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Mycorrhizae, biocides, and biocontrol. 1. Herbicide–mycorrhiza interactions in soybean and cocklebur treated with bentazon [1]

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Abstract

Interactions between herbicides and vesicular–arbuscular mycorrhizal (VAM) fungi are little-known but may differentially affect the development of tolerant and susceptible plants. We conducted this greenhouse study to determine if VAM fungi modify the effects of the herbicide bentazon (3–isopropyl–1H–2,1,3–benzothidiazin–(4)3H–one 2,2–dioxide) on soybean (*Glycine max* (L.) Merr.) and common cocklebur (*Xanthium strumarium* L.). The experiment was designed as an eight-treatment, 2 × 2 × 2 factorial. Individual potted soybean or cocklebur plants were grown in a high (28 $mg\,kg^{-1}$) P-content soil. The plants were colonized by VAM fungi (a mixture of *Glomus etunicatum* Becker and Gerdemann, *Glomus leptotichum* Schenck and Smith, and *Glomus mosseae* (Nicol. and Gerd.) Gerd. and Trappe) and sprayed with bentazon. Alternatively, they were exposed only to VAM fungi or to the herbicide, or to neither of these factors. The effects of VAM fungi on plant dry mass were small, but larger in cocklebur than in soybean, especially for the herbicide-treated plants. Root/shoot ratios in cocklebur were larger and shoot dry matter content smaller than those in soybean. The VAM effect in the herbicide-treated plants was greater than in the nontreated ones for both parameters. Colonized root length in cocklebur was drastically reduced by the herbicide (43%), as were leaf dry weight and N, P, and K concentrations. Changes were small, and generally not significant in soybean. Gradual necrosis of treated cocklebur shoots was related to an accelerated loss of shoot dry matter, especially in VAM plants. The data suggest that changes in source–sink relations following herbicide treatment favor enhanced export of shoot dry matter to the roots in susceptible relative to tolerant plants. This biomass may be preferentially available for export from susceptible-plant roots to the soil system through the VAM mycelium.

Keywords: Glomus spp.; *Glycine max*; Weed control; *Xanthium* strumarium

1. Introduction

Farmers rank weeds as one of the top challenges to higher yields (Cramer and Brusko, 1991), and have relied mainly on herbicides to counter this challenge over the last four decades (Wyse, 1994).

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[1] Mention of cultivar or brand name does not imply endorsement by USDA–ARS.

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However, increasing societal concern, (e.g. Nazario, 1991; McMurray, 1993) over the effects of herbicides on human health and the environment has led to more regulation and suggestions for alternative control tactics (Buhler et al., 1992; Shirley, 1993; Wyse, 1994). Biological weed control is one of the alternatives (Strobel, 1991), but vesicular–arbuscular mycorrhizal (VAM) fungi have not been previously considered as biocontrol agents. We are now beginning to realize, however, that responses by one plant to selective stresses (e.g. cultivation, Johnson and Pfleger, 1992; biocides, Ocampo, 1993; nutrition, Marschner and Dell, 1994), are communicated to other plants, and that VAM fungi are involved in this process because their mycelia form a living bridge between root systems (Goodwin, 1992; Martins, 1993).

Direct effects of herbicides on root colonization and sporulation by VAM fungi have been evaluated (Johnson and Pfleger, 1992; Ocampo, 1993; Trappe et al., 1984) and were variable and often species- and dosage-dependent (Dehn et al., 1990). However, many herbicides are not directly fungi-toxic but affect these obligately biotrophic organisms indirectly by altering host-plant functions (Garcia-Romera et al., 1988; Dehn, 1990; Sieverding, 1991). The resulting inhibition of the endophyte may have further effects on host-plant physiology, but these effects on the individual host are little-known, and even less well-known for plant associations.

Inhibitors of photosynthesis applied as foliar sprays are convenient herbicides for the investigation of indirect, plant-mediated effects on VAM fungi (Ocampo and Barea, 1982). We chose bentazon, because it is translocated acropetally and because its dose-rate effects on host-plants and symbionts are well-known (Potter, 1977; Bethlenfalvay et al., 1979). It is rapidly metabolized in tolerant plants but controls susceptible plants by inhibiting electron transport in Light Reaction II of photosynthesis (Zimdahl, 1993). Soybean and cocklebur were used because they are highly mycorrhiza-dependent, and have similar growth rates with leaves oriented to fully intercept sprays.

