soil systems

Review

Managing Root Parasitic Weeds to Facilitate Legume Reintroduction into Mediterranean Rain-Fed Farming Systems

Diego Rubiales

Institute for Sustainable Agriculture, CSIC, 14080 Córdoba, Spain; diego.rubiales@ias.csic.es

Abstract: Grain and forage legumes are important sources of food and feed, key for sustainable agriculture given the environmental services they provide. However, their cultivation is hampered in the Mediterranean Basin and Near East by the widespread occurrence of the root parasitic weed crenate broomrape (*Orobanche crenata*). Other broomrape species such as *O. minor*, *O. foetida*, and *Phelipanche aegyptica* are also of local importance. As for other parasitic weeds, a number of management strategies have been proposed, but considering that temperate legumes in the area are low-input crops, these strategies are largely uneconomical or hard to achieve, leaving the use of resistant cultivars as the most desirable option. Breeding for broomrape resistance is not an easy task, but significant progress has been achieved by classical breeding and selection and will profit from recent developments in phenomics and genomics. Here, achievements and prospects in broomrape management and resistance breeding are presented and critically discussed.

Keywords: *Orobanche*; crop protection; resistance breeding; faba bean; pea; vetches; grass pea

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1. The Key Role of Legumes in Cropping Systems

Legumes are the second most important family of cultivated plants after cereals. They not only play a key role in agri-food systems as sources of food and feed but also provide ecosystem services by improving soil fertility, biodiversity and environmental sustainability [1,2]. The legume-rhizobium association provides a source of renewable nitrogen for agriculture that is estimated to reduce total nitrogen fertilizer consumption in all farming systems by between 24% (grain legumes) and 38% (forage legumes) [3]. Global production of nitrogen fertilizers has increased more than fourfold in the last decades, accounting for more than 60% of all fertilizers used in agriculture, either in the form of ammonium, urea, or nitrate. A large part of these fertilizers is not used by plants but is leached and ends up in aquifers. Reduced use of nitrogen fertilizers in turn reduces fossil energy consumption and greenhouse gas emissions associated with the manufacturing process as well as nitrous oxide emissions from soils [4]. Nitrous oxide is a potent greenhouse gas whose main source is microbial activity in soils and waters enriched in nitrates by the massive application of nitrogen fertilizers. It is estimated that cropping systems that include a legume emit, on average, 18% less nitrous oxide, with this reduction rising to 33% in the case of pastures [3].

However, yields of most temperate legumes are relatively low due to limited investment in breeding compared to other crops. As a result, and despite the above-mentioned ecosystem services they provide, the cultivation of most legumes has declined in Europe since the onset of so-called modern agriculture in the middle of the 20th century; nevertheless, legume cultivation is growing worldwide [5]. It is true that, as a result of changes in eating habits, human consumption of grain legumes has markedly declined in the last five decades, a trend that fortunately is starting to reverse. But this decline in human consumption alone does not explain the reduction in cultivation in traditional legume-producing countries in the Mediterranean Basin and Near East, as production is insufficient to cover the domestic demand, forcing imports of about 60 to 80% of the pulses eaten.

The reduced consumption of legumes paired with an increased consumption of meat has led to an ever-increasing demand for feed legumes, resulting in increasing dependence of imported soybeans [6,7]. It is therefore highly desirable from a nutritional point of view to increase legume consumption, but it is naïve to propose that this is the main measure needed to reintegrate legumes into Mediterranean cropping systems. Promoting legume consumption without acting on the necessary measures to promote local legume cultivation would result in a further increase in imports, as in fact is already the case for all grain legumes, and particularly soybean, whose imports continue to rise. Thus, by not growing legumes locally, we continue to lose the ecosystem services they provide [8]. The solution can only be to develop cropping packages that make the crops profitable to farmers by adjusting cultivation techniques and developing adapted varieties [5,9–11].

