Effect of Dinitroaniline Herbicides on Plant Resistance to Soilborne Pathogens

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ABSTRACT

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Seeds were sown in noninfested soil with or without herbicide at 1 μg/g soil. After emergence, seedlings were either transplanted to *Rhizoctonia solani*-infested soil or inoculated with *Fusarium* or *Verticillium dahliae*. Generally, resistance to the diseases in herbicide-treated plants was increased. Trifluralin, nitralin, butralin, and dinitramine significantly increased resistance of eggplant, tomato, and pepper to *R. solani;* disease incidence was decreased by 30-90%. This increased resistance was dependent on inoculum and herbicide concentrations. Benefin and isopropalin did not affect plant resistance. Resistance of beans was not affected by trifluralin, nitralin, or butralin, but was significantly decreased by dinitramine in one case. Trifluralin increased resistance of cotton to *R. solani* in certain cases and decreased it in others. The herbicides did not affect resistance of corn and oats to *R. solani.* Resistance of eggplant and tomato to Fusarium and Verticillium diseases was greatly increased by trifluralin and nitralin, resulting in as much as a 97% reduction in disease. Increased resistance occurred in spite of phytotoxic effects of herbicides. Trifluralin was detected in the hypocotyls of treated eggplants and cotton at concentrations of 0.84 and 0.15 μg/g respectively. Growth of the pathogens in vitro was inhibited at concentrations much higher than those used in soil or found in tissues.

Additional key words: herbicide-pathogen interaction, solanaceous plants, *Fusarium oxysporum* f. sp. *lycopersici*, *Fusarium oxysporum* f. sp. *melongenae*.

The substituted dinitroanilines are a group of selective herbicides widely used in many vegetable and agronomic crops to control a wide spectrum of weeds. As with other pesticides, these herbicides exert inhibitory and stimulatory effects on nontarget pathogenic and nonpathogenic organisms. Of this group, trifluralin has been most extensively studied regarding these effects. In culture, growth of certain plant pathogenic fungi (e.g., *Sclerotium rolfsii, Fusarium* spp., *Rhizoctonia solani,* and *Aphanomyces euteiches*) was reduced by trifluralin (5, 8, 10, 13, 15). In a comparative study, *R. solani* was more sensitive to four dinitroanilines than was *F. oxysporum* f. sp. *lycopersici* (8). Some reports describe the stimulatory effects of low concentrations of trifluralin on the growth, reproduction, or germination of fungi either in culture or in sterile soils (8, 10, 15, 21), and its effect on disease incidence caused by *R. solani* in various crops (11). This effect is apparently due to the positive and negative effects the herbicide has on growth and virulence of the pathogen, on plant resistance, and on activity of the surrounding microorganisms (11). In this respect, trifluralin increased disease caused by *R. solani* in cotton (2, 7, 13, 14, 19) and bean (16), but not in all cases in cotton (2, 19). On the other hand, recent field and greenhouse studies showed significant disease control of *A. euteiches* by trifluralin in peas (10), and of *Plasmodiophora brassicae* in cabbage and to a lesser extent, by other dinitroaniline herbicides (6).

This study deals with the effects of dinitroaniline herbicides on the resistance of various plants to damping-off and wilt diseases when herbicide application and plant inoculation were made separately. In certain cases, the combined effects of the herbicide on all living components involved in disease also were studied. A brief report of a part of these results already has been published (9).

MATERIALS AND METHODS

Noninfested, loamy sand soil (12) was used in all experiments unless otherwise stated. The following herbicides were used as emulsifiable concentrates: *N*-butyl-*N*-ethyl-α,α,α,-trifluoro-2,6-dinitro-*p*-toluidine (benefin); 4-(1,1-dimethylethyl)-*N*-(1-methylpropyl)-2,6-dinitrobenzenamine (butralin); N^4, N^4-diethyl-α,α,α-trifluoro-3,5-dinitrotoluene-2,4-diamine (dinitramine); 2,6-dinitro-*N,N*-dipropylcumidine (isopropalin); 4-(methylsulfonyl)-2,6-dinitro-*N,N*-dipropylaniline (nitralin); and α,α,α-trifluoro-2,6-dinitro - *N,N*-dipropyl-*p*-toluidine (trifluraline). Water emulsions of the herbicides were mixed with the soil to give the desired final concentration in μg active ingredient per gram of soil. The following plants were used: eggplant (*Solanum melongena* L. 'Black Beauty'), pepper (*Capsicum annuum* L. 'Vindale'), tomato (*Lycopersicon esculentum* Mill. 'Rehovot 13'), snapbeans (*Phaseolus vulgaris* L. 'Spotted Bulgarian'), cotton (*Gossypium hirsutum* L. 'Acala Sj-l'), corn (*Zea* *mays* L. 'Newe Ya'ar 170') and oat (*Avena sativa* L. 'Mulga').

