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Interaction between Broomrapes and their Hosts

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Summary

Broomrapes (Orobanchaceae) are phanerogamic holoparasites that attack the roots of many crops. They vary in host range, some parasitizing a broad range of crops, whereas others are more specific. Broomrape seed germination occurs only in response to a chemical signal from the host root and produces a haustorium which connects directly to the host phloem via contact or transfer cells. The parasite competes successfully with the host sink organs for water and nutrients due to a mechanism assuring a higher osmotic pressure compared with the host plant. Several compatible and incompatible interactions between broomrapes and their hosts have been described. The determination of the osmoregulation and nutritional relationships between broomrapes and their hosts will provide a better understanding of the host-parasite interaction. This can be made by histological, physiological and biochemical or molecular methods which can also allow the development of new methods of control. This review assembles and discusses latest works on the communication and connection between broomrapes and their hosts with particular emphasis on incompatible interactions and osmotic and metabolic particularities of broomrapes in relation with their hosts.

Key Words: Broomrape, Phloem, Osmolarity, Metabolism, Interaction, Hosts

Geographic Distribution of Broomrapes and their Host Range

The genus *Orobanche* has more than 150 species among which only a few parasitize agronomic crops. The majority of broomrapes are found in the warm and temperate parts of the northern hemisphere, especially the Mediterranean region [1], but some species have spread to many other parts of the world. *Phelipanche aegyptiaca* (Pers.) Pomel (Synonym *Orobanche aegyptiaca*) occurs mainly in southeastern Europe, northeastern Africa, and the Middle East, whereas *Phelipanche ramosa* (L.) Pomel (Synonym *Orobanche ramosa*), which is closely related to *P. aegyptiaca*, is mostly found in the Middle East. *Orobanche cernua* and *Orobanche cumana* are mainly distributed in the Middle East, and southern and eastern Europe [1]. *Orobanche crenata* is restricted to the Mediterranean Basin and the Middle East [2]. *Orobanche foetida* is widely distributed in natural habitats in the Western Mediterranean Area including Portugal, Spain, Morocco, Algeria and Tunisia, [3, 4]. *Orobanche minor* is disturbed in habitats throughout the central and southern parts of Europe, and extends to the eastern coast of Africa and southwards [1] and has recently become a problem on red clover in Oregon, USA [5].

Broomrapes vary in host range, some parasitizing a broad range of crops, whereas others are more specific. *P. ramosa* L. has the widest host range, parasitizing many solanaceous crops such as potato, tobacco and tomato, members of Brassicaceae, Leguminaceae, and several other families. *P. aegyptiaca* has a host range similar to that of *P. ramosa*, and is also parasitic on carrot, legumes such as common vetch, and crucifers including oilseed rape [1]. In the Mediterranean Basin and Middle East, *O. crenata* Forsk. is an important pest in faba bean, pea, lentil, vetches, grass pea and other grain and forage legumes [2]. *O. cumana* Wallr. is extremely damaging to sunflower, however *O. cernua* Loefl. is almost exclusively a parasite of Solanaceae (tomato, tobacco, pepper and eggplant) [1]. *O. foetida* parasitises wild herbaceous leguminous plants [4], but recently it is considered as an important agricultural parasite in faba bean in Beja region of Tunisia [3, 6, 7]. It has recently also been found in Morocco infecting common vetch [8]. This parasite presents a less broad host range compared to *O. crenata* [9]. *O. minor* has a wide host range among forage legumes in temperate climates and it is of economic importance on clover [5]. For more details, a recent review on the current status and the agricultural damage of parasitic weeds is available [10].

Communication Between Broomrapes and their Hosts: Growth and Development (Compatible Interaction)

Broomrapes are annuals that reproduce by seeds. Seeds are usually dark brown, oval shaped, measure 0.35 x 0.25 mm and weigh 3 to 6 µg [1]. Broomrape seed germination occurs only in response to a chemical signal from the host root. This chemical communication is critical for the survival of the parasite because it allows the tiny Orobanche seeds to recognize the presence of a nearby suitable host prior to germination, avoiding a suicidal germination. Numerous secondary metabolites as inducers of parasite germination mainly belonging to the strigolactones group of isoprenoid are involved in this interaction [11]. These compounds and their production are subject to intensive studies to find either analogous chemicals to induce suicidal parasite germination or genotypes with reduced induction levels [11]. The first described *Orobanche* germination stimulant, orobanchol, was isolated by [12] from red clover (*Trifolium pratense*) root

exudates. However, 2'-epiorobanchol and solanacol were characterized from root exudates of tobacco (*Nicotiana tabacum*), a host of *P. ramosa* [13]. In addition, two novel stimulants, sorgomol [14, 15] and a putative didehydro-orobanchol (strigol) isomer [13, 16], were identified in the root exudates of several Poaceae species and the Solanaceae species *N. tabacum* and tomato (*Solanum lycopersicum*). More recently, several Fabaceae plants were found to exude known strigolactones, such as orobanchol, orobanchyl acetate (alectrol), and 5-deoxystrigol, suggesting that these strigolactones are widely distributed in Fabaceae [17]. More detailed discussions on the structure, biological activity, chemistry and regulation of production of strigolactones can be found in other papers [18, 19, 20].

