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Biological Characteristics and Control of *Orobanche Crenata* Forsk., a Review

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Abstract

Orobanche crenata is a holoparasitic phanerogam which is particularly noxious to legumes, such as faba bean (*Vicia faba* L.), pea (*Pisum sativum* L.), chickpea (*Cicer arietinum* L.), lentil (*Lens culinaris* Medik.), etc., and commonly considered one of the major causes which has contributed to re-rizing the area designed to their cultivation. After a few brief references on the origin and diffusion of *O. crenata*, in this work summarises the results of research into biological aspects and control of this species. The information obtained especially concerns seed production, seed viability, seed longevity and dormancy, seed conditioning and germination, parasitism phases, the effects of parasite attacks on host plants and the means of control.

Key-words: seed production, seed characteristics, parasitism, damage, means of control, crenate broomrape.

1. Introduction

The genus *Orobanche,* from the Greek οροβος and αγχω, according to Fiori (1969), includes 120 species, 90% of which are indigenous to the warm temperate regions of the Northern hemisphere where, through commerce in seeds, some spread to South America and Oceania (Marudarjan, 1950; Sauerborn, 1991a; Mitich, 1993; Carter et al., 1996; Diaz and Norambuena, 2001; Rubiales et al., 2003a).

These species represent dreadful parasites to numerous crops, such as hemp (*Cannabis sativa* L.), carrot (*Daucus carota* L.), cabbage (*Brassica oleracea* (L.) Alef. conv. capitata L.), chickpea (*Cicer arietinum* L.), faba bean (*Vicia faba* L.), sunflower (*Helianthus annuus* L.), lentil (*Lens culinaris* Medik.), aubergine (*Solanum melongena* L.), lucerne (*Medicago sativa* L.), potato (*Solanum tuberosum* L.), pea (*Pisum sativum* L.), celery (*Apium graveolens* L.), tobacco (*Nicotiana tabacum* L.), vetch (*Vicia sativa* L.), etc. It has been estimated that in the Mediterranean region, Eastern Europe and Western Asia about 16 million hectares of agricultural land have been infested by *Orobanche* spp. (Sauerborn, 1991b).

2. Origin, diffusion and parasitized species

Listed among the most deleterious species, *O. crenata* Forsk., also known as O. *speciosa* D.C. in Lam & D.C. and *O. pelargonii* Caldesi by Greuter et al. (1989), is considered indigenous in the Mediterranean Basin (Cubero, 1983), but it can be found in many other central northern European countries like Estonia, the Czech Republic, the Netherlands, Northern France, Southern England, Switzerland, Austria and Northern and Central Germany (Kreutz, 1995).

According to Grenz and Sauerborn (2007), the establishment of this species is only possible in areas where a warm dry period is followed by warm wet conditions, and the presence of conditioned seed coincides with that of the host plant. These conditions predominate wher-

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ever there is a Mediterranean climate and in parts of the monsoon regions, savannah and dry winter areas of central America, Africa, Australia and Southern Asia. By contrast, its establishment is impossible in humid areas, both temperate and tropical, where the preponderance of dormancy-inducing wet conditions and lack of a warm-dry period which, facilitating dormancy release, prevents seed germination and thus establishment of the species.

Commonly called crenate broomrape, legume burn, flame grass, wolf grass, bull grass, scallion grass, wolf bean, *O. crenata* is a holoparasite devoid of chlorophyll and totally dependent on the host for organic carbon, water and nitrogen (Joel et al., 2007) and is particularly noxious to legumes (faba bean, pea, chickpea, lentil), being one of the major causes of the decline in their cultivation. Carrot (*Daucus carota* L.), safflower (*Carthamus tinctorious* L.), geranium (*Geranium* spp.), lettuce (*Lactuca sativa* L.) and many other species, either cultivated or wild, are also parasitized. To explain *O. crenata*'s relevance, it had by the beginning of the 1990s, already infested 63% of the faba bean crop in Morocco, Portugal, Spain and Syria (Sauerborn, 1991b) and this percentage would have been even higher if it had included all those areas abandoned due to over-infestation (Parker e Riches, 1993).

3. Plant Characteristics and Seed Production

O. crenata reproduces by seeds; its underground fraction being essentially made of the tubercle and pseudo roots, while above-ground it consists of a floral stem, also called flowering shoot, fleshy, erect, non-branching, 30-70 cm high, sparsely hairy, usually yellowish.