2. Broomrape as a Major Constraint in Legume Production

Cultivation of annual grain and forage temperate legumes is strongly hampered in the farming systems of the Mediterranean and Middle East by the widespread occurrence of broomrapes, which cause important yield losses [10]. The most widespread and damaging broomrape is crenate broomrape (*Orobanche crenata* Forsk.), but minor broomrape (*O. minor* Sm), foetida broomrape (*O. foetida* Poir), and Egyptian broomrape (*Pelipanche aegyptiaca* (Pers.) Pomel) can be of importance locally [11–16].

O. crenata is not a new problem in legume farming, having been described by authors from ancient Rome. Little progress has been made in its management since then, and unfortunately, the real situation is that instead of being controlled, it is a problem that is spreading to new areas that were considered free of infestation, even outside the Mediterranean Basin, to the north in Europe, to the south in Africa, and to the east in Asia, representing a situation that could worsen with climate change [16–18].

3. Understanding Broomrape Biologic Features Relevant to Management

The most relevant aspect of broomrape biology is that broomrapes are flowering plants that have evolved to feed on other plants, thereby losing photosynthetic capacity [11]. As flowering plants, broomrapes can be managed from a weed science point of view regarding their reproduction, seed dispersal, and chemical control with herbicides. However, unlike standard weeds, the damage of broomrapes is not due to competition for light and water from the soil but to the direct establishment of a permanent interaction with the roots of the host plants on which they feed and alter their physiology [19]. Broomrapes cause therefore true diseases and can be approached with a plant pathology perspective. The infected plant can defend itself against infection, in a similar way to how it defends itself against infections with any other pathogens like fungi, bacteria, or viruses [20,21]. And therefore, breeders can act by developing varieties that are more resistant to broomrape infection, in a similar way to how we would breed varieties resistant to fungi, bacteria, or viruses.

Several features make broomrape difficult to control [11,22]. One is its wide host range; for instance, the host range of *O. crenata* includes most legumes as well as crops such as carrot, lettuce, geranium, or celery. The host range of *P. aegyptiaca* is particularly wide, including many vegetable crops. Another difficulty is that infection with root parasitic plants occurs underground and is not detected until the broomrape emerges from the soil, by which time most of the damage has been done, and it is too late to attempt any control measures. Additionally, a single plant can produce a large number of seeds that have a great capacity for survival in the soil, germinating only when stimulated by signals emitted by host plants. Broomrape plants produce large numbers of seeds that are dispersed a short distance by the wind; thus, their distribution is typically agglomerated [23]. However, they can be spread over longer distances by manure of animals that feed on them, and above all, they can be spread by human action, either by the movement of contaminated machinery between farms or over even longer distances by the trading of crop seed lots containing soil residues and broomrape seeds [24]. Sanitation measures, disinfecting machinery and sowing seed are therefore essential in preventing expansion to new areas as well as in quarantine measures [25,26]. Diagnosis and quantification in soil or crop seed lots is also essential, with genomic tools being developed for this purpose [27,28].

Once the seeds have entered a farm, they are difficult to eradicate. The seeds have a long viability and germinate only in the presence of a host plant. They first need conditioning, associated with specific humidity and temperature conditions, which mimic the growing conditions of the host plant, thus ensuring that they germinate only when there may be plants available to be infected [29,30]. But this is not sufficient for germination; if the seeds are conditioned but are not stimulated by the proximity of a host plant, they return to their dormant state [31]. Broomrape seeds recognize a series of chemical signals emitted by neighboring host plants. The best-known group of broomrape germination stimulants are strigolactones [32,33], but there are many other metabolites that can induce broomrape germination [34]. For instance, a number of metabolites have been described in root exudates of pea or common vetch that differentially stimulate germination of seeds of different broomrape species, contributing to host specificity [35–37]. Once the seed germinates in the proximity of a root of a host plant, it emits a radicle that must find and anchor itself to the root, or it dies of starvation. Once anchored, it begins to feed on the host plant, developing a stem without functional roots, which eventually emerges to the surface and flowers, producing seeds that fall back to the ground, filling the seed bank, and repeating the cycle when a new host crop is found [11,13].

