Crop Protection

Intercropping with cereals reduces infection by *Orobanche crenata* in legumes

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Abstract

Orobanche crenata is a weedy root parasite that causes huge damage to legume crops. Control strategies have centred around agronomic practices and the use of herbicides, although success has been marginal. Our field experiments show that *O. crenata* infection on faba bean and pea is reduced when these host crops are intercropped with oat. The number of *O. crenata* plants per host plant decreased as the proportion of oats increased in the intercrop. Pot and rhizotron experiments confirmed the reduction of infection in faba bean intercropped with cereals. It is suggested that inhibition of *O. crenata* seed germination by allelochemicals released by cereal roots is the mechanism for reduction of *O. crenata* infection.
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1. Introduction

Over 4000 species of angiosperms are able to parasitize other plants. Unfortunately for farmers, some of these species pose severe constraints to major crops (Parker and Riches, 1993; Rubiales, 2001; Joel et al., 2006). By far the most economically damaging are root parasites of the genera *Striga* (witchweeds) and *Orobanche* (broomrapes). Witchweeds (*Striga* spp.) are very damaging in tropical Africa to cereals and legumes, which endangers food supplies in many developing countries. The broomrapes (*Orobanche* spp.) are widespread in Mediterranean areas in Asia and Southern Europe, attacking dicotyledonous crops and depend entirely on their hosts for all their nutritional requirements. *Orobanche crenata* (crenate broomrape) has threatened legume crops since antiquity, being of economic importance in faba bean (*Vicia faba*), pea (*Pisum sativum*), lentil (*Lens culinaris*), vetches (*Vicia* spp.), grass pea (*Lathyrus sativus*) and other grain and forage legumes (Rubiales et al., 2006).

Orobanche species exert their greatest damage prior to emergence and the majority of field losses therefore occur before diagnosis of infection. A wide variety of approaches—physical, cultural, chemical and biological—have been explored against root parasites, but most of them are ineffective, or insufficiently selective to the majority of susceptible crops. The intimate connection between host and parasite also hinders efficient control by herbicides. Unfortunately, in many crops no resistant varieties have been produced to date. Control strategies based on a single treatment are often only partially or inconsistently effective and are affected by environmental conditions. Overall, control strategies to date have not proven to be as effective, economical and applicable as desired (Parker, 1991; Joel, 2000; Joel et al., 2006).

Current means for controlling parasitic weeds are focusing on reducing the soil seed bank, preventing seed set and inhibiting seed movement from infested to non-infested areas. Rotation into non-host crops is generally the only valid recommendation for farmers, but this option is not always acceptable due to the importance of the host crops for the economy and incomes of subsistence farmers. There are some reports of potential 'trap crops' or 'false

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hosts' which offer the advantage of stimulating germination of the root parasites without themselves being parasitized. These reports are mainly based on pot experiments and there is a shortage of good evidence for practical benefits under field conditions (Parker, 1991). An alternative is the mixed cropping or intercropping. Intercropping is regarded as an ecological method to manage pests, diseases and weeds via natural competitive principles that allow for more efficient resource utilization (Liebman and Dyck, 1993). Many African farmers traditionally intercrop maize or sorghum with legumes to increase crop production achieving better returns on fertilizer, pesticide, energy and manpower resources. These intercrops also reduce the infection by *Striga hermonthica* (Carson, 1989; Carsky et al., 1994; Oswald et al., 2002). However, there is no evidence of beneficial effects of intercropping reducing the infection of *Striga gesnerioides* (infecting cowpea) or *Orobanche* species infecting legumes.

The objective of the present studies was to assess the feasibility of controlling *O. crenata* in grain legumes by intercropping with cereals.

2. Materials and methods

2.1. Field experiments

Field experiments were performed in the 2003–2004, 2004–2005 and 2005–2006 seasons at Córdoba, Spain. Faba bean (cv. Prothabon) and pea (cv. Athos) crops were grown on their own or intercropped with oat (cv. Cory), triticale (cv. Peñarroya) or barley (cv. Aspen) at the ratio of 1:1 (50% host:50% cereal). Experimental plots were 1.5×4 m, in randomized blocks with 6 replications.