The inflorescence, usually, has numerous flowers in a spike, dense above, often lax below, hairy; the corolla is usually 20-30 mm long, subglabrous, white; four stamens are inserted 2-3 mm above the base of the corolla (Tutin et al., 1981). Cross-pollination, normally entomophilous (Cubero, 1983), determines genetic variability (Verkleij et al., 1986; Cubero, 1991; Román et al., 2002) which contributes to explains why *O. crenata* is able to parasite on an increasingly greater number of species. Its fruit is a unilocular capsule 10-12 mm long (Tutin et al., 1981), which, when ripe, opens into two valves, and above all in early attacks, liberates a large number of very small brown seeds from $1\text{-}5x10^5$ per spike (Cubero, 1983; Linke and Saxena, 1991; López-Granados and García-Torres, 1991). Seed weights ranging from 3 to 7 µg (Linke, 1987; Parker and Riches, 1993), are oval, convex on one side and flat on the other with corresponding micropyle.

The seed has an undifferentiated embryo made of a group of cells surrounded by others rich in reserve substances (endosperm); externally it is covered in a tough seedcoat with an alveolar surface. The alveoli more or less form a pentagon 55-75 x 35-55 µm (Abu Sbaih and Jury, 1994).

4. Seed viability

Seeds may be viable (germinable or dormant) or non-viable. The former come mostly from the capsules of the lower and middle third of the spikes, while the latter mostly from the upper third and often, because of an underdeveloped endosperm, are particularly small (Linke and Saxena, 1991).

The results of in-vitro research (Khalaf, 1991) lead one to presume that seed viability is also influenced by area of origin.

The seeds are relatively long-lived (Kardy and Tewfik, 1956; Cubero and Moreno, 1979) which also depends on the environment and conservation conditions. Seed viability proved longer in the laboratory than in the soil where no variations due to depth were observed (Lòpez-Granados and Garcìa-Torres, 1999) or any due to heat/humidity variations (Kebreab and Murdoch, 1999). Referring to this latter, Linke and Saxena (1991) demonstrated that half life was reached after 9 years of storage at low relative humidity, and temperatures not exceeding 25 °C; after 15 years, at the same storage conditions, all seeds had lost viability. The same parameters were reached after 2.5 and 5 years, respectively, when stored at high relative air humidity and temperatures often over 30 °C during the hot season.

5. Seed dormancy

Viable seeds are subject to dormancy (Abu-Shakra et al., 1970; Edwards, 1972; El-Basyouni,

1979; Khalaf, 1991; Van Hezewijk et al., 1993; Salisbury and Ross, 1996). Dormancy, which affects about 50% of viable seeds (Lòpez-Granados and Garcìa-Torres, 1993), may be caused by different factors as yet insufficiently studied.

Among those most commonly cited, they point to the metabolic state of the seed, low endogenous gibberelline or high germination inhibitors in the seed, seed-coat characteristics, the absence of host plant stimulus and long seed exposure to humidity and temperatures unfavourable for germination (Khalaf, 1991; Van Hezewijk et al., 1993; Van Hezewijk et al., 1994; Matusova et al., 2005).

It has been observed that dormancy due to phenolic compounds in the seed disappears after washing in soil water or immersion in water for 2-4 weeks at 20 °C (Edwards, 1972; Edwards et al., 1976; El Basyouni, 1979).

The dormancy/non-dormancy cycle is typical of an annual weed with autumn germination.

6. Seedbank

The copious production of enduring long-life seeds capable of long dormancy accounts for its peculiar seedbank characteristics. It can reach very high values (approximately 4 million seeds m^{-2} in the 20 cm depth arable layer) most of which are viable (Lopéz Granados and García Torres, 1993). *O. crenata* seeds, also extracted from the soil, can be identified by DNA fingerprinting (Portnoy et al., 1997).

7. Seed conditioning

The seed must be conditioned, for example by exposure to a moist environment at about 18 °C for 11 days, in order to be stimulated by the host plant to germinate (Kasasian, 1973). Nevertheless, it has been ascertained that should the length of conditioning exceed the necessary time to ensure the highest percentage of germination, then the seed returns to dormancy. In research by Van Hezewijk et al. (1993) this phenomenon has been confirmed after prolonged exposure at 10-15 °C and less so at 20 °C.

Seed conditioning is a complex process involving metabolic events as well as those indispensable for germination (Joel et al. 1991) and due to which there is a drastic increase in respiration and the production of hormones and proteins for DNA (Bar-Nun and Mayer, 1993; Joel et al., 1991; Joel et al., 1995a; Joel, 2000).

