and fenugreek *(Trigonella foenum-graecum* L.) (Sauerborn and Saxena, 1986; Parker and Riches, 1993; Kleifeld *et al.*, 1994; Dhanapal *et al.*, 1996; Acharya *et al.*, 2002; Fernández-Aparicio *et al.*, 2008).

Suicidal Germination by SLs, Analogues and Mimics

As an alternative to trap and catch crops, which require that they are grown for a certain period on the contaminated field, suicidal germination can potentially also be provoked by applying compounds with stimulatory activity directly to the field. Also, in this case, the parasitic seeds would germinate in the absence of a host and then would not survive. Generally, the most active molecules inducing seed germination are the naturally occurring SLs. Unfortunately, the structures of natural SLs are very complex, and thus their synthesis for effective field applications is not feasible. Therefore, alternative approaches to producing germination stimulants have been explored, such as the synthesis of simpler and cheaper SL analogs, the use of natural compounds from other sources, and the use of other compounds from whatever origin with stimulatory activity.
Natural products that have similar activity as SLs have been isolated from a cultivar of sources. For example, dehydrocostus lactone was identified in the root exudates of sunflower as the natural germination stimulant for *O. cumana*, a root parasite specific of

sunflower (Joel *et al.*, 2011); dihydrosorgoleone was identified in the root exudate of sorghum and proved to stimulate the germination of *S. asiatica* seeds (Chang *et al.*, 1986); peagol and peagoldione were isolated from pea (*Pisum sativum*) root exudates and exhibited germination stimulatory activity in particular on *P. aegyptiaca* (Evidente *et al.*, 2009), whereas soyasapogenol B and trans-22-dehydrocampesterol were isolated from common vetch (*V. sativa*) exudates and stimulated germination of different broomrape species (Evidente *et al.*, 2011). However, most of these compounds proved to have only a modest stimulatory activity only under lab conditions. Thus, their use for controlling parasitic weeds is very far from being put into practice.

SL Degradation

A different approach proposed for controlling root parasitic weeds is the degradation of the SLs soon after they are released into the soil by the host roots, and before the stimulatory signal reaches the seeds of the parasite. In this case, the aim of this approach would not be a reduction of the seed bank over time, but rather to enable the growth of susceptible crops on infested fields. To achieve this, both chemical and biological approaches were explored.
For the chemical approach, borax, an inexpensive and eco-friendly salt, was successfully tested under laboratory conditions (Kannan and Zwanenburg, 2014).
For practical field applications, formulation of borax would be necessary, and the method should be optimized to avoid too high a concentration of boron in the long run due to its continuous use. For the biological approach, microbes able to degrade SLs were tested in lab conditions (Boari *et al.*, 2016). However, both strategies are still very far from practical field application.

Biological control

This approach is based on the use of living organisms (e.g., insects, pathogenic fungi, and bacteria) to suppress or reduce parasitic weed growth and diffusion. This control method was and still is considered very promising because the long underground growth stages of the parasitic plants are ideal targets for the biological control agents. However, although considerable attention and efforts have been given to this approach, until now no biological control agents have reached the field application.
Many insects have been collected on *Orobanche*, but most were not specific to parasitic plant species (Klein and Kroschel, 2002).
The fly *Phytomyza orobanchia* Kalt was reported to be host specific on *Orobanche*, but its effectiveness and the distribution of its population are limited because of the presence of antagonists and some cultural practices. Moreover, since only the insect's immature stages are seed-feeders, the impact is limited to the reduction of the seed bank into the soil over time. The results indicated that the biocontrol agents in most cases do not provide the level of control desired by farmers.
Soil microorganisms interfering with parasite life cycle are also very attractive. Numerous fungi and bacteria can infect parasitic weeds (Barghouthi and Salman, 2010), while other microbes may improve crop growth and deter parasitic attacks. Soils that naturally suppress populations of parasitic weeds occur (Zermane *et al.*, 2007). Vital and intensive interactions occur amongst the host plant, soil, and microorganisms in the rhizosphere of parasitic plants. Important biochemical interactions and exchanges of signal molecules occur between parasitic plants and soil microorganisms (Bouwmeester *et al.*, 2007).
Like other plants, also broomrapes can be attached by plant pathogenic fungi. There were early attempts in the former Soviet Union, Hungary, China, and Iran to exploit pathogens

including *Fusarium lateritium* Nees: Fries, *F. solani* (Martius) Saccardo, *F. oxysporum*, and *Rhizoctonia solani* J.G. Kuhn for broomrape biocontrol, including the formulation and distribution of a quite mysterious 'Product F' in Russia (Parker and Riches, 1993).
Later, many other fungal isolates were reported to be promising biocontrol agents for the control of *Orobanche*. Approximately 30 fungal genera are reported to occur on *Orobanche* spp., being *Fusarium* sp. the most frequently associated with diseased Orobanche (Watson, 2013). The Fusarium (FOO) isolate exclusively attacks *O. cumana* and susceptible biotypes of *O. aegyptiaca* (Thomas, 1998). Other Fusarium isolates [*F. oxysporum* (FOXY) and *F. arthrosporiodies* (FARTH)] attack *O. aegyptiaca*, *O. cernua*, and *O. ramosa* (Amsellem *et al.*, 2001). Strains of *F. oxysporum* and *F. solani* were isolated in southern Italy (Boari and Vurro, 2004).

Chemical control

Chemical control has been extensively explored since the '70s, and three main approaches have been taken into consideration, i.e., (a) soil fumigation (Foy *et al.*, 1989); (b) application of the herbicide through the soil (Hershenhorn *et al.*, 1998a ; Goldwasser *et al.*, 2001); (c) leaf application with translocation of the herbicide through the host plant foliage into the root-attached parasite (Goldwasser *et al.*, 2001 Eizenberg *et al.*, 2004).
Methyl bromide was a highly effective fumigant for controlling broomrape seeds in the soil, but it has been banned since many years due to its very negative impact on the environment; other registered fumigants (e.g., dazomet, metham sodium, 1,3-dichloropropene, methyl iodide, ethylene dibromide) have proved to be less effective in broomrape seed control. Obviously, this approach aims at eliminating all the seeds of the parasitic plant species. It is effective also against other organisms (even beneficial) living in the soil and can be applied only in absence of the crop.
A more 'natural' approach is the use of crops able to release allelopathic compounds acting as natural fumigants and able to inhibit seed germination (see above).
Broomrapes are more sensitive to herbicides in the underground stages of their lifecycle than in the above-ground developmental stages (Eizenberg *et al*., 2004, 2018). Therefore, understanding the dynamics of parasitism is necessary to effectively control the parasite using herbicides. In non-parasitic weeds, the herbicide rate can be specifically adjusted according to the phenological stage when weeds are observable. However, the target stage for broomrape control using herbicides occurs when the broomrapes are in their subsurface stages, for example at the stage of seedlings or small attachments.
Another issue that is critical for the success of chemical control is delivering the herbicide to the broomrape throughout the growing season, considering that the seeds of the parasites continuously germinate and infect new roots. A limited number of herbicide modes of action are appropriate for broomrape control.
As broomrapes completely lack chlorophyll, herbicides that inhibit the photosynthetic system cannot be considered. Moreover, the parasite tissues are directly connected with host root tissues, allowing systemic herbicides to move from host to parasite.
Thus, chemical control is complicated because: (i) chemical control can only be used as a prophylactic treatment, because in most cases the level of infestation is unknown, (ii) the parasite is directly connected to the host and, therefore, only highly selective herbicides can be used, (iii) if the herbicide reaches the parasite through the conductive tissues of its host, the host must be tolerant to the herbicide by mechanisms which are not based on its metabolic degradation or inactivation, (iv) the parasite germinates continuously throughout the season and throughout the entire cultivated soil-depth profile.

