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REVIEW

The impact of selenium on insects

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Selenium, a naturally occurring metalloid, is an essential trace element for many higher organisms, including humans. Humans primarily become exposed to selenium by ingesting food products containing trace amounts of selenium compounds. Although essential in these small amounts, selenium exhibits toxic effects at higher doses. Previous studies investigating the effects on insects of order Blattodea, Coleoptera, Diptera, Ephemeroptera, Hemiptera, Hymenoptera, Lepidoptera, Odonata, and Orthoptera revealed impacts on mortality, growth, development, and behavior. Nearly every study examining selenium toxicity has shown that insects are negatively affected by exposure to selenium in their food. However, there were no clear patterns of toxicity between insect orders or similarities between insect species within families. At this time, the potential for control will need to be determined on a species-by-species basis. We suspect that the multiple modes of action, including mutation-inducing modification of important amino acids as well as impacts on microbiome composition, influence this variability. There are relatively few studies that have examined the potential effects of selenium on beneficial insects, and the results have ranged from increased predation (a strong positive effect) to toxicity resulting in reduced population growth or even the effective elimination of the natural enemies (more common negative effects). As a result, in those pest systems where selenium use is contemplated, additional research may be necessary to ascertain if selenium use is compatible with key biological control agents. This review explores selenium as a potential insecticide and possible future directions for research.

Key words: toxicity, survival, growth, development, behavior

Introduction

Selenium (Se) is a naturally occurring metalloid element that exists in several states: an amorphous liquid and 3 different crystalline forms (NRC 1983). It is widely distributed in all earth materials at an average of 0.09 ppm, and black shales have concentrated amounts of up to 675 ppm (Lakin 1972). Se is also concentrated in ore deposits of uranium and phosphate rocks. In the western United States, Se is found in Cretaceous marine sedimentary rock (Presser et al. 1994).

Schwarz and Foltz (1957) first discovered the nutritional function of Se in rats, but its role in humans was unclear at the time. An interest in Se peaked during the 1970s when breakthrough research linked Se as an essential component to glutathione peroxidase (Combs 1990). More recently, researchers found an association between people living in Se-deficient areas and increased fatality rates from COVID-19 (Zhang et al. 2021). Selenium has become an essential trace element for humans and other animals.

The primary route of Se intake for humans is ingesting food products containing Se (NRC 1983). The Institute of Medicine (2000) reported the Recommended Dietary Allowance for Se to be 55 µg (0.7 µmol)/day for both men and women. Sodium selenite and sodium selenate have been used in the agricultural industry to supplement feed to prevent any disorders arising from Se deficiency (NRC 1983). For example, Finnish soils naturally low in Se are fertilized with Se (Aspila 2005). Keshan disease, a cardiomyopathy endemic to China, is the only human disease caused by Se deficiency (Institute of Medicine 2000). In animals, Se deficiency can lead to severe symptoms such as lipid peroxidation, liver necrosis, and cardiac injury.

The duality of Se presents a complex situation. On the one hand, it is an essential trace element, but on the other, it can exhibit toxic effects on the consumer at slightly higher concentrations. The Tolerable Upper Intake Level, the level at which there is no observed selenosis, is set at 400 µg (5.1 µmol)/day for adults (Institute of Medicine 2000). In human case studies, Se toxicity can manifest as symptoms of diarrhea, fatigue, hair loss, nail discoloration or brittleness, and even death (See et al. 2006, MacFarquhar et al. 2010). In lab animals such as rats, acute toxicity of Se resulted in vomiting, dyspnea, tetanic spasms, death from respiratory failure, and pathological changes to organs (NRC 1983).

Based on early reports, Se may have been the first systemic insecticide explored for use on pest species (Gnadinger 1933, Reed et al. 1962). Hurd-Karrer and Poos (1936) provided cereal plants with Se concentrations ranging from 1 to 12 ppm in sodium selenate. Twospotted spider mite, *Tetranychus urticae* Koch (Acari: Tetranychidae), and bird cherry-oat aphid, *Rhopalosiphum padi* (L.) (Hemiptera: Aphididae), placed on 2-month-old plants grown in concentrations greater than 0.003 ml/liter died within a few days. Similar results were observed using 1-month-old plants. Complete inhibition of aphid infestations was achieved without adverse effects on the plants, showing its potential utility as a systemic insecticide. However, the authors issued a precautionary statement due to the awareness of its toxicity to mammals. Shortly after, Mason and Phillis (1937) explored the use of Se to protect cotton plants from the pink bollworm, *Pectinophora gossypiella* (Saunders) (Lepidoptera: Gelechiidae). Trelease and Trelease (1937) studied an interesting system of the 2-grooved milkvetch plant, *Astragalus bisulcatus* (Hook.) A. Gray, which accumulates Se and its associated selenium-tolerant insects. Seeds contain around 1475 ppm, an extremely high Se content. Nonetheless, the chrysomelid (*Acanthoscelids fraterculus* [Horn]) and seed-feeding chalcid wasps (*Bruchophagus* sp.) thrived on Se levels that could kill rats.