Increased respiration, which for *O. aegyptiaca* seed reaches a peak 3 days after conditioning (Bar-Nun and Mayer, 1993), shows that seed preparation for germination involves very active changes. Once past the peak, the seed goes into stand-by, but maintains its receptivity to the stimulus for a relatively long period. The oxygen absorption peak is significantly higher if during conditioning oxygenised gibberellin is applied (Bar-Nun and Mayer, 1993), which also reduces the minimum useful exposure time to the stimulant (Joel et al., 1991; Joel et al., 2000) and promotes germination (Nash and Wilhelm, 1960; Hsiao et al., 1988).

Conditioned seeds respond to very low concentrations (10^{-7}-10^{-15} M) of germination stimulants, such as strigolactones, which are normally released from host roots (Wigchert and Zwanenburg, 1999). Stimulant concentrations which are higher than optimal, inhibit seed germination (Joel et al., 1995a; Joel, 2000).

8. Seed germination

Seed germination is barely influenced by the increase in soil pH from 5 to 8.5 (Van Hezewijk et al., 1994**)** and by the lowering of the osmotic potential from 0 to -0.5 MPa. This latter parameter, on the contrary, shortens germ tube length. (Nandula, 1998).

Acid scarification with dilute concentrations of H_2SO_4 (0.5 N) for short periods of time (from 1 to 20 min) or prechilling treatments at temperatures of around 0 °C from 24 h to 6 d increased seed germination (Lòpez-Granados and Garcìa-Torres, 1996).

Lag time strongly increased with decreasing temperatures and at 5 °C it was 20 days. Germination percentage was maximal within a narrow temperature range, from approximately 15 to 20 °C; at 0 and 35 °C no germination took place (Kasasian, 1973; Van Hezewijk et al., 1991).

The identification of the stimulants exuded by host roots was not easy also because of their low concentration and probable transformation by soil micro-organisms (Steinkellner et al.,

2007). It is widely held, however, that they can be active or precursors to conversion into germination inducers.

In the root excretions of the faba bean at least 8 gibberellines capable of stimulating germination have been found (El-Ghamrawy et al., 1990; El-Ghamrawy and Neumann, 1991), but none includes gibberellic acid (GA_3). Since the latter cannot induce germination alone, while if added to stimulants it increases noticeably (Hassan et al., 1980), it has been suggested that its presence in the seed is to perceive the stimulant (El-Ghamrawy et al., 1990; El-Ghamrawy and Neumann, 1991). This is different in relation to the host plant (Restuccia and Mauromicale, 1991); in faba bean the stimulus reaches the maximum effectiveness nearing the phase change from vegetative to reproductive, more precisely a week before and about five days after the start of flowering in the autumn/spring crop and in the spring/summer crop (El-Ghamrawy and Neumam, l991). This data on the autumn/spring cycle of the cultivated faba bean would seem to confirm the results of Restuccia and Mauromicale (1991), who verified that the highest percentages of germination are assured by the root extracts from the main shoot of plants at the development stage of the 8^{t}-10^{th} leaf.

Very little is known about the mechanism behind receiving the stimulus and initiating germination, even if it has been hypothesised that initiation is made possible by physiological changes taking place within the seed itself such as the transformation of inhibitors and/or the increase in stimulators (Evenari, 1949; Mayer and Shain, 1974).

9. Parasitism phases

Germination begins with the enlarging of the micropyle zone of the seed, which is followed by the emergence of the germ tube, a yellowy-white tubular organ, whose apex formed of active meristematic cells, seems slightly swollen. Once past the seedcoat, the germ tube elongates by division and cellular distension (Parker and Riches, 1993), and most probably guided by a chemiotrophic gradient, in the 2-3 days after the start of germination, makes contact with the host plant root.

Since this contact must be made before the endosperm reserve runs out, even at risk of seed death, it is only believed possible if the seed-root distance amounts to a few millimeters in length (Kardy and Tewfic, 1956; Ter-Borg, 1986). Frequently, contact is with secondary host roots (Aber, 1984), above all in the area of prolongation and active absorption (Foy et al., 1989) or in relation to root nodules (Kukula and Masri, 1985). This latter observation holds that there is a relationship between *O. crenata* and *Rhizobium* (Musselman, 1980; Morozov et al., 2000; Mabrouk et al. 2007). It should be noted, however, that in the pea, an inoculum with compatible *Rhizobium* strains (P.SOM and P. 1236) can protect the pea against *O. crenata* attack by reducing active host root exudation and by preventing parasite attachment and growth of installed tubercles. As the attacks decrease, peroxidase and phenylalanine ammonia lyase activity increases in the pea roots (Mabrouk et al., 2007).