Herbicide application through the soil is intended to control germinating broomrape seeds or young attachments on host roots.

The effectiveness of this mode of application depends mainly on the phytotoxicity of the herbicide to the parasite and its selectivity to the host crop (Hershenhorn *et al.*, 1998b; Goldwasser *et al.*, 2001). Approaches for the selective control of broomrape using systemic herbicides are based on the aromatic amino acid synthesis inhibitor glyphosate, or the branched-chain amino acid synthesis, acetolactate synthase (ALS) inhibitors, imidazolinones and sulfonylureas (El-Rokiek *et al.*, 215). Sulfonylurea herbicides are applied to the host plant and are rapidly translocated to the roots and the parasite (when attached) via acropetal and basipetal translocation.

Imidazolinone herbicides are absorbed and translocated through the host to the meristematic tissues where the ALS enzyme is highly active. Herbicide effectiveness and timing of application vary depending on the crop species (host) and herbicide. To achieve successful control, the developmental stage of the parasite should be known.

In the past, as it was unpredictable, an empirical approach to broomrape control was used. The time for herbicide application was estimated according to the calendar and did not consider thermal or physiological time. Protocols were based on the application of herbicides belonging to the sulfonylurea or imidazolinone families, or glyphosate, applied at low rates two to four times to crop leaves or to soil, starting 3 weeks after planting. However, the success of these control methods was limited or at least variable.

Developing Models for Optimising Chemical Control of Root Parasitic Weeds.

The recent advent of new technologies allows the monitoring of parasite development under the soil surface, facilitating the development of modelling approaches for precise parasite control at its desired subsurface developmental stage. Therefore, new protocols based on predictions of the exact developmental stage of the parasite have been introduced.

The modelling approach describes and facilitates the prediction of host–parasitic weed interactions and population dynamics, by dealing with the order of specific phenological events such as seed germination, attachment to the host, tubercle development or parasitic weed emergence. The rate of germination of parasite seeds is estimated in terms of a particular number of germinating seeds in the host rhizosphere.

Thermal time-based models (cumulative growing degree days) to predict the dynamics of broomrape parasitism have been developed for *O. cumana* in sunflower, *P. aegyptiaca* in tomato and *O. minor* in red clover (Ephrath and Eizenberg, 2010; Vurro *et al.*, 2017).

The objective of these models is to predict the timing of specific developmental stages of the parasite which are sensitive to the herbicide, in order to facilitate optimal chemical control.

For example, the integration of soil-applied herbicides together with post-emergence applied herbicides for *P. aegyptiaca* control in processing tomato proved to be particularly effective when following the application of a combination of one to three sulfosulfuron applications between 200 and 600 growing degree days (GDD) and one or two imazapic applications at a later growth stage. Overhead irrigation using either moving pivot or sprinkler irrigation for delivering sulfosulfuron into the soil was essential for successful applications.

Herbicide-Resistant Crops for Broomrape Control. Herbicides used for broomrape management are not adequately selective to the crops. Long-term control could be attained if the crops do not metabolise the herbicide, that is, have target-site resistance.

When the host is target-site resistant to herbicides, systemic herbicide rates could be optimised for parasitic weed control.

Target-site resistances have allowed foliar applications of herbicides inhibiting enolpyruvylshikimate phosphate synthase (EPSPS) (glyphosate), acetolactate synthase (ALS) (e.g., chlorsulfuron, imazapyr) and dihydropteroate synthase (asulam) for *Orobanche*

control in experimental conditions with various crops (Gressel, 2009, and references therein). Large-scale use of imazapyr as a seed dressing of imidazolinone-resistant maize has been commercialised for *Striga* control (Gressel, 2009).
Herbicide-resistant hosts could be obtained by classical breeding (Clearfield cultivars), genetic engineering and mutagenesis. So far, it seems that only classical breeding and genetic engineering have the potential for commercialisation. Further research should be invested in breeding crops resistant to herbicides, either genetically modified or by mutagenesis or Clearfield selected. Even though the introduction of genetically modified crops is currently limited, herbicide companies are highly motivated to release Clearfield cultivars.
Crop resistance to herbicides could represent a useful instrument for controlling parasitic weeds. However, the use of herbicide-resistant crops should be carefully managed to reduce the risk of developing herbicide resistances in the parasites.
In addition, research into the mechanism of herbicide action in host–parasite systems may open the way to using new herbicide families for the chemical control of parasitic weeds.

Other control methods

Cultural, mechanical, and physical practices have been attempted for parasitic weed control, including crop rotation, fallowing, transplanting, hand-pulling, nitrogen fertilization, time and method of planting, intercropping, and solarization (Parker and Riches, 1993).
The impact of these methods is quite modest, or evident only in the long run. Moreover, in general, only a few can be considered control methods (i.e., hand-pulling and solarization) whereas all the others tend to give some advantages to the crop with respect to the parasite (e.g., escape the germination, grow faster, or produce more biomass to better tolerate the attack of the parasite). These methods could contribute preventing the distribution of parasite seeds from infested to uninfected areas.
Hand-pulling. This method could be effective for some crops, especially in fields with a relatively low infestation or where the land cover by crops is low, but it is very expensive and time-consuming. However, parasitic plants can be removed only after their emergence, when most of the damage has been accomplished.
Thus, removing mature plants from an infested field before seed dispersal will reduce only the number of seeds, not increase the host yield in the short term (Verkleij and Kuiper, 2000).
Solarization. The exploitation of summer sunlight to reach high temperatures (55 °C) under clear polyethylene mulch covering the soil for several weeks is another approach to achieve the destruction of the parasitic weed soil seedbank.
Soil solarization was successfully applied in some European Countries and the Middle East for crops of tomato, eggplant, faba beans, lentil, and carrot, where the environmental conditions are favourable to the use of this method (Sauerborn *et al.* 1989; Mauromicale *et al.*, 2005).

Genetic Strategies

Due to their growth behaviour, amount, and longevity of seeds released, and, generally, a large cultivar of hosts, the control of parasitic plants can be difficult.
The production of resistant crop cultivars, achieved by a number of different means, can represent a durable and reliable alternative to reduce their impact on cultivations (Table 2).

Table 2. Examples of various genetic approaches pursued to obtain resistant genotypes to *Orobanche* and *Phelipanche* spp. in vegetables and legumes

