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# Effects of some cereal root exudates on germination of broomrapes (*Orobanche* spp. and *Phelipanche* spp.)

Bazı tahıl kök salgılarının canavar otlarının (*Orobanche* spp. and *Phelipanche* spp.) çimlenmesi üzerine etkileri

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#### ABSTRACT

Species of broomrape (Orobanche spp. and Phelipanche spp.) are among the most damaging parasitic weed species worldwide. These species reproduce through abundant seed production. Their seeds are protected by complex dormancy mechanisms, in particular a need for hostspecific chemical germination cues. Broomrape seeds have been shown to remain viable in the soil for many years. While the depletion of the soil seed bank, e.g. using trap crops that induce suicide germination of broomrape seeds, could potentially be a way to control these weeds, the practical uptake of this approach has remained very limited. To explore the potential of an array of cereal species to serve as trap crop, laboratory experiments were conducted to qualitatively check for the existence of cereal-broomrape interactions and to quantify possible effects on Orobanche/Phelipanche seed banks. For this purpose, seeds of the following cereals were used: wheat, rye, barley, oats, maize, rice, sorghum and pearl millet. Several accessions of O. crenata, O. cumana and P. ramosa were used as parasite species. As host species, pea, sunflower and tomato were grown. Cereal and parasite species were crosswise-combined to assess interactions. Maize was found to be most effective in stimulating the germination of the broomrapes. Among the parasite species, P. ramosa proved most ready to germinate in the presence of cereal root exudates. The interaction was observed in various combinations of maize cultivars and P. ramosa accessions. As a result, strong evidence of germination induction in P. ramosa seeds by maize was collected.

### MAKALE BİLGİSİ

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### ÖZ

Canavar otu türleri (Orobanche spp. and Phelipanche spp.) tüm dünyada en zararlı parazit yabancı ot türleri içerisinde yer almaktadır. Bu türler çok sayıda tohum oluşturarak çoğalırlar. Tohumları, çimlenmenin gerçekleşebilmesi için konukçuya özgü kimyasal bir maddeye ihtiyaç duyan karmaşık bir dormansi mekanizmasıyla korunmaktadır. Canavar otu tohumlarının toprakta uzun yıllar canlı kalabildiği görülmektedir. Tuzak bitki kullanımı ile canavar otu tohumlarının çimlenmesi teşvik edilerek topraktaki tohum bankasının azaltılması bu tür yabancı otların mücadelesinde potansiyel bir yöntem olmakla birlikte, bu yaklaşımın pratikte kullanımı oldukça sınırlı kalmıştır. Bazı tahıl türlerinin tuzak bitki olarak potansiyelini araştırmak amacıyla bir seri laboratuar denemeleri kurulmuş ve tahıl-canavar otu arasındaki etkileşim ile birlikte, Orobanche/Phelipanche tohum bankasına muhtemel etkisi test edilmiştir. Bu amaçla tahıllardan; buğday, çavdar, arpa, yulaf, mısır, çeltik, darı ve hint darısı, parazit türlerden ise O. crenata, O. cumana ve P. ramosa 'ya ait çeşitli populasyonlar kullanılmıştır. Bezelye, ayçiçeği ve domates konukçu bitki türü olarak yetiştirilmiştir. Aradaki etkileşimin belirlenebilmesi için tahıllar ve parazit türler çaprazlama olarak eşleştirilmiştir. Canavar otlarının çimlenmesini en fazla mısır bitkisinin teşvik ettiği bulunmuştur. Parazit türler içerisinde ise tahıl kök salgılarının çimlenmeyi en fazla teşvik ettiği tür P. ramosa olarak belirlenmiştir. Mısır çeşitleri ve P. ramosa populasyonları arasındaki interaksiyonlar gözlemlenmiştir. Sonuç olarak, mısır bitkisinin P. ramosa tohumlarının çimlenmesini teşvik ettiğine dair kuvvetli kanıtlar elde edilmiştir.

### 1. Introduction

The genera Orobanche and Phelipanche contain over 170 species of holoparasitic herbaceous plants in the family Orobanchaceae (Joel 2009). Most species of Orobanche and Phelipanche are highly specialized parasites of one or few host plant species that occur in natural ecosystems at rather low population densities. Some *Orobanche* and *Phelipanche* species thrive upon agricultural crops though, particularly in the Mediterranean and cool temperate climate zones. Although only few weedy species are economically important, the cropping area threatened by Orobanche was calculated as 16 million ha in the Mediterranean and West Asian region alone (Sauerborn 1991). Species of *Phelipanche* and *Orobanche* are among the most damaging parasitic weed species worldwide. A review of literature over the period from 1991 to 2008 suggests that many million hectares are infested and that the losses amount to billions of US\$ annually (Parker 2009).

