Effect of Selenium-treated Alfalfa on Development, Survival, Feeding, and Oviposition Preferences of *Spodoptera exigua* (Lepidoptera: Noctuidae)

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Environ. Entomol. 31(6): 953–959 (2002)

ABSTRACT We examined the effect of irrigating alfalfa (*Medicago sativa* L.) with selenium-contaminated water on the oviposition response, larval feeding preference, development and survival of the beet armyworm, *Spodoptera exigua* Hübner, a generalist herbivore. Alfalfa was grown in sand cultures under three levels of sodium selenate irrigation: (1) control with no Se added; (2) a low rate of 0.0066 g sodium selenate/60 liters water; (3) and a high rate of 0.20 g sodium selenate/60 liters water. The low concentration treatment resulted in 2.88 ± 0.52 μg Se/g plant dry weight and did not affect percent survival to adult eclosion compared with the control at 1.26 ± 0.11 μg Se/g dry weight. The high rate generated 305.81 ± 52.14 μg Se/g dry weight of alfalfa and significantly fewer insects survived compared with insects fed control alfalfa at 1.11 ± 0.12 μg Se/g dry weight. High Se levels, but not low levels, decreased the relative growth index for larvae. In two-choice bioassays (treated/control) neonate larvae did not discriminate between control and Se-treated plants at high or low levels. Fourth instars did not discriminate between plants with low Se levels and control plants, but preferred to consume plants with high, usually lethal concentrations of Se. Females preferred ovipositing on plants with low Se concentrations over control plants, but did not discriminate between plants with high Se levels and untreated controls. This indicates that although females and late instars may be able to differentiate between Se-treated and control alfalfa they do not avoid plants containing high concentrations of Se. Thus, alfalfa with high Se-treatment levels is resistant to *S. exigua*, and may serve as a population "sink," where females oviposit and few offspring survive to reproduce.

KEY WORDS *Spodoptera exigua*, alfalfa, biomagnification, phytoextraction, phytoremediation, selenium

SELENIUM (SE) IS essential to humans and other vertebrates as a micronutrient (Daniels 1996). However, intoxication of fish, fowl and other wildlife, domestic animals, and humans by Se is surprisingly common (Heinz et al. 1990, Presser et al. 1994, Daniels 1996). The primary effect apparently arises from incorporation of Se into amino acids instead of the normal moiety, sulfur; thus, disulfide bonds within proteins are disrupted, resulting in incorrect folding, and consequently malformed, nonfunctional proteins and enzymes (Lemly 1997). Presumably, substitution of Se is also a primary factor causing toxicosis and mutagenesis in insects.

Previous studies demonstrated that terrestrial insects can accumulate Se (Simmons et al. 1988, Hogan and Razniak 1991), but most of this research focused on Se in specific insect physiological systems rather than the ecological consequences of Se accumulation in host plants and insects. For example, studies with *Musca domestica* L. (Diptera: Muscidae) were designed to demonstrate a lack of Se-dependent glutathione peroxidase activity (Simmons et al. 1989a, 1989b). In other studies, increased mitochondrial respiration was observed in *Corcyra cephalonica* Stainton (Lepidoptera: Pyralidae) when 2 μg/g Se as sodium selenate was added to diet (Lalitha et al. 1994). Additional investigations of enzyme activity indicated that cadmium (Cd) interaction with Se in the insect gut had a positive effect (up to 2 μg/g Se) on Madagascar hissing roaches, *Gromphadorhina portentosa* Schaum (Dictyoptera: Blaberidae), even at toxic Cd levels, but there was enzyme inhibition with Se alone (Nakonieczny 1993). More recently, *Drosophila melanogaster* L. (Diptera: Drosophilidae) on medium without Se had reduced fertility and survival as compared with those with 10^{-6} to 10^{-8} M Se, but 10^{-5} M Se was toxic (Martin-Romero et al. 2001).