Effect of herbicides on host resistance.—Seeds were sown in the noninfested soil with or without herbicides. After emergence, the pretreated seedlings were removed, thoroughly washed, and transplanted to herbicide-free soil, concomitantly with pathogen inoculation. This was done either by infesting soil with washed mycelia of *Rhizoctonia solani* Kuehn at various concentrations (12) or by inoculating tomato with various concentrations of washed conidia of *Fusarium oxysporum* f. sp. *lycopersici* (Sacc.) Snyd. & Hans., race 2, or by inoculating eggplant with *Fusarium oxysporum* f. sp. *melongenae* Matuo & Ishigami, as described (1). Plants were then grown under greenhouse conditions at 24-30 C, unless otherwise stated, and examined daily (12). Disease incidence was expressed either as a percentage of diseased seedlings or as a disease index (18). Inoculation of tomato and eggplant seedlings with *Verticillium dahliae* Kleb. was carried out in a manner similar to that of *Fusarium*, except that the conidia were produced on Czapek-Dox agar and inoculated seedlings were maintained at a constant temperature of 24 C. In certain cases, soil naturally infested with *R. solani* also was used. Greenhouse experiments were carried out in six replicates of 20 seedlings each, and were repeated at least once with similar results, unless otherwise stated. Isolations made from randomly selected diseased seedlings yielded the

TABLE 1. Effect of dinitroaniline herbicides on plant resistance to damping-off disease caused by *Rhizoctonia solani*

Herbicide	Eggplant[a]		Pepper[a]	Tomato[a]		Bean[a]	
	Inoculum concn, mg mycelium/kg soil						
	50	200	100	100	200	60	NI[b]
Trifluralin	11.3[c]	79.2[c]	84.3[c]	31.8[c]	44.3[c]	102.4	81.3
Nitralin	50.0[c]	89.5	27.3[c]	9.1[c]	52.4[c]	61.6	127.0
Butralin	13.2[c]	72.7[c]	65.3[c]	36.4[c]	49.2[c]	...	101.2
Dinitramine	...	49.0[c]	...	...	49.0[c]	157.6	169.2[c]
Benefin	137.5	85.5	68.7	...	...	...	...
Isopropalin	150.0	89.5	103.0	...	...	...	...

[a]Seeds were sown in noninfested herbicide-free soil, or in soil treated with herbicide at a concentration of 1 μg/g. The pretreated seedlings were transplanted to soil inoculated with various concentrations of *R. solani*. Results are expressed as relative disease incidence in the herbicide-treated diseased plants, where disease percentage in the herbicide-free control = 100.
[b]Field soil naturally infested with *R. solani*.
[c]Significantly different ($P = 0.05$) from their respective herbicide-free controls.

TABLE 2. Effect of nitralin concentration on resistance of eggplant seedlings to *Rhizoctonia solani*

Inoculum concentration (mg/kg)	Days after inoculation	Percentage of diseased plants at various nitralin concentrations (μg/g)			
		0	0.2	1	5
50	1	11.6	5.0	0.8[a]	1.6[a]
100	1	82.5	51.6[a]	35.0[a]	42.5[a]
200	1	89.1	90.8	83.3	45.0[a]
50	17	15.8	16.6	0.8[a]	6.6[a]
100	17	94.1	92.5	56.6[a]	73.3[a]
200	17	90.0	97.5	86.6	52.5[a]

[a]Significantly different from the herbicide-free control, at the same inoculum concentration ($P = 0.05$).