An additional field experiment was performed during the 2004–2005 and 2005–2006 seasons, in which the host crops faba bean (cv. Brocal) and pea (cv. Messire) were intercropped with oat (cv. Cory) at various ratios. These ratios were 1:0 (host sole crop, either faba bean or pea), 0:1 (oat sole crop), 1:1 (50% host:50% oat), 2:1 (66% host:33% oat) and 1:2 (33% host:66% oat) (Table 2). Experimental plots were 2×2 m, in randomized blocks with 4 replications.

No inoculation was done as the plots were known to be heavily and uniformly infested of *O. crenata* seeds from previous trials (Rubiales et al., 2003b, 2006). Numbers of emerged *O. crenata* plants and of host plants were counted at plant maturity and expressed as numbers of emerged *O. crenata* plants per host plant.

2.2. Pot experiments

The effect of intercropping faba bean (cv. Brocal) with cereals on infection by *O. crenata* was studied in pot experiments (Table 1) in a greenhouse maintained at $20 \pm 5\,°C$. Faba bean plants were grown individually (one per pot) or mixed with oat, barley or triticale (one plant of faba bean with one cereal plant) in large pots filled with 10 l

Table 1

Infection of faba bean or pea host crops by *O. crenata* when intercropped with oat, triticale or barley in field experiments performed at Córdoba during the 2003–2004 and 2004–2005 seasons; in greenhouse pot experiments or in rhizotrons (Fig. 1)

| | Field | | | Pots in the greenhouse | Rhizotrons (glass plates) in growth chamber | | | |
| | 2003–2004 season | 2004–2005 season | 2005–2006 season | | | Distribution in the plate profile (broomrape attachments/host plant) | | |
	No. emerged broomrapes/host plant	No. emerged broomrapes/host plant	No. emerged broomrapes/host plant	Total no. broomrapes/host plant	No. broomrape attachments/host plant	Upper 0–10 cm	10–20 cm	20–30 cm
Faba bean sole crop	1.57	0.26	2	13.1	215	105	84	27
Faba bean + oat	0.45*	0.02*	1.26*	6.0*	110*	58*	45	7*
Faba bean + triticale	1.14	0.07	1.56	8.6	201	57*	100	45
Faba bean + barley	1.39	0.09	1.85	6.4*	—	—	—	—
Pea sole crop	0.39	0.48	2.73	—	115	58	47	11
Pea + oat	0.23	0.05*	1.63*	—	104	49	46	9
Pea + triticale	0.17*	0.27	2.33	—	88	29*	39	19
Pea + barley	0.26	0.1*	2.41	—	—	—	—	—

— Non determined.

*Statistically significant from sole crop (LSD, $P < 0.05$).

of black peat:perlite:vermiculite (2:2:1, v:v) mixed with 400 mg (about 90,000 seeds) of *O. crenata* seeds collected during the previous season from plants parasitizing faba bean (Rubiales et al., 2004, 2006). Each combination was represented by 10 pots in a completely randomized design. Three months after sowing the plants were removed from the pots, the roots gently washed with water and the number of *O. crenata* tubercles per plant counted and their developmental stage recorded using a 1–7 scale (ter Borg et al., 1994) (1, small tubercle 1–3 mm; 2, crown roots starting to develop; 3, bud ⩽ 1 cm; 4, first development of spike below ground surface; 5, emergence of spike; 6, flowering; 7, setting of seeds).

