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Feeding Preferences of *Spodoptera exigua* in Response to Form and Concentration of Selenium

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Minimal information is available on the impact of various organic and inorganic forms of the ecologically and agriculturally important pollutant, selenium (Se), on insect herbivores. We conducted bioassays with artificial diet to examine the feeding responses of a generalist herbivore, *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae), to various forms and concentrations of Se. Two different-aged cohorts of larvae were examined in choice tests with control diets vs. test diets incorporating lethal concentrations (LC_{10}, LC_{30}, LC_{50}, and LC_{70}) of sodium selenate, sodium selenite, seleno-DL-cystine, and seleno-DL-methionine. Tests initiated with neonates showed larvae significantly preferred control diet over diet with sodium selenate, sodium selenite, or selenocystine, but at most concentrations showed no preference between selenomethionine and control diet. Choice tests initiated with third instars demonstrated a preference for control diet over sodium selenate treatments, and sodium selenite treatments. In contrast, no significant responses were found in tests initiated with third instars offered the choice between selenocystine or selenomethionine and untreated controls. Additionally, comparisons of consumption demonstrated that inorganic selenium compounds were antifeedants whereas the organic selenium compounds tested have little antifeedant activity. The toxicity of all of the tested forms of selenium, in combination with the lack of antifeedant activity of some compounds, has the potential to affect both the distribution and diversity of terrestrial herbivores in both agricultural and natural systems. Arch. Insect Biochem. Physiol. 42:64–73, 1999.

Key words: selenomethionine; selenocystine; phytoremediation; antifeedant; pollution; herbivory

INTRODUCTION

Selenium (Se) is an essential trace nutrient important to humans and most other animals as an antioxidant, functioning as the metal cofactor for important enzymatic activity requiring glutathione peroxidase (Mayland, 1994). When present in high concentrations, Se is substituted for sulfur in sulfur to sulfur linkages of proteins. This results in an inability to form a helix structure, leading to non-functioning, malformed proteins (Lemly, 1998). The element Se can be acquired by plants, is readily biomagnified in the

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food chain, and is known to cause toxicosis in wildlife, domestic animals, and humans (Heinz et al., 1990; Frankenberger and Benson, 1994; Daniels, 1996).

Soil Se accumulation associated with agricultural irrigation, geochemical processes, mining, and a variety of other industrial sources frequently results in significant effects on animal health (Haygarth, 1994). Within the western United States, high Se levels around the Salton Sea (Imperial County, CA) and Kesterson National Wildlife Refuge (Merced County, CA) have resulted in symptoms of Se intoxication of animals (Presser and Ohlendorf, 1987; Heinz et al., 1990; Mayland, 1994; Daniels, 1996; Lemly, 1997). However, these are not just localized problems; approximately 160,000 ha of agricultural land in the San Joaquin Valley of CA are affected by salinity and high water tables, a combination that has been correlated with high Se concentrations in many regions of the world (Wu, 1994).

Selenium enters the food chain naturally through water and accumulates in drainage areas where evaporation concentrates soluble salts (Parker and Page, 1994). Selenium in soils generally occurs as inorganic forms, selenate (SeO_4^{2-}, Se^{6+}) and selenite (SeO_3^{2-}, Se^{4+}), both of which are water soluble and taken up by plants to varying degrees depending on soil properties such as pH, soil texture, and soil composition (Mikkelsen et al., 1989; Haygarth, 1994). In agricultural drainage water in the western United States, selenate is the most common form and is most often taken up by plants (Cutter, 1982; Banuelos and Meek, 1989; Carlson et al., 1991; Terry and Zayed, 1994).

Inorganic Se from sodium selenate is reduced to sodium selenite in plants and may then be substituted for sulfur in amino acid analogs such as selenocysteine, selenocystine, and selenomethionine (Cutter, 1982; Presser et al., 1994). Plant metabolism of these organic forms is complex, resulting in methylated compounds, polypeptides, and proteins (Cutter, 1982; Terry and Zayed, 1994). All the above forms of Se have been found in leaves, stems, and roots of plants, but amounts of each compound vary between plant species (Terry and Zayed, 1994; Ge et al., 1996). Plants have been categorized as high-, moderate-, or nonaccumulators of total Se independent of soil Se concentrations (Rosenfeld and Beath, 1964). Nonaccumulators, such as grasses and grains, rarely sequester more than 50 μg/g dry weight (5 mg/kg or 5 ppm) plant tissue, whereas plants considered moderate and high accumulators (legumes and crucifers) develop concentrations into the thousands of μg/g dry weight plant tissue.