TABLE 3. Effect of dinitroaniline herbicides on disease incidence in beans sown in a loamy sand soil naturally infested with *Rhizoctonia solani*[a]

Herbicide	Dosage[b] (kg/ha)	Diseased plants[c] (%)	Disease index[c,d] (D)	(D),[c] per cent of control
Control	0	47	1.01	100
Trifluralin	1.0	42	0.94	93
Trifluralin	1.5	47	0.91	90
Nitralin	1.0	45	0.78	77
Nitralin	1.5	51	0.76	75

[a]Field experiment carried out in four replicates of 15 m rows each.
[b]Herbicides were sprayed on the soil surface and then incorporated to a depth of 5 cm.
[c]Differences between treatments are not significant ($P = 0.05$).
[d]Diseased seedlings were rated on a 0-5 scale where 0 = no disease and 5 = seedlings completely girdled.

same pathogen used for inoculation. Noninoculated control seedlings showed no disease symptoms.

Effect on plant growth.—Pretreated seedlings were dried at 80 C to a constant weight, and by comparisons with the herbicide-free control, percent weight reduction was calculated.

Gas chromatography determinations.—Trifluralin concentration in the plants was determined by using a modified Smith's procedure (17). Extraction was made with a mixture of benzene and 2-propanol (2:1, v/v), and prepared for injection as described (17). A Packard 7400 gas chromatograph equipped with a tritium foil electron-capture detector operated at 25 VDC was used. The glass column (180 × 0.4 mm) was packed with 5% QF, on an 177- to 149-μm particle size (80-100-mesh) acid-washed Chromosorb W (Johns-Manville, USA). Operating temperatures were: injector port, 210 C; oven, 190 C; detector, 200 C. Results are expressed as μg trifluralin/g tissue (fresh weight).

Effect of growth of fungi.—Petri plates containing sterile water emulsions of the herbicides mixed with potato-dextrose agar (8) were inoculated with the test pathogens. The diameter of the colonies was measured at the end of the incubation period. Results were expressed as percent inhibition compared to the growth of the fungus in an herbicide-free medium (8).

RESULTS

Effect of dinitroaniline herbicides on plant resistance to R. solani.—Seedlings of eggplant, pepper, tomato, beans, cotton, corn, and oats were pretreated with herbicides and then inoculated with *R. solani* at different inoculum concentrations to determine their effects on plant resistance. The plant species differed in response to *R. solani* depending on the herbicide applied. Resistance of the three solanaceous plants to this pathogen was significantly increased by trifluralin, nitralin, butralin, and dinitramine at 1 μg/g (Table 1), but this effect was less pronounced with higher inoculum concentrations. Benefin and isopropalin did not alter plant resistance. Eggplant seedlings pretreated with nitralin and trifluralin at various concentrations showed that with a reduced concentration of the herbicides (0.2 μg/g) the increased resistance to *R. solani* was reduced (Table 2, Fig. 1). Likewise, the herbicide effect was less pronounced at high inoculum concentrations. The differences between herbicide-treated and nontreated plants diminished by the end of the experiment (Table 2). Increased resistance of eggplants and tomatoes to *R. solani* by trifluralin and nitralin at 1 μg/g occurred with four other isolates of the pathogen. Experiments carried out with pepper pretreated with nitralin, inoculated with *R. solani,* and maintained at a suboptimal temperature of 20 C in controlled environment chambers, once again showed an increase in plant resistance.

Experiments were carried out with eggplants sown in soil simultaneously mixed with trifluralin or nitralin and inoculated with *R. solani.* Diseased seedlings were recorded during the 26 days of plant growth in this soil. Under these conditions, the plants and the pathogen were exposed to the herbicide throughout the experimental period. Thus, disease incidence reflects the combined effects of the herbicide on the plant, on the pathogen, and on the soil microorganisms (11, 12). Results with trifluralin and nitralin showed no significant change in disease incidence; e.g., at inoculum concentrations of 3 mg mycelium/kg soil, the percentages of diseased seedlings were 28, 22, and 35 for nontreated, trifluralin-, and nitralin-treated soils, respectively. The corresponding percentages of diseased seedlings for 9 mg mycelium/kg soil were 80, 79, and 86.

