

# Identifying Sources and Mechanisms of Resistance in Crucifers for Control of Cabbage Maggot (Diptera: Anthomyiidae)

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J. Econ. Entomol. 94(4): 942-949 (2001)

**ABSTRACT** The cabbage maggot, *Delia radicum* (L.) is an important insect pest of cruciferous crops in upstate New York. This species causes considerable damage to seedlings and young plants by feeding on roots and stems, resulting in plant stand loss and yield loss. Five crucifer accessions (*Brassica oleracea* variety *italica* L., 'Green Comet'; *B. oleracea* L., 'Rapid Cycling' [Crucifer Genetics Cooperative 3-1]; *B. oleracea* variety *botrytis* L., a standard cauliflower cultivar 'Amazing'; *B. carinata* L.; and *Sinapis alba* L., 'Cornell Alt 543') were evaluated to identify sources and mechanisms of resistance for *D. radicum*. Of the accessions tested, *S. alba* Cornell Alt 543 demonstrated reduced oviposition by *D. radicum*, reduced weights and survivorship of larvae, pupae or adults, and reduced damage to plants. Thus, *S. alba* Cornell Alt 543 could be a potential source for resistance to be bred into cruciferous crops for control of *D. radicum*.

**KEY WORDS** *Delia radicum*, cabbage maggot, cabbage root fly, crucifers, host-plant resistance

PRECISE KNOWLEDGE ON sources and mechanisms of host-plant resistance to specific insect species is the first step in developing an insect-resistant cultivar. Information on the type of resistance is also useful for designing good assays for breeding new varieties (Stoner and Shelton 1988). Plant resistance to insects can be caused by antixenosis, antibiosis, tolerance, or some combinations of these (Painter 1951, Kogan and Ortman 1978). The mechanisms of resistance have a direct influence on the durability and ultimate success of an insect-resistant cultivar. For example, the integration of low to moderate levels of antixenosis, antibiosis, and tolerance can be effective in controlling a resident pest population that invades early in the development of a crop and increases gradually during the growing season (Kennedy et al. 1987). Also, the combination of both antixenosis and antibiosis can decrease the likelihood that the pest population will overcome the resistance, compared with either antibiosis or antixenosis alone, as long as alternative sources of the preferred host plant are available (Gould 1984).

The cabbage maggot, *Delia radicum* (L.), is an important insect pest of cruciferous crops in North America and Europe (Coaker and Finch 1971) and also infests a wide range of cruciferous weeds (Finch and Ackley 1977). The maggots of *D. radicum* cause damage to seedlings and young plants by feeding on roots and stems. Control measures have thus far depended on the use of chemical insecticides, such as

cyclodienes (Judge et al. 1968), carbamates, and organophosphates (Read 1970, Goble et al. 1972, McDonald and Swailes 1975). Due to intense selection, some populations of *D. radicum* have become resistant to these insecticides (McDonald and Swailes 1975, Young et al. 1987), and it is likely that these populations will develop resistance to other insecticides as well (Harris 1977). Because of the threat of resistance development and the potential adverse effects of insecticides on the environment, there is a need to evaluate alternative control strategies to replace the present chemical control strategies.

Host-plant resistance can reduce the need for chemical insecticides as a component of an integrated pest management program because it offers farmers economically and ecologically sound means of suppressing insect populations (Smith 1989). The use of insect-resistant cultivars can result in reduced insect pressure and fewer insecticide treatments. In many cases, even moderately insect-resistant cultivars are useful in enhancing the effects of predators, parasites, and pathogens of pest insects on a variety of crops (Kea et al. 1978, Hare and Andreadis 1983, Kartohardjono and Heinrichs 1984, Hamm and Wiseman 1986, Isenhour and Wiseman 1987, Richter et al. 1987, Bong et al. 1991).