The purpose of this research was to determine the independent and interactive effects of bentazon and VAM fungi on individual weed and crop plants. These individual-plant data would form the basis for future evaluation of similar interactions in associated crop and weed plants.

2. Materials and methods

2.1. Experimental design and statistics

The study used a completely randomized design with a 2 × 2 × 2 factorial arrangement of treatments and five replications. Factors were herbicide application, VAM colonization, and plant type. Single potted plants were the experimental units. Two levels of each factor were used: (1) spraying (+BEN) or not spraying (−BEN) with herbicide, (2) presence (+VAM) or absence (−VAM) of VAM root colonization, and (3) soybean or cocklebur as host. Data were subjected to analysis of variance and individual treatment differences were separated using the Student's *t*-test. Instead of an arbitrary indication of significance ($p >$ or < 0.05), actual probability values (p) are shown to permit individual interpretation by the reader (Nelson, 1989). We may interpret differences as significant up to $p = 0.1$.

2.2. Biological materials and soil

Soybean (*Glycine max* (L.) Merr., cv. Hobbit) and common cocklebur (*Xanthium strumarium* L.) seeds were pre-germinated, selected for uniformity prior to planting, planted in 1.5 L plastic pots, and thinned from three to one seedling per pot after one week of growth. Pots contained a steam-sterilized (70°C, 1 h) mixture of a silty–clay–loam soil and sand (1:1, v:v). The soil (pH 6.4) was collected from the Oregon State University Botany Farm (Willamette River flood plains near Corvallis) and contained ($mg\,kg^{-1}$): NH_4–N, 13.9; NO_3–N, 0.4; K, 363; P (total), 1000; P ($NaHCO_3$–extractable), 28; S, 4.6; Cu, 3.2; Fe, 62; Mn, 16.8; Zn, 9.4. Extractable bases were ($cmol\,kg^{-1}$): Ca, 11.7; Mg, 4.8; Na, 0.2. This high-P soil was used to minimize host responses to P uptake by VAM fungi, permitting focus on non-nutritional effects.

A mixture (40 mL of each) of soil inocula containing spores, hyphae and colonized root fragments of the VAM fungi *Glomus etunicatum*, *Glomus leptotichum*, and *Glomus mosseae* (isolates UT316A–2, FL184–1, and CA110, respectively, catalogued by the International Collection of Arbuscular and Vesicular–arbuscular Mycorrhizal Fungi) was mixed into the soils. Washings (100 mL, 45 μm sieve) of the inocula free of VAM propagules were also applied.

2.3. Growth conditions

Plants were grown in a greenhouse at Corvallis, Oregon, February to March, 1994 at 18–28°C. Sunlight was supplemented by 1000 W phosphor-coated metal halide lamps (General Electric) that extended daylight to 16 h and provided 400 $\mu mol\, m^{-2}\, s^{-1}$ of photosynthetically active radiation at soil surface. Pots were watered from below (300 mL tapwater in saucers) once a week for the first 3 weeks and twice a week thereafter, and fertilized at 14 and 28 days after planting with 3 g per pot of ''Grow More'' fertilizer concentrate (20–0–15, National Research and Chemical Company, Gardenia, CA), containing 20% NO_3–N, 15% K_2O, 6% Ca, and 1% S.

2.4. Herbicide application

Plants (+BEN) were sprayed with Bentazon (Basagran, BASF Corp., Research Triangle Park, NC) at the field-recommended (FR) rate of 1.12 kg AI ha^{-1} (2 pints $acre^{-1}$ of the liquid formulation containing 42% of active ingredient (AI)) 25 days after planting. Both soybean and cocklebur plants were at the recommended growth stage (7–8 leaves) for application at this rate. Bentazon was applied using two 8002 flat-fan nozzles (43 cm apart and 60 cm above the shoot tips) under 31 $\times$ 10^4 Pa (45 $lb\, in^{-2}$) of tank pressure. The spray also contained 2.3 $mL\, L^{-1}$ (FR of 1 pint per acre) of a surfactant oil (BAS 06400S, Crop Oil Concentrate, BASF Corp.). The −BEN control plants were sprayed with a suspension of the surfactant only.

2.5. Weed and crop responses

The plants were harvested 2 weeks after spraying (39 days after planting). Shoots were excised and weighed immediately. Dry weights were determined after drying for 3 days at 70°C. Leaf nutrient contents and concentrations (N, P, K) were determined by A and L Western Agricultural Laboratories, Modesto, CA, according to ''Official Methods of Analysis'' (AOAC, 1980).