In research by López Granados and García Torres (1993), about $3x10^{-3}$% of the seedbank became attached to the root and of these only 9% developed and emerged from the soil, probably reflecting high levels of intraspecific competition.

Once contact with the host root is made, the germ tube immediately forms an appressorium, followed by haustoria production. The germ tube stops extending itself, the apex expands and the peripheral cells become papillars. On the outer surface of these cells, protuberances begin to form covered by a cuticle which secretes a carbohydrate. Once accumulated it then discharges to create a thin adhesive layer which glues the parasite to the host (Baird and Riopel, 1985; Joel and Losner-Goshen, 1994).

The independent life phase, facilitated by the consumption of material stored in the seed, lasts a few days until the parasite finds a host, and attaches to it. The next parasitic life phase starts as soon as the intrusive cells of the haustorium (specialized transfer structure) make a physiological bridge with the host. At this point the parasite becomes dependent on nutrients from the host (Joel, 2000).

The penetration of the haustorium into the root tissue is facilitated by both the mechanical force generated by its growth (Dörr and Kollman, 1974) and its enzymatic activities which

change wall composition in the host tissues, thereby facilitating the separation of neighboring host cells (Joel and Losner-Goshen, 1994). The enzymes involved are thought to be polygalacturonase, carbomethylcellulase, ß-glycosidase (whose activity peaks 2-3 days after germination by which time the parasite must have attached itself to the host) and pectin methyl esterase (PME) (Aber and Sallé, 1983; Losner-Goshen et al., 1998). Furthermore, it is presumed that in the endodermis, whose cells are impregnated with cutin and suberin, haustorium penetration is facilitated by cutinase (Joel et al., 1998; Joel, 2000).

There is a direct connection between the haustorium and the host's xylem (Saghir et al., 1973; Dörr and Kollman, 1976; Pennypacker et al., 1979; Visser and Dörr, 1987), whereas for the phloem they have not as yet been clearly identified and seem to indirectly involve contact (Dörr and Kollman, 1975) or polymorphic cells (Pennypacker et al., 1979; Rajanna et al., 2005), on several occasions observed in direct contact with host sieve cells. Dörr and Kollman (1995) also noticed interspecific sieve pores derived from plasmodesmata at the points where both the host cells and those of the parasite differentiate into sieve elements (Nandula, 1998). Once the connection is established, the parasite development is fully coordinated by the host. Their synchronised life leads to the formation of continuous vessels which act like a bridge between the two (Joel, 2000).

Once the cauline cells of the parasite on the outside of the root take in organic ions, metabolites, hormones and water from the host, they begin to multiply rapidly, so a tubercle starts to form. It is an organ of nutritive accumulation whose external surface produces numerous conical protuberances from which pseudo roots grow. In research by Restuccia et al. (2005), the S_1 phase (Ter Borg et al., 1994) of the first tubercles were observed after 41 days (fully expanded 7th and 8th leaf on the main shoot) and 77 days (fully expanded 11th and 12th leaf on the main shoot) from the emergence of the host plant both in *Vicia faba major* and in *V. faba minor* cultivated in the autumn/spring cycle and respectively sown in the first ten days of November or about a month later. Similar results after sowing at the same time in November were obtained by Perez-de Luque et al. (2005a) for *Pisum sativum* and *P. fulvum* accessions grown in a controlled environment.

Normally 1-2 weeks after formation of the tubercle, a bud appears in the upper part encircled by scale leaves which give rise to the flowering shoot.

10. Emergence of the flowering shoot, seed ripening and dissemination

Generally, the flowering shoot emerges from the ground during the flowering-setting of the host plant (Van Hezewijk et al., 1993) and initially, above all if the air temperature is around 30 °C, it grows quite rapidly, even 1-2 cm a day. The seeds ripen about 6-8 weeks later, are scattered by wind, water, man, animals, vehicles and farm machinery (Zaitoun et al., 1991; Manschadi et al., 1996; Lolas, 1996 and 1997; López-Granados and García-Torres, 1998) and in the top 0-15 cm of the soil can be highly numerous, as just mentioned, reaching particularly high values (Lolas, 1996).

After the seeds ripen, the flowering shoot dies, whereas the tubercle may continue living for several years if the host is polyennial (Dawoud, 1995).

11. Physiological effects of parasitism

These effects may differ in relation to the susceptibility of the host plant to the attacks of *O. crenata* (Castillejo et al., 2004).