In contrast to their effect on solanaceous plants, trifluralin, nitralin, and butralin had no significant effect on resistance of beans to *R. solani,* whereas dinitramine significantly decreased bean resistance in one case (Table 1). This effect of dinitramine on beans was not consistent, however; it occurred only in some of the experiments. The effect of trifluralin and nitralin on beans also was examined in a field experiment in a soil naturally infested with *R. solani* (Table 3). No significant effect on the percentage of diseased plants or disease index was observed.

Cotton seedlings were pretreated with trifluralin at 2 μg/g soil and inoculated with *R. solani* at various inoculum concentrations. The results obtained in eight experiments were not consistent: increase, decrease, or no change in plant resistance was observed in the various experiments. Results were also variable with other isolates of the fungus, with another cultivar (Acala-1517), or with a lower temperature. When a higher concentration of the herbicide was used (10 μg/g) a decrease in plant resistance to *R. solani* was observed in most, but not all, experiments. For example, in one

TABLE 4. Effect of dinitroaniline herbicides on resistance of eggplant and tomato seedlings to the respective *formae speciales* of *Fusarium oxysporum* and to *Verticillium dahliae*

Herbicide	Percentage of diseased seedlings at various inoculum concentrations expressed as number of conidia/ml			
	F. oxysporum		*V. dahliae*	
	Eggplant	Tomato[y]	Eggplant	Tomato
	50,000	500,000	100,000	500,000
Control	80 a[z]	86 a	80 a	58 a
Nitralin	16 c	18 b	16 b	13 b
Trifluralin	62 b	8 b	21 b	3 b

[y]Race 2 of this pathogen was used.

[z]Numbers in each column followed by the same letter are not significantly different ($P = 0.05$).

experiment, disease indices for 0, 2, and 10 μg/g trifluralin at an inoculum concentration of 10 mg/kg were 0.79, 0.91, and 1.64; at an inoculum concentration of 25 mg/kg, 1.6, 1.53, and 2.97; and at an inoculum concentration of 50 mg/kg were 3.29, 3.55, and 3.59, respectively.

Many members of the Gramineae are particularly sensitive to dinitroaniline herbicides (3) and are resistant to the *R. solani* isolate used in our experiments. Corn and oat seedlings were pretreated with trifluralin, nitralin, butralin, benefin, and isopropalin at 0.5 μg/g and inoculated with *R. solani* at various concentrations. The herbicides caused a marked stunting of these seedlings that was obvious before inoculation. Plant resistance, however, was not altered, as disease symptoms were not observed in inoculated plants either pretreated with the herbicides or nontreated.

Effect of dinitroaniline herbicides on plant resistance to Fusarium and Verticillium diseases.—Nitralin and trifluralin had a pronounced effect in increasing plant resistance to Fusarium and Verticillium wilt diseases. The effects were more pronounced than those observed with *R. solani* (Table 4). Nitralin caused a significant reduction of 21% in Fusarium wilt of eggplant at a concentration as low as 0.2 μg/g (Fig. 2). Trifluralin was more effective than nitralin with tomatoes, but the reverse was true with eggplants. When another three isolates of race 2, or when one isolate of race 1 (using the susceptible tomato cultivar, Marmande) of the pathogen were used, nitralin also increased resistance of tomatoes to Fusarium wilt.

A partial increase in resistance of tomatoes to Fusarium wilt was observed when the herbicide was applied by spraying the emerged seedlings instead of incorporating it into the soil prior to planting. Seedlings grown in an herbicide-free soil were sprayed three times with 500 μg/ml of nitralin on the day of emergence (prior to inoculation) and on the third and the sixth day after inoculation. Soil was covered with a thick layer of polystyrene granules to prevent contact between the herbicide and soil. Percentages of diseased seedlings were 45, 1, and 23 in the nontreated soil, herbicide-treated soil, and sprayed seedlings, respectively.

Effect of dinitroaniline herbicides on plants and pathogens.—The herbicides had phytotoxic effects, to varying degrees, on the plants. Percentages of reduction in weight of tomatoes treated with trifluralin (1 μg/g) were 9.1 and with nitralin (1 μg/g), 12.6. In eggplant seedlings grown in nitralin-treated soil, the percentage reductions were 0.3, 14.3, and 17.9 at concentrations of 0.2, 1.0, and 5.0 μg/g, respectively.

