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# Non-host facilitators, a new category that unexpectedly favours parasitic weeds

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**Abstract** In Europe, the current decrease of herbicide application increases and diversifies weed flora in crops. As a consequence, there is an increase in the number of pests that use weeds to spread. This change is a major threat to crop production. For instance broomrape—*Phelipanche ramosa*—is an obligate parasite of dicotyledonous species that reduces crop yield by up to 80 % of oilseed rape in France. In highly infected fields, broomrape can in turn infect various weed species and thus persist and even proliferate in the absence of host crops. Up to now, three categories of interactions between broomrape and plant species have been identified in monospecific stands: host, non-host and false host. In multispecific stands, broomrape germination and attachment have never been studied despite the use of multispecific crop associations to protect host crops with non-host species in tropical conditions. Therefore, we studied parasite germination and attachment of monospecific vs. multispecific stands, associating broomrape with host plants (oilseed rape), non-host plants (field bindweed) or a combination of both. Experiments were conducted in vitro for 6 weeks and in pots for 3 months. We measured the percentage of germinated broomrape seeds in the

presence of field bindweed or oilseed rape. We analysed the attachment of the parasite on its host. Results unexpectedly show a nearly threefold increase in the infection of host oilseed rape in the presence of field bindweed. We thus proposed a new plant species category called ‘non-host facilitator’ and a new parasitic interaction process named ‘facilitation’. The underlying mechanism is still unknown though we observed that field bindweed was able to support secondary parasite attachments originating from primary attachments on a nearby oilseed rape root system. Our discovery implies the rethinking of parasite management in arable crops, particularly the rotation or association of host with non-host crops, since the non-host crops could actually be non-host facilitators.

**Keywords** *Phelipanche ramosa* (L.) Pomel · *Brassica napus* L. · *Convolvulus arvensis* L. · Parasitism · Weeds · Host plant · Non-host facilitator · Facilitation

## 1 Introduction

In Europe, the current decrease in herbicide use may increase and diversify weed flora in crops, together with a series of companion bioaggressors spreading via weeds (Barzman and Dachbrodt-Saaydeh 2011; Melander et al. 2013; Meynard et al. 2003; Parker and Riches 1993; Press and Graves 1995). Among crop bioaggressors, *Phelipanche* and *Orobanche* genera are obligate parasites of dicotyledonous roots causing severe damage to numerous economically important crops throughout the world, especially in the Mediterranean area (Parker 2009; Rubiales et al. 2009). Broomrape—*Phelipanche ramosa* (L.) Pomel (syn. *Orobanche ramosa*) (Joel 2009)—is the most devastating species and has by far the widest range of hosts such as Solanaceae, Brassicaceae and legumes (Joel et al. 2007; Parker 2009; Parker and Riches 1993). In France,

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broomrape (Fig. 1a) can reduce crop yield by up to 80 % in its favourite crop, i.e. oilseed rape (*Brassica napus* L., Fig. 1b), but also in hemp and tobacco (Brault et al. 2007; Gibot-Leclerc et al. 2003, 2012, 2013). To date, no herbicide has been authorized for controlling broomrape in crops. Several strategies have been developed to control broomrape, including false hosts and catch crops which stimulate germination of broomrape without being infected themselves and use of resistant or tolerant varieties, but none are fully successful (Parker 2009; Parker and Riches 1993; Rubiales et al. 2009). In fields strongly infected by broomrape, the parasite can infect numerous weed species and thus persist and even proliferate in the absence of host crops (Boulet et al. 2001, 2007; Gibot-Leclerc et al. 2003). The ability of various weed species to stimulate and attach parasite germinations has already been demonstrated in controlled conditions for individual species (Boulet et al. 2001, 2007; Gibot-Leclerc et al. 2003).

To date, three distinct types of interactions between broomrape and plant species have been identified in monospecific stands (Joel 2000; Parker and Riches 1993; Press and Graves 1995): (1) host plants stimulate parasite seed

germination and support subsequent parasite attachment up to seed production; (2) false-host plants stimulate parasite seed germination without attachment and (3) non-host plants neither stimulate parasite germination nor support attachment. But broomrape germination and attachment in multispecific stands have never been studied, though multispecific crop associations are being used in tropical conditions to protect potential host crops through the beneficial effect of non-host species (Hearne 2009; Khan et al. 2000; Kuchinda et al. 2003). Consequently, the objective of the present paper was to compare these two parasite stages in monospecific vs. multispecific stands. In vitro and pot experiments were carried out, associating broomrape with host plants, non-host plants or a combination of both. Oilseed rape was chosen as a host species because it is the most frequent and sensitive host of broomrape (Gibot-Leclerc et al. 2003, 2012); the chosen non-host species was field bindweed (*Convolvulus arvensis* L.) because this weed is frequent in oilseed rape (Fried and Reboud 2007) and is considered a non-host species to broomrape (Boulet et al. 2001, 2007).