4. Management Strategies

There have been numerous efforts to develop control measures for broomrape management in legume cropping systems [10,11,13,18,38–40]. Unfortunately, the result has not been satisfactory, and the problem remains unresolved in practice. The approaches followed have ranged from agronomic practices to biological control and have given rise to great scientific discovery; unfortunately, they have had limited commercial application since they have either provided only partial protection or simply are not economically affordable for a low-input field crop, as are most of the legumes that we are dealing with. In practice, the only measures that have had some commercial application for legumes, as well as most field crops, are chemical control strategies with herbicides and genetic resistance [38–40].

The first measure always mentioned is hand weeding, namely, removing emerged plants from the field and destroying them. This is labour demanding and is worthwhile only in cases where infestations are still light. The second most recommended agronomic practice is delaying the sowing date [29,41,42], which may reduce the infection, but which in rain-fed cropping systems in Mediterranean climates is associated with a reduction in productive potential by not taking advantage of winter rains [43]. Other recommended practices are no tilling to reduce the incorporation of seeds into the soil [44] or very deep ploughing to plant the seeds quite deep [45].

Solarization can be very effective [46] and can be economical for cash crops in small areas such as greenhouses or orchards, but it is hardly feasible to solarize large farms with low-input crops. Another alternative is the cultivation of highly susceptible species, namely, “catch crops” that are infected and destroyed before the broomrape produces seeds, either by incorporating them into the soil as green manure or used for silage.

Soil fertilization can contribute to broomrape control as infestations are more severe in poor soils [47]. Under nutrient starvation, particularly P, but also N, strigolactone production by plants is increased to promote mycorrhizal colonisation, which is reduced when plants are fertilized [48]. On the other hand, urea and ammonium can have a toxic effect on the seeds and broomrape plants [49].

Another agronomic practice with potential is intercropping. A similar case with some success in subsistence agricultural systems in sub-Saharan Africa is the control of *Striga hermonthica* on corn or sorghum intercropped with *Desmodium* species, a mixture that was actually explored for the control of cereal stemborer insects, which are repelled by *Desmodium* and attracted to a border crop that is used to remove them from the field [50].

This intercropping was also found useful for controlling *Striga* [51]. This technique, called "pull and push", which is very labor-demanding, has some success on small family farms, but its extrapolation to other agricultural systems is not simple. Thus, it has been shown that a series of species can reduce infection with *O. crenata* in several legumes when they are mixed, such as fenugreek, oats, or berseem clover [52–54]. However, it is necessary to adjust cultivation practices so that they can be adopted by farmers.

The allelopathic effect of a series of crops on broomrape can be exploited not only in mixed crops but also in rotations. Thus, a series of crops have been described that can induce germination of broomrape seeds without being infected, having potential as "trap crops" that reduce the seed bank in the soil [55–58]. The principle is the same as that of "suicidal germination" by applying germination stimulants to the soil [59,60]. The theoretical basis is brilliant, and in both cases, it is based on germinating broomrape seeds that then die when they cannot find roots of a host crop to infect, either with crops that stimulate them but are not infected or by directly applying the germination stimulants to the soil in the absence of susceptible crops. However, in both cases the reduction is not complete, so several crop cycles would be needed for effective control. In the case of the direct application of synthetic germination stimulants to the soil, there is the added difficulty of finding an effective method of incorporation into the soil and of its persistence and cost. And once again, the economic factor must be considered since the measure must not only be effective in reducing the seed bank in the soil but also be economically viable for the farmer to adopt.

Within biological control, there have been efforts to promote the use of various insects, such as *Phytomiza orobanchia*, which is specific to *Orobanche*, whose larvae pupate inside broomrape capsules and destroy a large number of seeds [61]. The reality is that this insect is widely distributed naturally, having been found even in wild populations of many broomrape species, and that even if they destroy a percentage of seeds, there are so many thousands of seeds that a single broomrape plant is capable of producing that the effect of the parasite is minimal in areas with high infestation. After many years of study, there is no conclusive result or commercial application, even with breeding and release of adults. Other types of widely studied biocontrol agents are fungi [62] and bacteria [63] that have shown certain levels of control in pot studies under controlled conditions, but conclusive results from field studies have not yet been reported, highlighting above all the difficulty of finding a viable method of application and persistence [64]. The use of a series of natural metabolites produced by fungi or plants has also been proposed [65,66], which has shown an effect in the laboratory, but the mode of extraction or synthesis of these metabolites as well as their incorporation into the field must be optimized to make them applicable. Additionally, application of the amino acid methionine [67,68] or of growth regulators such as uniconazole [69] has been proposed, but this requires validation under field conditions.