Toxicity of Se to insects varies by species and developmental stage, as well as with the form and concentration of Se *Tribolium confusum* Duval (Coleoptera: Tenebrionidae) larvae fed a casein diet containing sodium selenite at concentrations of 2,500, 5,000, and 10,000 μg/g showed decreased development rates and 20, 50, and 100% mortality, respec-

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tively, to the adult stage (Hogan and Cole 1988). In contrast, only 4 μg/g sodium selenate fed to *C. cephalonica*, a stored products pest, decreased weight by 30%, but at 2 μg/g these insects showed significant weight gain compared with controls (Lalitha et al. 1994). For *Spodoptera exigua* Hübner, the lethal concentrations in an artificial diet needed to kill 10–70% of the experimental population (LC_{10} and LC_{70}) were 14.9 and 24.8 μg/g wet weight for sodium selenate, 4.8 and 11.9 μg/g sodium selenite, 9.0 and 18.9 μg/g selenocystine, and 13.9 and 25.1 μg/g selenomethionine, respectively (Trumble et al. 1998).

In food preference bioassays at these toxic concentrations (LC_{10} and LC_{70}), neonate *S. exigua* preferred control diets over sodium selenate or sodium selenite treatments, but preferred controls over selenocystine or selenomethionine only at their highest concentrations (Vickerman and Trumble 1999). Third-instar larvae also selectively avoided sodium selenate and sodium selenite, but they exhibited no antifeedant activity or concentration dependent response to selenocystine or selenomethionine.

Herbivorous insects are exposed to high concentrations of Se at Se-contaminated sites throughout the western United States and many Pacific Rim countries. Currently, remediation strategies at these sites include removal of soil Se through microbial and plant volatilization, and by plant harvest and removal. Both agricultural and uncultivated plant species have been proposed for use in reclamation programs (phytoremediation) for Se-contaminated soils (Khattak et al. 1991, Nyberg 1991, Bañuelos et al. 1996, Wu et al. 1996, Bañuelos et al. 1997, Losi and Frankenberger 1997).

Alfalfa (*Medicago sativa* L.) has been proposed for Se phytoremediation because it accumulates more Se than many other forage plants (Mayland 1994, Wu 1998), and was therefore selected for our bioassays. Alfalfa accumulates moderate levels of Se from the soil, and may be mixed with livestock feed where soil Se is deficient (Nyberg 1991). Other authors have indicated that forage grown in deficient soils can be amended through soil and foliar application of ground plant tissue containing high Se levels (Haygarth 1994, Gissel-Nielsen 1998, Gupta and Gupta 2000).

Use of plants in Se-remediation programs will result in the increased availability of Se, yet little is known about the response of herbivores to Se in plants. Recent studies with several *Atriplex* spp. have shown that Se-irrigation may increase resistance to *S. exigua* (Vickerman et al. 2002). Additionally, canola plants (*Brassica* spp.) such as Indian mustard grown on Se-treated soils became resistant as hosts to cabbage looper, *Trichoplusia ni* Hübner, whereas control plants were defoliated by the pest (Bañuelos et al. 1999). The authors hypothesized that phytophagous insects may avoid feeding on Se-rich plants and thus reduce the likelihood of biotransfer from plant to insect.

Our objectives in this study were to use a model insect-plant system to describe development and survival of herbivore larvae fed alfalfa plants containing different concentrations of Se; examine feeding preferences of two different age classes of larvae to determine if they can detect and avoid Se at sublethal and lethal treatment levels in alfalfa; and to measure oviposition response to Se-treated alfalfa plants to determine if the adult female will detect and avoid alfalfa plants containing sublethal or lethal Se concentrations.

Materials and Methods

Condor CT alfalfa seed was obtained commercially from Western Farm Services (Riverside, CA). Alfalfa plants were grown in coarse grained silica sand cultures in greenhouses at the University of California, Riverside, using 10 containers (7.6 liter) for each treatment, which were irrigated four times daily from 60-liter reservoirs containing half-strength modified Hoagland's nutrient solution (after Khattak et al. 1991). Treatment solutions included tap water plus nutrients: (1) a control, with no Se added resulting in 1.26 ± 0.11 μg Se/g plant dry weight for plants grown concurrently with low treatment plants, and 1.11 ± 0.12 μg Se/g dry weight for plants grown concurrently with high treatment plants; (2) low treatment with 0.0066 g sodium selenate/60 liters water resulting in plants containing 2.88 ± 0.52 μg Se/g plant dry weight; (3) high treatment with 0.20 g sodium selenate/60 liters water resulting in plants containing 305.81 ± 52.14 μg Se/g plant dry weight. Leaf samples were collected four times during each of the three experimental subunits (survival and development, feeding preference, and oviposition preference bioassays). Plants were dried for 48 h in a 60°C oven, then were ground in a Wiley Mill. Selenium analysis was performed by the University of California, Division of Agriculture and Natural Resources Laboratories at Davis, using nitric/perchloric acid digestion/dissolution of samples, and determination by vapor generation using inductively coupled argon plasma spectrometric analysis (Tracy and Moeller 1990).