Orobanche/Phelipanche species reproduce by seeds and the seeds have to be stimulated by root exudates of their host plants in order to germinate. The copious production of enduring longlife seeds capable of long dormancy accounts for their peculiar seedbank characteristics. Soil seed density can reach very high values in weedy species (for example, approximately 4 million seeds m<sup>-2</sup> in the 20 cm depth arable layer for O. crenata), most of which can remain viable for more than ten years e.g. in O. crenata (Lopéz Granados and García Torres 1993). Therefore, even after years without host plant cultivation, once host plants were cultivated again, seeds of broomrape germinated and the crop was re-infected (Rubiales et al. 2003). While efforts to actively reduce the parasite population have to take into account the soil seed bank, the choice of methods that effectively kill Orobanche and Phelipanche seeds is limited. Solarization is costly and cumbersome in large scale fields, so is fumigation, and the use of methyl bromide is banned. This leaves the use of trap crops, i.e. plants whose root exudates induce suicidal germination of parasite seeds, as a potentially cost-efficient and pragmatic means of reducing seed load in the soil. An ideal trap crop would be one that can be integrated into the crop rotation, with maximum benefit at little or no opportunity cost.

Anecdotal as well as experimental evidence suggest that some non-host cereal species, such as oats (Avena sativa) and maize (Zea mays), can induce germination in seeds of parasitic weeds of the genera Orobanche and, in particular, Phelipanche. Maize in particular was shown by Labrada and Perez (1986, 1988), Zehhar et al. (2003) and Abebe et al. (2005) to stimulate germination in P. ramosa seeds. Fernandez-Aparicio et al. (2009) demonstrated very different degrees of host specificity in several weedy Orobanche and Phelipanche species, with P. ramosa and P. aegyptiaca germinating in the presence of root exudates from a variety of plants. Similarly, Arslan and Uygur (2013) showed the effects of the root exudates of ten different crop species on P. ramosa and P. aegyptiaca germination. A compound from rye (Secale cereale) root exudates, ryecarbonitriline A, induced germination of O. cumana, suggesting that rye has potential as a trap crop in sunflower production (Cimmino et al. 2015). More recently, Ye et al. (2016) reported that maize can be used as trap crop for depleting the seed bank of P. aegyptiaca through a study with ten different commercial maize cultivars.

The aim of the present study was to observe how the germination of some broomrape species would be affected by

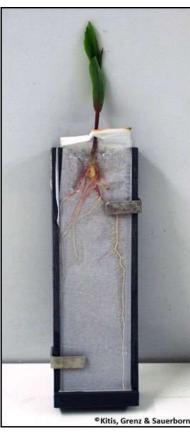
the root exudates of common cereal species. This in order to corroborate or refute the reported experimental results and anecdotal information about germination induction in broomrape species by cereals. Laboratory experiments were conducted to qualitatively check for the existence of cereal-*Orobanche/Phelipanche* interactions and to quantify possible effects on parasite soil seedbanks. In the study, a different set of broomrape accessions, cereal species and varieties and a different methodological approach were chosen in comparison to published studies. From a practical viewpoint, our work should serve to explore the potential of an array of cereal species to serve as *Orobanche* or *Phelipanche* trap crop.

### 2. Materials and methods

### 2.1. Screening of cereal-broomrape combinations

Experiments were set up in the Department of Agroecology, Institute for Plant Production and Agroecology in the Tropics and Subtropics, University of Hohenheim, Germany, in 2017. Stimulatory activity on Orobanche and Phelipanche seeds of the following cereals was determined: bread wheat (Triticum sativum Lam. cv. "Tomi"), rve (Secale cereale L. cv. "Hacada"), barley (Hordeum vulgare L. cv. "Passion"), oat (Avena sativa L. cv. "Tomi"), maize (Zea mays L. cv. "Amadeo"), rice (Oryza sativa L., unknown cv. from Camargue, France), sorghum (Sorghum bicolor (L.) Moench cv. "Wad Ahmad") and pearl millet (Pennisetum glaucum (L.) R. Br., unknown cv. from Niger). Parasite species tested included crenate broomrape (Orobanche crenata Forsk.) collected in Adana, Turkey, in 2002, sunflower broomrape (Orobanche cumana Wallr.) collected from Călărași, Romania, in 2003 and branched broomrape (Phelipanche ramosa L.) from Sandhausen, Germany, collected in 2002-2003. Cereal and parasite species were crosswise combined to assess interactions. In addition, one host plant per parasite was added as a check. For this purpose, pea (Pisum sativum L. cv. "Kleine Rheinländerin"), sunflower (Helianthus annuus L. cv. "Albena") and tomato (Solanum lycopersicum L. cv. "Rentita") were used for O. crenata, O. cumana and P. ramosa, respectively.

