THE EFFECTS OF VARIOUS ROOT EXUDATES ON BROOMRAPE GERMINATION

by

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INTRODUCTION

Weeds are the major impediment to food production and economic development in many regions of the world (44). They cause losses by their competition with crops for nutrients, space, light, carbon dioxide and water (44).

Phanerogamic root parasites are flowering plants inflicting yield losses by directly removing nutrients and water from host crops. The broomrapes (Orobanche spp.) are one group of such parasites. They are generally temperate in distribution, but some species are found in tropical and arctic regions (54). The inoculum is seeds. These are disseminated by wind, water and man. The approaches to control include (a) the use of herbicides, (b) biological means, and (c) such cultural means as trap and catch crops. Catch and trap crops function because broomrape seeds require a stimulant provided by the host's root exudates to induce germination. Trap crops are nonhost plants. Catch crops are host plants that are harvested before the parasite produces seed.

The subject of the present study was branched broomrape (Orobanche ramosa L.). This particular species is a problem weed in semi-arid nonindustrialized countries. In these countries, cultural controls are often more affordable than herbicides.

LITERATURE REVIEW

General Biology

Orobanche ramosa is most commonly found in eastern Europe, mid- and northern Asia, India and Mediterranean countries. It was first reported in the United States in Kentucky in 1890 and subsequently in Illinois and Wisconsin on hemp (*Cannabis sativa* L.), and also in California on hemp and tomato (*Lycopersicon esculentum* Mill.) (19). Durbin postulated that it was introduced on hemp seeds imported from the Orient (19). Since 1929 it has become a serious problem in California tomato plantings due to widespread seed dissemination by machinery and irrigation (19).

The broomrape plant consists of one to several flowering stalks with achlorophyllous leaves reduced to scales. The stalk is yellowish-tan, being devoid of chlorophyll (10,50), generally pubescent, and arises from a thickened base (54). The inflorescence is racemose or spicate and consists of small, tubular, lavender, bisexual flowers with glandular trichomes (42,54). Pollination is generally by bees although other insects, birds and wind may play a minor role (42,54). Several seedpods are produced per inflorescence. From 1000-2000 small dark brown seeds are contained in each seedpod. Seeds are finely reticulate, contain an undifferentiated embryo (1) and are disseminated by wind and water (42). They remain viable in soil for up to ten years (31). Germination occurs once the seed has been preconditioned in moist soil at the proper temperature (optimum is 20 C) and then

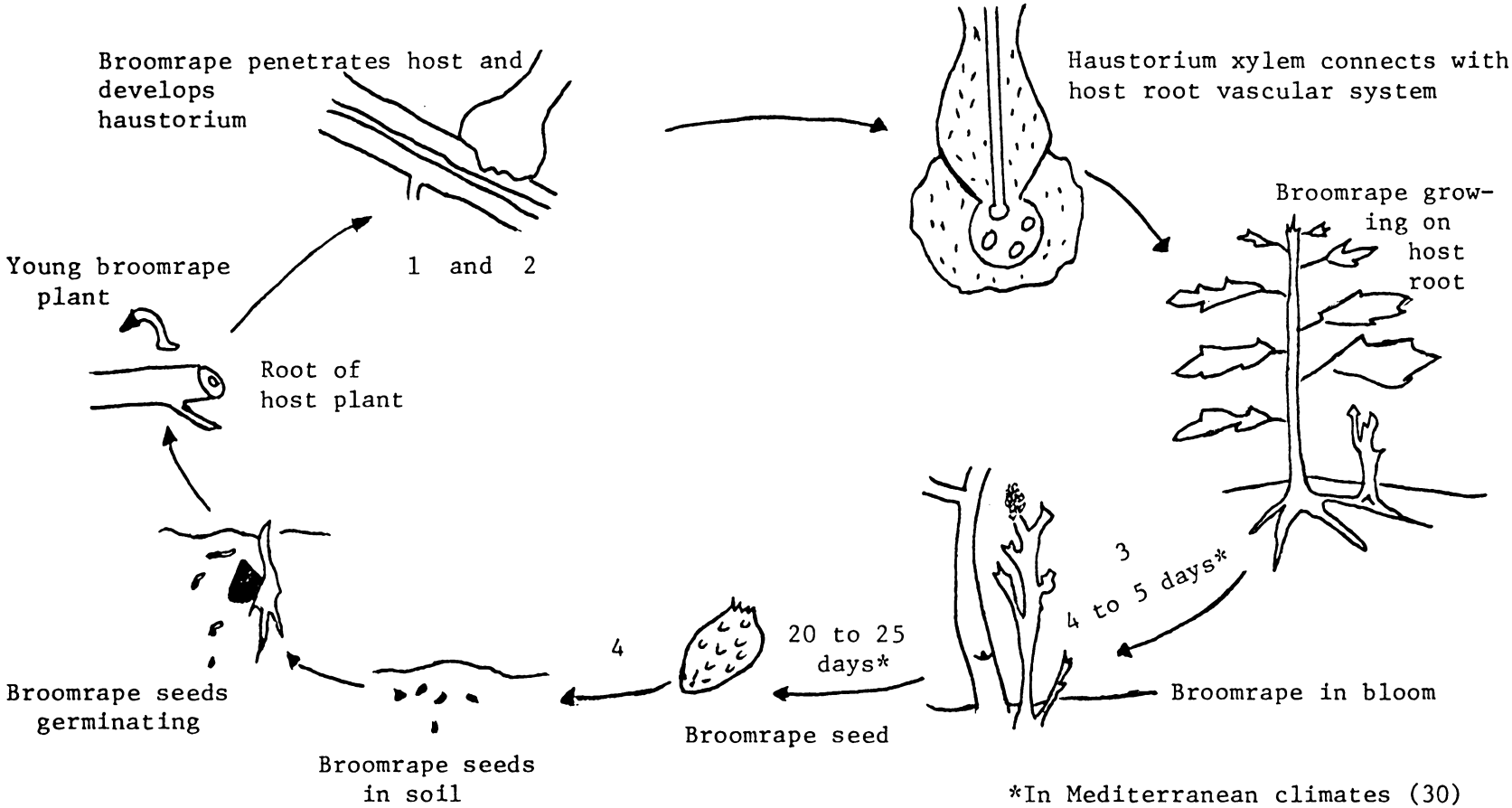
exposed to a stimulating compound from host root exudates. A radicle is sent out from the seed, the host root is penetrated and a haustorium develops to connect the parasite and host. The broomrape plant obtains most of its nutrients and water from the host via the xylem and phloem in the haustoria. Flowering stalks develop in about one week and seeds are produced about three weeks later (32).