In a search for plant resistance to *D. radicum*, several authors have evaluated antibiosis resistance and tolerance to cruciferous crops (Nikitina 1938; Whitecomb 1945; Swailes 1959, 1960; Abu Yaman 1960; Doane and Chapman 1962; Pond et al. 1962; Way and Murdie 1965; Pond and Moore 1965; Matthewman and Lyall 1966; Radcliff and Chapman 1966a; Mukerji 1969) based on plant injury and on insect survival on different plant species. In Great Britain, some authors (Ellis 1992; Ellis and Hardman 1983, 1988; Freuler

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1978) have discovered moderate levels of antibiosis resistance to *D. radicum* in a range of *Brassica* species (red cabbage, glossy Brassica, kale, and swedes), but the levels of resistance have not been considered high enough to form the basis of a breeding program to produce resistant varieties. In Scotland and Scandinavia, Bradshaw et al. (1989) reported that swedes have been bred for resistance to both *D. radicum* and *D. floralis* (Fallen). However, these resistant varieties have to be integrated with insecticides to achieve successful control of these pests. More recently, Ellis et al. (1999) identified high levels of antibiosis resistance to *D. radicum* in wild *Brassica* species, but these wild species lacked antixenosis resistance. Some authors have demonstrated that antixenosis to egg-laying of *D. radicum* occurs in crucifers (Ellis and Hardman 1975; Ellis et al. 1976, 1985; Freuler and Gagnebin 1984).

In a preliminary study conducted in our laboratory (Shroeder et al. 1995), we saw indications that *Sinapis alba* L. 'Cornell Alt 543' may serve as a source of resistance. In greenhouse trials, significantly more *D. radicum* eggs were deposited on *S. alba* Cornell Alt 543 but the larvae had significantly lower survival rates. The purpose of this study was to examine more closely the potential for *S. alba* Cornell Alt 543 and other *Brassica* species to resist attack by *D. radicum* and to determine the mechanisms of such resistance to it.

### Materials and Methods

**Insects.** A *D. radicum* population from a laboratory colony maintained in the Department of Entomology, New York State Agricultural Experiment Station, Cornell University, Geneva, NY, and reared on turnips as described by Read (1965), was used for all experiments. This colony is our standard insecticide-susceptible colony, which we have used for >10 yr for insecticide and host plant resistance bioassays.

**Plants.** Five crucifer accessions were tested: (1) *B. oleracea* variety *italica* L., 'Green Comet'; (2) *B. oleracea* L. 'Rapid Cycling' (Crucifer Genetics Cooperative 3-1); (3) *B. oleracea* variety *botrytis* L., a standard cauliflower cultivar 'Amazing'; (4) *B. carinata* L.; and (5) *Sinapis alba* L., Cornell Alt 543. As noted above, preliminary studies (Shroeder et al. 1995) had indicated a potential for resistance in *S. alba* Cornell Alt 543. *Brassica oleracea* variety *botrytis* Amazing was chosen as a standard because cauliflower is generally considered to be very susceptible to *D. radicum* and *B. oleracea* variety *italica* Green Comet was chosen because it is a major cultivar for commercial broccoli production. *Brassica oleracea* Rapid Cycling was chosen because it may provide a good vehicle for incorporating resistance into breeding lines. *Brassica carinata* was chosen because it has shown resistance to black rot (*Xanthomonas compestris* pv *compestris*), which is being incorporated into *B. oleracea* breeding lines.

Seeds of the cruciferous accessions were sown in cells of Speedling Styrofoam Trays (Speedling, Sun City, FL) filled with Cornell Mix (1:2 peat moss:ver-

miculite). Four weeks after planting, the plants were transplanted individually to 15-cm plastic pots containing a mixture of Cornell Mix and sand (1:1) and were watered as needed. The plants of each accession were grown and maintained under greenhouse conditions at  $21 \pm 1^\circ\text{C}$ , with  $60 \pm 3\%$  RH, and a photoperiod of 16:8 (L: D) h, using artificial lighting of six 1,500-W metal halide lamps.

**Antixenosis Experiments.** Greenhouse-grown crucifer accessions were used to assess *D. radicum* ovipositional preference in the greenhouse. The experiments were initiated when each crucifer accession had approximately four to five true leaves. Five free-choice experiments were conducted in the greenhouse at the New York State Agricultural Experiment Station, Cornell University, Geneva, NY. All the accessions in these experiments were arranged in a randomized complete block design with three plants as replicates during the fall of 1999 and the spring of 2000. In the center of transparent plastic lid-covers with a diameter of  $\approx 10$  cm and a depth of 2 cm, we cut a circle of  $\approx 0.15$  cm diameter. A cut was made from this circle to the perimeter of the plastic lid-covers and a cover was placed around the base of the main stem of each plant. Each lid-cover was filled with the sand as a site for egg deposition.