PVC (polyvinyl chloride) root chambers ca. 20 cm high, 6 cm wide and 3 cm deep were filled with autoclaved quartz sand. Surface sterilized seeds (200 to 300) of the respective parasitic weed species were sprinkled on a strip of moist glass fiber filter paper placed on the sand. The front of each chamber was tightly closed by a plexiglass lid fixed with clamps. One pre-germinated seed per cereal or host species was placed between lid and filter paper at the top end of the chamber (Figure 1). Chambers were wrapped in black plastic foil to block the light and placed obliquely in plastic bowls containing a 3-4 cm deep layer of tap water. Per cereal/host x parasite combination, five root chambers were prepared, giving a total of 9x3x5= 135 chambers. Rice, maize, sorghum and pearl millet were grown in a climate chamber set at a constant temperature of 30°C, all other crops were grown at 25°C. Starting 3 weeks after establishment, crops were fertilized once a week with 10 ml of a 1% solution of Wuxal<sup>TM</sup> complete fertilizer. From the sixth week after establishment onward, germination and attachment were quantified by counting 100 randomly selected seeds per root chamber under a dissecting binocular.



**Figure 1.** Root chambers used in the experiments (20 x 6 x 3 cm).

# 2.2. Screening of maize cultivars for their ability to induce germination of P. ramosa seeds

Based on the results of the first experiment, a screening of maize cultivars for their ability to stimulate the germination of P. ramosa was conducted. Prior to testing, seeds were surface sterilized by immersion in 1% NaOHCl for 5 minutes, rinsed in distilled water and spread on petri dishes to dry. Surface sterilized seeds of P. ramosa accessed from Sandhausen, Germany, in 2002-2003 were exposed to roots of nine different maize cultivars, namely 'Amadeo', 'Dr. Deliels Körnermais', 'Janetzkis Astra', 'Mahlsberger', 'Mahndorfer', 'Pautzfelder', 'Pommernmais x Schindelmeier', 'Schindelmeier' and 'V. Wynens Körnermais'. The first is a hybrid, while the latter eight are population breeds (landraces). Thus, high genetic heterogeneity was assured. As a control, tomato cultivar 'Rentita' was used, tomato being a host crop of P. ramosa. The experiment was established, maintained and evaluated in a similar manner as described above (root chambers, 5 repetitions, counts of 100 seeds per chamber).

# 2.3. Screening of P. ramosa and P. aegyptiaca accessions for sensitivity to maize root exudates

In parallel to the screening of maize cultivars, accessions of *P. ramosa* and the closely related *Phelipanche aegyptiaca* Pers. were screened for susceptibility to root exudates of maize cultivar 'Amadeo'. Seeds from six *P. ramosa* populations from Germany, Algeria, Morocco, Nepal, Egypt and Israel were surface sterilized, sprinkled on filter paper and exposed to maize roots in root chambers as described above. Again, tomato cultivar 'Rentita' was used as a check. A list of accessions is provided in table 1.

**Table 1.** *Phelipanche ramosa/aegyptiaca* accessions used in the experiments.

Broomrape Species	Location	Collection Year
Phelipanche ramosa	Germany	2002-2003
Phelipanche ramosa	Algeria	1996
Phelipanche ramosa	Morocco	1995-1996
Phelipanche ramosa	Nepal	1994
Phelipanche aegyptiaca	Egypt	1997
Phelipanche aegyptiaca	Israel	2006

# 2.4. Determination of viability and germinability of Phelipanche seed accessions

Viability and germinability were determined for the seed accessions used in the prior experiment. For this purpose, *P. ramosa* and *P. aegyptiaca* seeds used in the experiments were assessed by tetrazolium (Linke et al. 1991) and GR24 (Kroschel 2001) tests, respectively. Prior to testing, 6-7 mg seeds per accession were surface sterilized by immersion in 1% NaOHCl for 5 minutes, rinsed in distilled water and spread on petri dishes to dry.