Genetic approach	Parasitic plant	Host plant	Remarks	References
Intra / Interspecific hybridization	*P. ramosa, P. aegyptiaca*	Tomato	Various processing tomato varieties derived from breeding line PZU-11	Avdeyev and Scherbinin, 1977; Avdeyev *et al.*, 2003
	O. crenata	Pea	Advanced breeding lines derived from wide crosses with resistant *P. fulvum*, *P. sativum* ssp. *elatius*, *P. sativum* ssp. *syriacum*, and with pea landraces	Rubiales *et al.*, 2020
	O. crenata, *O. foetida, P. aegyptiaca*	Faba bean	Two breeding lines	Fernández-Aparicio *et al.*, 2012
	O. foetida (partial resistance)	Chickpea	Three genotypes	Nefzi *et al.*, 2016
Mutagenesis (fast-neutrons)	*O. cernua*, *O. crenata, P. aegyptiaca, P. ramosa*	Tomato	A mutant with low expression of the *SlCCD7* gene and SLs deficiency	Koltai *et al.*, 2010; Dor *et al.*, 2010, 2011
Mutagenesis (EMS)	*P. ramosa*	Tomato	Six M2 mutant genotypes	Kostov *et al.*, 2007
Mutagenesis (gamma rays)	*O. foetida* (partial resistance)	Faba bean	Two mutant lines	Mejri *et al.*. 2018
Mutagenesis (gamma rays)	*O. foetida* (partial resistance)	Chickpea	Five mutant lines	Brahmi *et al.*, 2016
TILLING	*P. ramosa*	Tomato	A mutant with altered SL synthesis	Minoia *et al.*, 2010; Disciglio *et al.*, 2016
	P. aegyptiaca, O. minor	Tomato	Two Micro-Tom genotypes with a point mutation in the *CCD8* gene and a branched phenotype	Hasegawa *et al.*, 2018
Molecular assisted selection	*O. crenata*	Pea	Two QTLs for resistance detected, overall explaining 21% of total variation	Valderrama *et al.*, 2004
	O. crenata	Pea	Four QTLs explaining 33% of phenotypic variation identified in a RIL population	Fondevilla *et al.*, 2010
	O. crenata	Faba bean	Three QTLs explaining 74% of phenotypic variation identified	Román *et al.*, 2002
Transgenesis	*P. aegyptiaca*	Tomato	Transgenic plants expressing in roots the insect-derived sarcotoxin IA gene	Radi *et al.*, 2006
	P. aegyptiaca	Carrot	ALS-transgenic genotypes resistant to the imazapyr herbicide	Aviv *et al.*, 2002
	P. aegyptiaca	Potato	Transgenic plants resistant to the Asulam- herbicide	Surov *et al.*, 1998
RNAi (parasitic plant genes)	*P. aegyptiaca*	Tomato	Transgenic host plants expressing the parasitic M6PR-mRNA in an inverted-repeat configuration	Aly *et al.*, 2009
	P. aegyptiaca	Tomato	Transgenic host plants expressing a multiple-sequence RNAi construct targeting three *P. aegyptiaca* key genes (*PaACS, PaM6PR, PaPrx1)*	Dubey *et al.*, 2017
RNAi (host plant genes)	*P. ramosa*	Tomato	Silencing of either *CCD7* or *CCD8* host genes. Plant phenotype severely affected	Vogel *et al.*, 2010; Kohlen *et al.*, 2012
Genome editing	Various *Phelipanche* and *Orobanche* species	Tomato	Knock-out of diverse genes involved in SL biosynthesis (*D27*, *CCD7*, *CCD8, MAX1, P450 CYP722C*) or transport (ABCG44 and ABCG45). Varying levels of pleiotropic effects on phenotype and AMF colonization	Bari *et al.*, 2019, 2021a, 2021b; Wakabayashi *et al.*, 2019; Nicolia *et al.*, 2021a

Conventional breeding

Diverse genetic sources of resistance to *Orobanche* spp. and *Phelipanche* spp. have been identified in cultivated vegetable and legume cultivars as well as corresponding wild relatives. The release of germination stimulants or haustorium-inducing factors in low amounts or in a different and/or less-inducing composition is responsible for pre-attachment resistance mechanisms, leading to the escape of parasitic-seed germination or haustorium-initiation. On the other hand, a resistance reaction directed to the establishment of the parasite depends on the accumulation of phenolic compounds (callose or suberin) in the cortex of a non-susceptible host plant, while a post-establishment resistance, gradually reducing parasite viability, is based on the accumulation into host vascular cells of mucilage-like substances that block nutrient translocation (Yoder and Scholes, 2010).
Only moderate levels of resistance against *P. aegyptiaca*, *P. ramosa* and *O. cernua* were detected in tomato cultivars (Dalela and Mathur, 1971; Qasem and Kasrawi, 1995; Avdeyev *et al.*, 2003; El-Halmouch *et al.*, 2006; Hershenhorn *et al.*, 2009; Draie, 2017). In some cases, an effect of host plant age on the response to *P. aegyptiaca*, likely depending on the varying composition of root exudates, was found (El-Halmouch *et al.*, 2006; Hershenhorn *et al.*, 2009). The tomato line PZU11 was reported to be completely resistant to *P. ramosa* and *P. aegyptiaca* only in field tests carried out in Russia, where is still used in breeding programmes (Avdeyev and Scherbinin, 1977; Foy *et al.*, 1987; Avdeyev *et al.*, 2003; Hershenhorn *et al.*, 2009). Partial resistance against *Orobanche* and *Phelipanche* spp. was also shown by the tomato mutant line *high pigment 2^{dg}* (*hp-2^{dg})* derived by the Manapal cultivar (Konsler, 1973), correlated to a low SL presence in root exudates (López-Ráez *et al.*, 2008b). Some wild tomato relatives (*Solanum pennellii*, *S. hirsutum*, *S. pimpinellifolium* and *S. chilense*) showed absent or reduced amounts of emerged *P. aegyptiaca* shoots. Besides having the lowest capacity in inducing *P. aegyptiaca* seed germination, root exudates of *S. pennellii* displayed an inhibiting effect on developing tubercles, with an incompatible interaction following the haustorium penetration (El-Halmouch *et al.*, 2006). Possible loci and genes involved in the resistance of the wild species to *P. aegyptiaca* were identified in two introgression lines (ILs) of *S. pennellii* LA716 in the genetic background of the tomato M82 (Bai *et al.*, 2020).
Pavan *et al.* (2016) selected a pea landrace highly resistant to *O. crenata*, with good yields in strongly infested soils. Compared to control, its root exudates showed a reduced concentration of SLs and stimulation of *O. crenata* seed germination. Advanced pea breeding lines resistant to *O. crenata* were obtained from a wide cross-programme between *P. fulvum, P. sativum* ssp*. elatius, P. sativum* ssp. *syriacum* and pea landraces. Such resistance occurred at the level of either reduced tubercle formation or further development. Remarkably, in broomrape-infested fields these lines gave higher yields than the parental pea cultivar Messire (Rubiales *et al.*, 2020).
In faba bean, several cultivars, derived mostly from the Egyptian donor line Giza402, showed variable degrees of resistance against *O. crenata*, based on a reduced penetration of the latter through the host vasculature (Nassib *et al.*, 1982; Maalouf *et al.*, 2011; Fernández-Aparicio *et al.*, 2012). On the other hand, two breeding lines, Quijote and Navio, showed a lower induction of *O. crenata*, *O. foetida* and *P. aegyptiaca* seed germination, due to reduced release of germination stimulants in the root exudate (Fernández-Aparicio *et al.*, 2012). In further experiments, the cultivar Baraca showed a broad-spectrum resistance and resulted to be the most resistant against all three species mentioned above (Rubiales *et al.*, 2016).
Chickpea accessions, resistant to *O. crenata* due to the reduced parasite seed germination, were also identified (Rubiales *et al.*, 2003). Moreover, three chickpea genotypes partially

resistant to *O. foetida* showed a lower number of both attached and developed tubercles per host plant (Nefzi *et al.*, 2016).

Mutation breeding

Conventional mutagenesis was also applied to induce resistance to parasitic weeds in tomato and chickpea. Compared to the parental line M82, the tomato line *Sl-ORT1* (*S. lycopersicum Orobanche Resistant Trait 1*), obtained by fast-neutron treatments, showed to be resistant against diverse *Orobanche* and *Phelipanche* species. In the mutant line, SL deficiency, together with reduced transcription of the gene *SlCCD7* involved in SL biosynthesis, were found to be associated to the resistant phenotype. The latter was characterized also by increased branching, due to the lack of growth suppression of axillary buds related to SLs deficiency, and reduced AMF colonization (Dor *et al.*, 2010, 2011; Koltai *et al.*, 2010). Kostov *et al*. produced a large EMS-mutagenized tomato population, and six M2 plants were more resistant to *P. ramosa* infestation (Kostov *et al.*, 2007). More tomato genotypes resistant to *P. ramosa, P. aegyptiaca* and *O. minor* were identified in TILLING (Targeting Induced Local Lesions IN Genomes) collections produced in Red Setter and Micro-Tom backgrounds. In the former case, the resistant genotype displayed an altered SL synthesis (Minoia *et al.*, 2010; Disciglio *et al.*, 2016;), while the Micro-Tom mutants were characterized by a point mutation in the *CCD8* gene and by a branched phenotype. On the other hand, compared to the wild type, flower and fruit traits showed no significant differences (Hasegawa *et al.*, 2018). Resistance against *O. foetida* was attained in five radiation-induced chickpea mutants, where the occurrence of either the alteration of SL exudation or the release of germination inhibitors was hypothesized (Brahmi *et al.*, 2016), and in two faba bean mutants, which showed lower induction of seed germination and enhancement of some enzyme activities (Mejri *et al.*, 2018).