The majority of living plants, however, are thought to accumulate Se at levels less than 100 μg/g (Banuelos et al., 1997). The so-called "nonaccumulating" species contain greater amounts of the protein-bound selenomethionine, whereas high accumulator plants have only trace amounts of selenomethionine and large amounts of the inorganic forms such as sodium selenate and sodium selenite (Mayland, 1994; Wu, 1998). Native plants and other herbaceous plants occur at contaminated sites where Se is leaching out of drainage areas into the surrounding soil. For example, near Kesterson Reservoir, dry weight concentrations of common plants have Se concentrations in the range of 20 to 183 μg/g dry weight (Wu et al., 1993).

Removal of Se from contaminated soil has been a focus of recent research. Reclamation efforts include volatilization by certain fungi and plants, and microbial reduction into either volatile or elemental forms (Terry and Zayed, 1994, 1998; Wu, 1994; Losi and Frankenberger, 1997). The use of plants in remediation programs (phytoremediation) for Se contaminated soils has also been studied with both agricultural and non-cultivated species suggested as potential candidates (Khattak et al., 1991; Nyberg, 1991; Parker and Page, 1994; Banuelos et al., 1996, 1997; Wu et al., 1996). Phytoremediation serves a dual purpose: plants grown in seleniferous soils can be added to feed of animals foraging on plants grown in Se poor soils, or spread on agricultural land with Se-poor soil (Mayland, 1994; Gissel-Nielsen, 1998).

Although much is known about the effects of Se compounds on vertebrates, minimal information is available on insects despite their importance in the food web for higher trophic levels and their roles as key herbivores and recyclers. Previous studies demonstrated that insects do accumulate Se, but most of the research has focused on using Se to disrupt specific enzyme systems (Simmons et al., 1988, 1989a,b; Nakonieczny, 1993) rather than the ecological consequences of Se toxic-

ity (but see Wu et al., 1995). Additional studies have used very high concentrations (1,250–10,000 μg/g) of Se added to stored grain products in order to look at toxicity to insects (Hogan and Razniak, 1991). However, Trumble et al. (1998) demonstrated that terrestrial herbivores suffer high mortality at concentrations corresponding to levels in nonaccumulator plants. Additionally, increased developmental times and substantially increased mortality were documented to vary with the form and concentration of selenium.

In these experiments, we examined the hypothesis that insect herbivores may detect and selectively avoid specific forms of selenium. Such responses would impact the plant choices for phytoremediation programs. Our specific objectives were to document the effects of selected selenium compounds on larval food choice and consumption.

MATERIALS AND METHODS

Insects

Spodoptera exigua (Hübner) (Lepidoptera: Noctuidae) was chosen as a test organism because of a broad host range that includes plants in the families Lilaceae, Fabaceae, Solanaceae, Malvaceae, Chenopodiaceae, Apiaceae, Asteraceae, and Amaranthaceae. These plant families include many non-cultivated species commonly found in Se contaminated areas (Metcalf and Flint, 1962; Peterson, 1962; Wu et al., 1997). In California, *S. exigua* has been found in abundance using native and introduced plant species as hosts in uncultivated areas adjacent to the Salton Sea (Pearson et al., 1989). In addition, this species has highly mobile larvae that are known to move within and between plants to select feeding sites (Berdegué et al., 1998).

The insects used in this study were reared in our laboratory at the University of California, Riverside. The colony was field collected in Orange Co., CA, and maintained on artificial diet modified from Patana (1969). Field-collected adults were added to the colony every 6 to 12 months to maintain genetic diversity. The laboratory colony was maintained at 28 ± 2°C, and 14:10 h (L:D) photoperiod with fluorescent lighting. The ages of the cohorts in these studies were standardized by using neonates within 12 h of eclosion, or third instars isolated onto agar during the premolt from second to third stadia.

Preference Bioassays

Sodium selenate, sodium selenite, seleno-DL-cystine, and seleno-DL-methionine, all water soluble selenium compounds, were obtained from Sigma Chemical Company (St. Louis, MO). These compounds were individually incorporated into artificial diet (modified from Patana, 1969) at lethal concentrations LC_{10}, LC_{30}, LC_{50}, and LC_{70} in Table 1 (based on log-dose probit lines developed by Trumble et al., 1998). All concentrations in diets are reported as wet weights, but can be converted to dry weights by multiplying by 2.31 for comparison. Concentrations reported for this study reflect the total weight for the compound, not the Se component alone. All tests were conducted at 28 ± 2°C, and 14:10 h (L:D) photoperiod.

Five to seven neonates were placed in bioassay arenas constructed from 30-ml plastic cups with 4% agar (w / v) in the bottom. Holes at opposite sides of the cups just above the agar allowed insertion of polypropylene microcentrifuge tubes (1.5 ml) completely filled with artificial diet. One tube contained a treatment diet and the other an untreated control diet. Each arena was replicated 26–30 times for each of the four compounds studied.