For viability testing, seeds were immersed in 1 ml of a 1% aqueous solution of TTC (triphenyl tetrazolium chloride) in Eppendorf vials. Vials were wrapped in aluminum foil to avoid any exposure to light, and stored in the dark at 33°C for 13 days. Subsequently, the TTC solution was washed off using distilled water, seeds were bleached for 4 minutes in 5% NaOHCl and placed on Whatman G/F filter paper. Viability was assessed using a dissecting binocular. Seeds with red or pink embryo were considered viable, colorless and black seeds were counted as non-viable.

Germinability of seeds preconditioned on moist filter paper for one week was quantified by exposure of some 200 seeds each on four filter paper quadrats per accession, placed in Petri dishes to 1 ppm aqueous solution of the synthetic strigolactone, GR24, in the dark at room temperature for one week. Seeds with a clearly visible germ tube were considered germinated.

### 2.5. Statistical analysis

The experiments were set up for five replicates in a randomized complete plot design and all experiments were repeated two times. Since there were no statistically significant differences between two experiments, the mean results of the two experiments were used. Statistical analysis of the results was made with the help of R statistical software (Version 1.0.143 ©2009-2016 RStudio, Inc.). The data collected on all parameters was subjected to analysis of variance (ANOVA). Multiple comparisons of mean values were performed with the LSD Test at rate of 95% confidence.

### 3. Results

### 3.1. Effects of cereal roots on broomrape germination

Host-induced germination percentages were lowest in *O. cumana* and highest in *O. crenata*. The average ability to stimulate parasite germination was highest in maize, followed by oats. The least effective cereals regarding parasite stimulation were millet and rice. This may in part be attributable to poor growth of both cereal species in the root chambers. From the parasite species, *P. ramosa* proved most sensitive to cereal root exudates. This fits well with the much wider host range of this species, compared with e.g. *O. cumana*. The

highest germination percentages were recorded for *P. ramosa* exposed to maize and oats roots (Table 2).

While 15%, 16%, 33% of the germinated seeds of *P. ramosa, O. cumana* and *O. crenata* managed to attach to host roots respectively, no attachment of broomrape species to cereal roots was observed. However, germ tubes of many *P. ramosa* seeds did grow towards the nearest maize root. In some instances, germ tubes reached a root, but failed to attach, which was sometimes accompanied by a thickening of the maize root epidermis. These findings may indicate the release of some germination cue from maize roots.

# 3.2. Induction of Phelipanche ramosa germination by maize cultivars

All tested maize cultivars stimulated germination in seeds of *P. ramosa* accession 'Germany' (Sandhausen) at a rate of more than 60% (Figure 2). The lowest germination percentage (48%) was recorded in the host plant, tomato. Maize cv. 'Amadeo' exhibited a similarly high stimulatory activity as in the first experiment, and was only exceeded by the population varieties,

'Dr. Deliels Körnermais' and 'Mahndorfer'. Hence, there seems to be quantitative, but not qualitative variation among maize cultivars regarding the release of compounds stimulating the germination of *P. ramosa*.

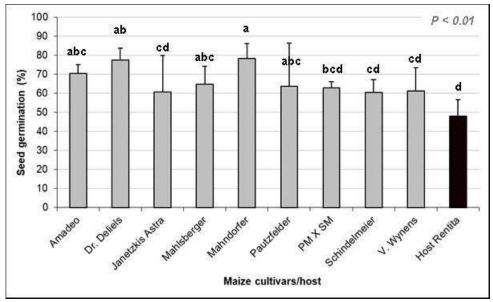
### 3.3. Phelipanche spp. viability and germinability

The viability of all branched/Egyptian broomrape accessions except those from Nepal ('Chitwan') and Morocco exceeded 60% (Table 3). GR-24-assessed germinability was close to zero in these two seed batches, as well as in the accession from Algeria. The batch from Egypt had a germinability of less than 20%. Apparently, viability and germinability had decreased due to prolonged storage. The two most recent accessions (Germany and Israel) were the most viable and germinable. Seeds of the Algerian and Egyptian accessions seemed to be dormant (viable, but not germinating under suitable conditions) to a high degree. It is unclear what factors induced this dormancy. Alternatively, temperature, moisture or GR24 concentration may have been suboptimal for germination induction in these accessions.