QTL mapping and molecular marker-assisted breeding

In some cases, genomic regions associated with resistance to broomrape were identified by employing molecular markers, genetic maps, and Quantitative Trait Loci (QTL) analysis (Fondevilla *et al.*, 2010). In faba bean, three QTLs for broomrape resistance against *O. crenata*, scored as the number of emerged broomrapes, were found in a F_2 population screened with isozymes, RAPD, seed protein genes and microsatellites. They explained 74% of the observed phenotypic variation (Román *et al.*, 2002). In an F_2 population of pea plants, two QTLs for *O. crenata* resistance were detected, but they explained only a moderate portion of the observed variation (Valderrama *et al.*, 2004). In a subsequent work, four QTLs associated with field resistance, explaining a maximum of 33% of phenotypic variation, were identified in a RIL (Recombinant Inbred Lines) population derived from a cross between the wild *Pisum sativum* ssp. *Syriacum,* resistant to *O. crenata*, and a susceptible pea cultivar. Afterward, QTLs governing specific mechanisms of resistance, such as lower induction of *O. crenata* seed germination, lower number of established tubercles per host root length unit, and slower development of tubercles were highlighted (Fondevilla *et al.*, 2010).

Biotechnological approaches

Classical transgenic strategies have been employed to generate herbicide-resistant genotypes, which were insensitive to the herbicidal treatment, the active principle reaching and damaging the attached parasite, while moving through the root apparatus. In

acetolactate-synthase (ALS) transgenic carrots resistant to imazapyr (Aviv *et al.*, 2002) and in transgenic asulam-resistant potatoes (Surov *et al.*, 1998), effective control of *P. aegyptiaca* was achieved. In another strategy, the insect-derived *sarcotoxin IA* gene was expressed under a root-specific promoter in tomato. Pathogenicity assays with *P. aegyptiaca*-inoculated seeds showed the necrosis and abnormal growth of tubercles due to sarcotoxin effect, while tomato plants were not affected by the transgene (Radi *et al.*, 2006).
A key *Orobanche* gene (*Mannose 6-phosphate reductase*), involved in mannitol biosynthesis, was silenced in *P. aegyptiaca* after translocation of a M6PR-siRNA from engineered tomato plants. Because of the suppression of M6PR-mRNA, more necrotic tubercles and fewer underground shoots were observed (Aly *et al.*, 2009). Similarly, tomato transgenic genotypes expressing a multiple-sequence RNAi construct targeting three *P. aegyptiaca* key genes – *PaACS* (1-amino- cyclopropane-1-carboxylate synthase), *PaM6PR* and *PaPrx1* (peroxidase) showed the reduction of the number of tubercles (Dubey *et al.*, 2017). When the RNAi approach was addressed to the tomato host genome, silencing two key genes involved in SL biosynthesis, *CCD7* and *CCD8*, the level of SLs in both mutants decreased as well as *P. 76amose* root colonization, but plant morphology was severely affected by the SL deficiency, inducing dwarfing and increased branching in RNAi plants (Vogel *et al.*, 2010; Kohlen *et al.*, 2012).
More recently, various genes involved in SL biosynthesis or transport have been edited in tomato through CRISPR/Cas9 technology, which allows to obtain precise mutations in the site of interest (Wakabayashi *et al.*, 2019; Bari *et al.*, 2019; Bari *et al.*, 2021a; Bari *et al.*, 2021b; Nicolia *et al.*, 2021a). No or very low levels of SLs were detected in the root exudates of all mutants, which furthermore showed resistance to *P. aegyptiaca* infestation and, in one case, also to *O. crenata* and *S. hermonthica*. Except in one case (Wakabayashi *et al.*, 2019), mutants showed the expected branched phenotype.
Mutants in *SlCCD8* and *SlCCD7* genes were also obtained from protoplasts of tomato transfected with ribonucleoprotein complex (RNP) constituted by purified Cas9 and specific single guide RNAs (Nicolia *et al.*, 2021b).
This procedure could allow the rapid generation of DNA-free tomato mutants carrying novel alleles conferring resistance against *Phelipanche* spp. and *Orobanche* spp.

CONCLUSIONS AND PERSPECTIVES

Orobanche and *Phelipanche* spp. represent an insidious threat to vegetable and legume crops, with increasing damage due to climate changes. The lore about the complex interaction between those parasitic species and their hosts has been improved only recently, with potential positive impacts on the development of innovative agronomic and genetic strategies.
Several approaches for the management of these pests in the field have been developed and tested in the past few years. They include methods aiming to reduce the parasite seed banks in the soil, enable the growth of susceptible crops on infested fields, and suppress or reduce the growth and diffusion of parasitic weeds.
These objectives can be achieved by different agronomic, biological, or chemical methods, with different impacts on the environment and varying effectiveness in open field cultivations.
The latter two aspects must be wisely considered before adopting one or another approach, and a combined integrated management strategy is likely necessary for most situations.
The development of novel digital and modelling approaches to monitor the parasite development under the soil surface will facilitate the implementation of more effective and

environmentally sound control methods (Eizenberg *et al.*, 2012; Cochavi *et al.*, 2017; Lati *et al.*, 2019).
The cultivation of crop cultivars resistant to parasitic weeds is also a powerful approach for broomrape management (Hershenhorn *et al.*, 2009; Rubiales, 2003).
Nevertheless, it is fundamental to get more insights into the mechanisms by which the resistance occurs, with the aim to widen the genetic basis of resistance and limit the occurrence of new broomrape sub-species and ecotypes.
Several broomrape-resistant genotypes were identified in germplasm collections and used in conventional breeding approaches. Such approaches, however, are complex and long, and frequently led to incomplete resistance.
Molecular-assisted breeding and biotechnological approaches are faster, and some interesting results have been already obtained. Genome sequences and functional information derived by -omics studies, now available not only for host species but also for diverse parasitic species, as for instance *P. ramosa, P. aegyptiaca, S. asiatica* and *C. australis* (Yao *et al.*, 2016; Yoshida *et al.*, 2019; Yoshida and Kee, 2021), can help develop novel breeding approaches. Access to information about genome structure and function as well as to efficient transformation/regeneration procedures is necessary to implement such new biotechnological approaches in a wide range of vegetable and legume crops (Cardi *et al.*, 2017).
The integration of agronomical management practices with different genetic resistance mechanisms is, however, mandatory to build a more effective and durable strategy to manage parasitic plant infestations in vegetables and legumes (Fernández-Aparicio *et al.*, 2016, 2020; Jamil *et al.*, 2021; Zarban *et al.*, 2021).