Two third instars were tested in larger, 150-ml bioassay arenas similar to those used for neonates. Four holes just above the agar allowed insertion of microcentrifuge tubes (1.5 ml) filled with artificial diet and arranged with alternating treatment and control diets. Each bioassay arena was replicated 25 times for each compound initiated with third instars.

Preference data were obtained for all tests by recording position of the larvae twice daily at 1–2 h after initiation of photophase and 1–2 h before scotophase, for 4 days. Recording of data began the morning after the test was set up in

TABLE 1. Lethal Concentrations (LC) Used in Choice Tests (μg/g Wet Weight Artificial Diet)*

Compounds	LC_{10}	LC_{30}	LC_{50}	LC_{70}
Sodium selenate	14.9	18.5	21.4	24.8
Sodium selenite	4.8	7.0	9.1	11.9
Selenocystine	9.0	12.3	15.2	18.9
Selenomethionine	13.9	17.8	21.2	25.1

*Derived from Trumble et al. (1998).

order to allow the larvae time to acclimate to the arena. Proportion of larvae on treatment or control diets was calculated by dividing the number of larvae on a diet tube by the total number of larvae in the bioassay arena.

Consumption Test

Third instar bioassays also included a measure of consumption determined by weighing the diet tubes before and after the tests. Evaporative loss for each treatment was determined by weighing the microcentrifuge tubes (n = 8 tubes) from replicates of bioassay arenas without larvae that were held concurrently with test arenas containing insects.

Statistical Analyses

Differences ($P < 0.05$) were determined for all choice tests using Wilcoxon Signed Rank analysis (after Lance, 1992; Tallamy et al., 1997). Comparisons of consumption were made by transforming data into percentages (of total consumption) followed by Wilcoxon Signed Rank analysis (StatView, 1993). Consumption data were also analyzed for differences between concentrations (e.g., potential concentration-dependent effects) within treatment compounds using the Kruskal-Wallis Test (Minitab, 1998). All four concentrations within a treatment compound were compared, and if significant differences were found ($P < 0.05$) pair-wise comparisons were performed to determine where those differences occurred.

RESULTS

Preference Bioassays

The general patterns of responses were similar for sodium selenate and sodium selenite. Ad-