One potted plant of each accession was randomly arranged in a circular fashion in a wooden-framed cage (50 by 50 by 50 cm) fitted with Tygon mesh sides and a wooden door. For each experimental period, 10 male and 10 female *D. radicum* adults (4–5 d old) were released in the center of the cage and allowed to mate and oviposit for 48 h. During this period, the adults were provided with a 10% sugar water solution with yellow food coloring in a 250-ml flask with a cotton dental wick protruding out of the top. The adults were also fed a diet consisting of equal parts of brewer's yeast and debittered brewer's yeast mixed together and placed inside the cage on small weighing dishes.

After 48-h exposure to oviposition by *D. radicum*, the plastic lid-covers with the sand containing eggs were removed from each accession and poured into a container of water using the procedure described by Hughes and Salter (1959). When the sand had settled to the bottom of the container and the eggs had floated to the surface, the water containing the eggs was poured through cheesecloth held in a conical funnel supported by a tripod stand. To remove any eggs in the sand, water was added to the sand and stirred so that eggs floated to the surface and the water was again poured through the cheesecloth. The cloth containing the eggs was placed flat onto a paper towel. The eggs were removed with a fine camel's-hair brush, streaked out onto a filter paper, and counted.

**Antibiosis Experiments.** Greenhouse-grown crucifer accessions were used to test for their antibiotic effects on survival and growth of *D. radicum* larvae, pupae, or adults in the greenhouse. The experiments were initiated when the plants of each accession had approximately four to five true leaves. Six experiments were conducted in a greenhouse at the New York State Agricultural Experiment Station, Cornell Uni-

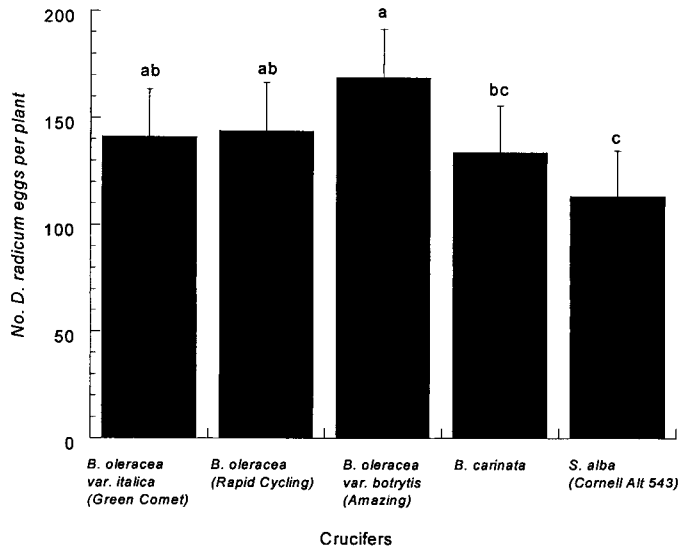


Fig. 1. Number of *D. radicum* eggs laid on plants of different crucifer lines. Means within a column flanked by a common letter are not significantly different ( $P \leq 0.05$ ).

versity, Geneva, NY. All the accessions in these experiments were arranged in a randomized complete block design with five plants as replicates during the fall of 1999 and the spring of 2000. *Delia radicum* eggs were prepared and 15 eggs (2 d old) were placed at the base of each plant with a fine camel's-hair brush. Upon hatching, larvae were allowed to feed on the plants for a 3-wk period. During this period, plants were watered as needed for their maintenance.

At 21-d post inoculation, the potted plants were brought to the laboratory where soil around the roots and the root themselves were examined for larvae and pupae. Individual larvae or pupae were counted and weighed, and pupae were transferred individually to small cups for eclosion to adults. The time for emergence of the adults was examined daily and their numbers and weights were recorded.