2.3. Growth chamber experiments

Distribution of cereal and legume roots and *O. crenata* infection with depth was studied in a separate experiment using rhizotrons (Rubiales et al., 2003a) (Fig. 1). This involved growing host and parasite over a glass microfibre filter sheet over 1 cm of sand held in the gap between two 50×30 cm glass sheets which were orientated vertically. It was therefore possible to grow large faba bean or pea plants and to follow the spatial distribution of the roots and the development of the broomrapes at different depths. This was not possible on faba bean using standard methods such as Petry dishes or polyethylene bags (Rubiales et al., 2006). Pea and faba bean plants were either grown on their own or mixed with oat, barley or triticale (one plant of faba bean or pea plus one of cereal plant). Cork strips were placed between the glass sheets, one on the left and one on the right hand sides. The bottom edge was sealed with a sponge which allowed a nutrient solution to penetrate. Crop seeds were placed on the sand at the top of the rhizotron system. Eight replicate systems were established

per crop combination. *O. crenata* seeds (50 mg) were spread over the microfibre sheet having been conditioned in Petri dishes with filter paper wet with distilled water for 10 days in the dark at 20 °C before use. The viability of the broomrape seeds had previously been determined by the tetrazolium method (López-Granados and García-Torres, 1996). After 45 days, the number of tubercles per plant was counted and root length estimated by the intercept method described by Tennant (1975).

Inhibition of *O. crenata* seeds germination by triticale and oat were studied with a minirhizotron experiment (Pérez-de-Luque et al., 2005) (Fig. 2). Twenty plants per species were grown individually in minirhizotrons consisting in 15×15 cm^2 Petri dishes with 8 mg of *Orobanche* seeds spread over a glass microfibre filter sheet. The dishes were placed with the germinating cereal or legume seed on top and the lids were removed to allow seedling emergence and growth. They were then sealed with parafilm, wrapped in aluminium foil and placed vertically in a growth chamber at 20 °C. *Orobanche* seeds were conditioned as indicated above. Five milliliter of the synthetic germination stimulant GR24 (10 ppm) (Mangnus et al., 1992; provided by Dr. Zwanenburg, University of Nijmegen, The Netherlands) were uniformly distributed to half of the petri dishes to promote *Orobanche* seed germination and determine inhibitory effect of root exudates. As a control 10 additional dishes were treated with GR24, but with no crop plants. Percentage of germination was determined seven days after GR24 application. The 500 broomrape seeds that were closest (< 3 mm) to the cereal roots were examined in each Petri dish under a stereoscopic microscope at $30 \times$ magnification to determine the percentage germination. Seeds having an emerged radicle were scored as germinated.
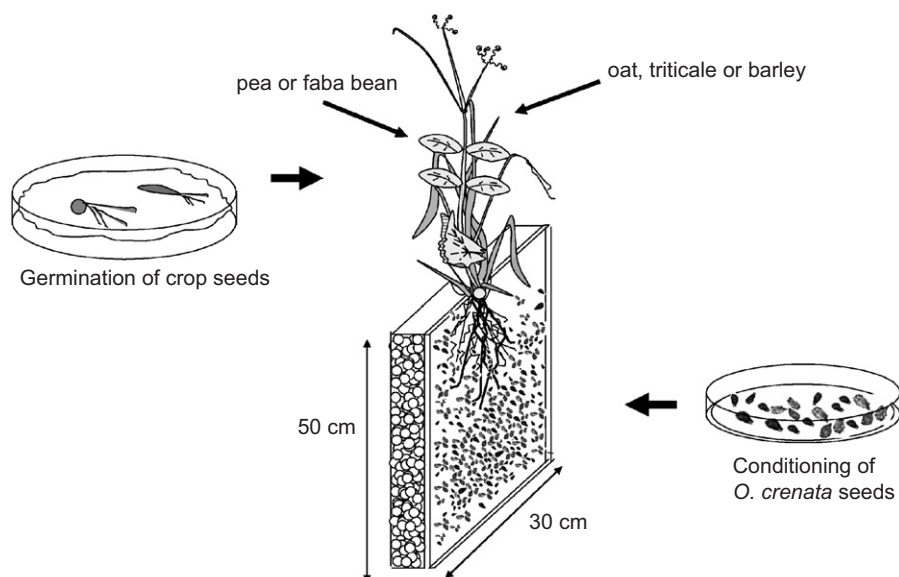