The removal of water, mineral ions, metabolites and hormones by the parasite gives rise to metabolic changes in the host which can either be interpreted as a defence against the parasite or as a stimulus to encourage its presence. Increases in iron in the faba bean seem to signal an ability to regulate the quantity and distribution of IAA in favour of *Orobanche* (Hassan et al., 1991). The accumulation in the parasite of mineral ions and sugars accentuates its sink behaviour, which following pseudo root growth, becomes dominant in the host-parasite system. In particular the accumulation of potassium:

– lowers water potential thus allowing the parasite to remove water from the host (Press et al., 1990), which, also due to reduced absorption by the parasite roots (Whitney,

1972), shows signs of withering even in relatively highly moist soil;
- favours the translocation of the host's metabolites towards the parasite (Salisbury and Ross, 1996);
- eases host phloem discharge;
- determines the biosynthesis of "compatible solutes" in the parasite. The first metabolic stage in producing these solutes is through the hydrolysis of sucrose in glucose and fructose. Glucose is consumed by the whole metabolism whereas fructose is converted into mannitol, which contributes to lowering osmotic potential without denaturing the enzymes (Stewart et al., 1984). Osmoregulation by the parasite allows it to absorb water even at very low water potentials and therefore to complete the cycle even under drought conditions.

12. Morphological, biological and productive effects of parasitism

The sink effect of the parasite on the host plant is very negative and apart from withering, there are morphological, biological and productive modifications which are generally more accentuated the more precocious and virulent the attacks. Among those most commonly noted is premature yellowing of the leaves of the lower half of the shoots (the most manifest symptom in late attacks), slowing of growth and the incomplete phenological development of the plant, scarce flowering and setting, and curtailment of faba grain yield. The latter varies from 5 to 100% and it correlates positively with the soil seedbank and the number of emerged shoots (Linke and Saxena, 1991; Zaitoun et al., 1991), with higher values where water and minerals are less available (in these conditions, in fact, the host suffers all the more from competition with the parasite) and is determined almost exclusively by a reduction in the number of pods per plant.

13. Means of Control

Controlling *O. crenata* is by no means easy mostly because of:
- its ability to produce numerous seeds even in adverse environmental conditions;
- its ease of seed dissemination;
- the ability of seeds to remain viable for a long time and to require only one external stimulant for germination;
- the close parasite-host connection;
- the lack of economical, practical, efficient, selective and eco-compatible means of control.

According to some authors, the development of effective control strategies depends on a better knowledge of parasite biology and physiology (Kuijt, 1969; Kasasian, 1973; Linke, 1992; Lutzeyer et al., 1994).

Of the numerous means of control adopted to date (Ciferri, 1955; Sauerborn et al., 1987; Lòpez-Granados et al., 1997), some occur before the infestation sets in (preventative), others afterwards (curative or therapeutic). Setting aside initiation, they are usually divided into agronomic, chemical, physical and biological (Weldeghiorghis, 1998) and they can be deployed singularly or in combination (Pieterse et al., 1992).

13.1 Agronomic means

These are almost all preventative means; in general, they are not very effective and insufficiently studied. Manual removal or destruction of the shoots just after emergence or, anyway, before the seeds ripen are the oldest practices and still in use in developing countries. Already by 1767, it was estimated that in the 12 years needed to free Tuscany (Italy) of the infestation, and during the 1920s the main incentive for control was a reward of £ 20 0.1 t^{-1} of shoots (Ciferri, 1955). Resorting to this was quite labour costly, and did not appreciably attenuate the parasite's effect on host plant growth or production (Kharrat and Halila, 1996). Upon shoot emergence, the tubercle has already accumulated over 90% of dried substances and so the damage is substantially done. The opportune removal of the shoots, nevertheless, does not allow the parasite seeds to ripen, and therefore, augment the seedbank. A similar effect is obtained by ploughing in the infested crop before the parasite seeds ripen.

Other agronomic means of control entail:
- the use of host species seed absolutely free of *Orobanche* seeds;
- the adoption of a succession of crops with a return to the host species in the same soil after long periods, whose effectiveness can be