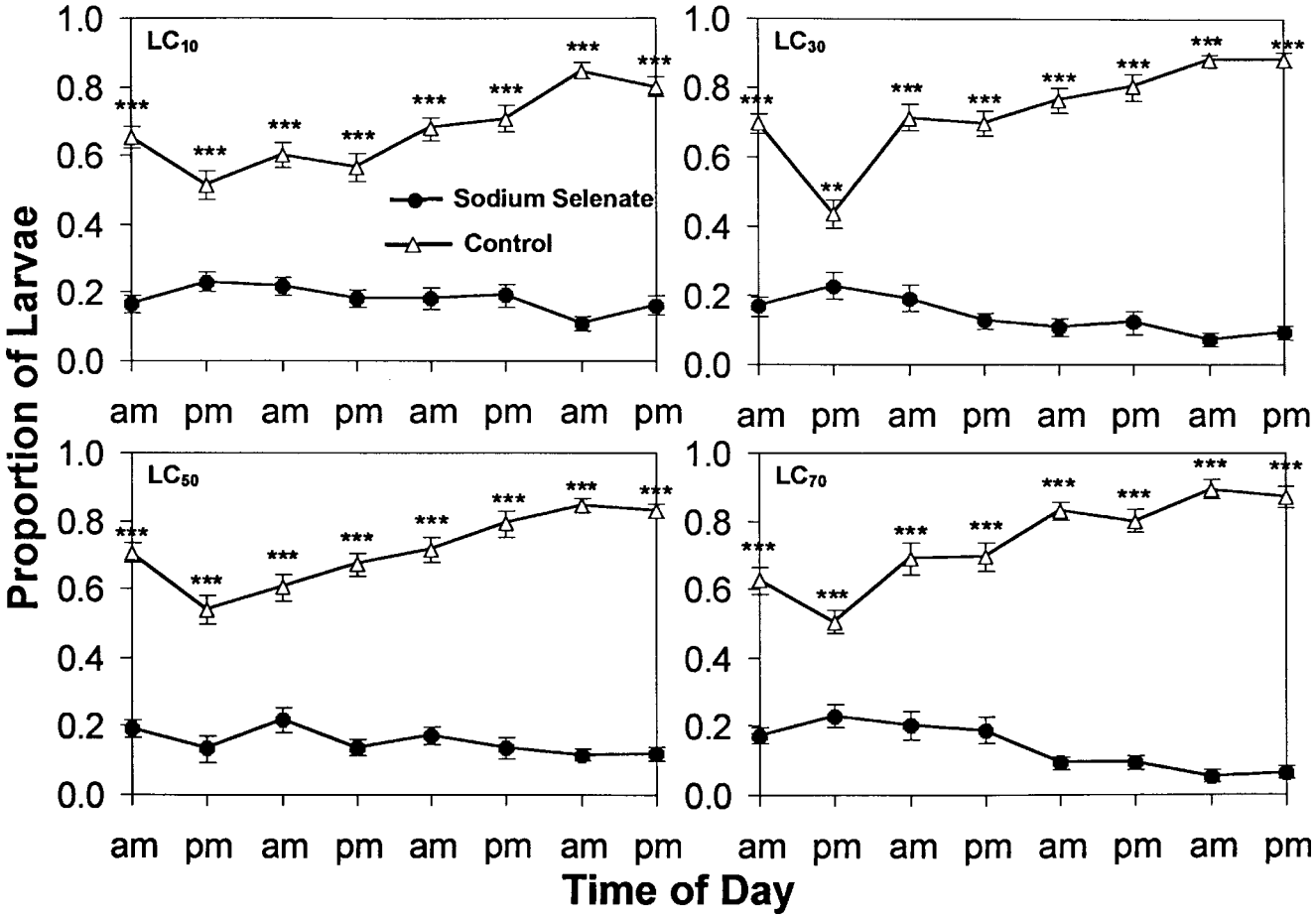

Fig. 1. Proportion of larvae on sodium selenate treatments compared to untreated controls in choice tests initiated with neonates (n = 30 for all concentrations). Asterisks above data points indicate significant differences at $P < 0.05$ (*), $P < 0.01$ (**), and $P < 0.001$ (***) Wilcoxon Signed Rank analysis (ns = not significant). Bars at each data point indicate the S.E.

ditionally, the responses were comparable for selenomethionine and selenocystine in tests initiated with third instars. Therefore, in order to minimize repetitive graphs, the results and discussion for the preference bioassays have been focused on sodium selenate and selenomethionine.

In tests initiated with neonates, significantly fewer larvae were found on diets containing sodium selenate than on control diets (Fig. 1). At the lowest concentration of sodium selenate (LC_{10}), a mean of 20% of the larvae were found on the treated diet throughout the test period. At the higher concentrations, approximately 15% of larvae were found on treated diets. Regardless of the concentration, larvae tended to accumulate on the control diet over time. Similarly, approximately 30% of early instar larvae were recorded on sodium selenite-treated diet at the two lower concentrations, decreasing to a mean of less than 25% at the higher two concentrations.

In contrast, early instars demonstrated no consistent avoidance of diets incorporating selenomethionine up to a concentration equivalent to the LC_{50} (Fig. 2). However, at the LC_{70} concentration, significantly more larvae were found on the control diet in five of the eight sample periods. Early instar larval responses to selenocystine were more variable, with significant preferences for control diet seen in 50–75% of the sample periods.

In tests initiated with third instars, larvae consistently preferred control diets over diets containing sodium selenate (Fig. 3). However, the difference was not as pronounced as seen for the first instars, nor did the proportion responding increase over time. For sodium selenite, the re-