Much drop damage occurs in the early stages of parasitism before the parasite has sprouted (46). Thus, control measures are directed toward preventing haustorial attachment as well as destroying the emerging plant before seed production. See Figure 1 for a schematic drawing of the life cycle.

Orobanche ramosa has a large host range. Solanaceous and leguminous plants are generally susceptible. Some host crops include tobacco, tomato, sunflower (Helianthus annus L.), hemp and melon (Cucumis melo L. and Citrullus vulgaris Shrad.). A complete host list is given in Tables 1 and 2.

Importance

The actual economic importance of branched broomrape is difficult to assess because of its widespread occurrence in underdeveloped countries. However it does cause considerable loss, especially in the Mediterranean basin (33,44,50). In one case, 70% of the plants were parasitized in a tobacco field near the Black Sea (32). Yields were decreased by as much as 40% in Afghanistan fields of melons, tomatoes and tobacco (4). In a California study, tomato production was reduced an average of 34% (16).



*In Mediterranean climates (30)

Mechanism of control:

1 trap crops
2 resistant varieties
3 catch crops post-emergent herbicides
4 quarantines

Figure 1. Schematic drawing of broomrape life cycle. Adapted from Agrios, 1969 (3) with modifications according to Kuijt, 1969 (42).

Table 1. A list of economically important broomrape hosts.

Common Name	Scientific Name
Brassicas	*Brassica* spp.[a,b]
Carrot	*Daucus carota sativa* (Hoffm.)[b]
Celery	*Apium graveoleus dulce* (Mill.)[b]
Cotton	*Gossypium* spp.[b]
Hemp	*Cannabis sativa* L.[a,b]
Lettuce	*Lactuca sativa* L.[b]
Melon	*Cucumis melo* L. *Citrullus vulgaris* Schrad.[b]
Parsnip	*Pastinaca sativa* L.[b]
Potato	*Solanum tuberosum* L.[a,b]
Safflower	*Carthamus tinctorius* L.[b]
Sunflower	*Helianthus annuus* L.[b]
Tobacco	*Nicotiana tabacum* L.[a,b]
Tomato	*Lycopersicon esculentum* Mill.[a,b]

[a]Durbin, 1953 (19)

[b]Kasasian, 1971 (33)

Table 2. A list of broomrape hosts of secondary importance.[a]

Scientific Name	Common Name
Amaranthus retroflexus L.	Pigweed
Armoracia lapathaefolia Gilib.	
Begonia semperflorens L.	Begonia
Capsella bursa-pastoris L.	Sheperd's purse
Coleus spp.	Coleus
Conium maculatum L.	Poison hemlock
Heliotropium peruvianum L.	
Lamium spp.	Mints
Lepidium virginicum L.	
Pelargonium spp.	Geranium
Perilla nankinensis L.	
Petunia hybrida Vilm.	Petunia
Solanum sarachoides Sendt.	Nightshade
Tropaeolum majus L.	
Veronica spp.	Veronicas
Vitis vinifera L.	
Xanthium spinosum L.	

[a]Durbin, 1953 (19)

Control Methods

Chemical. Control of Orobanche results in significant crop yield increases. Chemical control generally offers the most effective means, but it is not always the most practical. Other measures include breeding resistant varieties, cultural methods and biological control.

One class of chemicals which has achieved consistently good results is the soil fumigants. A typical example is one in which methyl bromide at 500 kg/ha in tobacco fields of the Black Sea area effected complete control (32). Similar results were obtained with 201.24 kg/ha (180 lb/acre) in California tomato seedbeds (55). The nematicides, Nemagon (dibromochloropropane), and Vapam (metham sodium) also significantly reduce broomrape infestation (7,60). Although soil fumigants provided excellent control, other studies have concluded that the cost of these chemicals is too high to be offset by yield increases (47,48).

Plant growth regulators have been found to have herbicidal activity against broomrape. Evtushenko (20) reported that MH-T (maleic hydrazide triethylamine), used to suppress auxillary bud formation in tobacco, killed 91.3% of O. ramosa as a post-emergent spray on tobacco. After treatment, tobacco root exudates were found to inhibit broomrape seed germination. MH-T moved into the broomrape via the host roots (20,21). Other compounds effecting good control include 2,4,5-T ([2,4,5-trichlorophenoxy] acetic acid) at 6 to 8 kg/ha, 2,4,-D ([2,4-dichlorophenoxy] acetic acid) as a directed spray and NAA (1-naphaleneacetic acid) applied to tomato prior to broomrape emergence

(2,22,33). Chloramben (3-amino-2,5-dichlorobenzoic acid) reduced Orobanche germination in petri plate studies and so is a possibility for pre-emergent control before the parasite can attach to and damage the host (34).