reduced by the long life span of the parasite seeds due to their dormancy during the absence of the host plants (Krishnamurthy and Rao, 1976; Al-Menoufi, 1991);
- the reduction of *Orobanche* soil seedbank with the use of normal hosts, e.g. faba bean, pea, lentil, that stimulate the parasite to germinate and develop, but are destroyed before parasite seed production – or "trap crops" – false hosts, e.g. flax (*Linum usitatissimum* L.), basil (*Ocymum basilicum* L.) and coriander (*Coriandrum sativum* L.), which also stimulate parasite germination, but do not permit attachment or parasite development (Al-Menoufi, 1991; Khalaf 1992; Parker and Riches, 1993; Schnell et al., 1994);
- the intercropping of host species (faba bean, pea, chickpea, lentil, etc.) with lupin (*Lupinus termis* Forsk.), turnip (*Brassica rapa* L.), fenugreek (*Trigonella foenum-graecum*, L.), oat (*Avena sativa* L.) etc., whose root excretions reduce *O. crenata* seed germination by allelopathic mechanisms and therefore its attacks (Al-Menoufi et al., 1996; Bakheit et al., 2002; Rubiales et al., 2004; Fernàndez-Aparicio et al., 2006; Fernàndez-Aparicio et al., 2007a; Fernàndez-Aparicio et al., 2007b; Evidente et al., 2007);
- early spring sowing (for pea from the end of February to the first 10 days of April in Northern Italy) which would allow the crops to ripen before the high summer temperatures interrupt the parasite seeds' dormancy;
- late autumn sowing (for faba bean from the end of November to mid December in Sicily – Southern Italy) to reduce the period of highest susceptibility of the host plant in the winter season, when the soil temperature is lower than the optimal temperature for germination of *O. crenata* seeds (15-20 °C);
- sowing the host seeds at the bottom of 25-30 cm furrows since a root located that deep is unlikely to encounter many germinable parasite seeds (Krishnamurthy et al., 1987);
- increasing of sowing density to decrease the number of *O. crenata* attachments per plant which does not always lead to a significant increase in grain yield (Pieterse and Aalders, 1986; Manschadi et al., 1997);
- the use of irrigation, e. g. drop irrigation, which does not facilitate parasite seed diffusion (Cubero and Moreno, 1979).

13.2 Chemical means

Of the numerous herbicides studied, imazethapyr and glyphosate have aroused interest (Kasasian, 1973; Schmitt et al., 1979; Jacobsohn and Kelman, 1980; Americanos, 1983; Kukula and Masri, 1984; Mesa-Garcìa et al., 1984; Garcìa-Torres et al., 1991; Jacobsohn and Eldar, 1992; García-Torres et al., 1996). The efficacy of glyphosate varies according to environmental, biological and technical conditions (El-Masry et al., 1991; Nadal et al., 2005). In faba bean infected with *O. crenata* at the predominant stages of already visible shoot bud or of well-developed shoot and vestigial roots, excellent control was achieved with a single glyphosate application of 60 g ha^{-1} applied with an experimental sprayer 2 m wide, furnished with SS8001 nozzles delivering 175 l ha^{-1} at 3 kg cm^{-2}. At later stages of development with the shoot emerged from the shoot bud, its susceptibility to glyphosate decreases (Mesa-García and Garcìa-Torres, 1985). The disparate effectiveness of glyphosate in relation to the parasite growth stage at the time of application is probably due to a dissimilar glyphosate quantities transported into the parasite. It was found that the best translocation of glyphosate from the host to the parasite occurs when *O. crenata* is in the turbercle stage (Müller and Distler, 1991).

Glyphosate also ensured positive effects in narbon vetch (*Vicia narbonensis* L.) and in parsley (*Petroselinum crispum* L.) with dose applications of 35-67 g ha^{-1} (Nadal et al., 2008). In this latter species, *O. crenata* and *O. aegyptiaca* were completely controlled by split foliar application of imazapic at 2.5-5.0 g ha^{-1}or glyphosate at 36-72 g ha^{-1}, applied on 5-7 leaf parsley before the first cutting and on the new growth after each cutting (Goldwasser et al., 2003).

The use of transgenic and mutant crops with target-site herbicide resistance is therefore a most promising solution for *Orobanche* and *Striga* infestation in many crops, and may fully control the parasite without affecting the crop and its yield (Abayo et al., 1998; Joel et al., 1995b, 2000; Surov et al., 1997).

In vitro, significant reductions in seed germination and growth of *O. crenata* have been obtained using nitrogen fertilizers, particularly those with ammonia and urea (Kukula and Masri, 1984; Pieterse, 1991; Van Hezewiik et al.,

1991), as well as with soil fumigation with ethylene bromide and methyl bromide (Zahran, 1970; Foy et al., 1989). It should be noted that methyl bromide fumigation, subject to increasing restrictions due to environmental risks, negatively affects the *Rhizobium* spp. activities (Parker and Riches, 1993).

To provoke parasite seed germination without host plant stimulation, adding gibberellins and compounds like strigol to the soil is hardly effective, probably due to the reduced stability of their molecules (Mangnus et al., 1992) depending on soil characteristics like pH and water content. On the contrary and worthy of further investigation, it appears that paclobutrazol, an inhibitor of gibberellin biosynthesis, significantly reduces the germination of *O. cumana* seed (Joel et al., 1991).