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REFERENCES

1. Abbes Z., Kharrat M., Delavault P., Chaïbi W., and Simier P. (2009). Nitrogen and carbon relationships between the parasitic weed *Orobanche foetida* and susceptible and tolerant faba bean lines. Plant Physiol. Biochem. 47: 153–159.
2. Acharya B.D., Khattri G.B., Chettri M.K., and Srivastava S.C. (2002). Effect of *Brassica campestris* var. toria as a catch crop on *Orobanche aegyptiaca* seed bank. Crop Protection 21: 533–537.
3. Aksoy E., Arslan, Z.F., Tetik Ö., and Eymirli S. (2016). Using the possibilities of some trap, catch and Brassicaceaen crops for controlling crenate broomrape a problem in lentil fields. International Journal of Plant Production 10: 53–62.
4. Al-Menoufi O. (1989). Crop rotation as a control measure of *Orobanche crenata* in *Vicia faba* fields. In Wegmann K., Musselman L. (Eds.), Progress in Orobanche research, Eberhard-Karl-Universitat, pp. 241–247.
5. Albert M., Belastegui-Macadam X.M., Bleischwitz M., and Kaldenhoff R. (2008). *Cuscuta* spp: "Parasitic Plants in the Spotlight of Plant Physiology, Economy and Ecology". In: Lüttge, U., Beyschlag, W., Murata, J. (eds) Progress in Botany. Progress in Botany, vol 69. Springer, Berlin, Heidelberg, pp. 267–277.
6. Aloni R. (2015). Ecophysiological implications of vascular differentiation and plant evolution. Trees - Struct. Funct. 29: 1–16.
7. Aly R., Cholakh, H., Joel D.M., Leibman D., Steinitz B., Zelcer A., Naglis A., Yarden O., and Gal-On A. (2009). Gene silencing of mannose 6-phosphate reductase in the parasitic weed *Orobanche aegyptiaca* through the production of homologous dsRNA sequences in the host plant. Plant Biotechnol. J. 7: 487–498.
8. Amsellem Z., Barghouthi S., Cohen B., Goldwasser. Y., Gressel J., Hornok L., Kerenyi Z., Kleifeld,Y., Klein O., Kroschel, J.*, et al.* (2001). Recent advances in the biocontrol of Orobanche (broomrape) species. BioControl 46: 211–228.

9. Auger B., Pouvreau J.B., Pouponneau K., Yoneyama K., Montiel G., Le Bizec B., Yoneyama K., Delavault P., Delourme R., and Simier P. (2012). Germination stimulants of *Phelipanche ramosa* in the rhizosphere of *Brassica napus* are derived from the glucosinolate pathway. Mol. Plant-Microbe Interact. 25: 993–1004.
10. Avdeyev Y.I., and Scherbinin B.M. (1977). Tomato Resistant to Broomrape, *Orobanche aegyptiaca*. Report of the Tomato Genetics Cooperative, Report No. 27, Department of Vegetative Crops, University of California (Davis).
11. Avdeyev Y.I., Scherbinin B.M., Ivanova L.M., and Avdeyev A.Y. (2003). Studying of tomato resistance to broomrape and breeding varieties for processing. Acta Hortic. 613: 283–290.
12. Aviv D., Amsellem Z. and Gressel J. (2002). Transformation of carrots with mutant acetolactate synthase for Orobanche (broomrape) control. Pest Manag. Sci. 58: 1187–1193.
13. Ba, J., Wei Q., Shu J., Gan Z., Li B., Yan D., Huang Z., Guo Y., Wang, X., Zhang, L., *et al.* (2020). Exploration of resistance to *Phelipanche aegyptiaca* in tomato. Pest Manag. Sci. 76: 3806–3821.
14. Barghouthi S., and Salman M. (2010). Bacterial inhibition of *Orobanche aegyptiaca* and *Orobanche cernua* radical elongation. Biocontrol Sci Technol 20: 423–435.
15. Bari V.K., Abu J., Kheredin S.M., Gal-on, A., Ron M., Britt A., Steele D., Yoder J. and Aly, R. (2019). CRISPR/Cas9-mediated mutagenesis of CAROTENOID CLEAVAGE DIOXYGENASE 8 in tomato provides resistance against the parasitic weed *Phelipanche aegyptiaca*. Sci. Rep. 9: 1–12.
16. Bari V.K., Nassar J.A. and Aly R. (2021a). CRISPR/Cas9 mediated mutagenesis of MORE AXILLARY GROWTH 1 in tomato confers resistance to root parasitic weed *Phelipanche aegyptiaca*. Sci. Rep. 11: 1–11.
17. Bari V.K., Nassar J.A., Meir A. and Aly R. (2021b). Targeted mutagenesis of two homologous ATP-binding cassette subfamily G (ABCG) genes in tomato confers resistance to parasitic weed *Phelipanche aegyptiaca*. J. Plant Res. 134: 585–597.
18. Boari A. and Vurro, M. (2004). Evaluation of *Fusarium* spp. and other fungi as biological control agents of broomrape (*Orobanche ramosa*). Biol. Control 30: 212–219.
19. Boari A., Ciasca,B., Pineda-Martos R., Lattanzio V.M., Yoneyama K. and Vurro M. (2016). Parasitic weed management by using strigolactone-degrading fungi. Pest Man. Sci. 72: 2043–2047.
20. Bouwmeester H., Li C., Thiombiano B., Rahimi M., and Dong L. (2021). Adaptation of the parasitic plant lifecycle: germination is controlled by essential host signaling molecules. Plant Physiol. 185: 1292–1308.
21. Bouwmeester H.J., Roux C., Lopez-Raez J.A. and Bécard G. (2007). Rhizosphere communication of plants, parasitic plants and AM fungi. Trends Plant Sci. 12: 224–230.
22. Brahmi I. Mabrouk Y. Brun G., Delavault P., Belhadj O. and Simier P. (2016). Phenotypical and biochemical characterisation of resistance for parasitic weed (*Orobanche foetida* Poir.) in radiation-mutagenised mutants of chickpea. Pest Manag. Sci. 72: 2330–2338.
23. Brun G., Spallek T., Simier P. and Delavault P. (2021). Molecular actors of seed germination and haustoriogenesis in parasitic weeds. Plant Physiol. 185: 1270–1281.
24. Cardi T., D'Agostino N., and Tripodi P. (2017). Genetic Transformation and Genomic Resources for Next-Generation Precise Genome Engineering in Vegetable Crops. Front. Plant Sci. 8: 241.
25. Casadesús A. and Munné-Bosch, S. (2021). Holoparasitic plant-host interactions and their impact on Mediterranean ecosystems. Plant Physiol. 185: 1325–1338.
26. Chang M., Lynr D.G., Netzly D.H. and Butler, L.G. (1986). Chemical Regulation of Distance: Characterization of the First Natural Host Germination Stimulant for *Striga asiatica*. J. Am. Che. Soc.: 108: 7858–7860.
27. Clarke C.R., Timko M.P., Yoder J.I., Axtell, M.J., and Westwood J.H. (2019). Molecular Dialog between Parasitic Plants and Their Hosts. Annu. Rev. Phytopathol. 57: 279–299.
28. Cochavi A., Rapaport T., Gendler T., Karnieli A., Eizenberg H., Rachmilevitch S. and Ephrath J.E. (2017). Recognition of *Orobanche cumana* below-ground parasitism through physiological and hyper spectral measurements in sunflower (*Helianthus annuus* L.). Front. Plant Sci. 8: 909.
29. Dalela G.G. and Mathur R.L. (1971). Resistance of Varieties of Eggplant, Tomato and Tobacco to Broomrape (*Orobanche cernua* Loefl.). PANS Pest Artic. News Summ. 17: 482–483.
30. Delavaul P. (2015). Knowing the parasite: Biology and genetics of Orobanche. Helia 38: 15–29.
31. Dhanapal, G.N., Struik, P.C., Udayakumar, M. and Timmermans, P.C.J.M. (1996). Management of Broomrape (*Orobanche* spp.) – A review. J. Agron. Crop Sci. 176: 335–359.
32. Disciglio G., Lops F., Carlucci A., Gatta G., Tarantino A., Frabboni L., Carriero F. and Tarantino E. (2016). Effects of different methods to control the parasitic weed *Phelipanche ramosa* (L.) Pomel. in processing tomato crops. Ital. J. Agron. 11: 39–46.
33. Dor E., Alperin B., Wininger S., Ben-Dor B., Somvanshi V.S., Koltai H., Kapulnik Y. and Hershenhorn J. (2010). Characterization of a novel tomato mutant resistant to the weedy parasites *Orobanche* and *Phelipanche* spp. Euphytica 171: 371–380.
34. Dor E., Yoneyama K., Wininger S., Kapulnik Y., Yoneyama K., Koltai H., Xie X. and Hershenhorn J. (2011). Strigolactone deficiency confers resistance in tomato line SL-ORT1 to the parasitic weeds *Phelipanche* and *Orobanche* spp. Phytopathology 101: 213–222.