Another herbicide used in broomrape control is allyl alcohol. Post-emergent applications in tobacco (49,56) and tomato (33) suppressed broomrape emergence and killed emerged parasite shoots.

Although herbicides such as these are efficient and effective, the chemical control of broomrape poses specific problems. Phytotoxicity to desirable species is often encountered (2,23,33,47) since both host and parasite are vascular plants and there is an intimate connection with the crop plant via broomrape's haustoria (see Figure 1) (51). Related to this, there is little connection between the mature parasite and the soil so that soil incorporated herbicides used to avoid phytotoxicity to desirable species are ineffective (44). The expense of herbicides is a deterrent to their use in underdeveloped countries (47,48). Because of these problems, other methods are used in conjunction with or instead of chemicals.

Resistance. Some success has been realized in discovering agriculturally acceptable resistant cultivars of sunflower (33,54), watermelon (Citrullus vulgaris) (31), rape (Brassica napus), mustard (Brassica spp.) (17), hemp and bean (Phaseolus spp.) (33). Resistance in Russian sunflower appears to be due to root tissue properties, perhaps the presence of phenols, as indicated by biochemical and grafting studies (33,35). No reports of tomato and tobacco resistance

were found.

Biological. The most promising means of biological control is the midge Phytomyza orobanchia Kalt. It is both effective and inexpensive (33). In Russian studies, almost complete control was obtained in tomato, cabbage (Brassica oleracea), melon and sunflower plots (33,36,39,46). After treatment with the midge, cabbage yields increased two and a half times over controls (36). The usual application method is to suspend bags containing puparia from posts set in the fields (9,36). Adults emerge when broomrape is flowering, and lay eggs. Stems and flowering shoots are destroyed (36) and seed viability is lost by the feeding action of the larvae on shoot and pericarp tissue. Three to four generations are produced per growing season (9, 36) and the midge overwinters (36). The Agricultural Research Council reported that the University of California at Berkeley has used Phytomyza to control broomrape (29). Disadvantages are that the midge may pollinate broomrape (12) and/or parasitize beneficial plants.

Another possibility for biological control is the fungus Fusarium orobanchus. It is especially destructive to young broomrape plants and seeds and causes minimal crop damage (8,38). However maximum results are obtained only under warm temperatures and constant high soil moisture (34,38). As with P. orobanchia, its host specificity is unknown.

Sclerotinia sclerotiorum (Lib.) de Bary forma orobanchus has been reported to produce a soft rot of O. cernua prior to or immediately after emergence (45). Its host specificity is also unknown.

Cultural. Mechanical removal is the oldest means of control. Regular roguing over several years can minimize Orobanche incidence to almost zero (33,40,57). However, some of the many disadvantages to its use on a large scale include: (a) hand cultivation is slow and ties up valuable man-hours, (b) it is unfeasible to remove all parasites because of continued reinfestations from alternate hosts, and (c) much damage is done before the parasite sprouts (42).

Trench plowing prior to spring planting (5) and sowing crops below the infested soil horizon (37) precludes root contact between host and broomrape and so reduces parasitism. Also, early sowing and harvesting, which removes the host plant before the broomrape seed can produce seeds, is recommended (12,34).

Control of soil moisture is somewhat effective. Flooding results in loss of seed viability (43). Results vary from complete elimination in melon patches in Russia to nine percent decline in Russian tobacco plots (37). Maintaining a low soil moisture content in tobacco fields reduced Orobanche incidence (33,37).

Although there are contradictory reports, proper application of phosphorus, nitrogen and potassium decreased broomrape severity by adversely affecting parasite vigor and enhancing early crop maturation (33). Alkaline soils tend to have increased Orobanche incidence (33).

Catch crops are another form of cultural control. These crops consist of hosts whose root exudates stimulate Orobanche to germinate. After emerging from the soil, broomrape plants are plowed under or treated with herbicides before seed production (59). They are often used in rotation with more valuable crop hosts (54). Kropac reported

that sowing a catch crop of white clover (Trifolium repens) and Italian ryegrass (Lolium spp.) mixture which was plowed under in autumn was effective in clearing Orobanche minor from red clover (Trifolium pratense) fields in Bohemia (41).

A method resembling the use of catch crops is the raising of trap crops. Trap crops are plants which induce Orobanche germination but do not allow a parasitic relationship to develop. This is probably accomplished by preventing haustorial attachment or by providing inadequate nutrition to sustain the pathogen (58). An advantage of trap cropping is that economically important crops are often used which can be harvested for a profit (34). Some trap crops for O. ramosa include alfalfa (Medicago sativa L.), clover (Trifolium spp.), mustard and flax (Linum usitatissimum L.) (see Table 3). In tobacco plots in Bulgaria, where mustard was raised and plowed under five days before tobacco was transplanted, broomrape incidence was six to eight times less and tobacco yield increased 400 to 500 kg/ha (6). Davies reported that cropping with flax followed by red clover lessened the number of O. minor plants and nearly doubled clover yield in plot experiments. Replicated field trials showed some broomrape reduction, but it was not significant at the five percent level (18).