**Tolerance Experiments.** The following experiments were performed as a measure of plant tolerance to withstand attack by a *D. radicum* population. The plants of each accession used for the antibiosis experiments were also recorded for damage during a 3-wk period. The number of dead and alive plants was recorded for each accession in these experiments, and the proportion of live plants was calculated as the ratio of live plants divided by the total numbers of plants used for each accession. The plants were considered dead if they contained no green leaves.

**Statistical Analysis.** All data on eggs laid by *D. radicum* (antixenosis), number of larvae, pupae, and adults and their weights (antibiosis), and proportion of undamaged plants (tolerance) were analyzed using analysis of variance (ANOVA) (SAS Institute 1995). The squares root transformation for count data of larvae, pupae and adults and the arcsine square root transformation for proportion of undamaged plants were used to stabilize variances before performing

analysis of the variance. When the *F*-test statistics for each response variable of treatments was significant ( $P < 0.05$ ), least significant differences for means and Student's *t*-test statistics for least square means were used for treatment comparison.

## Results and Discussion

**Antixenosis Experiments.** Antixenosis is characterized by the presence of factors that adversely alter insect behavior resulting in selection of an alternate host for oviposition. This may be due to morphological characteristics of the plant or the presence of phytochemicals that deter or repel insect herbivores from oviposition or larval feeding.

The ANOVA detected significant differences among accessions tested for numbers of eggs laid by *D. radicum* ( $F = 3.41$ ;  $df = 4, 16$ ;  $P < 0.05$ ). There was considerable variation in the numbers of eggs laid around the individual plants within an accession and between experiments during the egg-laying period. *Delia radicum* laid significantly fewer numbers of eggs on *S. alba* Cornell Alt 543 than on *B. oleracea* variety *botrytis* Amazing, *B. oleracea* Rapid Cycling, and *B. oleracea* variety *italica* Green Comet (Fig. 1). This is in contrast to our preliminary report (Shroeder et al. 1995) that indicated higher oviposition on *S. alba* Cornell Alt 543. However, results from the current study may be more plausible because *S. alba* Cornell Alt 543 has an abundance of plant hairs (trichomes) around the main stem of a plant (Brown et al. 1997) that may act as physical barriers to oviposition by *D. radicum*. Such an antixenosis trait of *S. alba* Cornell Alt 543 could be a potential source in the development of resistance.

Some authors have indicated that the egg-laying preference of *D. radicum* for radish cultivars is related

**Table 1. Number and weight of *D. radicum* larvae on five crucifers under greenhouse experiments, NYSAES, Geneva, NY**

Crucifers	n	Mean ± SEM	
		No. of survivors	Weights of survivors, mg
<i>B. oleracea</i> var. <i>italica</i> Green Comet	89	3.9 ± 0.3a	5.7 ± 0.3ab
<i>B. oleracea</i> Rapid Cycling	39	2.2 ± 0.2b	5.7 ± 0.7ab
<i>B. oleracea</i> var. <i>botrytis</i> Amazing	88	4.7 ± 0.5a	6.2 ± 0.4a
<i>B. carinata</i>	69	3.8 ± 0.4a	6.4 ± 0.4a
<i>S. alba</i> Cornell Alt 543	40	2.1 ± 0.2b	4.9 ± 0.4b

Means within a column followed by a common letter are not significantly different ( $P \geq 0.05$ ).

to the concentration of certain glucosinolates (Schnitzler 1975, Ellis et al. 1980). In a search for antixenosis resistance, Nair et al. (1976) suggested that egg-laying preferences of *D. radicum* were governed by the presence of glucosinolates and the absence of inhibitory chemicals. Other factors that affect antixenosis resistance to *D. radicum* include taxonomic, morphological, and physiological characteristics (Hardman and Ellis 1978). Plant age is particularly critical in determining the resistance of crops to egg-laying by *D. radicum* (Abu Yaman 1960, Maack 1977, Ellis et al. 1979), but in our study we examined young plants (four to five true leaf stage) because they are most susceptible to injury by *D. radicum*.