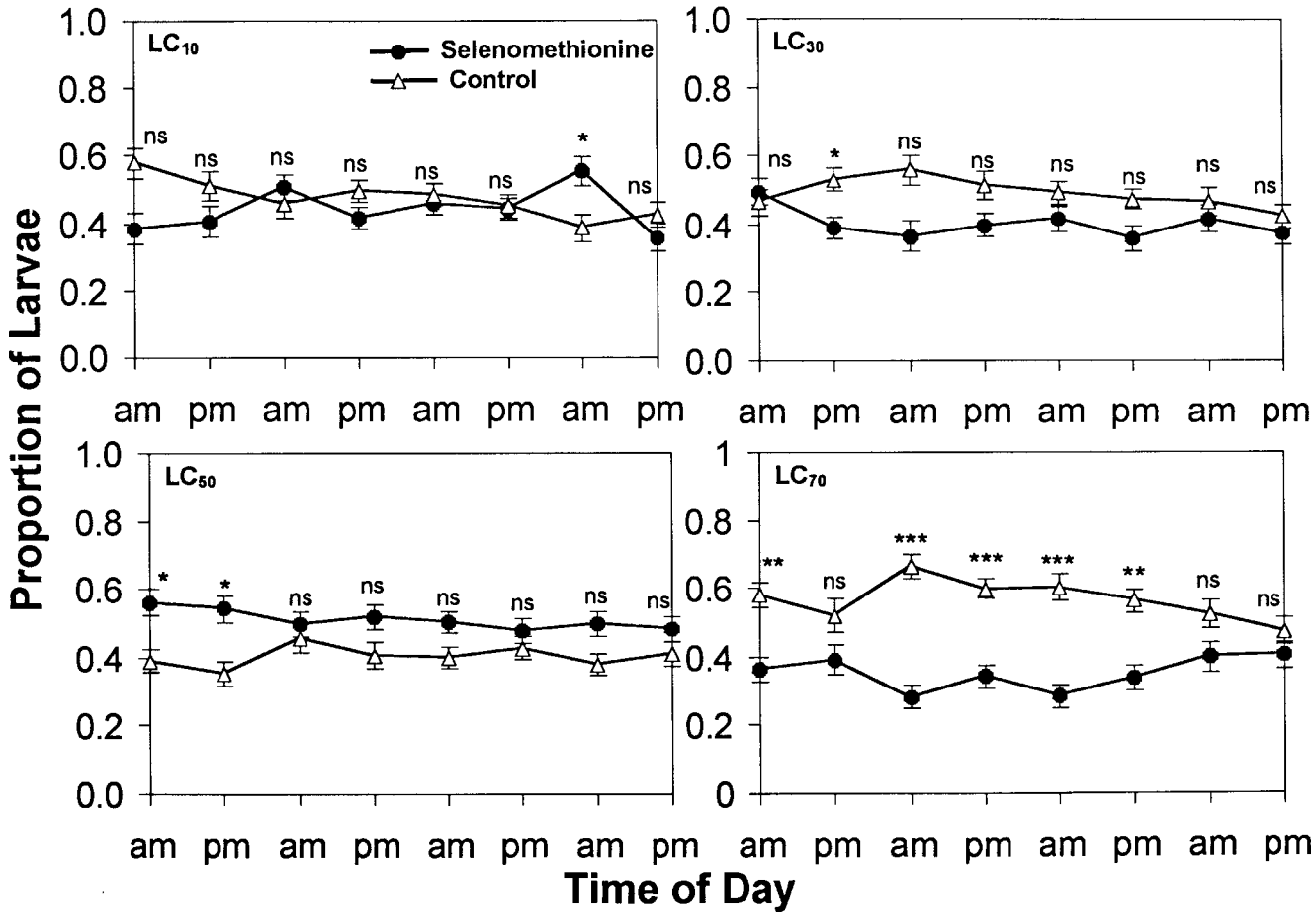

Fig. 2. Proportion of larvae on selenomethionine treatments compared to untreated controls in choice tests initiated with neonates (n = 30 for all concentrations). Asterisks above data points indicate levels of significance as in Figure 1.