Percent root colonization by VAM fungi was determined one day prior to herbicide application from root samples taken in soil cores (5 cm from the taproot, 2 cm diameter, spanning the entire depth of the pot). Fresh root samples were thoroughly washed, blotted dry, weighed, cleared in 5% KOH (w:v, 30 min, 90°C), washed in water, acidified (0.01 N HCL, 1 h), stained with trypan blue (0.05%) in lactic acid/glycerol (3:1, v:v, 15 min, 90°C), and assayed for percent VAM colonization and root length by the grid-line intersect method (Ambler and Young, 1977). At harvest, samples ($\approx$ 1 g) were taken from the entire root system at random, weighed, and assayed for percent VAM colonization and root length as above. Total root length and VAM-colonized root length could then be calculated from the sample and total root fresh weights. Effects on the response variables due to VAM fungi were calculated as percent changes [(VAM − nonVAM)/(nonVAM) $\times$ 100] and were shown in the tables as $\%\Delta$. Likewise, effects due to herbicide application [(BEN − nonBEN)/(nonBEN) $\times$ 100] were also presented in the tables as percent changes.

3. Results

3.1. Plant growth and root / shoot development

Application of bentazon significantly inhibited dry weight production by both cocklebur and soybean plants (Fig. 1, Table 1). The VAM growth effect in −BEN plants was small (due to high soil P content) but significant, especially in cocklebur (Fig. 1A). Dry weights of +VAM plants were greater in +BEN than in the −BEN treatments (cocklebur: +BEN, 22%, $p = 0.102$; −BEN 15%, $p = 0.033$; soybean: +BEN, 14%, $p = 0.059$; −BEN, 4%, $p = 0.099$), indicating that all VAM plants were generally more tolerant of the herbicide than nonVAM plants.

The herbicide reduced root and shoot fresh weights markedly in cocklebur, while in soybean only the −VAM plants were significantly affected (Table 2). VAM effects were significant only on cocklebur shoots. The roots of +VAM plants not treated with the herbicide were shorter (cocklebur, −24%; soy-

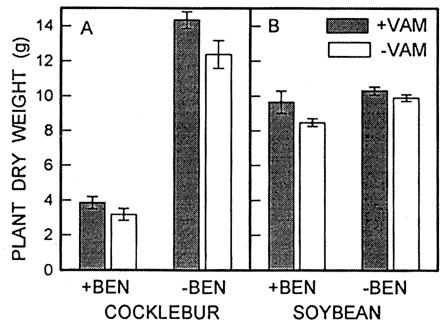

Fig. 1. Dry weights of cocklebur and soybean plants not colonized (+VAM) or not colonized (−VAM) by vesicular–arbuscular mycorrhizal (VAM) fungi 2 weeks after herbicide application. The foliage was sprayed (+BEN) or not sprayed (−BEN) with the herbicide bentazon. Bars represent the means and SE of five replications.

bean (−11%) than those of −VAM plants. In +BEN plants, VAM fungi inhibited root growth only in soybean. The almost identical lengths of herbicide-treated +VAM and −VAM cocklebur roots (Table 2) indicated that treatment reduced root growth more in −VAM than in +VAM plants. Interactions between VAM and BEN effects were not significant ($p > 0.3$) for root or shoot fresh weights of either plant, indicating that the factors were independent of one another.

Table 1
Two-way analysis of variance of endophyte (VAM) and herbicide (BEN) effects on soybean and cocklebur plants 2 weeks after herbicide application

Plant parameter	Cocklebur			Soybean		
	VAM	BEN	V × B	VAM	BEN	V × B
	p					
Plant dry weight	0.022	< 0.001	0.234	0.046	0.012	0.305
Shoot dry/ fresh weight	0.063	0.084	0.304	0.068	0.040	0.621
Root/shoot ratio	0.081	0.302	0.761	0.044	0.765	0.685
Root length	0.019	< 0.001	0.032	0.021	0.073	0.874
Leaf						
Dry weight	0.003	< 0.001	0.087	0.068	0.002	0.304
N content	0.054	< 0.001	0.526	0.050	0.215	0.476
P content	0.001	0.003	0.153	0.022	0.264	0.291
K content	0.016	< 0.001	0.818	0.110	0.169	0.075
N concentration	0.129	< 0.001	0.718	0.227	0.308	0.817
P concentration	0.004	< 0.001	0.001	0.042	0.622	0.330
K concentration	0.054	< 0.001	0.074	0.700	0.022	0.088