The importance of leaf color and leaf surface properties in determining egg-laying between cruciferous crops and *D. floralis* was demonstrated by Rygg and Somme (1972). Leaf color was first shown to influence *D. radicum* by Gibson and Treherne (1916), and this was confirmed later by many authors (Matthewman and Lyall 1966; Radcliff and Chapman 1966a, 1966b; Rygg and Somme 1972; Prokopy et al. 1983). Several authors have demonstrated that antixenosis to egg-laying of *D. radicum* occurs in crucifers (Ellis and Hardman 1975; Ellis et al. 1976, 1985; Freuler and Gagnebin 1984), but our observations suggest that, at least in *S. alba* Cornell Alt 543, this could be due to the presence of trichomes (Brown et al. 1997).

**Antibiosis Experiments.** Antibiosis effects may result from either chemical or morphological traits, and their resulting effects may be mild to lethal on the biology of the insect. Acute effects may result in the death of young larvae or chronic effects may lead to mortality in larvae, pupae, or adults. Individuals surviving antibiosis may suffer from small body size and low weight, prolonged developmental periods in immature stages, and low fecundity as surviving adult females.

The results showed that significantly fewer ( $F = 6.27$ ;  $df = 4, 315$ ;  $P < 0.05$ ) *D. radicum* larvae survived on *S. alba* Cornell Alt 543 and *B. oleracea* Rapid Cycling than on *B. oleracea* variety *botrytis* Amazing, *B. carinata* or *B. oleracea* variety *italica* Green Comet (Table 1). Larvae weighed significantly less ( $F = 3.0$ ;  $df = 4, 315$ ;  $P < 0.05$ ) on *S. alba* Cornell Alt 543 than

**Table 2. Number and weight of *D. radicum* pupae on five crucifers under greenhouse experiments, NYSAES, Geneva, NY**

Crucifers	n	Mean ± SEM	
		No. of survivors	Weights of survivors, mg
<i>B. oleracea</i> var. <i>italica</i> Green Comet	30	3.3 ± 0.4a	8.1 ± 0.3c
<i>B. oleracea</i> Rapid Cycling	17	1.9 ± 0.3bc	8.3 ± 0.4bc
<i>B. oleracea</i> var. <i>botrytis</i> Amazing	23	2.6 ± 0.4ab	9.8 ± 0.5a
<i>B. carinata</i>	36	2.9 ± 0.3ab	9.6 ± 0.5ab
<i>S. alba</i> Cornell Alt 543	18	1.5 ± 0.2c	7.7 ± 0.7c

Means within a column followed by a common letter are not significantly different ( $P \geq 0.05$ ).

on *B. carinata* or *B. oleracea* variety *botrytis* Amazing but their weights were not significantly reduced on the other crucifers tested. *Sinapis alba* Cornell Alt 543 exhibited a strong antibiotic effect on larval survivorship and their weights compared with the other accessions.

The results showed significant differences in numbers of pupae ( $F = 2.16$ ;  $df = 4, 116$ ;  $P < 0.10$ ) and their weights ( $F = 4.08$ ;  $df = 4, 116$ ;  $P < 0.05$ ) among crucifers. Significantly fewer pupae survived on *S. alba* Cornell Alt 543 than on *B. oleracea* variety *italica* Green Comet, *B. carinata*, and *B. oleracea* variety *botrytis* Amazing (Table 2). Likewise, significantly lower pupal weights were recorded on *S. alba* Cornell Alt 543 than on *B. carinata* or *B. oleracea* variety *botrytis* Amazing. The fact that fewer pupae survived and lower pupal weights were found on *S. alba* Cornell Alt 543, suggests that it was exerting an antibiotic effect.

The ANOVA indicated no significant differences in numbers of adults emerged ( $F = 0.67$ ;  $df = 4, 49$ ;  $P > 0.05$ ) among accessions, but there were significant differences in adult weights ( $F = 2.59$ ;  $df = 4, 49$ ;  $P < 0.05$ ). Adult weights were significantly lower on *S. alba* Cornell Alt 543 than on *B. carinata*, but weights did not differ significantly from survivors on other accessions (Table 3).