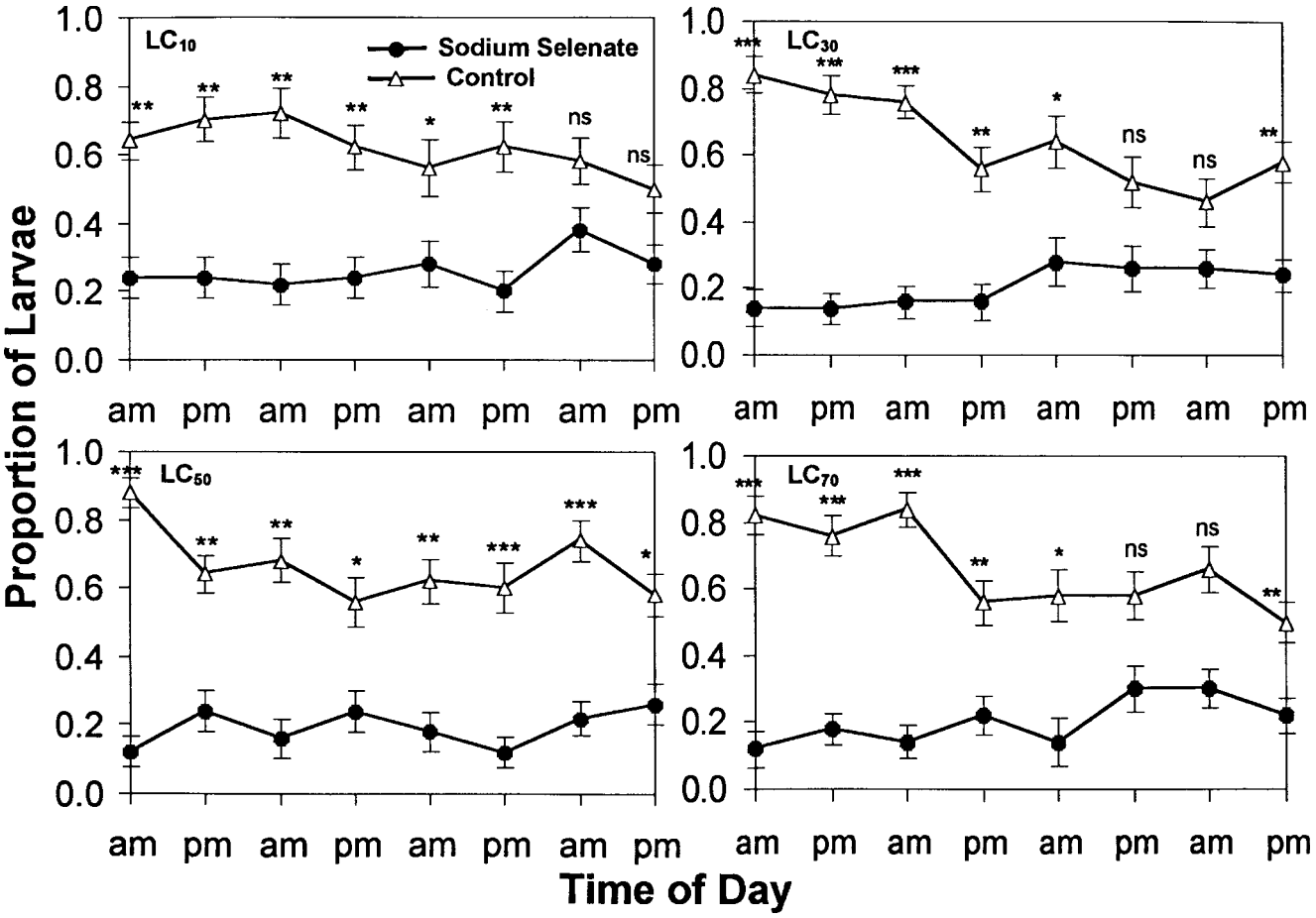

Fig. 3. Proportion of larvae on sodium selenate treatments compared to untreated controls in choice tests initiated with third instars (n = 25 for all concentrations). Asterisks above data points indicate levels of significance as in Figure 1.

sponse of larvae was even more reduced; responses were significantly different on less than 40% of the sample periods.

The related tests comparing preferences among older larvae for diets with or without selenomethionine indicated no significant responses (Fig. 4). The same pattern was observed for selenocystine as for selenomethionine. Thus, despite the reported toxicity of these forms of selenium (Trumble et al., 1998), third instar or larger larvae do not selectively avoid these compounds.

Consumption Test

Larvae consumed significantly less diet containing either sodium selenate or sodium selenite than control diets (Fig. 5). In addition, both of these compounds were less likely to be consumed at higher concentrations, indicating a concentration-dependent feeding response ($P < 0.001$, Kruskal-Wallis Test). These observations are consistent with the preference bioassays and suggest an antifeedant activity.

In contrast, larvae consumed equivalent amounts of diets with either selenomethionine or selenocystine as compared with control diets (Fig. 5). Concentrations between the LC_{10} and LC_{70} values did not influence the results ($P = 0.789$ and $P = 0.672$, respectively, Kruskal-Wallis Test). These results conform to the preference bioassays for selenomethionine and selenocystine initiated with third instar larvae, indicating that even highly toxic concentrations of these organic forms of selenium will not be detected or selectively avoided by *S. exigua* larvae.

DISCUSSION

Insects play a key role in plant population dynamics, especially as pollinators and as herbivores.