While having no effect on *O. crenata*, feeding the host plant kinetin (cytokinin is usually strongly removed by the host's parasite) increases growth and, if done during the pod growth phase, significantly increases faba bean production (El-Ghamrawy and Neumann, 1991).

13.3 Physical means

During the last 30 years, interest has been growing in soil solarization, warm mulching or solar pasteurization, also for its ecocompatibility. Research in different environments concluded that it significantly reduces or wipes out attacks by *O. crenata* (Mesa-García and García-Torres, 1986; Haidar and Sidahmed, 2000; Mauromicale et al., 2001; 2005; Restuccia et al., 2001; 2005; 2007) especially if combined with chicken manure and repeated for many consecutive years and that its effects continue to be appreciable into the following year (Sauerborn et al., 1989; Restuccia et al., 2005).

Soil solarization, despite its efficacy and ecocompatibility, is not widespread. The reasons for this have not been sufficiently studied. It seems, however, that they lie in the fact that during treatment (usually for periods lasting from 6-8 weeks) the soil cannot be used which renders it uneconomical.

13.4 Biological means

This tactic foresees the use of antagonistic agents and the cultivation of resistant/tolerant biotypes. The antagonistic agents are numerous (Del Serrone and Quacquarelli, 1988; Sauerborn and Kroschel, 1996; Sauerborn, 1993; Klein and Kroschel, 2002; Zermane et al., 2004; Sauerborn et al., 2007) and there is continuing interest in some phytopathogenous fungi (*Fusarium oxisporum*, *Urocladium botrytis*, *Mirothecium verrucasia, Trichoderma harzianum, T. viride*) and their phytotoxins (Müller-Scharer et al., 2000; Abdel-Kader et al., 2001; El-Kassas et al., 2005; Müller-Stover and Kroschel, 2005), as well as in the diptera *Phytomyza orobanchia,* which lays its eggs inside the capsules where their larvae can destroy up to 90% of the seeds (Sauerborn, 1991a; Amsellem et al., 2001) and bacteria isolated from the rhizosphere of faba bean, available to counteract *O. crenata* (Mabrouk et al., 2007). It should be noted, however, that the mycoherbicide strategy has drawbacks because of high cost and legislative restrictions. In addition, under standard cultivation conditions, the effectiveness of antagonist agents was generally lower than its potential because of unfavourable environmental conditions and interference from some agricultural practices (succession of crops, ploughing, burying or burning crop residues, plant health treatments, etc.).

Resistant biotypes have not always proved positive because of their polygenetic nature and the partial levels of parasite resistance verified (Romàn et al., 2002). A moderately resistant faba line has been identified, F 402, which is already used in a genetic improvement programme (Nassib et al., 1979, 1982, 1984), and several accessions with varying levels of parasite resistance (Cubero, 1991). F 402 was later released as cultivar Giza 402 (Nassib et al., 1979; 1982). Selected from Giza 402 under field conditions, VF 1017 was crossed with Spanish cultivars to produce Baraca (Cubero et al., 1994; Manshadi et al., 1997). Giza 402 and Baraca represent the only partially resistant cultivars currently available. Recently, appreciable levels of resistance to *O. crenata* attacks were observed in some accessions of narbon vetch (Nadal et al., 2007), lentil (Fernàndez-Aparicio et al., 2008a), chickpea (Rubiales et al., 2004) and pea (Rubiales et al., 2005). Partial resistance in pea is highly influenced by environmental conditions and is the consequence of a combination of several resistance mechanisms and may become apparent at different times during the parasite's biological cycle (Nassib et al., 1979; Manshadi et al., 1997; Pérez-de-Luque et al., 2008).

Recently these mechanisms were divided into three groups: pre-attachment, prehaustorial and posthaustorial (Pérez-de-Luque et al., 2008).

The pre-attachment mechanisms take place in the first stage of the infection process (germination of parasite seeds and chemical guidance of the germ tube towards host root). Three of these mechanisms are as follows:

- reduced production of lateral roots, more compact root system and low root length density (RLD), observed in faba bean (Nassib et al., 1979; Manshadi et al., 1997);
- low production of exuded germination stimulants from the host root, found in some accessions of a range of legumes including faba bean, vetches, peas, chickpea and grass peas (Aalders and Pieters, 1986; Ter Borg, 1999; Rubiales et al., 2003a; Rubiales et al., 2004; Pérez-de-Luque et al., 2005a; Rubiales et al., 2005; Sillero et al., 2005);
- host production of root inhibitory metabolite capable of decreasing *O. crenata* seed germination of which in fenugreek the most active is a new monosubstituted trioxazonane, characterized as the 2-butyl-[1,4,7,2] trioxazonane and named trigoxazonane (Evidente et al., 2007; Fernàndez-Aparicio et al., 2008b).