**Table 2.** Average germination percentage induced in *Orobanche* and *Phelipanche* seeds by cereal and host roots. 'Activity' denotes the average (for the three broomrape species) ratio of cereal-induced divided by the respective host-induced germination.

	Broomrape Species			
Cereals	O. cumana	O. crenata	P. ramosa	Activity (%)
Wheat	0 (±0)c	13.2 (±11.2)b	6.4 (±9.9)cd	12.0
Barley	2.2 (±1.3)bc	0.2 (±0.4)c	14.8 (±8.9)c	13.5
Oat	0.8 (±1.3)c	6.8 (±6.7)bc	37.8 (±8.8)b	32.0
Rye	0.4 (±0.5)c	4.6 (±3.6)c	9.2 (±9.6)cd	9.7
Maize	4.6 (±3.6)b	$1.0 (\pm 1.7)c$	77.0 (±6.4)a	61.7
Rice	0.8 (±0.4)c	0.2 (±0.4)c	4.6 (±2.7)cd	4.4
Sorghum	0.4 (±0.9)c	4.2 (±3.3)c	7.8 (±6.6)cd	8.5
Millet	0 (±0)c	0 (±0)c	$1.0 \ (\pm 0.7)d$	0.7
Host				
Sunflower	26.5 (±5.1)a			
Pea		59.6 (±7.9)a		
Tomato			46.4 (±21.2)b	

Different letters within a column indicate statistically significant differences at the 0.05 level.



**Figure 2.** Germination percentage of seeds of *P. ramosa* (accession Sandhausen, Germany, in 2002-2003) induced by different maize cultivars. Different letters at the top of the bars indicate statistically significant differences at the 0.05 level. Error bars indicate ±1 standard error.

Germination **Broomrape species** Location Viability Germinability Maize **Tomato** P. ramosa Germany 84.8 (±6.6)b 65.0 (±11.6)a 70.4 (±4.7)a  $48.0 (\pm 8.7)a$ P. ramosa Algeria 93.8 (±2.4)a  $0.5 (\pm 0.6)c$  $1.8 (\pm 2.5)d$  $0 (\pm 0)c$ P. ramosa Morocco 13.3 (±3.3)d  $2.7 (\pm 1.2)c$  $1.2 (\pm 1.1)d$  $3.2 (\pm 3.1)c$ P. ramosa Nepal  $4.8 (\pm 1.0)e$  $0 (\pm 0)c$  $2.0 (\pm 2.8)d$  $0.6 (\pm 1.3)c$ P. aegyptiaca Egypt 66.5 (±4.0)c 16.8 (±7.8)b 27.2 (±8.7)c 17.8 (±7.5)b P. aegyptiaca Israel  $82.0 (\pm 2.6)b$ 58.8 (±6.7)a 60.6 (±4.2)b  $45.0 (\pm 7.2)a$ 

**Table 3.** TTC-assessed viability and GR24-assessed germinability of *P. ramosa* and *P. aegyptiaca* accessions and their average germination percentage induced by maize (cv. Amadeo) and host (tomato cv. Rentita) species.

Different letters within a column indicate statistically significant differences at the 0.05 level.

# 3.4. Induction of germination of Phelipanche spp. accessions by maize

Maize cultivar 'Amadeo' stimulated germination in seeds of *P. ramosa* from Germany and *P. aegyptiaca* from Egypt and from Israel (Table 3). Some germination was observed in the other accessions, however due to low viability (Nepal, Morocco) and germinability (Algeria), germination percentages remained very low. Accordingly, germination induction by tomato as host was also close to zero in these accessions. Yet, results support the hypothesis that maize root exudates can stimulate germination of more than one strain of *P. ramosa* and the closely related *P. aegyptiaca*. Again, differences seem to be of a quantitative rather than qualitative nature.

#### 4. Discussion

All cereal species used in our study stimulated germination of broomrape seeds, albeit at very variable extent. Similarly, Fernandez-Aparicio et al. (2009) found in their study that, in general, all cereals induced germination of broomrape species. On the other hand, results of the study of Abebe et al. (2005) are of interest. When they used some plant species as trap crops against P. ramosa and O. cernua on naturally infested soil, they found all crop species used in experiment to reduce shoot number of broomrape species in following host crops by over 60%. The most effective trap species was found to be maize with 74% reduction of broomrape shoots. Ma et al. (2012) showed that some hybrid maize lines can induce germination of sunflower broomrape (O. cumana). Moreover, Ye et al. (2016) found strong evidence for maize cultivars inducing germination of Egyptian broomrape (P. aegyptiaca) through a study with ten commercial maize cultivars and different assay methods. In both studies, results suggested that maize can be used as trap crop to deplete the seed bank of broomrape species.