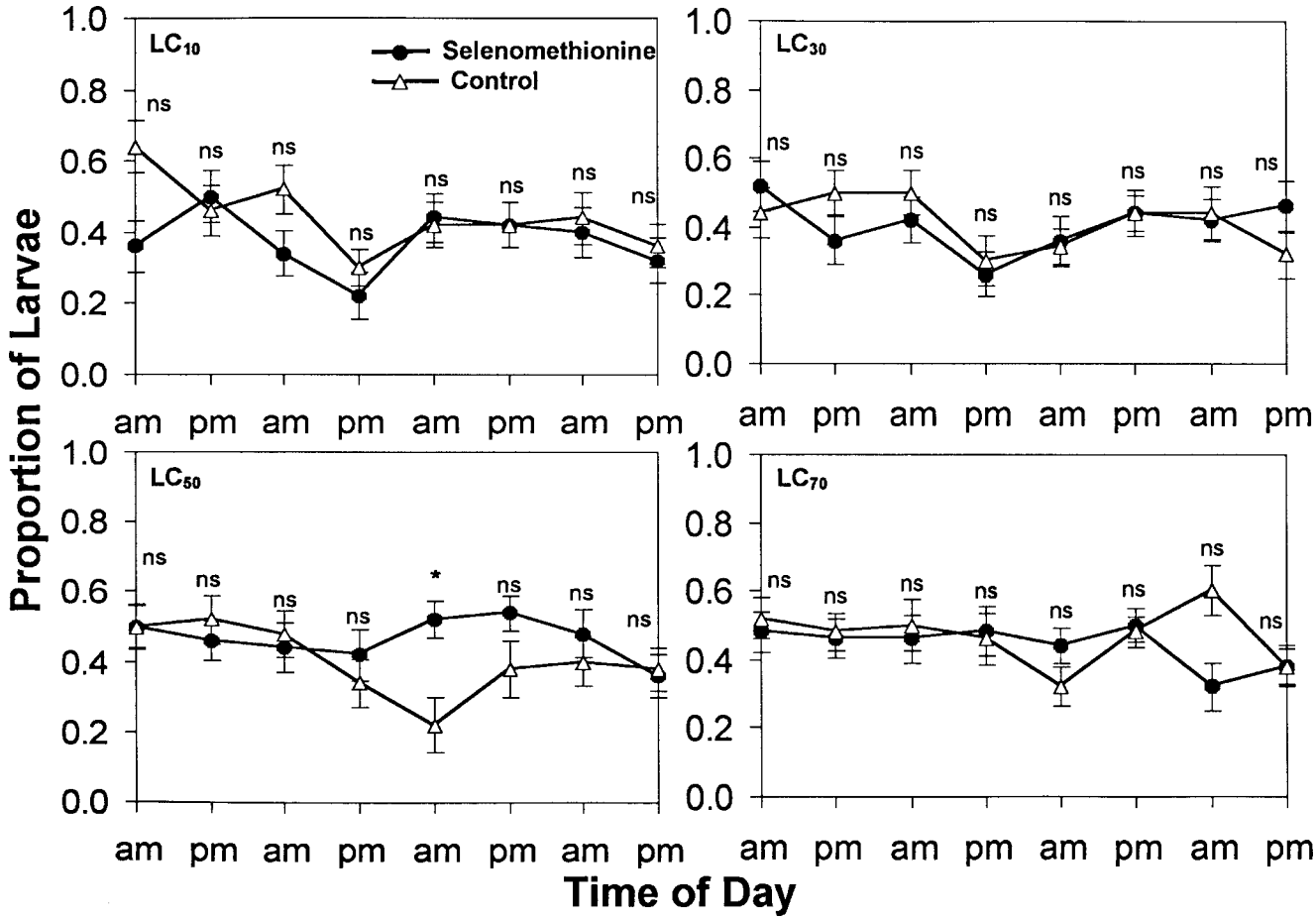

Fig. 4. Proportion of larvae on selenomethionine treatments compared to untreated controls, controls in choice tests initiated with third instars (n = 25 for all concentrations). Asterisks above data points indicate levels of significance as in Figure 1.

Thus, effective and sustainable soil reclamation strategies utilizing plants require thorough knowledge of insect-plant interactions in these systems. Although results from studies on artificial diets should be extrapolated to plants in a conservative fashion, our data suggest that concentration of Se in specific plant tissues would affect feeding site preferences and host plant selection. Such an effect could slow and confound phytoremediation efforts by: (1) returning Se to the soil through insect excretion (frass) and eventual degradation of toxified insects; (2) potentially interfering with plant growth and therefore volatilization through selective feeding on specific portions of plants; or (3) impeding remediation efforts using multiple plants by preferential removal of specific plant species.

In addition, acquisition of Se by terrestrial insects could result in biomagnification of this material in the food chain, resulting in increased levels of Se accumulation in many fish, birds, mammals, and in other invertebrates. Further, the decreased development rate reported for these herbivores could impact the relative amount of biomagnification. If populations decline as a result of reduced growth rates, biomagnification would be minimized. However, if immigration into contaminated areas is substantial, the availability of large numbers of Se-containing larvae could exacerbate the problem. Ultimately, if other herbivore species can detect and avoid these compounds, we suspect that elevated Se levels will reduce the biodiversity of natural ecosystems of insect herbivores such as *S. exigua*.

In this study, we determined that *S. exigua* larval responses to Se in artificial diets vary greatly depending on the form of Se encountered and the