Distribution of trifluralin was determined in tissues of eggplant and cotton (Table 5). Maceration of the tissues before extraction, which apparently subjected the external as well as the internal layers of the plant to the solvent, gave a higher recovery of trifluralin than did extraction of intact tissues. Trifluralin concentration in tissues increased with increasing herbicide concentration in soil and was higher in eggplant hypocotyls than in cotton hypocotyls. Trifluralin also was detected in tissues of eggplant shoots. This might be attributed either to translocation of the herbicide in the plant or to a direct uptake when the shoots were in contact with the soil during emergence. Hypocotyls of cotton seedlings pretreated with trifluralin at 1 μg/g were separated into external and internal layers with a razor blade and trifluralin concentration was determined in each part separately. In both parts, about 0.18 μg/g was detected.

TABLE 5. Concentration of trifluralin (T) in different parts of eggplant and cotton grown in T-treated soil

T concn in soil (μg/g)	Plant part	Extraction[a] method	T concn in plant tissue (μg/g) Eggplant	Cotton
0.2	Hypocotyl	A	0.14	0.07
1	Hypocotyl	A	0.84	0.15
1	Hypocotyl	B	0.13	...
1	Shoot	A	0.49	...

[a]A = 5 g of tissue were macerated and subsequently shaken with 2:1 benzene:2-propanol for 30 minutes. The purified extract was injected into the gas chromatograph. B = Extraction as in A, but without maceration of tissue.

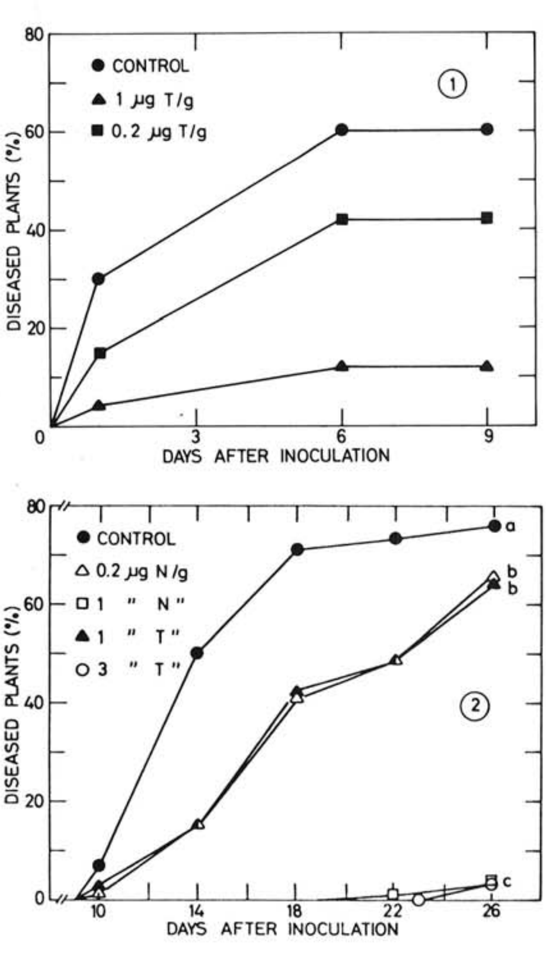

Fig. 1-2. 1) Effect of trifluralin (T) concentration in soil on disease progress in eggplant seedlings inoculated with *Rhizoctonia solani* (150 mg mycelium/kg soil). Differences between treatments, at each time period, are significant (P = 0.05). **2)** Effects of trifluralin (T) and nitralin (N) on disease progress in eggplants inoculated with *Fusarium oxysporum* f. sp. *melongenae* at 50,000 conidia/ml. Treatments with the same letter are not significantly different (P = 0.05).

Separation was not possible with the tiny eggplant seedlings.