The root/shoot (R/S) ratios of the two plants show that the relative development of roots and shoots was significantly different in +VAM and −VAM plants, but was not affected by the herbicide (Table 1, Fig. 2). Similar leaf dry weights in both plants (Table 3) gave the appearance of equal plant development. Yet, cocklebur had more roots than

Table 2
Soybean and cocklebur shoot and root fresh mass and root lengths 2 weeks after herbicide application [a]

Parameter		Cocklebur				Soybean			
		− VAM	+VAM	%Δ	*p*	− VAM	+VAM	%Δ	*p*
Root length (m)	−BEN	**181**	**137**	−24	0.030	**133**	**118**	−11	0.028
	+BEN	**70**	**69**	− 1	0.705	**122**	**105**	−14	0.072
	%Δ	−57	−50			− 8	−11		
	p	< 0.001	< 0.001			0.107	0.105		
Root fresh wt (g)	−BEN	**57**	**56**	− 2	0.994	**32**	**29**	− 9	0.957
	+BEN	**17**	**18**	6	0.559	**27**	**29**	7	0.418
	%Δ	−70	−68			−16	− 1		
	p	< 0.001	< 0.001			0.025	0.384		
Shoot fresh wt (g)	−BEN	**51**	**63**	24	0.090	**35**	**37**	6	0.266
	+BEN	**14**	**19**	36	0.061	**31**	**37**	19	0.111
	%Δ	−73	−70			−11	0		
	p	< 0.001	< 0.001			0.017	0.995		

[a] Roots were colonized (+VAM) or not colonized (−VAM) by vesicular–arbuscular mycorrhizal (VAM) fungi. The foliage was either sprayed (+BEN) or not sprayed (−BEN) with the herbicide bentazon. Percent changes (%Δ) were calculated for −VAM vs. +VAM comparisons (horizontally) and −BEN vs. +BEN comparisons (vertically). Probability values (p) were calculated by t-test.

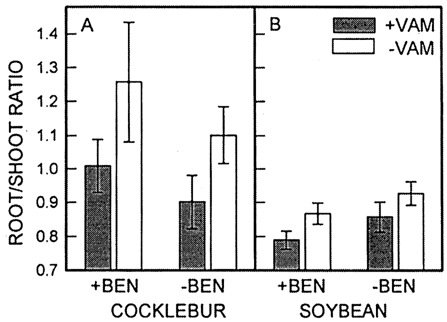

Fig. 2. Root/shoot fresh weight ratios of cocklebur and soybean plants. Treatments and statistics are as in Fig. 1.

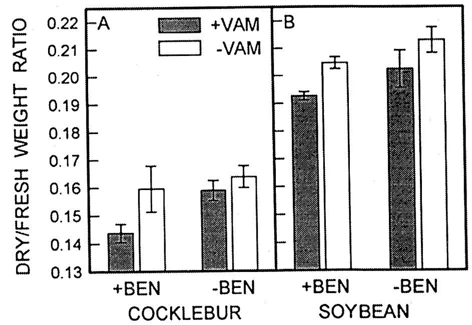

Fig. 3. Shoot dry/fresh weight ratios of cocklebur and soybean plants. Treatments and statistics are as in Fig. 1.

soybean of the same age (Fig. 2, Table 2). The R/S ratios of +VAM plants were lower than those of −VAM plants in all treatments (Fig. 2), but bentazon application tended to increase the ratios in cocklebur, and decrease them in soybean, regardless of VAM status. This trend was significant ($p = 0.093$) as indicated by the BEN × Plant interaction (ANOVA, VAM × BEN × Plant). This phenomenon may have biological meaning as an indicator of biomass-reallocation (here to roots in cocklebur and to shoots in soybean) under carbon stress (bentazon effect). If so, it will depend on differences in intra-plant sink strength and on plant tolerance of the herbicide.