Fig. 1. Rhizotron experiment to study *O. crenata* infection on faba bean or pea as sole crops or intercropped with oat, triticale or barley.
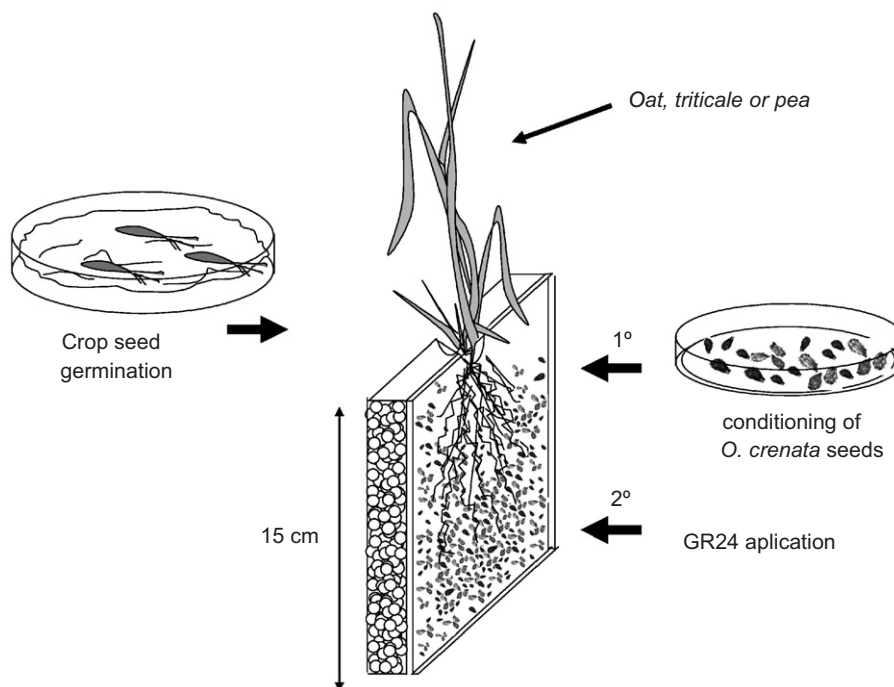
Fig. 2. Minirhizotron experiment to study inhibition of *O. crenata* seed germination by root exudates of avena, triticale or pea.

2.4. Statistical analysis

Statistical analyses were performed using Statistix 8.0 statistical package (Analytical Software, Tallahase, USA). Before performing analyses of variance, the normality and homogeneity of variances were checked. When necessary, percentage data were transformed to angles ($y = \arcsine\sqrt{x/100}$ where x is percentage germination) and again checked before applying analysis of variance. Comparisons of means were performed by LSD (Least Significant Difference, pair wise comparisons, Table 1) or Tukey tests (multiple comparisons, Tables 2 and 3). Null hypotheses were rejected when $P \leqslant 0.05$.

3. Results

The field experiments (Table 1) showed that *O. crenata* infection on faba bean and pea was reduced when these host crops were intercropped with oat. A tendency for a reduction of infection was also observed in intercrops with triticale and barley, but differences were usually not statistically significant. This beneficial reduction in *O. crenata* infestations when intercropping faba bean and pea with oat was confirmed in experiment 2 (Table 2). The number of *O. crenata* plants per host plant decreased as the proportion of oats increased in the intercrop. Pot experiments (Table 1) also confirmed the reduction of infection in faba bean intercropped with oat and barley while the rhizotron (glass plates) experiments confirmed a significant reduction of infection of faba bean intercropped with oat. The distribution of roots in the soil profile was also measured in both sole and intercrops. When intercropped

Table 2
Infection of faba bean or pea host crops by *O. crenata* when intercropped with oat at various host:oat ratios

	No. emerged broomrapes per host plant	
	Córdoba 2004–2005	Córdoba 2005–2006
Faba bean sole crop (1:0)	1.13 a[a]	4.39 a
Faba bean + oat (2:1)	0.68 ab	4.21 a
Faba bean + oat (1:1)	0.37 bc	3.08 b
Faba bean + oat (1:2)	0.20 c	2.84 b
Oat sole crop (0:1)	0 c	0 c
Pea sole crop (1:0)	1.37 a	2.45 a
Pea + oat (2:1)	0.89 b	0.85 b
Pea + oat (1:1)	0.6 bc	1.35 b
Pea + oat (1:2)	0.28 cd	0.83 b
Oat sole crop (0:1)	0 d	0 c