Spodoptera exigua was chosen as a model insect for this study because this species is a generalist herbivore and a crop pest of economic importance in areas of the United States where selenium is a problem. In California, the host range of *S. exigua* includes native and introduced plants in the families Lilaceae, Fabaceae, Solanaceae, Malvaceae, Chenopodiaceae, Apiaceae, Asteraceae, and Amaranthaceae that can be found in both cultivated and uncultivated areas (Metcalf and Flint 1962, Peterson 1962, Pearson et al. 1989). In addition, this species has highly mobile larvae that can select feeding sites by moving between plants (Berdegué et al. 1998), thereby permitting larvae to potentially choose between hosts with variable Se concentrations.

All insects were obtained from a laboratory colony maintained at 28 ± 2°C and a photoperiod of 16:8 (L:D) h with fluorescent lighting. The colony was field collected in Ventura County, CA, USA, and maintained on artificial diet modified from Patana (1969). Field-collected adults were added to the colony approximately every 6–12 mo to maintain genetic diversity. The ages of the cohorts in these studies were

standardized by using neonates (first instars within 12 h of eclosion) or fourth instars obtained by isolating them during the premolt from the third instar. Bioassays were conducted at 28 ± 2°C and a photoperiod of 16:8 (L:D) h with fluorescent lighting.

Survival and Development. Experiments were initiated with neonate larvae contained individually in labeled containers (30 ml) with non-nutrient agar covering the bottom to maintain humidity (after Diawara et al. 1992). Larvae were fed plant tissue ad libitum. Insect mortality and developmental stage of newly dead and survivors were recorded daily; pupal weight was recorded the day after pupation. Developmental stages were numbered as follows: instars 1–5 were stages 1–5, stage 6 was the prepupal stage, stage 7 was the pupa, and stage 8 the adult moth.

Mean days to pupation, days to adult, and percent survival to pupation and adult were calculated for all treatments. Survival to pupation was included to establish if any plants were toxic primarily to larval stages. Survival to the adult stage was used to determine if additional mortality occurred during the pupal stage. In addition, a measure of growth, the relative growth index (RGI; Zhang et al. 1993), was calculated for larval stages at day 9, the day before any in the alfalfa control group developed into the pupal stage. This index describes the relative values (on a scale from 0 to 1) of what developmental stage could have been achieved on control alfalfa plants, versus what was achieved on plants under Se-irrigation. Five replications of 10 observations each were made for both the low treatment and corresponding control (a total of 50 larvae), and eight replications of 10 observations were made for the high treatment and control (80 larvae).

Feeding Preference Bioassays. Bioassay arenas were constructed from 100 mm plastic petri dishes. Ten neonates were placed in dishes lined with agar. For tests with older larvae, two fourth instars were placed in dishes lined with Whatman glass fiber filter paper (Whatman, Hillsboro, OR) moistened with deionized water. Two alfalfa leaves of the same treatment were placed at each of the four ordinal points, alternating pairs of the Se-treatment and control. Each arena was a replicate (for fourth instars, $n = 88$ arenas for low Se and 90 arenas for high Se, totaling 176 and 180 larvae, respectively; for first instars $n = 50$ arenas for both treatments, a total of 500 larvae per treatment). Preference data were obtained for all tests by recording larval position every half hour for 5 h; time 1 corresponded to one-half hour after experimental setup to allow insects time to begin feeding. Proportion of larvae touching Se or control plants was calculated by dividing the number of larvae on a treatment by the total number of larvae. Consumption was determined only in tests with fourth instars by measuring leaf area (LiCor Leaf Area Meter, LiCor, Lincoln, NE) before and after the bioassay.