## 2 Materials and methods

### 2.1 Seed origin

Parasite seeds were collected from natural populations of broomrape (B-oilseed rape pathovar, Brault et al. 2007) that had severely infected fields of oilseed rape in Saint-Jeand'Angély (45° 56' 39" N, 00°31' 16" W; Charente-Maritime, France) in 2001. Once harvested, the seeds were sifted to clean them. Oilseed rape seeds (Lignée Aviso) were harvested in Le Meix (47° 36' 04" N, 04° 56' 30" E; Côte-d'Or, France) in 2007. Field bindweed seeds were bought from Herbiseed in 2010. After collection, all seeds were kept in watertight glass containers at room temperature (approximately 20 °C) until the beginning of the experiments.

### 2.2 In vitro experiment

The method was developed and explained in detail by Gibot-Leclerc et al. (2012). Either host (oilseed rape) or non-host (field bindweed) seedlings were put into plastic boxes with broomrape seeds set on paper discs. The development of the parasite on field bindweed or oilseed rape roots was assessed after 6 weeks under a stereomicroscope. The percentage of germinated broomrape seeds in the presence of field bindweed (or oilseed rape) was counted, and the early developmental stages of the parasite on its host were recorded.

The experiment consisted of two plastic boxes, each with five paper discs; one box contained three field bindweed



**Fig. 1** *P. ramosa* (broomrape). **a** Broomrape floral scape, **b** high broomrape density in a severely infected oilseed rape plot (Gibot-Leclerc et al. 2012)

seedlings, the other three oilseed rape seedlings. It was repeated four times, in exactly the same experimental conditions starting on April 6, 2010; April 26, 2010; May 17, 2010; and June 7, 2010, respectively. In total, four boxes were thus prepared per plant species (either field bindweed or oilseed rape), each containing three plants and five paper discs with 15–25 parasite seeds per disc, resulting in a total of 60 parasite discs and approximately 1,200 parasite seeds per plant species.

### 2.3 Pot experiments

The method was developed and explained in detail by Gibot-Leclerc et al. (2013). Field bindweed and oilseed rape seeds were sown into pots as follows: 25 pots with two plants of field bindweed per pot, 25 pots with two plants of oilseed rape per pot, and 25 pots with one plant of field bindweed and one plant of oilseed rape per pot. The 75 pots were placed on a completely randomised design in a growth chamber, with the same growth conditions as in the *in vitro* experiment. Approximately 50 ml of tap water was added daily. Broomrape development on field bindweed and oilseed rape was assessed 3 months later. The root systems of field bindweed and oilseed rape were taken out of the pots. After washing with tap water, root systems were observed under a stereomicroscope to detect the presence of broomrape. The parasite was described by counting the numbers of individuals having reached the following ontogenic stages according to Gibot-Leclerc et al. (2012): (a) seed germination and contact with host root, (b) attachment on host root, (c) young tubercle, (d) old tubercle, (e) bud, (f) underground stem, (g) stem emergence, (h) flowering and (i) fructification.

### 2.4 Statistics

The effect of the host species on the germination rate of parasite seeds in the *in vitro* experiment was analysed with a generalized linear model, using PROC GENMOD of SAS with a binomial distribution and taking account for overdispersion with a dispersion parameter estimated by Pearson's chi-square statistic divided by its degrees of freedom:

$$g(\text{germinated seeds}/\text{total seeds}) = \text{constant} + \text{host species effect} + \text{repetition effect} + \alpha \cdot \text{total seeds} \tag{1}$$

where

$$g(y) = \log_n \left( \frac{y}{1-y} \right) \tag{2}$$

The effect of the host species and the host association in the pot experiment was evaluated with an analysis of variance, using PROC GLM of SAS:

$$\text{parasite variable} = \text{constant} + \text{host species effect} + \text{host association effect} + \text{species} \times \text{association interaction} + \text{error} \tag{3}$$

The analysed parasite variables were the number of germinated seeds, the number of fixed shoots and the mean growth stage of the fixed shoots. The latter was calculated as follows:

$$\text{mean growth stage} = \frac{\sum_i (i \cdot \text{number of shoots at stage } i)}{\text{total number of shoots}} \tag{4}$$

with  $i=1$  to 8 for shoots at attachment, young tubercle, old tubercle, bud, underground stem, stem emergence, flowering and fructification, respectively.