The study of Zehhar et al. (2003) clearly showed that maize as non-host of broomrape stimulated seed germination of *P. ramosa* seeds by up to 70%. This study also showed how maize is resistant against broomrape attack. According to Zehhar et al. (2003), in most cases, the broomrape penetrated the maize root but was stopped at the endodermis by the formation of an encapsulation layer. Moreover, a thickening of endodermis cell walls near the penetrating parasite was also observed. This observation had first been made by Dorr et al. (1994) who investigated susceptible and resistant sunflower varieties against *O. cumana*.

Germination of broomrapes seeds can thus be stimulated by maize, but the germ tube does not succeed to penetrate the inner parts of maize roots and connect to xylem and phloem. It is known that the molecules inducing germination of broomrapes

are strigolactones which play a role in host recognition by parasitic plants (Yokota et al. 1998; Cardoso et al. 2011). Over 14 strigolactones have been identified in root exudates of various plant species up to now (Yoneyama et al. 2009). In maize roots, several strigolactones are released, the major compound being strigol (Siame et al. 1993). In addition to strigol, sorgomol and 5-deoxystrigol were found in maize root exudates. According to researchers, 5-deoxystrigol is one of the major germination cues of gramineous plants, with stimulants differing among cultivars within the same species (Ayman et al. 2006). Recently, Jamil et al. (2012) reported the detection of novel germination stimulants, tentatively called SL1 and SL2, in maize root exudates based on LC-MS/MS analysis. Isolation and structure of SL2 were determined; it was named methyl zealactonate and strongly induced germination stimulation activities in Striga hermonthica and P. ramosa (Xie et al. 2017).

Our results and those of other studies suggest that cereals, especially maize, do induce germination of broomrape seeds. This phenomenon could be put into practical use. In previous studies, the use of host catch crops (Linke et al. 1993; Acharya et al. 2002) and trap crops (Hershenhorn et al. 1996; Ross et al. 2004; Aksoy et al. 2016) were suggested as approaches to reduce broomrape infection in infested soil. Lins et al. (2006) showed that red clover (Trifolium pratense) plants also had fewer O. minor attachments when grown in field soil taken from plots where wheat or triticale had been grown, compared with plants grown in soil where no wheat or triticale had been grown. Ma et al. (2012) suggested that maize can be used to reduce the soil seed bank of O. cumana in infested sunflower fields, but further studies are needed to confirm whether maize can significantly reduce the O. cumana seed bank under field conditions. Similar confirmations are needed for the broomrape species, P. ramosa and P. aegyptiaca. When maize is used as a trap crop, with increased sowing density, the amount of exudates from maize roots will increase and hence there will be a better chance of contact with more broomrape seeds in the soil. The maize could still be used as fodder or green manure, or it could be part of the crop rotation. The maize can used as preplant before host crops and it can be removed after a short growing period, provided a rapid development of the root system and sufficiently early release of broomrape germination cues. This practice would be effective in greenhouses especially. In greenhouses e.g. in southern Turkey, there is a fallow period after the main crop harvest. In this time, maize can be grown, then incorporated into the soil. All applications mentioned above will be somewhat effective, but it should not be forgotten that only one tactic is not sufficient to control broomrape species. Thus, other control strategies should be combined for effective integrated broomrape management. The education of farmers and workers about broomrape control

tactics is also very important in the management of infested areas.

### 5. Conclusion

In this study, stimulating effects of some cereals on broomrape seed germination were investigated. The most effective cereal was determined to be maize, followed by oats. *P. ramosa* was found to be the most sensitive broomrape species, showing a clear reaction to maize as well as oats. All maize cultivars used in this study induced more germination of *P. ramosa | P. aegyptiaca* accessions than tomato, a host crop. All these results show that the maize can be used as a tool to induce suicidal germination of *P. ramosa* and *P. aegyptiaca*, which have the widest host range compared to other broomrape species. It is necessary to evaluate the effectiveness of the obtained results under field conditions.

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