35. Draie R. (2017). Differential Responses of Commercial Tomato Rootstocks to Branched Broomrape. Res. Plant Sci. 5: 15–25.
36. Draie R., Péron T., Pouvreau J.B., Véronési C., Jégou S., Delavault P., Thoiron S. and Simier P. (2011). Invertases involved in the development of the parasitic plant *Phelipanche ramosa*: Characterization of the dominant soluble acid isoform, PrSAI1. Mol. Plant Pathol. 12: 638–652.
37. Dubey N.K., Eizenberg H., Leibman D., Wolf D., Edelstein M., Abu-Nassar J., Marzouk S., Gal-On A. and Aly R. (2017). Enhanced Host-Parasite Resistance Based on Down-Regulation of *Phelipanche aegyptiaca* Target Genes Is Likely by Mobile Small RNA. Front. Plant Sci. 8: 1574.
38. Eizenberg H., Aly R. and Cohen Y. (2012). Technologies for Smart Chemical Control of Broomrape (*Orobanche* spp. and *Phelipanche* spp.). Weed Sci. 60: 316–323.
39. Eizenberg H. and Goldwasser Y. (2018). Control of egyptian broomrape in processing tomato: A summary of 20 years of research and successful implementation. Plant Disease 102: 1477–1488.
40. Eizenberg H., Goldwasser Y., Golan S., Plakhine D. and Hershenhorn J. (2004). Egyptian Broomrape (*Orobanche aegyptiaca*) Control in Tomato with Sulfonylurea Herbicides—Greenhouse Studies. Weed Technol. 18: 490-496.
41. El-Halmouch Y., Benharrat H. and Thalouarn P. (2006). Effect of root exudates from different tomato genotypes on broomrape (*O. aegyptiaca*) seed germination and tubercle development. Crop Prot. 25: 501–507.
42. El-Rokiek K.G., El-Metwally I.M., Messiha N.K. and Saad El-Din S.A. (2015) Controlling *Orobanche crenata* in Faba bean using the Herbicides Glyphosate and Imazapic with some additives. Int. J. Chem. Tech. Res. 8: 18–26.
43. Ephrath J.E. and Eizenberg, H. (2010). Quantification of the dynamics of *Orobanche cumana* and *Phelipanche aegyptiaca* parasitism in confectionery sunflower. Weed Res. 50: 140–152.
44. Evidente A., Cimmino, A., Fernández-Aparicio, M., Andolfi A., Rubiales D. and Motta A. (2010). Polyphenols, including the new peapolyphenols A-C, from pea root exudates stimulate *Orobanche foetida* seed germination. J. Agric. Food Chem. 58: 2902–2907.
45. Evidente A., Cimmino A., Fernández-Aparicio M., Rubiales,D., Andolfi A. and Melck D. (2011). Soyasapogenol B and trans-22-dehydrocam-pesterol from common vetch (*Vicia sativa* L.) root exudates stimulate broomrape seed germination. Pest Manag. Sci. 67: 1015–1022.
46. Evidente A., Fernández-Aparicio M., Cimmino A., Rubiales D., Andolfi A. and Motta A. (2009). Peagol and peagoldione, two new strigolactone-like metabolites isolated from pea root exudates. Tetrahedron Lett. 50: 6955–6958.
47. Fernández-Aparicio, M., Delavault, P. and Timko, M.P. (2020). Management of infection by parasitic weeds: A review. Plants 9: 1184.
48. Fernández-Aparicio, M., Emeran, A.A. and Rubiales, D. (2008). Control of *Orobanche crenata* in legumes intercropped with fenugreek (*Trigonella foenum-graecum*). Crop Prot. 27: 653–659.
49. Fernández-Aparicio, M., Moral, A., Kharrat, M. and Rubiales, D. (2012). Resistance against broomrapes (*Orobanche* and *Phelipanche* spp.) in faba bean (*Vicia faba*) based in low induction of broomrape seed germination. Euphytica 186: 897–905.
50. Fernández-Aparicio M., Reboud X., and Gibot-Leclerc S. (2016). Broomrape Weeds. Underground Mechanisms of Parasitism and Associated Strategies for their Control: A Review. Front. Plant Sci. 7: 135.
51. Fondevilla S., Fernández-Aparicio M., Satovic, Z., Emeran A.A., Torres, A.M., Moreno, M.T. and Rubiales, D. (2010). Identification of quantitative trait loci for specific mechanisms of resistance to *Orobanche crenata* Forsk. in pea (*Pisum sativum* L.). Mol. Breed. 25: 259–272.
52. Foy, C., Jacobsohn, R. and Jain R. (1987). Evaluation of tomato lines for resistance to glyphosate and/or *Orobanche aegyptiaca* Pers. In Parasitic Flowering Plants Proceeding of the 4th ISPFP, (Marburg, Germany: HC WEBER & WFORSTREUTER), pp. 221–230.
53. Foy C., Jain R. and Jacobsohn, R. (1989). Recent approaches for chemical control of broomrape (*Orobanche* spp.). Rev. Weed Sci. 4: 123–152.
54. Goldwasser Y., Eizenberg H., Hershenhorn J., Plakhine D., Blumenfeld T., Buxbaum H., Golan S., and Kleifeld Y. (2001). Control of *Orobanche aegyptiaca* and *O. ramosa* in potato. Crop Prot. 20: 403–410.
55. Goyet V., Billard E., Pouvreau J.B., Lechat M.M., PelletiernS., Bahut M., Monteau F., Spíchal L., Delavault P., Montiel G., *et al.* (2017). Haustorium initiation in the obligate parasitic plant *Phelipanche ramosa* involves a host-exudated cytokinin signal. J. Exp. Bot. 68: 5539–5552.
56. Goyet V., Wada S., Cui S., Wakatake T., Shirasu K., Montiel G., Simier P. and Yoshida S. (2019). Haustorium Inducing Factors for Parasitic Orobanchaceae. Front. Plant Sci. 10: 1056.
57. Gressel J. (2009) Crops with target-site herbicide resistance for Orobanche and Striga control. 560–565.
58. Gutjahr C., and Paszkowski U. (2009). Weights in the balance: Jasmonic acid and Salicylic acid signaling in root-biotroph interactions. Mol. Plant-Microbe Interact. 22 763–772.