## 3 Results and discussion

### 3.1 Validation of the oilseed rape host and field bindweed non-host status of broomrape

The *in vitro* experiment showed that broomrape germination was significantly higher in the presence of oilseed rape seedlings (germination rate=0.54, confidence interval [0.475, 0.603], Tables 1 and 2) than when next to field bindweed seedlings (chi-square=440,  $p<0.0001$ ); in the latter case, germination rate was negligible (0.008 [0.004, 0.016]). The monospecific pots in the second experiment confirmed these findings, i.e. oilseed rape stimulated considerably more parasite germination than field bindweed, and the germination stimulated by the latter was negligible (Fig. 2a). Moreover, this experiment showed that in monospecific stands, the parasite never attached to field bindweed roots whereas it successfully attached to oilseed rape where it usually exceeded the bud stage at the end of the experiment (Fig. 2b).

Our experiments thus confirmed the oilseed rape host and field bindweed non-host status of broomrape that have been extensively reported in the literature (Boulet et al. 2001, 2007; Gibot-Leclerc et al. 2003, 2012). However, the reason why field bindweed is a non-host remains unknown as our experiments were not conceived to establish whether parasite germinations were inhibited by a quantitative or qualitative deficit in root exudates that are necessary to trigger parasite germination (Bouwmeester et al. 2003; Humphrey et al. 2006; Cardoso et al. 2011) or by field bindweed synthesising and excreting parasitic-seed germination

**Table 1** Effect of host species on the germination rate of broomrape seeds in the in vitro experiment. Results of generalized linear model with a binomial distribution and a dispersion parameter

a. Likelihood ratio statistics for type 3 analysis				
Explanatory variable	DF	Chi-square	Probability>chi-square	
Host species effect	1	440.78	<0.0001	
Repetition	3	127.81	<0.0001	
Total broomrape seeds	1	2.49	0.1143	
b. Effect of host species on the mean estimated broomrape germination rates				
Host species	Broomrape germination rate			
	Mean	Confidence limits		
Field bindweed	0.008	0.004	0.016	a
Oilseed rape	0.540	0.475	0.603	b
c. Effect of the experiment onset date on the mean estimated broomrape germination rates averaged over host species				
Onset date	Broomrape germination rate			
	Mean	Confidence limits		
6 April 2010	0.034	0.017	0.067	a
26 April 2010	0.014	0.007	0.026	b
17 May 2010	0.358	0.250	0.483	c
7 June 2010	0.252	0.176	0.347	c

The analysed model was  $g$  (germinated seeds/total seeds) =  $\mu$  + host species effect + repetition effect +  $\alpha \cdot$  total seeds with  $g(y) = \log_e(y/(1-y))$ . Means of a given experimental factors followed by the same letter are not significantly different at  $p=0.05$ .

inhibitors and/or phytoalexins or coumarins (Serghini et al. 2001; Pérez de Luque et al. 2008).

### 3.2 Discovery of plant facilitators

Associating different host species significantly increased germination rates (Fig. 2a): germination next to field bindweed roots was significantly different from zero only when oilseed rape was also present in the pot. Unexpectedly, associating the germination-triggering oilseed rape with the non-triggering species field bindweed significantly

increased parasite germination next to oilseed rape roots and multiplied it by nearly three. The parasite germination surplus also translated into increased infection in multispecific vs. monospecific stands (Fig. 2a). Broomrape was only able to infect field bindweed in the presence of oilseed rape, and again, the infection of host oilseed rape was unexpectedly multiplied by almost three in the presence of field bindweed.

This major result makes it necessary to rethink the current species classification with regard to their susceptibility to root parasites. So far, three distinct types of interactions