Disadvantages of both trap and catch cropping are that a crop root must be within 10 mm of an Orobanche seed to stimulate germination (34). Shallow plowing (about five inches deep) prior to planting to place parasite seeds in close proximity to host roots and fertilization to increase the crop root system help overcome this problem (59). Also, seeds must be preconditioned by moisture to respond to stimulant (55).

Table 3. A list of trap crops for branched broomrape.[a]

Common Name	Scientific Name
Capsicums	*Capsicum* spp.
Castorbean	*Ricinus communis* L.
Clover	*Trifolium* spp.
Alfalfa	*Medicago sativa* L.
Millets	*Pennisetum* spp., *Setaria* spp.
Mustard	*Brassica nigra* (L.) Koch, *B. alba* (L.) Rabenh.
Rape	*Brassica napus* L.
Sesame	*Sesamum indicum* L.

[a]Kasasian, 1971 (33)

Finally, not all seeds may germinate after one exposure to the stimulant, so that the entire pest population will not be controlled in one season (46).

A measure similar to trap cropping which also causes broomrape germination but prevents parasitism is the soil incorporation of ground-up host remains. Experiments in which soil contained 0.4% by weight of sunflower stems, leaves and roots produced complete control in subsequent crop plantings (46).

Germination stimulants. The actual identity of the stimulant produced by catch and trap crops is still unknown. Paper chromatography by Brown, et al. (14) indicated that more than one compound may be involved. This is consistent with results obtained by Cezard where Centaurea scabiosa L. culture solutions which induce O. minor germination were examined (15). Its stability in weakly acid solutions and instability in alkaline solutions indicate the presence of a potential acidic or lactone grouping (14). According to Garas et al., Mallet also suspected an active lactone-like component in bean root extracts (24). Nash and Wilhelm observed that gibberellic acid induced O. ramosa germination (46), as did Karasu (32). However, in another study with O. crenata, gibberellic acid did not induce this response but only enhanced it once stimulating root exudates were applied (24). Other substances causing O. ramosa germination include vitamins with a pyridine nucleus (46). The active component in flax exudates was found to be inactivated by boiling for two hours, although it was inactivated more slowly at pH 3.62 to 4.37 (14).

Barcinsky reported that the activity of sunflower root extracts was stable after boiling for one half hour and induced greater germination of O. cumana at slightly acid pH (11).

Broomrape has often proved difficult to eradicate with herbicides for two reasons: (a) much damage is caused before its presence is noted because the parasitic relationship is established prior to sprouting of the weed (34), and (b) due to the vascular connection via haustorium, chemicals applied to the parasite may be easily translocated and cause phytotoxicity to the host (33). Trap and catch crops, which release germination stimulants, are alternative means of control. To most effectively reduce parasite incidence, catch and trap crops must be producing the stimulant when broomrape seeds will germinate. Thus, the primary objective of this study was to note the stimulant levels produced by various crop roots over time.

MATERIALS AND METHODS

Experiment One

Tomato, tobacco, sorghum (Sorghum vulgare L.), and flax were tested for their stimulatory activity on O. ramosa seed germination. These four plants were sprouted in a mixture of peat, vermiculite, and weblite at a ratio of 1:1:½ plus 4-9-3 fertilizer and 14-14-14 slow-release fertilizer. All tests were conducted in growth chambers under continuous light.

Tomato, tobacco and sorghum at the three-leaf stage and flax at the four-leaf stage were transplanted into containers with a cycling nutrient system by which root exudates were collected (Figure 2). Rooting medium was sand from which clay was removed by tap water rinsing through two screens, one with 0.841 mm^2 and the other with 0.025 mm^2 openings. This clay-free sand was used as the medium to avoid adsorption of root exudates to soil colloids.

Tomato seed planted was variety Rutgers 8828 treated with Captan-methoxychlor 75-3 at 0.06 ounces per 45.25 grams of seed. Sorghum was a hybrid grain sorghum variety R-920 lot 790-2KC from Texas. Tobacco seed was a Kentucky burley type of unknown lot number. Flax seed was an unstated variety, lot 178-1 BD from South Dakota.

Four containers with two plants each were prepared for each species. Controls consisted of containers identical to test containers but without plants. The experiment was carried out at 25 C under continuous lighting. To avoid a toxic accumulation of salts, plants