Oviposition Preference Bioassays. Selenium-treated and control plants were cut and placed in 250-ml Erlenmeyer flasks. Plant cuttings were 25–30 cm tall and 10 cuttings were placed in each flask. The flasks were arranged with alternating Se and control alfalfa within octagonal PVC cages (55 cm high by 100 cm diameter) covered in nylon organdy. Flasks were buried in sand so that the glass was completely covered, to more closely simulate plants and eliminate concerns about the potential inability of moths to walk on the glass. Pupae from the laboratory colony were sexed and separated by sex until eclosion, at which time two males and two females were isolated incylindrical mating cages (9 cm tall by 9 cm diameter). After 48 h, they were released into the oviposition cages and allowed to oviposit. Plants were replaced once on day 3 and the test was terminated on day 6. Percent eggs laid on Se-treated and control alfalfa was calculated for both treatment levels. Each cage was a replicate and each comparison was replicated twelve times, using a total of 24 individual females per treatment.

Statistical Analysis. Differences ($P < 0.05$) between controls and Se treatments in percent survival to pupation and adult eclosion, and in RGI were evaluated using the nonparametric Mann-Whitney *U* test for unpaired comparisons (Stat View 2000–2001). Analysis of variance (ANOVA) was used to evaluate differences ($P < 0.05$) in pupal weight, developmental stage at death, day of death, and number of days to pupation and to adult (Stat View 2000–2001). Because there were no significant replication effects, a one-factor ANOVA was performed for each comparison. Differences ($P < 0.05$) in comparisons of consumption, positional preference, and ovipositional preference were evaluated after transforming data into percentages followed by Wilcoxon signed-rank analysis for nonparametric paired comparisons (after Lance 1992, Tallamy et al. 1997; Stat View 2000–2001). Growth index (GI) and RGI values were calculated as described by Zhang et al. (1993):

$$GI = \frac{\sum_{i=1}^{i_{max}} [n_{(i)} \times i] + \sum_{i=1}^{i_{max}} [n'_{(i)} \times (i-1)]}{N \times i_{max}}, \quad [1]$$

where imax = 6, the highest attainable developmental stage of the insect at 9 d, n = the number of insects in each stadium, n′ = the number of insects that have died in a given stadium, and N = the total number of insects.

$$RGI = \frac{\text{GI of the test group}}{\text{GI of the control group}}. \quad [2]$$

Results

Survival and Development. Insect survival to the pupal and adult stages was not affected by a diet of low concentration Se-treated alfalfa compared with that of insects fed control alfalfa (Fig. 1; $Z = -0.104$; $P < 0.917$; $Z = -1.462$, $P < 0.144$). However, for insects fed high-concentration Se-treated alfalfa, survival to the pupal (33.8 versus 91.3% control) and adult stages

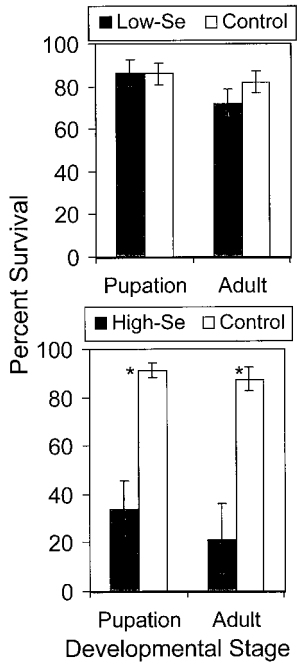

Fig. 1. Mean ± SE percent survival to pupal and adult stages for *S. exigua* larvae fed Se-treated or control alfalfa (*, $P < 0.05$; Mann-Whitney *U* test, Stat View 2000–2001).

(21.3 versus 87.5% control) was significantly reduced (Fig. 1; $Z = -2.888$; $P < 0.004$; $Z = -3.151$; $P < 0.002$).