In a more comprehensive study into Se as a systemic insecticide, Neiswander and Morris (1940) found a dose-dependent response in the decrease in *T. urticae* populations, providing complete control on tomato plants grown in nutrient solutions with 1 ppm sodium selenate. Other experiments showed that higher concentrations of Se might be required for adequate control of pests on ornamental plants due to the difference in Se accumulation in the foliage. Morris et al. (1941) reported on *T. urticae* control in corn plants. Similarly, they found that 1–2 ppm range resulted in no observed pest injury and complete pest eradication. Based on the reports provided by these earlier studies, the greenhouse industry started using Se as a systemic by 1945 in granular and capsule forms to control mites, although not extensively (Reed et al. 1962).

Due to the growing insecticide resistance issues, the demand for novel insecticides to control pests has increased (Sparks and Nauen 2015). Insecticides with new chemistry and different modes of action are needed to combat resistant populations of pests. Mechora (2019) supported the notion that Se may be effective as a repellent and a food fortifier on crops, although it has been reviewed within the context of other pollutants and metal contaminants (Jensen and Trumble 2003, Butler et al. 2009, Mogren and Trumble 2010). Here, we present what is presently known about Se and its impact on insects, its potential as an insecticide, and future research directions.

Recent Studies on Selenium and Insects

Although Se can be found naturally, anthropogenic activities can introduce it into areas at high levels, thus concentrating it, potentially outweighing all-natural sources combined (Fairweather-Tait et al. 2011). A shift from the insecticidal application of Se towards environmental toxicology occurred in the 1990s as concern for Se as an environmental toxin increased and warranted further investigation. In areas of contamination, such as the San Joaquin Valley of California, concern for aquatic fauna exposed to Se remained high (Presser et al. 1994, Lemly 1997). As a result, many studies examined the effects of Se on aquatic insects and herbivorous insects that could potentially feed on plants with bioaccumulated Se in their tissues (Maier and Knight 1993, Trumble et al. 1998, Hanson et al. 2004, Franz et al. 2011). Furthermore, Se has been reviewed within the context of other pollutants and metal contaminants (Jensen and Trumble 2003, Butler et al. 2009, Mogren and Trumble 2010). These studies expanded the knowledge of Se in the field of environmental toxicology. Bioaccumulating plants' potential for phytoremediation has also been investigated (Bañuelos et al. 2002, Vickerman et al. 2002a). Various inorganic and organic forms of Se have been tested against many insect orders that can potentially be exposed to Se in the environment, terrestrial or aquatic. Herein we have reviewed related literature from the 1990 to present day.

Impact on Mortality

Selenium compounds have been demonstrated to affect insects in a dose-dependent manner. The high water-solubility of most Se compounds makes them generally easy to work with in solutions and diet treatments. Studies investigating the toxicity of inorganic forms used Se salts (strictly selenate and selenite), while studies that evaluated organic forms commonly used selenomethionine and selenocysteine. Most studies included selenate due to its environmental relevance.