Activation of systemic acquired resistance by various means has been proposed in several legumes. For instance, salicylic acid and benzothiadiazole application activated resistance reducing *O. minor* infection in red clover [70] and *O. crenata* in pea [71] and faba bean [72]. Many other inductors of resistance have been postulated in other pathosystems but not tested so far in legumes against broomrape. Symbionts such as mycorrhizae and rhizobium may also have a protective effect since their colonization affects root exudates or by activating resistance [73–77]. However, the effect although significant is small. Therefore, we have to conclude that although the biological control of broomrape still holds great promise, it has not yet resulted in a commercial application. Alternatively, we can foresee "biocontrol" as using broomrapes for food [78] or in pharmaceutical and cosmetic industries [79].

Since broomrape is a plant, it can be controlled by a number of herbicides [11,80,81]. Chemical disinfection of the soil can be very effective, but like physical disinfection (i.e., solarization), it is recommended only for small areas [81,82]. Also, since most legumes are low-input rain-fed crops and the infection occurs in the roots, the number of herbicides that can be used is reduced, practically excluding contact herbicides that would require irrigation to be incorporated into the roots. This has limited the herbicides used to systemic ones, incorporated on the leaves and translocated to the roots. The most recommended has been glyphosate in faba beans, which even so, finds no problems for its wide adoption by farmers. Glyphosate is also toxic to crops, which is why repeated application of a very low dose is necessary in the initial stages of infection; thus, finding a balance between crop damage and infection control is difficult. This has been even more complicated in other crops such as peas that are more sensitive to glyphosate. Imidazolinones have been proposed, even in seed treatment. However, the control is only partial, and the treatments have to be repeated [13,83]. Understanding the temporal variation in parasitism dynamics to predict broomrape parasitism based on thermal time can help for a more effective chemical control [82,84]. Site-specific broomrape management can benefit from geographical information systems and global positioning systems to delineate the spatial variation in infestation within and between fields [82]. Nanoencapsulation of herbicides has been proposed to improve their effectivity but is still under development [85].

All of this makes the development of resistant varieties the most desirable measure since it would eliminate the need for farmers to use any type of control measure. But, on the one hand, genetic resistance is difficult to identify and requires long improvement processes, and on the other hand, genetic resistance does not usually provide complete protection; therefore, it is advisable to incorporate resistance into integrated management packages, which, in addition to complementing the protection, would prolong the durability of the resistance by keeping the populations of the pathogen low and thus reducing its ability to evolve [13,20,40,86–90].