For survivors, no significant differences were observed in pupal weight, days to pupation, or days to adult among insects fed low concentration Se-treated and control alfalfa (Table 1; $F = 2.235$; df = 1, 82; $P < 0.139$; $F = 1.188$; df = 1, 82; $P < 0.279$; $F = 0.009$; df = 1, 77; $P = 0.926$, respectively). The same was true for survivors on high concentration, Se-treated alfalfa (Table 1; $F = 0.476$; df = 1, 98; $P = 0.492$; $F = 1.903$; df = 1, 98; $P < 0.171$; $F = 0.103$; df = 1, 85; $P < 0.749$, respectively). Likewise, other developmental parameters such as developmental stage at death were not affected by the low level of Se in alfalfa among those insects that died (Table 1; $F = 0.380$; df = 1, 19; $P < 0.545$). However, insects that died in the high Se level treatment did so at an earlier developmental stage (on average, before larval stage 4) than insects that died on control plants (Table 1; $F = 7.434$; df = 1, 69; $P = 0.008$).

Because many of these insects did not develop into the pupal or adult stages, the RGI at day 9 is an important indicator of development rate during the larval stage. High concentration Se-treated alfalfa significantly increased the duration of each stadium as indicated by the RGI (Table 1; $Z = -2.836$; $P < 0.005$). The RGI of insects fed low concentration Se-treated alfalfa did not differ from that of control insects (Table 1; $Z = -1.671$; $P < 0.095$).

Feeding Preference Bioassays. In feeding preference tests initiated with neonates, differences in distribution were not significant among low Se-treated alfalfa and control alfalfa at each of the 10 observation periods (Fig. 2; all *P*'s > 0.05). Fourth-instar larvae significantly preferred the control plants at time interval 3 (Fig. 2; $Z = -2.284$; $P = 0.022$); however, at the next seven observations larvae showed no significant preference (Fig. 2; $P > 0.05$). Significantly more first-instar larvae were observed on control alfalfa at time interval 4 than on the high concentration Se-treated plants (Fig. 2; $Z = -2.284$; $P = 0.022$); however, at all other observation times the larvae did not discriminate between high concentration Se-treated plants compared with control alfalfa (Fig. 2; all *P*'s > 0.05). Fourth-instar larvae, given a choice of high Se-treated alfalfa and controls, showed no preference at six of the 10 time periods. However, at observation times 3, 5, 6, and 9 significantly more larvae were observed on the high Se plants, which were lethal to nearly 80% of the insects in the no-choice trials (Fig. 2; $Z = -2.00$; $P < 0.046$; $Z = -3.50$; $P < 0.001$; $Z = -2.05$; $P = 0.040$; $Z = -2.25$; $P = 0.024$, respectively).

No differences were found in consumption of control and low Se-treated alfalfa in two-choice bioassays with fourth-instar larvae (Fig. 3; $Z = -0.562$; $P = 0.574$). These results are consistent with those of the preference bioassays for low Se-treated plants for both first and fourth instars, indicating that Se at low con-

Table 1. Comparisons of developmental parameters (±SE) for insects fed either Se-treated or control alfalfa

Parameter	Mean ± SE	Mean ± SE	*P*
	Low-Se	Control	
Pupal weight (g)	0.067 ± 0.002	0.086 ± 0.012	0.139[a]
Days to pupation	12.12 ± 0.26	11.77 ± 0.20	0.279[a]
Days to adult	17.19 ± 0.26	17.16 ± 0.22	0.926[a]
Development stage at death	4.92 ± 0.60	4.29 ± 0.87	0.545[a]
Relative growth index (day 9)	0.673 ± 0.040	0.760 ± 0.017	0.093[b]
	High-Se	Control	
Pupal weight (g)	0.058 ± 0.002	0.061 ± 0.002	0.492[a]
Days to pupation	15.11 ± 0.61	14.27 ± 0.29	0.171[a]
Days to adult	20.59 ± 0.62	20.29 ± 0.49	0.749[a]
Development stage at death	3.77 ± 0.27	5.70 ± 0.42	0.008[a]
Relative growth index (day 9)	0.532 ± 0.067	0.876 ± 0.036	0.005[b]

[a] ANOVA.
[b] Mann-Whitney *U* test.