59. Hasegawa S., Tsutsumi T., Fukushima S., Okabe Y., Sait J., Katayama,M., Shindo Yamada Y., Shimomur K., Yoneyama K., *et al.* (2018). Low Infection of *Phelipanche aegyptiaca* in Micro-Tom Mutants Deficient in CAROTENOID CLEAVAGE DIOXYGENASE 8. Int. J. Mol. Sci. 19,: 2645.
60. Hershenhorn J., Eizenberg H., Dor E., Kapulnik Y. and Goldwasser Y. (2009). *Phelipanche aegyptiaca* management in tomato. Weed Res. 49: 34–47.
61. Hershenhorn J., Goldwasser Y., Plakhine D., Lavan Y., Herzlinger G., Golan S., Chile T., and Kleifeld Y. (1998b). Effect of Sulfonylurea Herbicides on Egyptian Broomrape (*Orobanche aegyptiaca*) in Tomato (Lycopersicon esculentum) under Greenhouse Conditions. Weed Technol. 12: 115–120.
62. Hershenhorn,â J., Plakhine D., Goldwasser Y., Westwood J.H., Foy C.L., and Kleifeld Y. (1998a). Effect of Sulfonylurea Herbicides on Early Development of Egyptian Broomrape (*Orobanche aegyptiaca*) in Tomato (*Lycopersicon esculentum*). Weed Technol. 12: 108–114.
63. Jamil M., Kountche B.A. and Al-Babili S. (2021). Current progress in Striga management. Plant Physiol. 185, 1339–1352.
64. Jia K.P., Baz L. and Al-Babili S. (2018). From carotenoids to strigolactones. J. Exp. Bot. 69: 2189–2204.
65. Joel D.M. (2000). The long-term approach to parasitic weeds control: Manipulation of specific developmental mechanisms of the parasite. Crop Prot. 19:753–758.
66. Joel D.M., ChaudhuriS.K., Plakhine D., Ziadna H. and SteffensJ.C. (2011). Dehydrocostus lactone is exuded from sunflower roots and stimulates germination of the root parasite *Orobanche cumana*. Phytochemistry, 72: 624–634.
67. Kannan C. and Zwanenburg B. (2014). A novel concept for the control of parasitic weeds by decomposing germination stimulants prior to action. Crop Prot. 61: 11–15.
68. Kebede M. and Ayana B. (2018). Economically Important Parasitic Weeds and Their Management Practices in Crops. J. Environ. Earth Sci. 8:104–115.
69. Kleifeld Y., Goldwasser Y., Herzlinger G., Joel, D.M., Golan =S. and Kahana D. (1994). The effects of flax (*Linum usitatissimum* L.) and other crops as trap and catch crops for control of Egyptian broomrape (*Orobanche aegyptiaca* Pers.). Weed Res. 34:, 37–44.
70. Klein O and Kroschel J. (2002). Biological control of Orobanche spp. with *Phytomyza orobanchia*, a review. BioControl 47: 245–277.
71. Kohlen W., Charnikhova T., Lammers M., Pollina T., Tóth P., Haider I., Pozo M.J., de Maagd R.A., Ruyter-Spira C., Bouwmeester H.J., *et al.* (2012). The tomato CAROTENOID CLEAVAGE DIOXYGENASE8 (SlCCD8) regulates rhizosphere signaling, plant architecture and affects reproductive development through strigolactone biosynthesis. New Phytol. 196: 535–547.
72. Koltai, H., Lekkala S.P., Bhattacharya C., Mayzlish-Gati E., Resnick N., Wininger S., Dor E., Yoneyama K., Yoneyama K., Hershenhorn,J., *et al.* (2010). A tomato strigolactone-impaired mutant displays aberrant shoot morphology and plant interactions. J. Exp. Bot. 61: 1739–1749.
73. Konsler T.R. (1973). Three mutants appearing in 'Manapal' tomato. Hortic. Sci. 8: 331–333.
74. Kostov K., Batchvarova R., and Slavov S. (2007). Application of chemical mutagenesis to increase the resistance of tomato to *Orobanche ramosa* L. Bulg. J. Agric. Sci. 13: 505–513.
75. Lati R.N., Filin S., Elnashef B., and Eizenberg H. (2019). 3-D Image-Driven Morphological Crop Analysis: A Novel Method for Detection of Sunflower Broomrape Initial Subsoil Parasitism. Sensors (Basel) 19: 1569
76. López-Ráez J.A., Charnikhova T., Gómez-Roldán, V., Matusova R., Kohlen W., De Vos R., Verstappen F., Puech-Pages V., Bécard G., Mulder P., *et al.* (2008a). Tomato strigolactones are derived from carotenoids and their biosynthesis is promoted by phosphate starvation. New Phytol. 178: 863–874.
77. López-Ráez J.A., Charnikhova T., Mulder P., Kohlen W., Bino R., Levin I. and Bouwmeester H. (2008b). Susceptibility of the tomato mutant high pigment-2dg (hp-2dg) to *Orobanche* spp. infection. J. Agric. Food Chem. 56: 6326–6332.
78. Maalouf F., Khalil S., Ahmed S., Akintunde A.N., Kharrat M., El K., Hajjar S. and Malhotra R.S. (2011). Yield stability of faba bean lines under diverse broomrape prone production environments. Fuel Energ. Abstr. 124: 288–294.
79. Mauromicale G., Monaco A., Longo A.M.G. and Restuccia A. (2005). Soil solarization, a nonchemical method to control branched broomrape (*Orobanche ramosa*) and improve the yield of greenhouse tomato. Weed Sci. 53: 877–883.
80. Mejri S., Mabrouk Y., Belhadj O. and Saidi M (2018). *Orobanche foetida* resistance in two new faba bean genotypes produced by radiation mutagenesis. Int. J. Radiat. Biol. 94: 671–677.
81. Minoia S., Petrozza A., D'Onofrio O., Piron F., Mosca,G., Sozio G., Cellini F., Bendahmane A. and Carriero F. (2010). A new mutant genetic resource for tomato crop improvement by TILLING technology. BMC Res. Notes 3: 69.
82. Nassib A.M., Ibrahim A.A. and Khali S.A. (1982). Breeding for Resistance to Orobanche. In Faba Bean Improvement, W.C. Hawtin G., ed. (Dordrecht: Springer Netherlands), pp. 199–206.
83. Nefzi F., TrabelsinI., Amri M., Triki E., Kharrat M. and Abbes Z. (2016). Response of some chickpea (*Cicer arietinum* L.) genotypes to Orobanche foetida Poir. parasitism. Chil. J. Agric. Res. 76, 170–178.