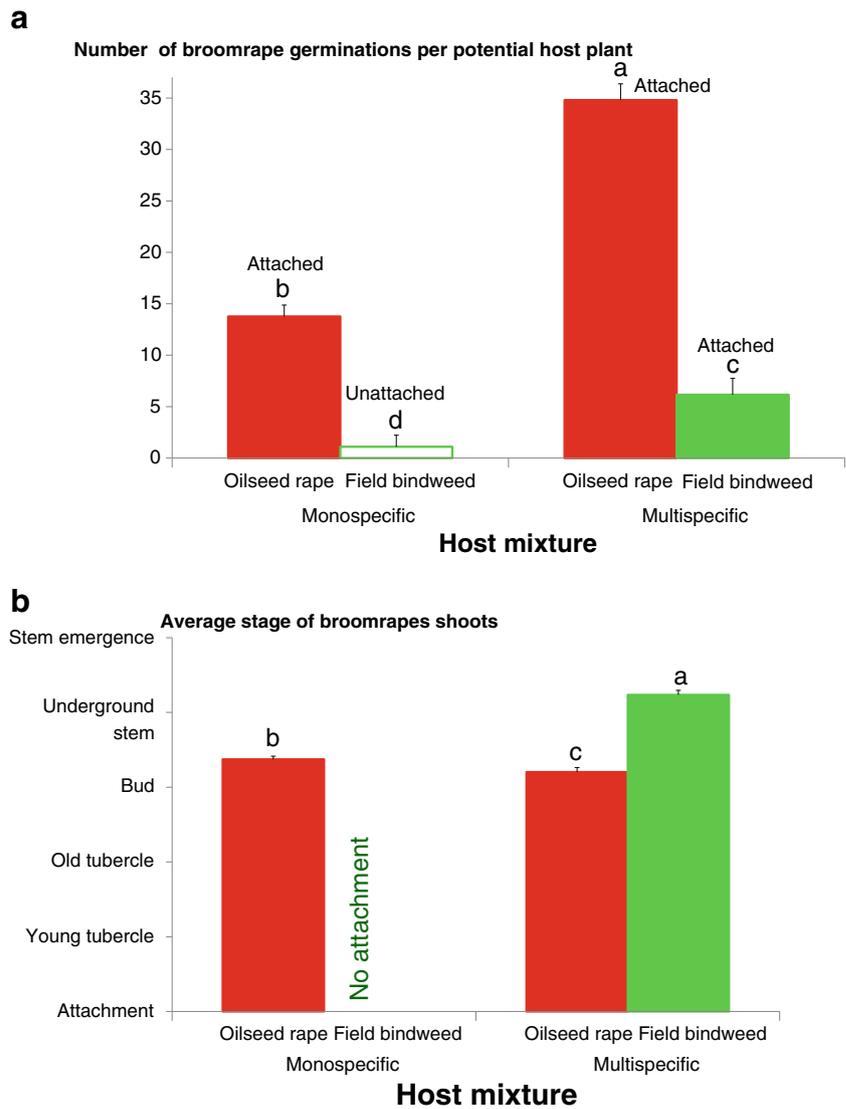
**Table 2** Effect of host species and host association on the germination of broomrape seeds as well as on the attachment and growth of the resulting parasite shoots

a. Variability in parasite variables explained by host species and species mixture. Partial $R^2$ of analysis of variance						
Explanatory variable	Number of germinated seeds		Number of attached shoots		Growth stage of attached shoots	
Host species	0.44		0.45		0.63	
Species mixture	0.18		0.19		0.02	
Interaction	0.07		0.06		0.00	
All	0.68		0.70		0.66	
b. Comparison of means						
Host species	Host species association	Number of germinated seeds		Number of attached shoots		Mean growth stage <sup>a</sup>
Oilseed rape	Alone	13.76	b	13.76	b	3.4 b
	With field bindweed	34.8	a	34.8	a	3.2 c
Field bindweed	Alone	1.1	ns d	0	ns d	
	With oilseed rape	6.16	c	6.16	c	4.2 a

The analysis of variance model was parasite variable = constant + host species effect + host association effect + species  $\times$  association interaction + error. Means of a given column followed by the same letter are not significantly different at  $\alpha=0.05$  (least significant difference test)

<sup>a</sup> Stages 1 to 8 are attachment, young tubercle, old tubercle, bud, underground stem, stem emergence, flowering and fructification, respectively.

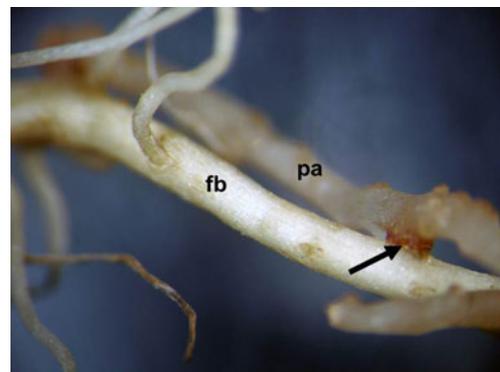
**Fig. 2** Effect of host species and host association on the germination of broomrape seeds as well as on the attachment and growth of the resulting parasite shoots. Least square means and standard errors from analyses of variance model of parasite variable=constant+host species effect+host association effect+species×association interaction+error. Bars headed by the same letter are not significantly different at alpha=0.05 (least significant difference test). **a** Germination and attachment success, **b** average growth stage of attached shoots at the end of the experiment