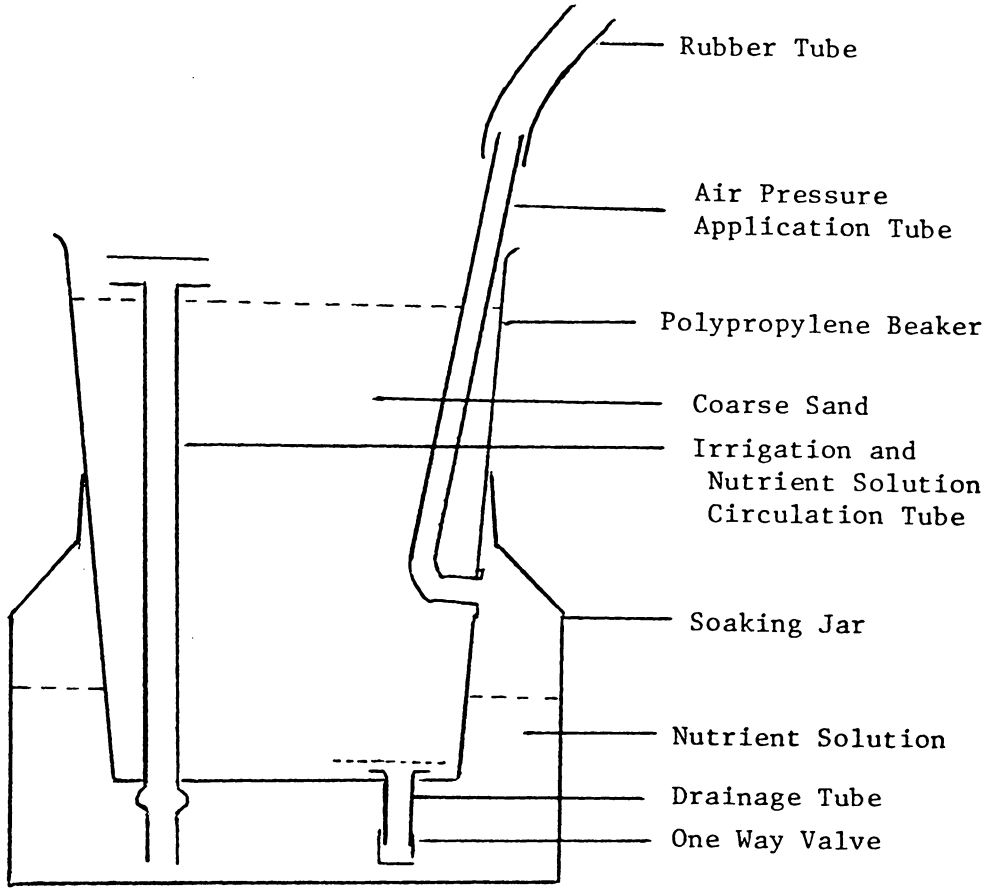


Figure 2. Schematic drawing of irrigation and exudate collection chamber (26).

were irrigated alternately with 200 ml of one-quarter strength Hoagland's solution (28) or distilled water twice daily.

At least two weeks prior to transplanting, O. ramosa seeds were preconditioned by placing 50 to 200 seeds on 2 cm wide discs of Whatman #2 filter paper, putting discs onto moistened filter paper in 15 cm wide petri plates, wrapping plates in aluminum foil and maintaining them at 20 C. This preconditioning is required for germination, both in laboratory (19,44,54) and field conditions (19). Broomrape seeds were from Lebanon and donated by Dr. A. R. Saghir, Professor of Weed Science and Chairman of Crop Production Protection Department at the American University of Beirut in Beirut, Lebanon.

After preconditioning, one disc of seeds was wrapped in a nylon-cotton bag and suspended by thread into the nutrient-root exudate solution in each soaking jar of the containers mentioned above (Figure 2). Effect of root exudates on germination was recorded 10 days after planting tomato, tobacco and sorghum and 21 days after planting flax (first seeding). Readings were taken for eight weeks.

Studies have shown that root exudates remaining too long in contact with Orobanche seeds might inhibit germination (15). For this reason, two weeks later new preconditioned O. ramosa seeds were placed in solutions of tomato, sorghum and tobacco containers. Germination was again noted (second seeding).

To determine actual plant age, 10 days should be added to "time in days" seen in Figure 3 for tobacco, sorghum and tomato and 6 days added to flax since they were planted before the readings were started.

Experiment Two

A second experiment was run with identical seed, containers, controls and growing conditions. However several variations were made. Soaking jars were wrapped in aluminum foil and polypropylene beakers were spray painted with aluminum paint to reduce algal growth in the containers. The root exudate-nutrient solutions were decanted daily just prior to watering to further discourage algae and ensure that broomrape seeds were exposed only to fresh root exudates. To test for stimulant production throughout development of the plants and avoid root injury from transplanting, crop plants were sprouted in the sand-filled beakers and Orobanche germination was recorded from planting until eight weeks later. The volume was kept constant at 200 ml by addition of nutrient solution or distilled water directly into the soaking jar after irrigation.

Preconditioned Orobanche seeds were placed along with ten seeds of either flax, tobacco, tomato or sorghum on wet filter paper in wrapped petri plates at 20 C. The test plant seeds were removed before they had germinated and Orobanche germination noted after one week. This was done to test for any stimulus that test plant seeds themselves may have provided.

RESULTS

Experiment One

First seeding. Orobanche ramosa germinated first in flax and responded more slowly to tomato, tobacco and sorghum exudates (Table 4 and Figure 3). Flax exudates gave the most abundant germination, tobacco the next, then tomato and sorghum the least.

Ten days following the initial response, germination rates in root exudates of tomato, tobacco and flax leveled off. An increase in germination was seen ten days after the leveling off was noted for tobacco and tomato and 18 days later for flax (Table 4 and Figure 3). Germination rates in sorghum root exudates exhibited a slow increase throughout the duration of the experiment.

Second seeding. Orobanche ramosa seeds germinated within the same time interval for root exudates of sorghum, tomato and tobacco, but tobacco and sorghum exudates prompted a faster initial response than in the first seeding (Figure 1). Percent germination was generally higher in tomato than tobacco exudates and a leveling off occurred as with the first seeding. Sorghum exudates gave germination percentages similar to the first seeding (Table 4 and Figure 3).

Experiment Two

First seeding. Broomrape germination occurred simultaneously after eight days in all exudates. Flax, tomato and sorghum had sprouted six days and tobacco five days prior to this reading. Tomato,

Table 4. Percent germination of broomrape upon exposure to root exudates accumulated throughout the experiment from crop plants at different ages (Experiment 1).