Growth of the pathogens in culture was inhibited by the herbicides at concentrations much higher than those used in soil or found in the plant tissues. The ED_{50} of trifluralin, nitralin, and butralin was above 50 μg/ml for *R. solani,* and for nitralin and trifluralin it was above 100 μg/ml for *F. oxysporum* f. sp. *lycopersici*. Conidial germination of this fungus was not affected by 100 μg/ml nitralin or trifluralin.

DISCUSSION

Resistance of solanaceous plants to Rhizoctonia, Fusarium and Verticillium diseases was significantly increased by certain dinitroaniline herbicides. This effect was manifested in experiments with various isolates of the pathogens and at different temperature regimes. The specific combination of a certain herbicide and a certain plant determines the resultant effect on plant resistance. For example, (i) trifluralin, nitralin, butralin and dinitramine increased resistance to Rhizoctonia diseases of solanaceous plants but not that of beans; dinitramine even decreased bean resistance in certain cases and the same was true with trifluralin in cotton; (ii) the effectiveness of trifluralin and nitralin was dependent on the specific plant (Table 4, Fig. 2). The effect of herbicides on disease was influenced by inoculum concentration as was also shown in other studies (6, 7, 12).

Our results do not support the notion that reduced plant growth necessarily leads to decreased resistance due to weakening of the plant. Increased resistance of solanaceous plants also occurred at phytotoxic levels of the herbicides or at suboptimal temperatures. Severe stunting of corn and oats caused by herbicides did not affect their resistance to *R. solani.* An increase in eggplant resistance caused by trifluralin still occurred at nonphytotoxic levels of 0.2 μg/g (Fig. 1). Biehn and Dimond (4) reported that tomato plants showed less Fusarium wilt when compounds that injure roots were applied before root inoculation with *F. oxysporum* f. sp. *lycopersici.*

In our studies, results regarding effects of trifluralin on cotton were variable in that we found both increased and decreased resistance. Higher doses of this herbicide frequently resulted in decreased resistance. In the field, trifluralin is usually incorporated into the soil to various depths. Therefore, sites of high concentrations of herbicide can be expected. This, and differences in inoculum concentration and soil type (which in turn affects herbicide activity), as well as possible interaction with other pathogens, may partially explain the varying results obtained by different workers (2, 7, 13, 14, 19), but not those obtained in our experiments because these were carried out under controlled conditions. Neubauer and Avizohar-Hershenson (13) obtained a very pronounced decrease in cotton resistance to *R. solani* by application of trifluralin at 0.75 and 1.5 μg/g. Since they used sterilized sand, it can be assumed that the effect of trifluralin obtained in this system resembles that occurring in a loamy sand soil treated at higher concentrations. The factors involved in trifluralin-cotton-*R. solani* interactions need further clarification. Cotton contained lower concentrations of trifluralin in the tissues than eggplants (Table 5), and showed no accumulation of herbicide in the external tissues of hypocotyls. Differences in trifluralin distribution in soybean and cotton plants have also been reported (20).

The mechanisms of increased resistance to pathogens cannot be attributed to a direct fungitoxicity of the herbicides unless the degradation products in the plant tissues are much more fungitoxic than the parent compounds. Other possibilities would be the herbicide effect on virulence rather than on pathogen growth, or herbicide accumulation in very high levels in the infection court. In addition, alterations in plant defense mechanisms and in composition and structure of the tissues should be considered. Because increased resistance was found with the three different diseases, the mechanisms involved may be nonspecific.

Even though the herbicides increase plant resistance, their application to infested soil in which the tested plants are grown may still have a different effect on disease incidence. This effect occurs when the various living components involved in disease are affected in different manners (11). For example, the suppressive effect of trifluralin on soil microorganisms (13) may be balanced by increased plant resistance as was shown with diphenamid in tomato (12). Even so, it may be possible to benefit from the increased resistance by growing seedlings in herbicide-treated noninfested soil before transplanting, or by spraying the plants as shown in our experiments. The outstanding effects of trifluralin and nitralin in increasing resistance of tomatoes and eggplants to Fusarium and Verticillium diseases, which occurred even at extremely low concentrations of the herbicides (Fig. 2), should be considered as a potential means of disease control. In this respect, control of root rot and the concomitant increase in yield of peas obtained under field conditions with trifluralin applied at commercial doses (10), are very encouraging.

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