The field experiment was performed at Córdoba, Spain during the 2004–2005 and 2005–2006 seasons.
[a]Means followed by the same letter for a given host crop indicates that differences were not statistically significant (Tukey test, $P < 0.05$).

with triticale, roots of faba bean and pea tended to grow deeper. This could be due to an allelophatic effect of triticale inhibiting growth of upper roots of faba bean. Infection of faba bean and pea by *O. crenata* was significantly reduced in the upper soil layer (0–10 cm). A deep root growth might be relevant under field conditions as broomrape seeds are more likely to be present in the upper layer of soil. Oat roots grew deeper than triticale and did not influence the root growth patterns of the peas or faba beans. In these experiments, the broomrape seeds were spread evenly on the plates, and so the same level of

Table 3
Percentage of germination of *O. crenata* seeds in the vicinity of oat, triticale and pea roots in Petri dishes to which the synthetic germination stimulant GR24 was or was not exogenously applied

	Without GR24	With GR24
Control	0	54.5 a
Oat	0	45.2 b
Triticale	0	30.2 c
Pea	55	53.2 a

Experiment performed in rhizotrons (Fig. 2).
Means followed by the same letter for GR24 treatments indicates that differences were not statistically significant (Tukey test, $P < 0.05$).

broomrape reduction occurred in all soil layers. Under natural field conditions, it is speculated that intercropping with triticale, which influenced deeper growth of the host's roots, might have a greater effect under real field conditions where low numbers of seeds are expected to be located in the upper soil layers.

Oat and triticale roots failed to stimulate germination of *O. crenata* seeds (Table 3). Moreover, they significantly inhibited the germination of seeds that had been stimulated to germinate by exogenous applications of GR24.

4. Discussion

Intercropping is a method for simultaneous crop production and soil fertility building (Willey, 1985). Intercropping was a common practice before the 1950s, when mechanization, plant breeding, synthetic fertilizers and pesticides were increasingly utilized as agriculture intensified. Intercrops of legumes and grasses in pastures are, however, still widely used, and although arable intercropping of cereals, grain legumes and oil seeds for feed and human consumption has declined in industrialized countries, it is still a common practice in many areas with less intensified agriculture. There is however, a renewing interest in intercropping linked to a need to reduce nitrogen costs and soil (Francis, 1986). There is also interest in intercropping in organic farming to produce animal feed sources of organic origin, with a need to increase organic cereal and grain legume (protein) crop production, to balance the European organic feed deficits.

Intercropping had already been proposed as a low-cost method of controlling *Striga*, but no conclusive evidence was available on its feasibility for broomrape control. Reports on effects of intercropping on *O. crenata* control are conflicting, with Bakheit et al. (2002) reporting a beneficial effect of intercropping fenugreek (*Trigonella foenum-graecum*) and faba bean, while Khalaf (1994) denies this effect. In the present paper, consistent control of *O. crenata* infection was achieved in faba bean and pea when they were intercropped with oats. Other cereals like barley or triticale had lower and less consistent effects, which nevertheless merit further research.

A suggested mechanism for the beneficial effect of intercropping on the control of *Striga* is that the intercropped non-host legumes might be acting as trap crops, stimulating suicidal *Striga* germination (Parker and Riches, 1993). However, our in vitro trials (Table 3) show that the three cereals studied did not induce *O. crenata* seed germination. This lack of induction of germination of *O. crenata* seeds by cereals contrasts with the reported stimulation of *O. minor* (small broomrape) germination by cereals like barley, corn, oats, and wheat (Mallory-Smith et al., 2004). The known specificity of germination requirements by the various *Orobanche* species is therefore confirmed and while cereals might act as effective trap or catch crops for *O. minor*, they may not induce suicidal germination of *O. crenata*. They might, however, be helpful when intercropped with host crops interacting with broomrape seed germination and/or haustoria formation, as well as on competing with host plants for soil and water.