84. Nicolia A., Andersson M., Hofvander P., Festa G. and Cardi T. (2021b). Tomato protoplasts as cell target for ribonucleoprotein (RNP)-mediated multiplexed genome editing. Plant Cell Tissue Organ Cult. 144: 463–467.
85. Nicolia A., Cuccurullo A., Contaldi F., Yoneyama K., Camerlengo,F., Festa G., Navarro A., D'Agostino N., Facchiano A., Scafuri B., *et al.* (2021a). CRISPR/Cas9-mediated mutagenesis as a strategy to develop resistant tomato plants against Orobanche. In Proceedings of the 2nd PlantEd Conference Plant Genome Editing: The Wide Range of Applications, A. Santino, ed. (Lecce: Institute of Sciences of Food Production-National Research Council), p. 23.
86. Parker C. (2009). Observations on the current status of Orobanche and Striga problems worldwide. Pest Manag. Sci. 65: 453–459.
87. Parker C. and Riches C.R. (1993). Parasitic Weeds of the World: Biology and Control. CAB International. United States from University of Arizona Press.
88. Pavan S., Schiavulli A., Marcotrigiano A.R., Bardaro N., Bracuto V., Ricciard,iF., Charnikhova T., Lotti C., Bouwmeester H. and Ricciardi L. (2016). Characterization of Low-Strigolactone Germplasm in Pea (*Pisum sativum* L.) Resistant to Crenate Broomrape (*Orobanche crenata* Forsk.). Mol. Plant-Microbe Interact. 29: 743–749.
89. Péron T., Candat A., Montiel G., Veronesi C., Macherel D., Delavault P. and Simier P. (2017). New insights into phloem unloading and expression of sucrose transporters in vegetative sinks of the parasitic plant *Phelipanche ramosa* L. (Pomel). Front. Plant Sci. 7: 2048.
90. Qasem J.R., and Kasrawi M.A. (1995). Variation of resistance to broomrape (*Orobanche ramosa*) in tomatoes. Euphytica 81: 109–114.
91. Radi A., Dina P. and Guy A. (2006). Expression of sarcotoxin IA gene via a root-specific tob promoter enhanced host resistance against parasitic weeds in tomato plants. Plant Cell Rep. 25: 297–303.
92. Raupp F.M. and Spring O. (2013). New sesquiterpene lactones from sunflower root exudate as germination stimulants for *Orobanche cumana*. J. Agric. Food Chem. 61: 10481–10487.
93. Roitsch T., and Ehneß R. (2000). Regulation of source/sink relations by cytokinins. Plant Growth Regul. 32: 359–367.
94. Romá B., Torres A.M., Rubiales D., Cubero J.I. and Satovic Z. (2002). Mapping of quantitative trait loci controlling broomrape (*Orobanche crenata* Forsk.) resistance in faba bean (*Vicia faba* L.). Genome 45, 1057–1063.
95. Rubiales D. (2003). Parasitic plants, wild relatives and the nature of resistance. New Phytol. 160: 459–461.
96. Rubiales D., Fernández-Aparicio, M., Vurro, M. and Eizenberg, H. (2018). Editorial: Advances in Parasitic Weed Research. Front. Plant Sci. 9: 236.
97. Rubiales D., Fondevilla S. and Fernández-Aparicio M. (2020). Development of Pea Breeding Lines with Resistance to *Orobanche crenata* Derived from Pea Landraces and Wild *Pisum* spp. Agronomy 11: 36.
98. Rubiales D., Pérez-de-Luque A., Joel, D.M., Alcántara C., and Sillero J.C. (2003). Characterization of resistance in chickpea to crenate broomrape (*Orobanche crenata*). Weed Sci. 51: 702–707.
99. Rubiales D., Rojas-Molina M.M. and Sillero J.C. (2016). Characterization of resistance mechanisms in faba bean (*Vicia faba*) against broomrape species (*Orobanche* and *Phelipanche* spp.). Front. Plant Sci. 7: 1747.
100. Runyon J.B., Tooker J.F., Mescher M.C. and De Moraes C.M. (2009). Parasitic Plants in Agriculture: Chemical Ecology of Germination and Host-Plant Location as Targets for Sustainable Control: A Review. In Organic Farming, Pest Control and Remediation of Soil Pollutants., E. Lichtfouse, ed. (Dordrecht: Springer Netherlands), pp. 123–136.
101. Sauerborn J. and Saxena M. (1986). A review on agronomy in relation to Orobanche problems in faba bean (*Vicia faba* L.). In ter Borg S. (Ed.), Proceedings of a workshop on biology and control of Orobanche, Landbouwuniversiteit, pp. 160–165.
102. Sauerborn J., Linke K-H., Saxena M.C. and Koch W. (1989). Solarization; a physical control method for weeds and parasitic plants (*Orobanche* spp.) in Mediterranean agriculture. Weed Res. 29: 391–397.
103. Saxena M., Linke K. and Sauerborn J. (1994). Integrated control of Orobanche in cool-season food legumes. In Pieterse A., Verkleij J., Borg S. (Eds.), Biology and management of Orobanche. Royal Tropical Institute pp. 419–431.
104. Seto Y., Sado, A., Asami K., Hanada A., Umehara M., Akiyama K. and Yamaguchi S. (2014). Carlactone is an endogenous biosynthetic precursor for strigolactones. Proc. Natl. Acad. Sci. USA. 111: 1640–1645.
105. Surov T., Aviv D., Aly R., Joel D.M., Goldman-Guez T. and Gressel J. (1998). Generation of transgenic asulam-resistant potatoes to facilitate eradication of parasitic broomrapes (*Orobanche* spp.), with the *sul* gene as the selectable marker. Theor. Appl. Genet. 96: 132–137.
106. Thomas H., Sauerborn J., Müller-Stöver D., Ziegler A., Bedi, J.S. and Kroschel, J. (1998). The Potential of *Fusarium oxysporum* f. sp. *orthocerasas* a Biological Control Agent for *Orobanche cumana* in Sunflower. Biol. Cont.: 13: 41–48.

107. Torres-Vera R., García, J.M. Pozo, M.J. and López-Ráez J.A. (2016). Expression of molecular markers associated to defense signaling pathways and strigolactone biosynthesis during the early interaction tomato-*Phelipanche ramosa*. Physiol. Mol. Plant Pathol. 94: 100–107.
108. Valderrama M.R., Román B., Satovic Z., Rubiales D., Cubero J.I. and Torres A.M. (2004). Locating quantitative trait loci associated with Orobanche crenata resistance in pea. Weed Res. 44: 323–328.
109. Verkleij J., and Kuiper E. (2000). Various approaches to controlling root parasitic weeds. Biotech. Develop. Monitor: 41: 16–19.
110. Vogel J.T., Walter M.H., Giavalisco P., Lytovchenko A., Kohlen W., Charnikhova T., Simkin A.J., Goulet C., Strack D., Bouwmeester H.J., *et al.* (2010). SlCCD7 controls strigolactone biosynthesis, shoot branching and mycorrhiza-induced apocarotenoid formation in tomato. Plant J. 61: 300–311.
111. Vurro M., Pérez-de-Luque A. and Eizenberg H. (2017). Parasitic Weeds. In Hatcher P.E., Froud-Williams R.J. (Ed.), Weed Research: Expanding Horizons, John Wiley & Sons Ltd, pp. 313–353.
112. Wakabayashi T., Hamana M., Mori, A., Akiyama R., Ueno K., Osakabe K., Osakabe Y., Suzuki H., Takikawa H., Mizutani M., *et al.* (2019). Direct conversion of carlactonoic acid to orobanchol by cytochrome P450 CYP722C in strigolactone biosynthesis. Sci. Adv. 5: 1–11.
113. Waters, M.T., Gutjahr, C., Bennett, T. and Nelson, D.C. (2017). Strigolactone Signaling and Evolution. Annu. Rev. Plant Biol. 68: 291–322.
114. Watson A.K. (2013). Biocontrol. In Joel D.M., Gressel J., Musselman L.J. (Ed.), Parasitic Orobanchaceae: Parasitic Mechanisms and Control Strategies, Springer Berlin Heidelberg, pp. 469–497.
115. Yao Z., Tian F., Cao X., Xu Y., Chen M., Xiang B. and Zhao S. (2016). Global Transcriptomic Analysis Reveals the Mechanism of *Phelipanche aegyptiaca* Seed Germination. Int. J. Mol. Sci. 17: 1139.
116. Yoder J.I., and Scholes J.D. (2010). Host plant resistance to parasitic weeds; recent progress and bottlenecks. Curr. Opin. Plant Biol. 13: 478–484.
117. Yoshida S. and Kee Y.J. (2021). Large-scale sequencing paves the way for genomic and genetic analyses in parasitic plants. Curr. Opin. Biotechnol. 70: 248–254.
118. Yoshida S., Kim S., Wafula E.K., Tanskanen J., Kim Y.M., Honaas L., Yan, Z., Spallek, T., Conn C.E., Ichihashi Y., *et al.* (2019). Genome Sequence of *Striga asiatica* Provides Insight into the Evolution of Plant Parasitism. Curr. Biol. 29: 3041-3052.e4.
119. Zarban R.A., Hameed U.F.S., Jamil M., Ota T., Wang J.Y., Arold S.T., Asami T. and Al-Babili S. (2021). Rational design of *Striga hermonthica*-specific seed germination inhibitors. Plant Physiol. 88: 1369-1384.
120. Zermane N., Souissi T., Kroschel J. and Sikora R. (2007). Biocontrol of broomrape (*Orobanche crenata* Forsk. and *Orobanche foetida* Poir.) by *Pseudomonas fluorescens* isolate Bf7-9 from the faba bean rhizosphere. Biocontrol Sci. Technol. 17: 483–497.