Based on the survivors of postdevelopmental stages and their weights, *S. alba* Cornell Alt 543 exhibited an

**Table 3. Number and weight of *D. radicum* adults on five crucifers under greenhouse experiments, NYSAES, Geneva, NY**

Crucifers	n	Mean ± SEM	
		No. of survivors	Weights of survivors, mg
<i>B. oleracea</i> var. <i>italica</i> Green Comet	18	2.2 ± 0.3a	4.2 ± 0.5ab
<i>B. oleracea</i> Rapid Cycling	6	2.0 ± 0.5a	4.5 ± 0.7ab
<i>B. oleracea</i> var. <i>botrytis</i> Amazing	14	1.5 ± 0.2a	4.1 ± 0.4ab
<i>B. carinata</i>	13	2.1 ± 0.4a	5.4 ± 0.6a
<i>S. alba</i> Cornell Alt 543	6	1.2 ± 0.2a	2.8 ± 0.7b

Means within a column followed by a common letter are not significantly different ( $P \geq 0.05$ ).

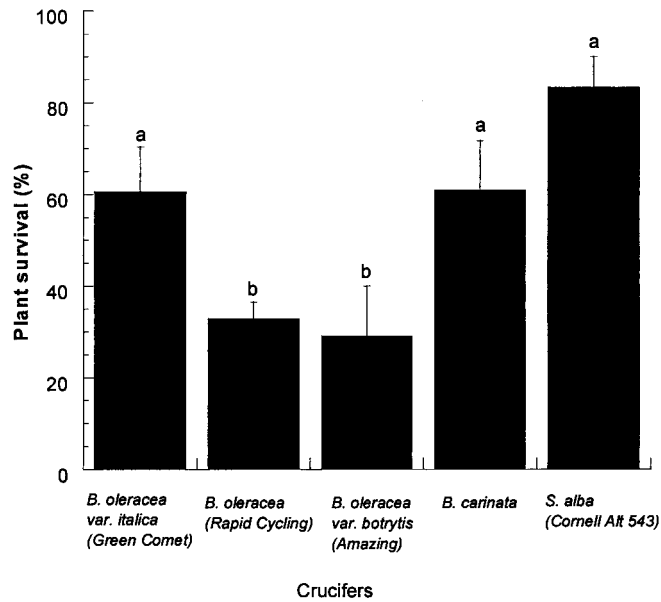


Fig. 2. Effect of *D. radicum* on plant damage 3 wk after egg inoculation for different crucifer lines. Means followed by a common letter are not significantly different ( $P \leq 0.05$ ).

antibiotic effect compared with other accessions. This may have been due to the presence of structural properties of the root or stem of *S. alba* Cornell Alt 543 plants. Plants of *S. alba* Cornell Alt 543 tend to have a more profuse root structure and a harder main stem than the other accessions tested (Shroeder et al. 1995, Brown et al. 1997). In these studies, the reduced body size and weight of larvae, pupae, and adults may have been due to antibiotic effects of rapid growth of *S. alba* Cornell Alt 543 (Painter 1951). For example, Hinds (1906) indicated that rapidly growing cotton boll tissues killed larvae of the boll weevil, *Anthonomus grandis grandis* Boheman; and Adkisson (1962) demonstrated a similar effect on larvae of the pink bollworm, *Pectinophora gossypiella* (Saunders). Also, the presence or absence of certain allelochemicals (toxins, inhibitors, and nutrients) in *S. alba* Cornell Alt 543 might have resulted in reduced survivorship and weight. Several authors have demonstrated antibiotic effects of cruciferous crops on the survivorship of larvae of *D. radicum* (Whitecomb 1945, Abu Yaman 1960, Swailes 1960, Pond et al. 1962, Radcliff and Chapman 1966a, Mukerji 1969). However, none of these authors examined antibiotic effects on body size and weight of *D. radicum*. Some authors have identified moderate levels of antibiosis resistance to *D. radicum* in *Brassica* species (red cabbage, glossy Brassica, kale, and swedes) (Ellis 1992; Ellis and Hardman 1983, 1988), but the levels of resistance were not high enough to breed *D. radicum* resistant varieties. Ellis et al. (1999) identified high levels of antibiotic resistance in some wild *Brassica* species to *D. radicum*.