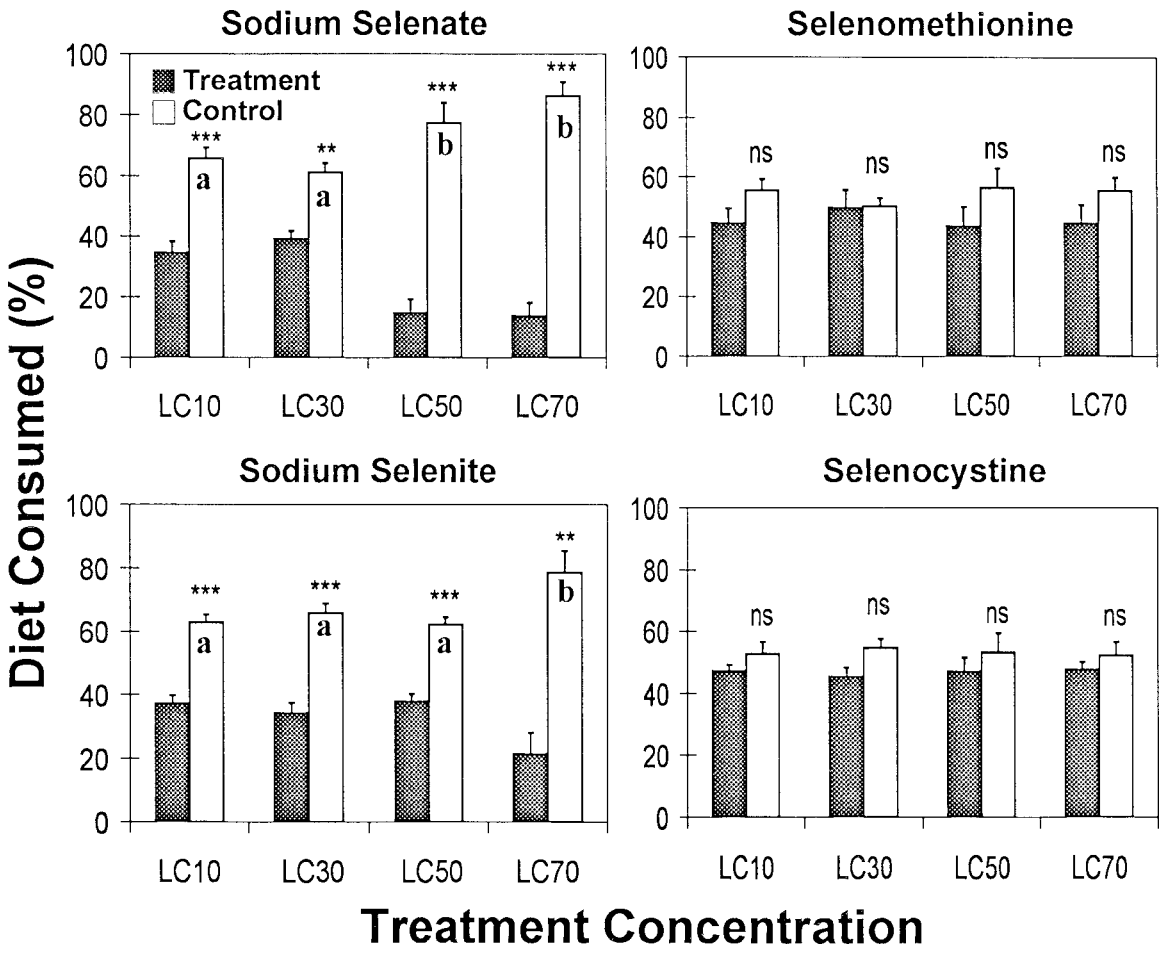

Fig. 5. Percent consumption of treated and untreated (control) diets in two-choice preference tests initiated with third instar larvae (n = 25 for each tested compound at each concentration). Asterisks above paired columns indicate levels of significance as in Figure 1. Bars at each data point indicate the S.E. Differences in response between concentrations within each treatment compound are indicated with different letters, Kruskal-Wallis test ($P < 0.01$).

age of the larvae. Responses of early instars varied such that avoidance of sodium selenate > sodium selenite > selenocystine > selenomethionine. For all of these compounds, the degree of response appeared to increase over time of contact. However, selenomethionine, which is as toxic as the other compounds, was not avoided by early instars except at the highest concentration tested (Fig. 2). These data are consistent with the developmental data using analysis of co-variance of relative growth rate and relative growth index described by Trumble et al. (1998).

Older larvae show slightly more tolerance to, but still selectively avoided, both sodium selenate and sodium selenite (Fig. 3). In contrast, tests using older larvae did not indicate antifeedant activity or a concentration-dependent response to either selenocystine or selenomethionine (Figs. 4 and 5) despite known toxicity of *S. exigua* to these compounds (Trumble et al., 1998). These preference and consumption data demonstrate an antifeedant effect of inorganic selenium compounds and not organic selenium compounds (Figs. 3–5) on older instar larvae. Understanding the impact of variable avoidance of these compounds by these highly mobile larvae (see Smits et al., 1987; Berdegué et al., 1998) in plant systems, therefore, will be critical to predicting ecological effects of Se contamination.

Regardless of the age-related effects, the concentrations of Se compounds used in this study (Table 1) are similar to concentrations found in many plants. In the few examples available, plants reportedly contain greater amounts of the

protein-bound selenomethionine than inorganic Se compounds (Mayland, 1994; Wu, 1998). Thus, the lack of avoidance of selenomethionine could have substantial ecological consequences. However, because Se compounds in plants frequently occur as mixtures (Wu, 1998), determining if there are synergistic or antagonistic affects on herbivore development and survival is necessary.

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