between broomrape and plant species are known: host, non-host and false host (Joel 2000; Parker and Riches 1993; Press and Graves 1995). We now propose a new species category, i.e. non-host facilitator, and a new parasitic interaction process, i.e. facilitation, in which the infection of oilseed rape (host) by broomrape increases when field bindweed (non-host) is located nearby. Our experiment was unable to identify the causes of the facilitation process as no root exudates were monitored. Moreover, no explanation was found in the literature.

This demonstration makes it necessary to rethink parasite management in arable crops. Crop rotation with non-host crops is a general recommendation for farmers, but our results indicate that this strategy is possibly much less effective than assumed. Some of the non-host crops may actually be non-host facilitators just as a weed species identified as a non-host may increase the infection of crop hosts through facilitation. This risk could also exist in crop

associations. Until now, the facilitation process has never been observed in the field. The opposite effect, i.e. a



**Fig. 3** External view of secondary broomrape attachment (arrow) on a non-host species (field bindweed, fb) root system after a primary attachment (pa) on a host species (oilseed rape) root system in broomrape/field bindweed/oilseed rape pathosystem pot cocultivation. Magnification, ×33

decrease in parasitic infections in multispecific canopies, has nonetheless already been reported. Thus, legume intercropping with cereals has been reported to be efficient to cope with *Orobanche crenata* (Fernandez-Aparicio et al. 2007). Moreover, in Germany, the weedy parts of otherwise heavily infected tobacco fields were observed to be free of *P. ramosa*, an effect attributed to germination-inhibiting root exudates (Höniges et al. 2009).

The new facilitation process demonstrated here and the interspecific germination-inhibiting effect reported in the literature make it necessary to evaluate both crop and weed species for their ability to trigger and/or attach the parasite, and these both in monospecific and multispecific stands. Moreover, since parasite seeds can survive in the soil for several years (Dhanapal et al. 1996; Rubiales and Fernandez-Aparicio 2012), parasite control cannot be simply reasoned at the annual scale but must be optimized at the multiannual scale. Because of this long-term effect and the multiplicity of the cultural techniques that potentially influence parasite dynamics, either directly or via weeds, developing models that quantify the effect of cropping systems on parasite dynamics in interaction with non-parasite weeds becomes crucial. This was attempted in a preliminary work (PHERASYS, Colbach et al. 2011), but the knowledge of many parasite life stages (soil-borne processes occurring outside host plants, influence of trophic host/parasite relationships on the key stages of the parasite life cycle and host growth) and of weed susceptibility to the parasite is still insufficient.

### 3.3 Secondary attachments

Our results also show an external view of secondary parasite attachments on field bindweed from broomrape established on nearby oilseed rape (Fig. 3, arrow). Such secondary attachments have already been reported on host species (Joel 2000; Joel et al. 2007). In these cases, broomrape first attached on a host root, then penetrated into host tissues and developed a primary haustorium. When the old tubercle stage was reached, the proliferation of cells located around the caulinary meristem led to the formation of a wreath of lateral adventitious roots. These roots were then able to make contact with another host species and produced secondary haustoria attached perpendicularly to the surface of the root of the second species.

Our results show that once attached to a preferred host (here oilseed rape), the parasite is also able to parasitize other nearby species that do not support a primary attachment (here field bindweed). The parasite shoots observed here on field bindweed were fully functional insofar as they were able to grow and develop, even progressing further—in terms of developmental stage—than shoots attached to oilseed rape (Fig. 2b). However, our experiment was not designed to demonstrate whether

the parasite actually drew its nutrients from the secondary field bindweed host or from the initial oilseed rape host. Thus, we now need to conduct experiments to confirm that secondary haustoria between field bindweed and broomrape are fully functional in terms of anatomy, e.g. by determining if phloem-mobile dyes move between field bindweed and the parasite.

## 4 Conclusion

The present work was the first to study broomrape germination and attachment in monospecific vs. multispecific stands using in vitro and pot experiments and resulted in the first demonstration of a new parasitic interaction process, i.e. facilitation. Furthermore, the identification of the new ‘non-host facilitator’ species category makes it necessary to rethink parasite management in arable crops, particularly the rotation or association of host with non-host crops as the latter could actually be non-host facilitators. Consequently, future work is necessary to demonstrate our results in field conditions.

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