All forms, organic and inorganic, have varying degrees of toxic effects on insects (Table 1). Several studies have comprehensively examined at least 1 of each inorganic and organic form. Investigation on honeybee, *Apis mellifera* (L.), whether through single and chronic doses on foragers or an artificial larval diet, have shown that selenate is the most toxic form (Hladun et al. 2012, 2013a). Only 9% of the larvae successfully pupated in a diet spiked with selenate at 1 mg/L (Hladun et al. 2013a). Trumble et al. (1998) tested 4 different forms in spiked artificial diet against the beet armyworm, *Spodoptera exigua* (Hübner), and reported that selenite had the lowest LC_{50} value of 9.14 µg/g. Another study looked at the effects of Se on the tobacco budworm *Heliothis virescens* (F.) through spiked artificial diet (Popham and Shelby 2007). Total mortality was observed with seleno-DL-methionine 100 µg/g, while selenite caused 60% larval mortality at the same concentration. In contrast to S. *exigua*, an inorganic form was more toxic to *H. virescens,* even though both species are from the same family. This indicates that the toxicity profile of the various forms of Se cannot be reliably predicted by systematic relationships even at the family level. The Argentine ant *Linepithema humile* (Mayr), an urban and agricultural pest species, exhibited varying degrees of toxic effects from ingestion of all forms of Se (de La Riva et al. 2014, de La Riva and Trumble 2016). When Se was added to 25% sucrose solutions, seleno-L-methionine was most toxic and provided an LC_{50} of 87.83 mg/liter (de La Riva et al. 2014). Selenate was the second most toxic form, with a reported LC_{50} value of 131.6 mg/liter at 7 days. A subsequent study with another hymenopteran, the honeybee, also demonstrated selenate toxicity resulting in queen mortality and 100% failure of larvae to complete the transition to the pupal stage (de La Riva and Trumble 2016). Ultimately, there is good evidence that the most toxic forms of Se vary substantially across insect orders.

Selenium is known to have detrimental effects on aquatic fauna. Many investigations revealed the toxicity of Se on aquatic insect larvae, especially Dipterans (Debruyn and Chapman 2007). When 4th instars *Chironomus decorus* Johannsen were reared in solutions of selenate, selenite, and seleno-DL-methionine, the authors reported LC_{50} values of 23.7, 48.2, 194 mg/liter at 48 h, respectively (Maier and Knight 1993). *Chironomus riparius* (Meigen) (Diptera: Chironomidae) exposed to field-collected or laboratory water spiked with Se exhibited higher mortality in seleno-L-methionine regardless of the water used in 40-h acute tests (Ingersoll et al. 1990). Chronic exposure of larvae to mixtures of both inorganic Se forms (selenate: selenite, 6:1) resulted in reduced adult emergence. Franz et al.

Table 1. Impact of selenium on the survival of insects

Order	Species	Se Form	Testing method	Observations	Reference
Odonata	*Sympetrum corruptum*	Selenate	*C. quinquefasciatus* 2nd instars reared in 15 µg/g	No differences in survival when in treatment or exposed to prey	Jensen (2006)
Orthoptera	*Acheta domesticus*	Selenate	*B. juncea* leaf grown in 20 µM solution / Grown in treated solution with treated prey and without	100% mortality by day 11	Freeman et al. (2007)