**Tolerance Experiments.** Tolerance describes the inherent genetic ability of a plant to outgrow or recover from damage by an insect infestation. Never-

theless, tolerance often occurs either in the form of antibiosis or antixenosis or their combination. The assessment of tolerance involves different methods from those used to evaluate antixenosis and antibiosis. Tolerance in plant resistance can be determined by comparing yield of insect-infested and noninfested plants of the same cultivar, percent yield loss based on the ratio yield of infested and noninfested plants, or plant mortality depending on the nature of the damage to the plant species. In a Brassica cole crop such as cabbage, cauliflower, or broccoli, the most important period to prevent damage by *D. radicum* is during the seedling period or soon after plants are transplanted.

Our studies were designed to assess damage from an infestation that occurred when plants had four to five true leaves. The results showed that *S. alba* Cornell Alt 543, *B. oleracea* variety *italica* Green Comet, and *B. carinata* had a significantly higher proportion of live plants (Fig. 2) than *B. oleracea* Rapid Cycling and *B. oleracea* variety *botrytis* Amazing ( $F = 6.33$ ;  $df = 4, 12$ ;  $P < 0.05$ ). The low proportion of damaged plants of *S. alba* Cornell Alt 543 indicated its inherent ability to better tolerate an attack by *D. radicum*. Of the accessions tested, *S. alba* Cornell Alt 543 showed the lowest percentage of plant mortality that may be due to antibiosis or antixenosis or the combination of both traits. Several authors have studied the effect of *D. radicum* for tolerance in cruciferous crops (Whitecomb 1945, Swailes 1960, Abu Yaman 1960, Pond et al. 1962, Radcliff and Chapman 1966a, Mukerji 1969). Plant mortality has been used in both greenhouse (Soni et al. 1984) and field experiments (Ellis et al. 1979) as a measure of plant tolerance in cruciferous crops. Some plant tolerance to *D. radicum* in cauliflowers has been reported by Maack (1977), and it is



well known that the different cruciferous crops show a range of tolerances to this pest species (Hardman and Ellis 1978).

Of the accessions tested, *S. alba* Cornell Alt 543 demonstrated reduced oviposition by *D. radicum* flies, reduced weights and survivorship of larvae, pupae, or adults, and reduced damage to plants. The antibiotic and antixenotic effects of *S. alba* Cornell Alt 543 on *D. radicum* were more clearly able to be documented in our study because we used equal numbers of *D. radicum* per plant. However, in the case of tolerance to injury, our studies were not able to differentiate whether the reduced damage to *S. alba* Cornell Alt 543 was the result of fewer larvae feeding on the plant due to the antibiotic effect of the plant, or whether the plant was able to compensate for injury, or a combination of both. However, it does appear that *S. alba* Cornell Alt 543 could be a potential source for a resistance breeding program.

*Sinapis alba*, which is currently grown for condiment use (Hemmingway 1976), has other desirable agronomic traits such as tolerance to drought and high temperature (Downey et al. 1975), high seed yield, and resistance to shattering of pods (Gareau et al. 1990). Furthermore, *S. alba* is resistant or tolerant to many major pests of *Brassica* oilseed crops in the Pacific Northwest region of the United States of America, such as flea beetle *Phyllotreta cruciferae* (Goeze) (Putnam 1977, Lamb 1980, Brown et al. 1999); the weevil *Ceutorhynchus assimilis* Paykull; cabbage aphid, *Brevicoryne brassicae* L.; and diamondback moth, *Plutella xylostella* L. (McCaffrey et al. 1999). *Sinapis alba* genotypes have also shown high levels of resistance to *Alternaria* diseases (Brun et al. 1987).

### Acknowledgments

We express our sincere thanks to Zohara Yaniv (The Volcanic Center, Israel) for providing seeds of *Sinapis alba* Cornell Alt 543, and Phillip Griffiths (Department of Horticultural Sciences, New York State Agricultural Experiment Station, Cornell University, Geneva, NY) for reviewing an earlier version of the manuscript. We also appreciate two anonymous reviewers and the editor for their critical comments and suggestions in improving the manuscript. This research was supported in part by USDA Pest Alternative Program Grant # 9864631.

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Received for publication 20 July 2000; accepted 22 January 2001.

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