5. A Focus on Resistance Breeding

5.1. Genetic Basis of Resistance

Monogenic resistance has been identified in sunflower against *Orobanche cumana* [90] and in cowpea against *Striga gesnerioides* [91] but not in any legume crops against any broomrapes. This presents advantages and problems similar to those encountered in genetic improvement for resistance to any kind of disease; although monogenic resistance simplifies breeding progress, new races of the pathogen can emerge that break down these resistances [92]. Although it is easier to manage in breeding, monogenic resistance is not a panacea since the ability of pathogens to evolve into new races that overcome these resistances is well known. The risk of the appearance of new races depends not only on the genetic basis of the resistance (i.e., easier in monogenic resistance than in polygenic resistance) but also on the manner of reproduction and dissemination of pathogens [89,93]. Thus, it is known that the greatest risk occurs in organisms that combine sexual reproduction (new genetic combinations) and asexual reproduction (fixation of these new successful combinations), which can involve several complete cycles of reproduction in a breeding season. Cultivation can play a role in dissemination by influencing aerial dispersal over long distances; rust rot is the typical example where new races can appear in a matter of 2–5 years. In the case of broomrape, the risk is moderate since this plant reproduces sexually, with only one cycle per year, and except for accidental cases of movement of seeds by human action over long distances, the natural dispersal of seeds is a few meters [89]. Thus, in the case of *O. cumana*/sunflower, although new races have appeared, this did not happen as fast as observed in rusts but took several decades [92]. In the case of broomrapes infecting legumes (*O. crenata*, *O. minor*, *O. foetida* and *P. aegyptiaca*), no races have been described so far, and there is not even a consensus that there are *formae speciales*, despite the existence of variability in the pathogen as it is partially allogamous [89,94]. Only some weak levels of host specificity have recently been suggested in *O. crenata* populations growing on lentil [95]. Contrary to *O. crenata*, which has been known to infect legumes over centuries, *O. foetida* seems to be a relatively recent problem. Natural non-weedy populations of *O. foetida* are widespread in the western Mediterranean, infecting wild legume species only, not legume crops. However, only a few decades ago, weedy populations of *O. foetida* on faba bean were reported in the Beja region of Tunisia that became established in that area [96]. It seems that evolution of these populations might have been driven by response to host selection pressures including recognition of root exudates [97–99].

One possible explanation is that since monogenic resistance with complete expression has not been identified and exploited on a large scale but different levels of incomplete resistance has, the pathogen has not suffered this selection pressure, and in any case, since these are generally minority crops that occupy small extensions and are rarely repeated in the farm rotation, although more virulent populations have developed, they have not been established, or at least there is no evidence of establishment [89]. But without a doubt, we cannot rule out that if varieties with complete resistance are developed and become popular by repeatedly growing them in large areas, as has been the case with sunflowers, races that evolve to overcome this resistance will appear.

In the case of legumes, progress in broomrape resistance breeding has been slow, as they are rather minor crops in which relatively little has been invested in the last half century [5,9,100]. Most studies on broomrape resistance in legumes have concluded that there is low heritability and that inheritance is complex, highly influenced by the environment. Mapping studies have been performed in pea and faba bean, identifying a series of quantitative trait loci (QTLs) with a small effect, often not reproducible between years [100–106]. Field screenings are most needed but do not allow dissection of the various resistance mechanisms that might be operative and lack sufficient control of crucial environmental factors and of homogeneity of inoculum in the soil [87]. Attention is needed to improve phenotyping, complementing field screenings with dedicated minirhizotron methods or similar approaches allowing the identification of QTLs involved in specific mechanisms of resistance.

This has made the use of marker-assisted selection difficult. Still, the reality is that classical breeding programs have been successful in developing varieties with certain levels of resistance. Because of this, progress has been slower, but perhaps also because of this, there has not been a high selection pressure on the pathogen and no races of *O. crenata*, *O. minor*, *O. foetida*, or *P. aegyptiaca* have been described so far. Still, valuable sources of resistance have been identified in germplasm of most legume crops, including faba bean [107–112], pea [113–115], lentil [116–118], vetches [119–127], chickpea [128–131], grass pea and related *Lathyrus* species [132–136], or barrel medic [137,138], among other legume species. Some of these sources have been exploited in breeding programs, resulting in the release of resistant cultivars particularly in the case of faba bean [43,108] and pea [139–142].

5.2. Focus on Mechanisms of Resistance Operative

The basis of the durability of resistance is diversity, both at the cropping system level and at the level of genes and operative mechanisms [89,93]. There is consensus on the convenience of avoiding the use of monogenic resistance, recommending the use of polygenic resistance, which is what we only have at the moment in the case of legumes. Therefore, it seems that instead of complaining about the lack of monogenic resistance, we should congratulate ourselves and look for effective ways to accumulate information on the various QTLs or minor genes available, despite the greater complexity of their management in genetic improvement. Even so, given the predictable moderate risk of appearance and establishment of new races described in the previous section, the use of monogenic resistance should not be excluded, as long as the virulence of the parasitic populations is monitored to design strategies for the use of these genes, in space and time, to prolong their durability [93,138]. Another important point to discuss is that it is possibly not only the genetic basis of resistance that matters but also the nature of the resistance mechanism [89,93,143]. Thus, there is a series of monogenic resistances that have proven to be durable [144]. Curiously, these examples have in common that they are not based on a hypersensitive reaction due to cell death of the infected cell, like most of the major genes used in breeding, but rather on prehaustorial mechanisms, making cell penetration difficult. It is therefore highly recommended to explore the existence of resistance mechanisms acting in various phases of the infection process, which can be exploited separately, or preferably, combined in the same genotype [145]. And it is that combining two different resistance mechanisms that provide different barriers could be more effective than combining two genes that regulate the same mechanism.