The prehaustorial mechanisms are involved when the parasite establishes contact with the host root, penetrating into the host tissues and forming vascular connections with the host. The intrusive *Orobanche* cells can be stopped at three different levels (Pérez-de-Luque et al., 2008):

- in the cortex, observed in resistant pea, faba bean, chickpea, etc. (Rubiales et al., 2003a; Pérez-de-Luque et al., 2005b; Echevarría-Zomeño et al., 2006) and due to the reinforcement of the host cell walls by protein cross-linking callose depositions and suberisation (Echevarría-Zomeño et al., 2006; Pérez-de-Luque et al., 2006a, 2007) and probably due to the accumulation and excretion of toxic phenolic compounds into the apoplast at the infection point (Serghini et al., 2001; Echevarría-Zomeño et al., 2006; Lozano-Baena et al., 2007);
- at the endodermis, observed in vetch and faba bean and due to the lignification of endodermal and pericycle cell walls (Pérez-de-Luque et al., 2005b, 2007);
- inside the central cylinder, observed in *Medicago truncatula* (Lozano-Baena et al., 2007) and probably due to the accumulation of phenolic compounds which are toxic for the parasite (Pérez-de-Luque et al., 2006c; Lozano-Baena et al., 2007).

The posthaustorial mechanisms are involved after the parasite has developed a haustorium and established connection with the host, becoming one with the plant, acting as a sink for water and nutrients (Pérez-de-Luque et al., 2008). The necrosis and death of established *Orobanche* tubercles is, in some cases, related to the presence of gel or gum-like substances within host vessels (Pérez-de-Luque et al., 2005b; Pérez-de-Luque et al., 2006b) or to the production of toxic host compounds (phenolics) delivered into the parasite through the vascular system (Pérez-de-Luque et al., 2006c; Lozano-Baena et al., 2007).

13.5 Integrated control

The results showed that single methods are not sufficient for effective parasite control and suggest developing integrated control methods for different ecological and socio-economic conditions. The trials were conducted almost exclusively on faba bean grown in the Mediterranean region. The suggested strategies provide a combination of seed treatments with benomyl, the application of calcium-cyanamide and glyphosate (Petzoldt, 1979); of tillage, fertilizer and glyphosate (Kukula and Masri, 1984); of delayed sowing and herbicide treatment (glyphosate rate of 2x80 g ha^{-1} or imazaquin at 2x40 g ha^{-1}); of delayed sowing, herbicide treatment (glyphosate treatment at a rate of 2x80 g ha^{-1} or imazaquin at 2x40 g ha^{-1}) and soil solarization (Linke and Saxena, 1991); of resistant cultivars and early sowing (Pérez-de-Luque et al., 2004). During the trials conducted by Linke and Saxena (1991), combining herbicide treatment with delayed sowing proved successful in *Orobanche* controls with the highest economic efficiency. Resistant cultivars allow early sowing (with low *O. crenata* attack), thus avoiding yield losses due to the short crop cycle with late sowing (Pérez-de-Luque et al., 2004).

14. Conclusions

Especially in the last quarter of the previous century, *O. crenata* was the subject of much research, mainly conducted in Europe (Spain,

Germany, Netherlands, UK, Italy, France, etc.), the Middle East (Israel, Syria, the Lebanon, etc.), Northern Africa (Egypt, Tunisia, Morocco, etc.) and Asia (India, Turkey, Nepal, etc.). However, the overall results do not identify decisive solutions for controlling this holoparasitic phanerogam. In fact, even those solutions considered promising by researchers have not yet been widely used for various reasons (high cost compared to host crop income, risk of environmental pollution, variable effectiveness in relation to environmental conditions, etc.). On the other hand, the results have increased our knowledge of parasite biology, host resistance mechanisms and the effectiveness of many control methods, all of which are certainly significant for the development of future research programmes. With reference to the *O. crenata* control, there may be the opportunity for further study:

- by agronomic means, especially if they are able to reduce the seedbank;
- by use of systemic herbicides, which, through the host plant, eliminates the parasite during the first stages of its biological cycle when it is developing underground;
- by solarization, in relation to the film characteristics, the frequency and duration of treatment, organic manuring;
- by host resistant or tolerant cultivars even in environments different to the one from which they originated;
- by strategies of integrated control.

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