After germination, the seed produces a 'germ tube' or radicle which elongates by cell division and extension [1], and attaches to host roots mainly in the region of root elongation and absorption [21]. The tip of the radicle enlarges as soon as it attaches to the host root and forms a 'haustorium'. Subsequently, the haustorial tissue penetrates the host root by enzymatic degradation, rather than mechanical destruction [22], and establishes connections with the host vascular system. It is by these connections that the parasite derives its nutrients and water from the host. The part of the broomrape seedling outside the root of the host swells to form a tubercle. Under favorable conditions, a shoot bud develops on the tubercle producing a flowering spike which elongates, and emerges above the soil [1].

Orobanche-Hosts Interfaces

During the early stages of penetration, the parasitic plant releases enzymes that allow penetration of intrusive cells between host cells [23] and an adhesive substance that facilitates internal anchoring of the parasite to host cell walls [24]. Several studies described close association of orobanche haustorium with vascular host roots [25, 26]. Direct connections between haustorial tissue and the host xylem were observed [25, 27, 28]. However, for the connection between the host phloem tissue and the haustorial cells, contact cells have been reported [29]. These cells probably absorb nutrients from the sieve cells via the sieve areas and transport the nutrients to the parasite. Dorr and Kollman [30] have reported interspecific sieve pores derived from interspecific plasmodesmata at the point where broomrape and the host cells differentiate into sieve elements. Transfer cells linking the phloem of host and parasite have also been reported [31]. Several studies described the presence of xylem and phloem in broomrape haustorial tissues [30, 31].

On the other hand, the high K/Ca ratios registered in *O. feotida* parasitizing faba bean [32], *P. ramosa* parasitizing tobacco [33] and *O. cernua* parasitizing tobacco [34], attest that these parasites are connected essentially to the host root phloem. Indeed, the degree of broomrape dependence on host phloem is regulated by the occurrence of symplasmic connections through plasmodesmata between host and parasite phloem tissues [30, 31]. Recently, the pathosystem faba bean-*O. foetida* showed that some RFO (Raffinose Family Oligosaccharide) compounds were transferred from the host to the parasite. Given that RFO loading and unloading in plants consists of transport through plasmodesmata [35], symplasmic phloem connections between faba bean and *O. foetida* can be expected [32]. On the other hand, the absence or low activity of nitrogen assimilating enzymes in broomrape [36] may indicate that the parasite must have access to organic nitrogen forms from the host plant.

Osmotic and Metabolic Particularities of Broomrapes in Relation with their Hosts

The parasite competes successfully with the host sink organs for water and nutrients due to a mechanism assuring a higher osmotic pressure compared with the host plant [37, 38]. The sink strength of the parasite is based mainly on the immediate cleavage of the host-derived sucrose into glucose and fructose mediated by a putative invertase, thus doubling the osmotic value of the sugar component. In this way, the resistance of some faba bean cultivars was explained by their higher osmotic values compared to susceptible cultivars [37, 38], and then lowering the magnitude in osmolarity between host and parasite. Several studies have emphasized the primary role of hexoses and mannitol in the osmotic adjustment of Orobanche [1, 39]. In addition, excess carbon is massively incorporated into starch [32, 38]. Nevertheless, the mechanisms involved in the osmotic adjustment of broomrapes needs clarification.

Determination of the organic solutes profiles of broomrapes and their hosts will provide a better understanding of the biochemistry and physiology of the host-parasite interaction. Hibberd et al. [34] showed that more than 99% of carbon taken up by the parasite *O. cernua* comes from the phloem of tobacco. This carbon transfer occurs primarily in the form of sucrose in the broad bean-*O. crenata* system [40], and in the form of sucrose and Stachyose (ROF) in the faba bean-*O. foetida* system [32, 38]. Thus, Aber et al. [40] demonstrated translocation of organic substances, particularly sucrose, to *O. crenata* tubercles from $^{14}CO_2$ fixation by broad bean plants. It has also been shown that ^{14}C-labeled photoassimilates accumulated in *O. ramosa* after fixation of $^{14}CO_2$ by tomato plants [27]. In addition, in the Helianthus-*Orobanche cumana* system, when aerial parts of sunflower were subjected to $^{14}CO_2$, radioactivity was detected in the parasite [25]. In the parasite, carbon is accumulated in the form of mannitol and starch and mainly hexoses, [32, 38, 39] suggesting the implication of an invertase enzyme which was recently measured in *O. foetida* and which looks related to the degree of susceptibility of the host genotype [32].