Treatment Plant Spp.	Percent Germination											
	Nov 9	Nov 14	Nov 18	Nov 22	Nov 28		Dec 2		Dec 12		Dec 20	
	Old[a]	Old[a]	Old[a]	Old[a]	Old[a]	New[b]	Old[a]	New[b]	Old[a]	New[b]	Old[a]	New[b]
Tomato[c]	0	0.4	1.8	6.8	10.2	0.8	39.9	6.2	42.6	28.2	42.6[e]	28.2
Tobacco[c]	0.25	0.25	1.5	37.7[e]	31.2[e]	0	45.9	9.4	68.4	20.0	68.4	20.8
Flax[d]	--	--	--	0	20.1	--	39.2	--	39.2	--	70.8	--
Sorghum[c]	--	--	1.4	4.5	4.5	0	5.1[e]	1.4	8.9[e]	4.6	8.9	6.0

[a]Broomrape seeds placed in exudates two days after transplanting treatment plants into exudate collection containers.

[b]Broomrape seeds placed in exudates on November 28 to test for germination inhibition in old seeds due to prolonged contact with exudates.

[c]Transplanted into irrigation containers 6 days after planting.

[d]Transplanted into irrigation container 17 days after planting.

[e]Significantly different from other readings of same day at $\alpha = 0.5$ using Duncan's Multiple Range Test.

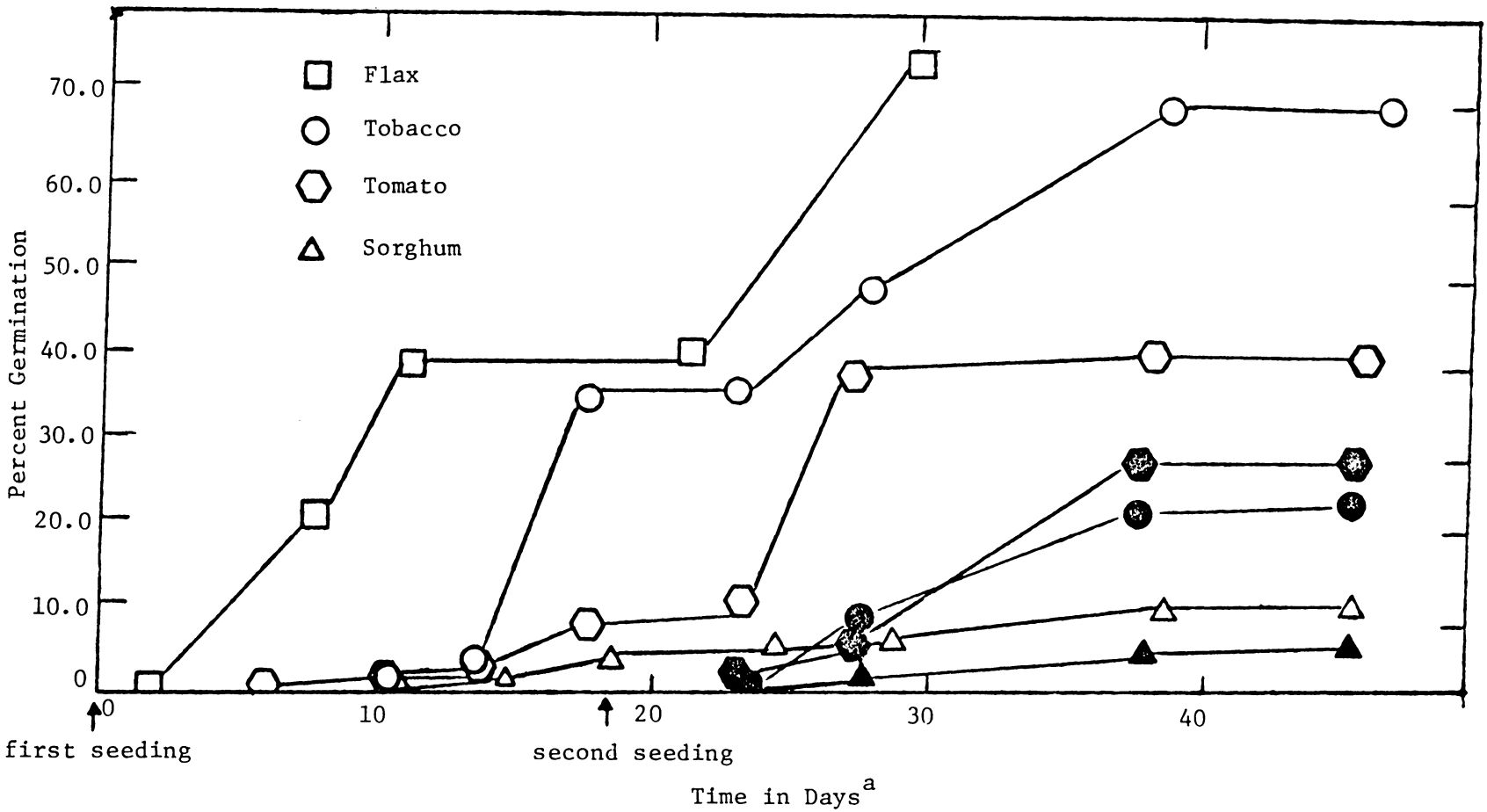


Figure 3. Broomrape germination rates upon exposure to root exudates accumulated throughout the experiment from crop plants at different ages.

[a]To obtain true plant age, add 10 days to tobacco, sorghum and tomato and 21 days to flax.

tobacco and sorghum exudates first produced germination percentages similar to initial exposure to older plants' exudates of the first test but stopped after two weeks. Seeds in flax exudates germinated most abundantly, although this response decreased to a low level in containers with two-week old plants. Increased germination was noted after one week (Table 5 and Figure 4).