		Selenite	2 wk old crickets fed torula yeast-based diets (0.1, 0.3, 1, 3, 10 µmol Se/kg) for 5 wk	Decreased survival at 0.3 and 10 µmol vs 1 µmol Se/kg based on hazard ratios	Ralston et al. (2006)
	Various spp.	Selenate	*S. pinnata* grown in 40µM (high) or 2 µM (low) solution	High 10% survival rate vs low 70% survival rate (7 DAE)	Freeman et al. (2007)
Hemiptera	*Podisus maculiventris*	Selenate	*M. scalaris* larvae reared in 125 µg/g	No effect on predator survival	Jensen (2006)
		Selenate	*S. exigua* larvae reared on diet 109 µg/g and 135 µg/g dry weight	59% (low) 58% (high) survival vs 89% (control)	Vickerman and Trumble (2003)
	Myzus persicae	Selenate	*B. juncea* plants 0, 10, 20, or 40 µM (nonchoice)	Stage at death and day of death not sig treated vs control ~0% aphids found on treated 7DAE indicate lethality	Hanson et al. (2004)
			Detached leaves (0, 0.1, 1, 5, 10, or 20 µM Se for 7 d) (nonchoice)	Mortality observed from 1 µM and higher	Hanson et al. (2004)
			Systemic 0, 0.1, 5, or 10 µM 7DAE	Decrease in aphid pop. as increase conc. up to 75% decrease in 10uM	Hanson et al. (2004)
				20% decrease in pop. similar to 0.1 as systemic	Hanson et al. (2004)
Hymenoptera	*Apis mellifera*	Selenate	Topical 20 µM sprayed every other day Single dose mortality assay (0.6–6,000 mg/ml) in 1M sucrose	Up to 67% mortality at 5 days	Hladun et al. (2012)
			Chronic dose mortality assay 20 µl daily (0.6–6,000 mg/ml) in 1M sucrose for 5 d	Up to 89% mortality at 5 days	
		Seleno-methionine	Single dose mortality assay (0.6 to 6000 mg/mL) in 1M sucrose	Up to 59% mortality at 5 days	
			Chronic dose mortality assay 20 µl daily (0.6 to 6000 mg/ml) in 1M sucrose for 5 days	Up to 81% mortality at 5 days	
		Selenate	Larva: artificial diet (0, 0.2, 0.4, 0.6, 1, 2 mg/liter) Forager: 19.2µl of 50% sucrose solution (0, 30, 60, 120, 240, 480 mg/liter)	Larval mortality; LC_{50} = 0.72 mg/liter at 8 days Forager mortality; LC_{50} = 58 mg/liter at 72 h Decreased prepupation; 9% pupation at 1 mg/liter	Hladun et al. (2013a)
		Selenite	Larva: artificial diet (0, 0.2, 0.4, 0.6, 1, 2 mg/liter) Forager: 19.2 µl of 50% sucrose solution (0, 30, 60, 120, 240, 480 mg/liter)	Larval mortality; LC_{50} = 1.0 mg/liter at 8 days Forager mortality; LC_{50} = 58 mg/liter at 72 h Decreased prepupation; no effect on pupation %, no larvae pupated	Hladun et al. (2013a)
		Methylselenocysteine	Larva: artificial diet (0, 4, 6, 7, 9, 10 mg/liter) Forager: 19.2µl sucrose solution (0, 104, 125, 150, 200, 250 mg/liter)	Larval mortality; LC_{50} = 4.7 mg/liter at 8 days Forager mortality; LC_{50} = 161 mg/liter at 72 h Decreased prepupation up to 95%; no effect on pupation	Hladun et al. (2013a)
		Selenocystine	Larva: artificial diet (0, 2, 4, 6, 8, 10 mg/liter) Forager: 19.2 µl of 50% sucrose solution (0, 104, 125, 150, 200, 250 mg/liter)	Larval mortality; LC_{50} = 4.4 mg/liter at 8 days Forager mortality; LC_{50} = 148 mg/liter at 72 h Decreased prepupation up to 68%; no effect on pupation	Hladun et al. (2013a)
		Selenate	1 M sucrose solution (6 mg/kg); Pollen-sucrose patty (6 mg/kg) for 7 days	Increased worker mortality vs control	Burden (2016)
		Methylseleno-L-cysteine	1 M sucrose solution (6 mg/kg); Pollen-sucrose patty (6 mg/kg) for 7 days	Increased worker mortality vs control	Burden (2016)