It is therefore interesting to break down the broomrape infection process to identify the possible mechanisms operating at different stages of the infection process [114,145]. Genetically inherited phenological or root morphological traits might help to prevent infection, reducing the chances of contact in time and space, respectively. For instance, both very early or very late genotypes can escape infection [113,133], either by competition for nutrients of the early formed pods or through the late development of most roots when conditions are less favorable for broomrape establishment.

This would be followed by mechanisms that affect the germination and growth phase of broomrape radicles, either by reducing germination by lower exudation of germination stimulants, or by emitting metabolites with an inhibitory effect. Broomrape seeds germinate only when they recognize chemical signals exuded by the roots, which are thought to be primarily strigolactones [32,33]. There are many strigolactones known from different plants, and it is thought that the differential recognition of one or the other, together with other possible metabolites by different broomrape species, is what determines their host specificity [146–148]. A first working hypothesis would be the selection of genotypes that produce fewer strigolactones, but this would be counterproductive since strigolactones are not only signals that favor mycorrhization but also hormones that regulate the correct branching and architecture of the plant. It would therefore be desirable to have efficient methods to determine the strigolactones required by each broomrape species and to quantify them in the plant, so that we can select genotypes with differential levels of production, namely, to avoid those that stimulate the broomrape species but do produce others that allow a correct mycorrhization and architecture. In the absence of this level of knowledge, it has been possible to empirically identify faba bean genotypes displaying a strong resistance in the field, which was due to non-induction of germination of *O. crenata* seeds [109]. Interestingly, this mechanism was also operative against *O. foetida* and *P. aegyptiaca* and was associated with low production of the two strigolactones studied [148]. However, selected plants showed excellent performance in the field, suggesting that other (unquantified) strigolactones might be produced. The genetic basis of this resistance has not been studied, but there are indications that it could be monogenic. In fact, this mechanism has previously been described as monogenic in sorghum against *S. hermonthica* [149]. Similarly, tomato [150,151] and chickpea [130,152] mutants with reduced induction of broomrape seed germination likely due to reduced exudation of strigolactones have shown to be resistant to broomrape. This mechanism has also been described in other legumes such as pea [113–115], lentil [116,117], vetches [122–125], chickpea [128,129], or barrel medic [137,138], among others. In pea, two QTLs were associated with low induction of *O. crenata* seed germination [105]. A later study postulated monogenic inheritance of the trait [153].

Selection could also be exerted for higher exudation of metabolites inhibiting broomrape seed germination or radicle growth. Thus, a series of metabolites with such an effect have been identified [33], although little is known about the genotypic variability for this trait in legumes. A chemotrophic effect has also been postulated, such that a higher concentration of a series of metabolites could cause a directed growth of the broomrape radicle towards the host root [114] and affect the formation of the haustorium once the root has been contacted [154]. Until now, it was thought that a chemical signal was necessary for the differentiation of the haustorium in *Striga* and other parasitic plants but that this was not necessary in broomrape. However, it has recently been shown that broomrape radicles also respond to certain chemical signals to differentiate a haustorium [155], which in theory would make it possible to design genotypes that do not release these signals. Once a haustorium has differentiated on a host root, penetration is produced by a combination of mechanical pressure and enzymatic activity, so that a vascular interconnection occurs between both plants [156]. From here, broomrape acts as a sink for water and nutrients so that it develops at the expense of the host plant. The plant can develop different types of barriers preventing or delaying the infection. A first barrier can be by reinforcement of the cell walls of the cortex by protein cross-linking or with the deposition of suberin or callose, followed by lignification of endodermal and pericycle cell walls or later by occlusion or sealing of host vessels by gel- or gum-like substances, peroxidase-related lignification, mucilage production, or haustorium disorganization, preventing the parasite's survival [156–159].