Second seeding. Renewed germination was observed in exudates of one month old tomato plants but declined to zero after five days (Table 5 and Figure 4). No germination was seen in tobacco and sorghum exudates. In flax containers, seed response declined to the lowest point during the first ten days. A slight increase was observed with 36 day old flax which subsequently dropped to zero.

Preconditioned Orobanche seeds placed along with the test plant seeds in wrapped petri plates failed to germinate after one week. Analysis of variance and Duncan's multiple range tests (52) were done on the date of experiment one and two. The results are found in Tables 3 and 4. No germination was noted for controls in either experiment.

Table 5. Percent germination of broomrape upon exposure to root exudates decanted daily from crop plants at different ages (Experiment 2).

Treatment Plant Spp.[b]	Percent Germination[a,c]							
	Feb 16	Feb 21	Feb 24	March 3	March 11	March 18	March 23	March 28
Tomato	5.0	0	0	0	0	4.1	4.1	0
Tobacco	2.0	1.5	0	0	0	0	0	0
Flax	4.3	13.2	13.0	8.2	6.3	0.1	1.8	0
Sorghum	1.7	5.4	0	0	0	0	0.1	0

[a]All broomrape seeds placed in exudates on February 8.

[b]All plants planted in exudate collection containers on February 8.

[c]No readings for the same day were found to be significantly different at $\alpha = 0.05$ using Duncan's Multiple Range Test.

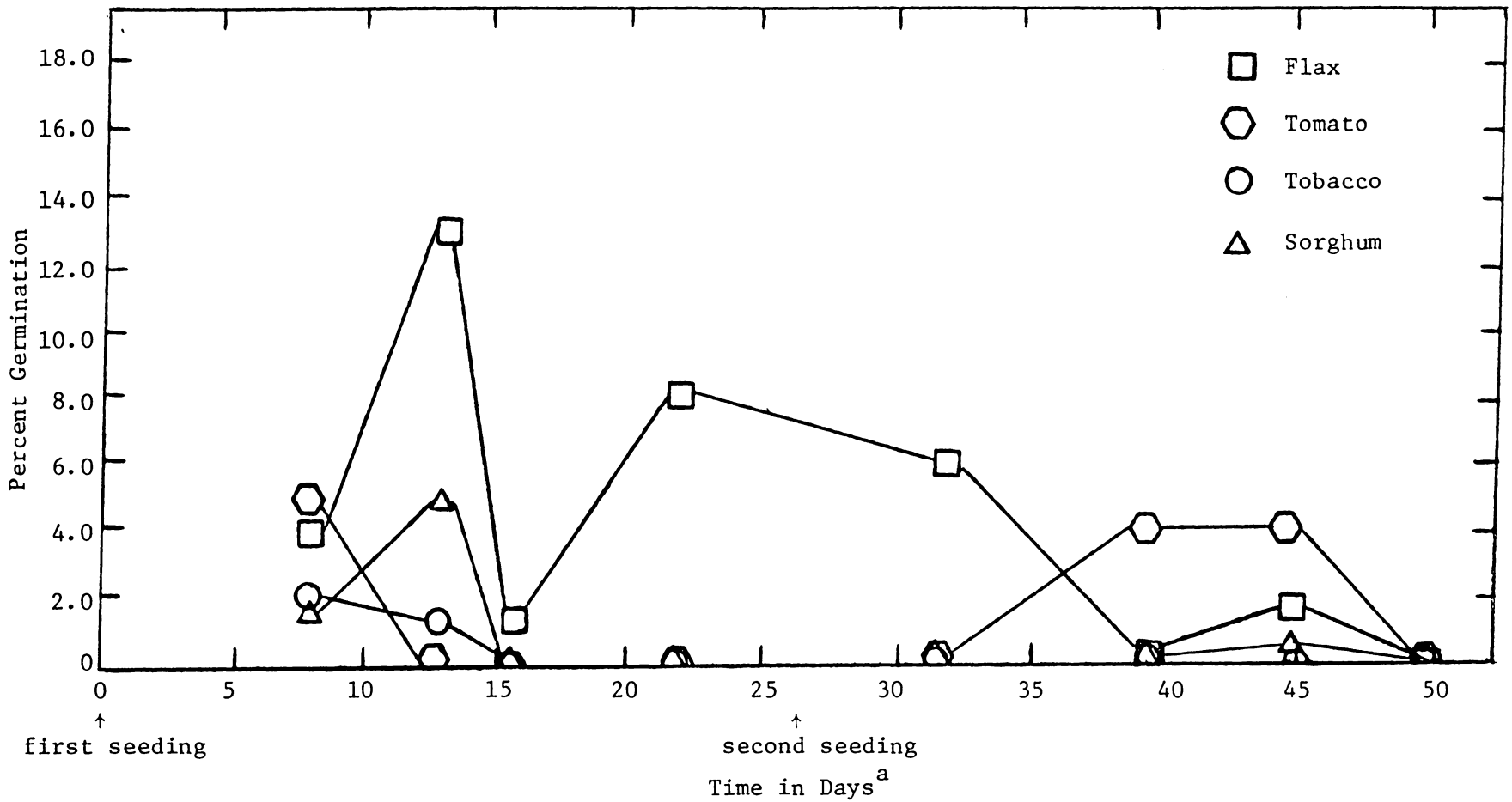


Figure 4. Broomrape germination rates upon exposure to root exudates decanted daily during the experiment from crop plants at different ages (Experiment 2).

[a]Equals actual plant age.