Shading by intercrops has also been suggested as a mechanism for *Striga* control. Shading reduces soil temperature, especially where the intercrops quickly cover the inter-row area (Carsky et al., 1994; Oswald et al., 2002; Tenebe and Kamara, 2002). In contrast to the hemi-parasitic *Striga*/summer cereal hosts, shading is unlikely to play any major role in *O. crenata*, as *O. crenata* infects cool season legumes, infection starting in February–March (Rubiales et al., 2003a) when mean air temperatures are $10–15\,°C$, so that shading is likely to have less impact on soil temperature than in summer crops infected by *Striga*. Additionally, *Orobanche* is holoparasitic with no photosynthetic capacity at all, so it is unaffected by the lack of light.

Nitrogen fixed by the legumes has also been pointed as a reason for *Striga* control. Incidence of *Striga* is known to negatively correlate with soil fertility, particularly nitrogen availability (Cechin and Press, 1993). In contrast to the *Striga*/cereal systems, N is unlikely to play any effect on *Orobanche* spp., as the host legumes increase N by rhizobial nitrogen fixation. However, it is not possible to exclude a competition effect by the cereals or any potential effect on microbial interactions in the rhizosphere. For instance, the nitrogen-fixing bacterium *Azospirillum brasilense* has been reported to inhibit germination and radicle growth of *O. aegyptiaca* (Dadon et al., 2004) and *S. hermonthica* (Miché et al., 2000). Also arbuscular mycorrhizal fungi have been reported to increase phosphorous uptake and to reduce infection by weedy root parasites (Salonen et al., 2000). Only recently it has also been found that arbuscular mycorrhizae hyphal branching is induced by the same plant sesquiterpenes that stimulate *Orobanche* and *Striga* seed germination (Akiyama et al., 2005).

From the present experiments it is suggested that allelopathy is the major component for reduction of *O. crenata* infection in faba bean and pea crops that are intercropped with cereals. The finding that germination of seeds exposed to the synthetic germination stimulant, GR24, is inhibited in presence of cereal roots (Table 3)

suggest that cereal roots might be exuding substances that inhibit *O. crenata* seed germination. Such inhibitory effects on *Orobanche ramosa* germination have recently been described in the wild tomato accession *Lycopersicum pennellii* and the mechanism suggested was an *excess* of stimulatory substances (El-Halmouch et al., 2006). In this research, the possibility of inhibition due to overproduction of germination stimulants is unlikely, as there was no variation in germination as a function of distance from the cereal's roots, as might be expected given a concentration gradient of host root germination stimulants (Whitney and Carsten, 1981). Once a broomrape seed had successfully germinated, no differences were observed in its success in attaching to the host's roots whether grown with sole host crop or intercropped. This suggests that any potential allelopathic effect is on the broomrape seed germination and there is no effect on radicle or haustorial formation. Allelopathy has been reported to be the cause for the reduction of *S. hermonthica* infection in intercropping with *Desmodium uncinatum* by inhibition of the development of *Striga* haustoria although not of seed germination (Khan et al., 2002). Also, coumarins excreted by sunflower roots have been shown to inhibit *Orobanche cumana* seed germination and seedling growth (Serghini et al., 2001). The allelopathic activity of cereals is well known (Chon and Kim, 2004), with a number of compounds like vanillic, *o*-coumaric acids or scopoletin having already been suggested as responsible for the allelopathic effects of various cereals (Pérez and Núñez, 1991; Baghestani et al., 1999). Considerable genetic variation in allelopathic activity has been found within cereals (Baghestani et al., 1999; Grimmer and Masiunas, 2005) which may allow for selection of more allelopathic cultivars. Identification of the compounds released from cereals, in particular oat, involved in the suppression of *O. crenata* may give more opportunities for developing reliable intercropping strategies, as well as new approaches in the molecular biology of *O. crenata*.

Acknowledgements

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