3.2. Shoot dry matter content

Root colonization by VAM fungi lowered the shoot dry/fresh weight ratio (Fig. 3, Table 1). Such differences in shoot dry matter contents in −VAM vs. +VAM plants have been reported earlier (e.g. 13% in *Allium*, Snellgrove et al., 1982) and were related to high leaf P concentrations and to an enhanced export of C from the shoot to the mycorrhiza

Table 3
Cocklebur and soybean leaf dry weights and nutrient concentrations 2 weeks after herbicide application. (Treatments and statistics are as in Table 2)

Leaf parameter		Cocklebur				Soybean			
		−VAM	+VAM	%Δ	*p*	−VAM	+VAM	%Δ	*p*
Dry mass (g)	−BEN	**4.6**	**5.9**	28	0.005	**4.8**	**4.9**	2	0.245
	+BEN	**1.6**	**2.0**	25	0.095	**3.9**	**4.5**	15	0.045
	%Δ	−65	−66			−19	−8		
	p	< 0.001	< 0.001			0.001	0.095		
Nutrient concentration (mg g^{-1})									
N	−BEN	**38.4**	**36.1**	−6	0.149	**35.7**	**37.7**	6	0.288
	+BEN	**53.5**	**52.0**	−3	0.112	**37.3**	**40.2**	8	0.080
	%Δ	39	44			4	7		
	p	< 0.001	< 0.001			0.256	0.223		
P	−BEN	**3.1**	**2.1**	−32	0.090	**2.6**	**2.8**	8	0.272
	+BEN	**4.9**	**7.2**	47	0.003	**2.5**	**3.1**	24	0.001
	%Δ	58	243			−4	11		
	p	0.007	< 0.001			0.273	0.217		
K	−BEN	**29.6**	**30.0**	1	0.417	**20.9**	**19.9**	−5	0.200
	+BEN	**38.1**	**49.4**	30	0.031	**21.2**	**22.6**	7	0.004
	%Δ	29	65			1	14		
	p	0.067	< 0.001			0.304	0.107		

(fungus-root). Since C fluxes and C availability within a plant affect below-ground relationships between plants (Newman et al., 1992), herbicide and VAM effects on shoot dry matter content (fresh/dry weight ratio) may be of consequence not only to the individual plant, but to its neighbors as well. Our data (Fig. 3) showed the percent change in dry matter content (+VAM vs. −VAM) to be significant only in herbicide-treated plants (cocklebur: +BEN, 11%, $p + 0.001$; −BEN, 3%, $p = 0.235$; soybean: +BEN, 6%, $p = 0.056$; −BEN, 3%, $p = 0.195$). The herbicide altered shoot dry matter content only in +VAM plants (percent change, −BEN vs. +BEN) in cocklebur: +VAM, 10%, $p = 0.071$; −VAM, 3%, $p = 0.144$; and in soybean: +VAM, 7%, $p = 0.007$; −VAM, 4%, $p = 0.335$. The within-plant VAM × BEN interaction for dry matter content was not significant ($p > 0.3$) for either plant, showing that the factors acted on this response variable independently of one another (as they did on most other variables).

3.3. Leaf nutrients

Herbicide main effects on cocklebur leaf dry weights and nutrient concentrations (N, P, and K) were highly significant (Table 3). In soybean, herbicide effects were small, but VAM effects were significant in the +BEN plants only. High P concentrations (Table 3) and low dry matter contents (Fig. 3) were related in the leaves of +VAM plants, while the reverse of this relationship was true in the −VAM plants of the +BEN treatment. Such a relationship between +VAM and −VAM plants had been noted by others (Stribley et al., 1980; Snellgrove et al., 1982), who interpreted it as an increased demand for C by VAM roots. It is noteworthy that this effect was significant under our conditions only in the C-stressed +BEN plants.

3.4. Herbicide effects on the mycorrhiza

The effect of the herbicide on endophyte and mycorrhiza development is shown by the differences in colonized root length in the bentazon-tolerant soybean and the susceptible cocklebur plants (Table 4). In soybean, the small decline (−BEN vs. +BEN) in colonized root length (−11%) compares well with a similar decline in shoot dry wt. (−10%), suggesting reduced carbon export to root and endophyte: a plant-mediated herbicide effect. The disproportionately larger decline in cocklebur shoot dry mass (−72%) relative to the decline in colonized root length (−43%) is ascribed to the inhibition of photosynthesis by the herbicide and the resulting loss of mycorrhiza-mediated nutrient-uptake in this herbicide-intolerant plant.