DISCUSSION

According to the data collected, flax root exudates generally give the greatest broomrape seed germination (Figures 3 and 4). These results support those obtained by Hameed, et al. (27) and Brown, et al. (14). Sorghum exudates produced the lowest germination throughout the duration of the two experiments (Figures 3 and 4). This low germination conflicts with the observations of Kasasian and Parker (34). The variation in results may be attributed to different races of O. ramosa, as has been recognized for O. cumana (50) and O. aegyptiaca (12), to changes in the experimental situation or to different varieties of sorghum. Tomato and tobacco exudates also seem to be effective germination stimulants. Work with O. minor using liquid chromatography indicates that several substances inducing germination are produced by one host root (14,15). This could also be true for O. ramosa, in which case the presence, absence or alteration in proportions of these compounds would account for the various germination percentages found.

Results from the second experiment indicated that sprouting and young test plants induced a significant amount of broomrape germination (Figure 4). Since O. ramosa seeds soaked with crop seeds in petri plates did not germinate, the stimulant is probably not leached from the seeds or exuded by germinating crop seedlings but rather is produced by sprouting and young plants. This could be due to initiation of photosynthesis and subsequent exudation of byproducts from the roots. The investigations of Sunderland (53) who found stimulant synthesis

depended on a sugar supply, tend to support this speculation. He also found that stimulant synthesis decreased with root cell maturity and that the stimulant was utilized during growth in length of these cells.

The decrease in O. ramosa germination noted in the second experiment and second seeding of the first experiment indicate that root exudate concentration is directly related to germination since less exudate accumulation occurred during these experiments (Figures 3 and 4). Similar results have been noted with O. minor (13). Thus the broomrape response seems to be caused by an actual stimulant rather than a concentration decrease of an inhibitor released by the roots.

The stimulant does not appear susceptible to breakdown by microorganisms or algae since no increase in germination percentages was noted in the second experiment.

The results obtained for the flax readings support each other well. The small reduction in germination seen in 23 to 33 day old flax suggests that detectable levels of stimulant were still being produced. This is reflected by an increase in germination rates in the first experiment where the exudates were accumulated. As germination continued to decrease in the second experiment until Orobanche response was almost zero, accumulation ceased in experiment one and germination leveled off. Production of more stimulant was noted by an increased response in the first experiment and paralleled by renewed germination in the second experiment (Figures 3 and 4). Fluctuations of germination seen in the second experiment with flax exudates compared to other test plants may be due to changes in the amounts of substances produced or to a greater sensitivity of broomrape seeds to flax exudates

(Figure 4). The latter explanation would also account for the higher germination percentages seen in the first experiment.

The tomato exudate data were not as consistent as the flax data. The rising broomrape response generally noted for from 15 to 38 day old plants in accumulated exudates was not seen in the changed exudates of experiment two until tomatoes were between 32 and 39 days old (Figure 3). One suspects that this is because the released stimulant was not accumulated in the second experiment and so a detectable concentration was not produced until plants were 32 to 39 days old. That exudation was significantly increased at this time can be seen by the heightened Orobanche response for 34 to 38 day old tomatoes (Figure 3). A leveling off was then noted in second experiment exudates which corresponds to continued accumulation and so a slight increase in germination of first experiment seeds. Also, in the first experiment, plants were transplanted into the containers which may have damaged roots and so changed exudation (25). A third explanation for the above discrepancy is that the metabolism of algae and microorganisms in the accumulated exudates (experiment one) either enhanced the activity of stimulants present or actually produced the stimulant. These last two hypotheses might account for the high levels of Orobanche response to tobacco exudates seen in experiment one compared to most of the second experiment (Figures 3 and 4).

Similar results were obtained for sorghum, i.e., germination noted in the first experiment but none seen for plants of similar age in experiment two (Figures 3 and 4). However, such low germination rates were found in accumulated exudates that stimulant concentrations may

have been too small to be detected in experiment two. Also, as mentioned above, microorganisms may have been responsible for some of the activity in the first experiment or mechanical damage during transplanting may have altered exudation.

The germination rates obtained for the second seeding of experiment one support those obtained for plants of the same age in the first seeding, except that tomato percentages were greater than tobacco. This was because the new Orobanche seeds were not exposed to exudates from younger tobacco plants which produced a significant increase in germination when plants were between 23 and 28 days old.

It should be remembered that the actual stimulant produced by the test plant was released prior to when germination was noted due to a lag period in which the broomrape seed initiated cell growth. This lag may be as long as three to five days (34). However, the plant age at which the response was observed is used here since the actual delay is now known.

The effectiveness of trap and catch crops depends on the production of germination stimulant when Orobanche seeds are ready to germinate. Assuming that the stimulant does not accumulate in the soil, the highest levels are produced when the crops tested here are young. Thus, late spring plantings when the soil is warm and moist, optimum conditions for Orobanche germination (34), would produce maximum germination. Even under this situation complete control will not be obtained, as can be seen by the low germination percentages obtained in experiment two. This was found to be true in field (18) and laboratory studies (46).

Several methods may prove helpful in enhancing germination of Orobanche in the field. Fall harvesting of crops would allow the exudates to accumulate in the soil during dry summer months. According to the data of this study, accumulation results in much higher germination percentages. Soil incorporation of crop residues has been found to provide increased control (34,36). The use of catch and trap crops in conjunction with herbicides and biological control would decrease the amount of heribicide necessary and increase overall eradication. In addition, a synthetic soil-incorporated germination stimulant, which acts in the same manner as a trap crop, has been developed (30) and could be used alone or with other control measures.

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