5.3. Resistance to Herbicides

As indicated above, broomrape can be managed in legume farming systems with systemic herbicides (i.e., glyphosate, imidazolinones, and sulfonylurea) at low rates with repeated treatments. Control could be improved by enhancing the tolerance of the crops to these herbicides, so higher rates could be applied [160]. Natural variation in herbicide tolerance has been identified in several legumes, including tolerance to imazethapyr and metribuzin in faba bean [161] and lentil [162,163]. Mutation breeding has been effectively exploited to develop herbicide-resistant mutants [164,165], offering scope for improving the chemical control of broomrape by using higher rates of herbicides. An alternative strategy is using transgenic techniques, although engineered legume crops harboring herbicide-resistance transgenes are not yet available for broomrape management [166–168].

5.4. Potential Applications of Biotechnology in Broomrape Resistance Breeding

The basis of any genetic improvement program is genetic diversity on which to act using various tools until obtaining resistant varieties that are also agronomically attractive and of good quality [5,89,99]. If the needed genetic diversity is not available, it can be generated by classical or directed mutagenesis [150–152] or by new biotechnological tools [100,166,167]. But it may be sufficient to explore and exploit the existing natural variability within the crop or related species. Thus, there are a large number of insufficiently characterized collections where we could find the desired characters [145]. A battery of field, pot and minirhizotron screening protocols have been proposed to promote the identification of sources of resistance in most species as described above. An often neglected limitation is the availability of fast but sufficiently reliable screening techniques that allow us to find what we need [87]. Hyperspectral imaging is being adjusted for early detection of broomrape infection to help with precise herbicide application in terms of time and space [169], with continuous attempts also to automate image phenotyping in seedling responses in rhizotrons [170], which is still too laborious and time-consuming. As a result, sources of resistance to broomrape are limited and poorly characterized. In spite of these constraints, pea and faba bean breeding has successfully led to the release of resistant cultivars [139–142]. Adoption of modern technologies rapidly developing in legumes will facilitate breeding. Despite the fact that modern genetics was born with Mendel's genetic studies of the pea and, similarly, the bean played an important role in the onset of cytogenetics, progress in the knowledge of these crops proceeded much more slowly later than in other crops, like cereals. Fortunately, in recent years, we have been experiencing spectacular advances in genomic and phenomic techniques in legumes [171], opening enormous opportunities for their application in breeding. Thus, in only a few years, annotated genomes of peas, faba beans, lentils, and most of the legumes have become available. Even in those species not yet sequenced, the reduction in genotyping costs is facilitating molecular analysis [172–174]. Although similar progress in genome sequencing has not been achieved for broomrape species, spectacular progress is being made in sequence information on other parasitic weeds [175,176] that will help in understanding parasite virulence and host resistance mechanisms. The integration of information obtained from QTL analysis with gene and protein expression analysis in response to broomrape infection [177,178] can shortcut conventional breeding or marker-assisted selection to identify candidate genes that could be used for selective gene silencing (RNAs, siRNA) [179] or DNA base editing (CRISPR/Cas9) to deliver broomrape resistance [180–182]. Although legumes are considered recalcitrant to stable genetic transformation protocols, progress is being achieved [183,184]; therefore, transient transformation or TILLING may be used for the functional characterization of candidate genes.

6. Conclusions

A number of strategies have been proposed for crenate broomrape management, but considering that temperate legumes in the area are low-input crops, they have been found to be largely uneconomical or hard to achieve, leaving the use of resistant cultivars as the most desirable option. Breeding for broomrape resistance is not easy, but significant progress has been achieved by classical breeding and selection and will benefit in the short term from recent developments in phenomics and genomics.

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