On the other hand, for nitrogen metabolism of broomrapes, several studies indicated that absence or low activity of nitrogen assimilating enzymes in broomrape [36] may indicate that the parasite must have access to organic nitrogen forms from the host plant. There are only few studies on the effect of broomrapes on the composition of host amino acids. *O. aegyptiaca* had similar amino acid profiles than its host, but parasitism induced changes in the composition of both free and bound amino acids in carrot [41]. In this pathosystem, Arginine was the major amino acid in both host and parasite. In contrast, N metabolism in *O. foetida* parasitizing faba bean consisted mainly of the accumulation of Asparagine/Aspartate [32, 38]. Thus, a model for the implication of Asparagines synthetase and Glutamine oxaloacetate aminotransferase enzymes was proposed in *O. foetida* [38]. *O. foetida* did not influence significantly the phloem composition in a susceptible faba bean. In contrast, it

induced a marked decrease in the levels of all the amino acids in the phloem exudates of a resistant one, without affecting significantly the carbohydrate and organic acid levels. On the other hand, the parasite *O. cernua* exerted a large impact on the nitrogen relations of the host tobacco, notably nitrate uptake was stimulated and the amino acid content of xylem sap was lower. The major amino acid detected in both host and parasite was Glutamine [34].

Incompatible Interactions: Host Plant Resistance/Tolerance

Once the parasite has germinated or penetrated to host tissues; the host can detect the presence of this foreign organism and reacts to it. This was found to apply also in compatible interactions [42, 43].

Several studies indicated incompatible interactions between orobanche and their hosts. These incompatible interactions are characterized by the lignification of host root [1, 44], the induction of toxic phytoalexins in host tissues [1, 45] and the development of necrotic lesions on the host root encompassing the attachments of the parasite radical like in the Vetch-*P. aegyptiaca* system [46]. Necrosis is also an incompatible interaction described for many legumes, including common vetch, faba bean, pea, chickpea and lentil against *O. crenata* [26, 47, 48, 49, 50], sunflower against *O. cernua* and *O. cumana* [25, 44] and *Vicia* against *P. aegyptiaca* [46]. Cell wall deposition, vessel occlusion and broomrape cellular disorganization were also demonstrated in incompatible interaction between sunflower and *O. cernua* [25].

At the biochemical level, incompatibility between host and parasite tissue has been correlated with an increase in the level of phenolics and peroxidase activity and the accumulation of substances inside host xylem vessels in several pathosystems, including purple vetch-*O. aegyptiaca* L. [46], sunflower-*O. cumana* Wallr. [45], faba bean, chickpea, vetch and lentil-*O. crenata* [26, 37, 49, 50, 51]. Broomrape infection induced also an induction of H_2O_2 and camalexin synthesis in the *A. thaliana-O. ramosa* system [43] and the activation of the phenylpropanoid and isoprenoid pathways in the host in the *Arabidopsis thaliana-P. ramosa* system [42] and tobacco-*P. aegyptiaca* system [52].

The retarded development of established tubercles in some genotypes was observed in several pathosystems [49, 53]. In the case of the faba bean-*O. foetida* system, the limited growth of broomrape fixed on the resistant genotype was due to low soluble invertase activity, low osmotic potential of the infected roots and low organic nitrogen level in the host phloem sap [32].

Some other incompatible interactions are showed before connection between host and parasite. Thus, a reduction in root biomass or a deeper host root system can reduce the chance of contact between the host and the parasite. This form of escape has been reported as a resistance mechanism operating in faba bean [47, 54], chickpea [48], pea [49] and lentil [55] against *O. crenata*. Genotypes with low stimulation of broomrape germination have been found in vetch, pea, chickpea, grass pea [48, 49, 53, 56] against *O. crenata*, faba bean against *O. feotida* and *O. crenata* [54, 57, 58] and sunflower against *O. cernua* [25]. The differences in germination of broomrape seeds between genotypes could be due to differences in the amount of germination stimulants exudated, differences in production of inhibitors or a combination of both. This difference can also be due to differences in the receptors for the germination stimulants in the parasites between Orobanche species.

Conclusion

Broomrapes are serious parasitic weeds causing great losses in many major crops. Various cultural and chemical strategies have been assayed to control broomrapes but without sufficient success. The use of histological, physiological and biochemical methods contributed to the better understanding of the interaction and the parasite biology. These methods may also allow the comprehension of causes of incompatible interactions and the development of new methods of control. To date, the molecular bases of the plant–parasitic plant interaction remain mostly unknown, and much work in this approach remains to be done.

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