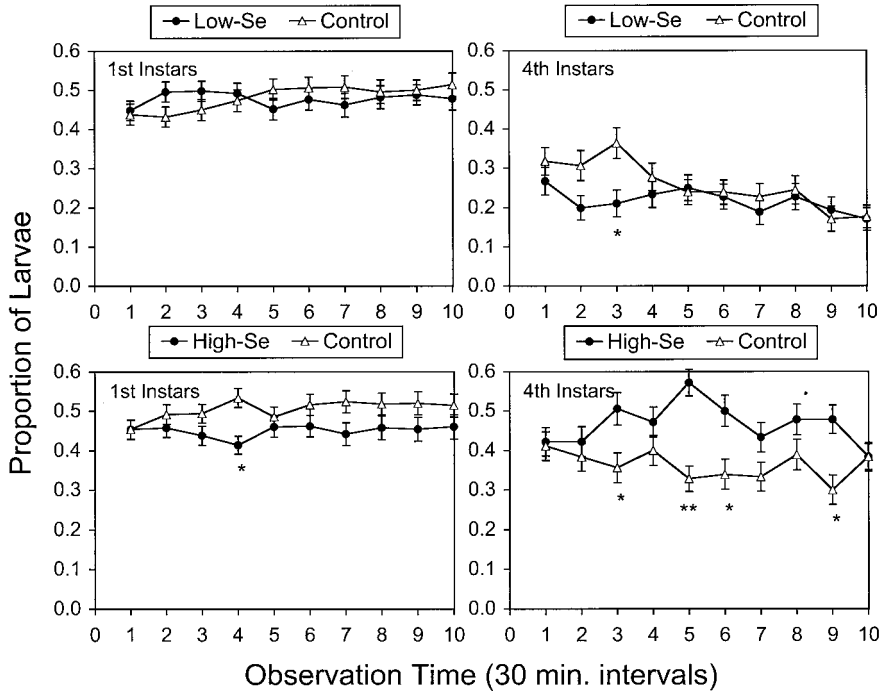

Fig. 2. Mean ± SE proportion of *S. exigua* larvae found on Se treatments or untreated controls in choice tests with first instars or fourth instars determined at 30 min. intervals (*, $P < 0.05$; ***, $P < 0.001$; Wilcoxon signed-rank, Stat View 2000–2001).

centrations tested will not be detected or selectively avoided by *S. exigua* larvae in alfalfa. However, fourth instars consumed more alfalfa at the high Se concentration than the control plants (Fig. 3; $Z = -5.301$; $P < 0.001$). These data reflect the observed positional preference and show that the fourth instars are not simply arrested on the plant without feeding, but are in fact consuming more of the high Se plants.

Oviposition Preference Bioassays. Alfalfa plants under all irrigation treatments in our bioassays were suitable for oviposition and were not burned or

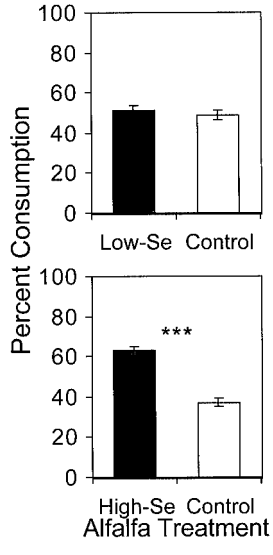

Fig. 3. Mean ± SE percent consumption of Se-treated and control alfalfa in two-choice tests conducted with *S. exigua* fourth instars (***, $P < 0.001$; Wilcoxon signed-rank, Stat View 2000–2001).

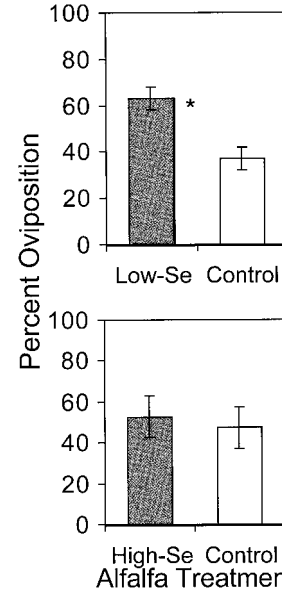

Fig. 4. Mean ± SE percent oviposition by *S. exigua* on Se-treated alfalfa and control alfalfa in two-choice tests. (*, $P < 0.05$; Wilcoxon signed-rank, Stat View 2000–2001).

stunted by Se content. Females preferred to oviposit on low concentration Se-treated plants over controls (Fig. 4; $Z = -2.353$; $P < 0.019$; mean number of eggs: 419 ± 61, low Se; 295 ± 66 control). However, in contrast to the larval preference, no differences were found in oviposition preference of control compared with high concentration Se-treated alfalfa (Fig. 4; $Z = -0.471$; $P < 0.638$; mean number of eggs: low Se, 189 ± 41; control, 221 ± 61).