The percentages of root colonization at harvest (Table 4) were remarkably uniform, not only within, but even among soybean and cocklebur treatments. Thus, the ratio of colonized root length to total root length (percent colonization) was a less accurate indicator of host-endophyte response (−BEN vs. +BEN: $p = 0.401$) than the direct comparison of colonized root lengths (−BEN vs. +BEN: $p = 0.009$): in the former the difference was not signifi-

Table 4
Root colonization by vesicular–arbuscular mycorrhizal (VAM) fungi [a]

VAM root data		Cocklebur −BEN	+BEN	%Δ	p	Soybean −BEN	+BEN	%Δ	p
Length (m) at harvest		**52.3**	**29.6**	−43	0.009	**52.9**	**47.2**	−11	0.120
Colonization (%)									
Before spraying		**40.6**	**44.8**	10	0.658	**34.8**	**34.0**	−2	0.925
At harvest		**38.0**	**44.9**	18	0.401	**44.8**	**45.4**	1	0.910
	%Δ	−6	1			28.7	33.5		
	p	0.993	0.831			0.042	0.097		

[a] Plants were sprayed (+BEN) or not sprayed (−BEN) with the herbicide bentazon. Percent changes (%Δ) were calculated for −BEN vs. +BEN comparisons (horizontally) and for comparisons of percent VAM colonization before spraying and 2 weeks later, at harvest (vertically). Probability values (p) were calculated by t-test.

cant, while in the latter there was an almost two-fold difference for cocklebur. An indication that negative VAM responses to the herbicide were mediated by the host plant is given by the colonization percentages before spraying with bentazon and at harvest (Table 4). Fungal growth in +BEN plants ceased with root growth by cocklebur (%Δ, NS), while in −BEN plants root growth was matched by fungal growth (%Δ, NS). Fungal growth in soybean was apparently faster than root growth in both +BEN and −BEN plants (%Δ, $p < 0.098$).

4. Discussion

Our study of herbicide-effect modification by VAM fungi used a highly reductionist approach: individual crop and weed plants grown in sterilized soil. This eliminated competition between associated plants (Newman et al., 1992), minimized soil-microbial effects other than those of VAM fungi (Linderman, 1992), and permitted us to focus on crop or weed responses to herbicides as modified by VAM fungi. These responses were: (1) biomass production, (2) resource allocation to root or shoot as measured by root vs. shoot development, (3) changes in source–sink relationships between root and shoot as indicated by shoot dry matter content, and (4) mycorrhiza development.

The results showed that: (1) Under our soil conditions (high P content) the effect of VAM fungi on plant biomass was small but greater in cocklebur than in soybean (suggesting that cocklebur was more VAM-dependent than soybean), (2) there was a small, but measurable enhancement of recovery (shoot weight) from herbicide effects due to VAM fungi (confirming Ocampo and Barea, 1985), (3) similar shoot development in soybean and cocklebur plants was accompanied by greater root growth (and therefore greater total biomass and larger R/S ratios) in cocklebur, (4) lower shoot dry matter contents in herbicide-treated +VAM than in −VAM cocklebur plants, and (5) a greater decline in colonized and total root length in cocklebur than in soybean due to herbicide application.

Deductions (and projections to associated plants to be discussed in subsequent reports) from these findings are as follows. Greater soil penetration by its larger root system may provide cocklebur with some of its competitive ability. This larger root mass also represents greater sink strength and demand (Zeevaart, 1979) for resources from within the plant (shoot), and also (potentially) from associated plants via their common VAM mycelia (Goodwin, 1992; Newman et al., 1992). Inhibition of photosynthesis and shoot growth by bentazon changed source–sink relations (Hendrix, 1979) within the cocklebur plant (but much less so in tolerant soybean), resulting in an export of dry matter from the increasingly necrotic, nonfunctional shoot (weak sink) to the still functional root. In intra-plant competition, the +VAM root was a stronger sink (George et al., 1994) for shoot dry matter than the −VAM root in both herbicide-treated cocklebur and soybean. This permits us to draw inferences to inter-plant competition. Herbicide-caused shoot necrosis affects susceptible-plant roots eventually, changing the latter from strong sinks to sources of nutrients (exudation and hyphal transport, Newman and Eason, 1989). The VAM fungi that colonize these roots are the immediate sinks and through them the roots of associated plants (crops) that also share these fungi. Although root growth in cocklebur apparently ceased after herbicide treatment, percent root colonization did not decline, providing for hyphal contact with the soil and potentially with the roots of associated plants.

Based on the effects of bentazon on individual cocklebur and soybean plants, we infer a predisposition of the greatly weakened weed plant not only to become a less active competitor, but also to become a contributor, or source, of its accumulated biomass. The receiver organisms in closest contact, the weed's VAM endophytes, are likely to be the most immediate beneficiaries. Since these VAM fungi are at the same time endophytes of other neighboring plants under normal circumstances (field conditions), crop- and weed-plant responses to VAM-herbicide treatments described above may be interdependent.

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