Discussion

Acquisition of Se by terrestrial insects could result in biomagnification in the food chain, resulting in increased levels of Se accumulation in other invertebrates, fish, birds, and mammals. A reduced development rate and survivorship in insect herbivores could influence the relative amount of biomagnification. If populations decline, biomagnification would be minimized. However, if immigration into contaminated areas is substantial, large numbers of Se-containing larvae available to predators could exacerbate the problem.

High-concentration Se-treated alfalfa significantly reduced survival of this insect herbivore. This suggests that Se may enhance plant resistance to some insect herbivores, which is in agreement with earlier studies (Bañuelos et al. 1999, Vickerman et al. 2002), but the effect of Se in plants on insects is concentration-dependent. The low Se concentration used in our study had no significant effect on insect survival, development, or food preference. The lack of *S. exigua* larval responses to Se- treated plants could have substantial consequences for insect population development. Larvae that actively select, or do not avoid, plants with toxic levels of selenium will be eliminated from the population.

Spodoptera exigua developmental response to high levels of Se in plants was variable. Although development during the larval stage, as described by the RGI, was significantly reduced and although a significant number of insects died in earlier stages than the controls, the few that made it to pupation did not weigh significantly less than the controls and did not take significantly longer to develop into the pupal and adult stages. This suggests that a few insects are relatively more resistant to Se than others. The possibility of this resistance as a genetic trait should be investigated further.

Developmental stage at death is important as an indicator of potential plant damage (consumption greatly increases after molting into stage 4), and can serve as a predictor of the potential for Se biomagnification. A relatively early developmental stage at death reduces the average size of individual insects available to the next trophic level, particularly to predators, and so reduces the potential for Se biotransfer. However, by the same reasoning this may be detrimental to populations of beneficial insects such as parasitoids if the herbivore does not develop adequate size or survive long enough for the parasitoid to complete development.

Higher Se levels were required in plants to produce a toxic effect on *S. exigua* equivalent to that caused by selenium in artificial diets (Trumble et al. 1998). This may be explained in part if some of the total Se content in plants is insoluble and therefore biologically unavailable (McNeal and Balistrieri 1989). It is also possible that Se irrigation of alfalfa plants results in chemical changes in the plant that were not measured in these experiments, but that affect insect nutrition or preference. This is suggested by the unexpected (although limited) preference of fourth-instar larvae for plants with high Se levels, a result differing from those of preference tests using various forms of selenium in artificial diets (all forms were either neutral or antifeedants; Vickerman and Trumble, 1999).

Our data suggest that ovipositing females (even in the confines of a cage) and fourth-instar larvae can discriminate between Se-treated and nontreated alfalfa plants, but surprisingly they do not avoid lethal levels of Se in alfalfa. At high (lethal) Se levels, alfalfa is toxic to most *S. exigua* larvae and may serve as a population "sink," where females oviposit and few offspring survive to reproduce. Thus, there is an additional advantage to using phytoremediation programs (at least with alfalfa) over other Se remediation strategies if local pest insect populations are reduced. However, there may be a simultaneous risk, if the phytoremediation program results in biomagnification of Se in the food chain.

Acknowledgments

We thank W. G. Carson, and M. D. Arias for their laboratory assistance and G. S. Kund for constructing the sand culture irrigation system. We also thank D. R. Parker for his advice on the solution components for the irrigation system. The statistical advice of R. J. Beaver (Department of Statistics at the University of California Riverside) is gratefully acknowledged. We also appreciate the reviews of R. T. Cardé, T. D. Paine, T. W. Sappington, and two anonymous reviewers. This work was supported in part by a grant from the University of California Toxic Substances Research and Teaching Program, and a University of California Graduate Dean's Dissertation Research Grant.

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Received for publication 31 January 2002; accepted 28 May 2002.