Table 1. Continued

Order	Species	Se Form	Testing method	Observations	Reference
	Bombus impatiens	Selenate	Microbiota-inoculated bees with 0.75 mg/liter selenate in 40% sucrose for 10 days	Inoculated bumble bee microbiome significantly increased bee survival when exposed to selenate. In the preliminary experiment (exp. 1), the inoculated microbiome significantly increased bee survival 42% increased survival for no bees survived to 10 d	Rothman et al. (2019a)
		Selenate	10, 1, 0.1, 0.01, 0.001, and 0 mg/liter spiked into 60% sucrose For 14 days	LC_{50}: 0.75 mg/liter at 7 days LC_{50}: 0.09 mg/liter at 14 days	Rothman et al. (2020)
	Linepithema humile	Selenate	0, 0.5, 2.7, 5.4, 13.5, 27, and 54 μg Se/ml in 25% sucrose	LC_{50}: 131.57 mg/liter at 7 days LC_{50}: 34.8 mg/liter at 14 days	de La Riva et al. (2014)
		Selenite	0, 2, 4, 10, 20, 30, 40, and 50 μg Se/ml in 25% sucrose	LC_{50}: 44×10^5 mg/liter at 7 days LC_{50}: 709.89 mg/liter at 14 days	de La Riva et al. (2014)
		Seleno-L-methionine	0, 2, 4, 10, 20, 30, 40, and 50 μg Se/ml in 25% sucrose	LC_{50}: 87.83 mg/liter at 7 days LC_{50}: 27.68 mg/liter at 14 days	de La Riva et al. (2014)
		Methylseleno-cysteine	0, 2, 4, 10, 20, 30, 40, and 50 μg Se/ml in 25% sucrose	LC_{50}: 29×10^3 mg/liter at 7 days LC_{50}: 176.17 mg/liter at 14 days	de La Riva et al. (2014)
		Selenate	25% sucrose (0, 5, or 10 mg Se/ml)	Queen mortality 5 mg Se/ml died sooner than control 5 mg–100% mortality 8 wk 10 mg–100% mortality 11 wk; Offspring did not develop beyond the larval stage	de La Riva and Trumble (2016)
Lepidoptera	*Cotesia marginiventris*	Selenate	*S. exigua* larvae feeding on *M. sativa* irrigated with 3.3 mg/liter Se	No effect on the number surviving as pupae and adults; no effect on mortality during the pupal stage	Vickerman et al. (2004)
	Spodoptera exigua	Selenate	Larval artificial diet (5–7 conc)	LC_{50}: 21.41 μg g^{-1}	Trumble et al. (1998)
		Selenite	Larval artificial diet (5–7 conc)	LC_{50}: 9.14 μg g^{-1}	Trumble et al. (1998)
		Seleno-DL-methionine	Larval artificial diet (5–7 conc)	LC_{50}: 15.21 μg g^{-1}	Trumble et al. (1998)
		Seleno-DL-cystine	Larval artificial diet (5–7 conc)	LC_{50}: 21.18 μg g^{-1}	Trumble et al. (1998)
		Selenate	1st instar larvae fed leaves collected from different *Atriplex* lines for 30 days	Reduced mean day of death on treated	Bañuelos et al. (2002)
		Selenate	(1 mg/liter with sulfate and chloride salts 90 days exposure) Feeding *M. sativa* irrigated with 0.0066 g/60 liter and 0.20g/60 liter of water	No effect on survival to pupal and adult stages (low); reduced survival to pupal and adult stages (high)	Vickerman et al. (2002b)
	Plutella xylostella Stanleyi	Selenate	Nonchoice bioassay: *S. pinnata* leaves watered with 80 mM Se for 3 days	No effect on larval survival	Freeman et al. (2006)
	Plutella xylostella G88	Selenate	Nonchoice bioassay: *S. pinnata* leaves watered with 80 mM Se	Decreased larval survival	Freeman et al. (2006)
	Pieris rapae	Selenate	Nonchoice bioassay: *B. juncea* watered with 20 μM Se i) Newly hatched larvae allowed to feed for 9 days ii) 9 days old larvae allowed to feed for 2 days	i) 100% mortality by 9 days ii) 100% mortality by 2 days	Hanson et al. (2003)
		Selenate	Nonchoice bioassay: *S. pinnata* leaves watered with 80 mM Se	Decreased larval survival	Freeman et al. (2006)

Table 1. Continued

Order	Species	Se Form	Testing method	Observations	Reference
	Heliothis virescens	Selenate	Diet (1, 100, 200, 500 μg/g)	Low larval mortality, 2% at 500 μg/g	Popham and Shelby (2007)
		Selenite	Diet (1, 5, 25, 50, 100 μg/g)	60% larval mortality at 100 μg/g	Popham and Shelby (2007)
		Seleno-DL-cysteine	Diet (1, 100, 200, 500 μg/g)	Low larval mortality, 12% at 500 μg/g	Popham and Shelby (2007)
		Seleno-DL-methionine	Diet; (1, 5, 25, 50, 100 μg/g)	100% larval mortality at 100 μg/g	Popham and Shelby (2007)
		Sel-Plex™ 2000[a]	Added into artificial diet (0, 1, 5, 25, and 50 μg/g)	100% larval mortality at 50 μg/g	Popham and Shelby (2007)
Diptera	*Drosophila melanogaster*	Selenite	Newborn adult flies on artificial media (final concentration of 10^{-8}, 10^{-7}, 10^{-6} 10^{-5}, 10^{-4} M)	> 90% mortality at 10^{-4} M Se by 35 days; 2× mortality at 10^{-5} M Se vs control or 10^{-8}, 10^{-7}, 10^{-6} M Se; No effect on mortality at 10^{-8}, 10^{-7}, 10^{-6} M Se	Martin-Romero et al. (2001)
	Chironomus decorus	Selenate	4th instar in toxicant solution	LC_{50}: 23.7 mg Se/liter at 48 h	Maier and Knight (1993)
		Selenite	4th instar in toxicant solution	LC_{50}: 48.2 mg Se/liter at 48 h	Maier and Knight (1993)
		Seleno-DL-methionine	4th instar in toxicant solution	LC_{50}: 194 mg Se/liter at 48 h	Maier and Knight (1993)
	Chironomus riparius	Selenate	48 h acute toxicity test in San Joaquin River water (7 conc)	LC_{50}: 16.2 mg/liter	Ingersoll et al. (1990)
		Selenite	48 h acute toxicity test in ASTM soft water (7 conc)	LC_{50}: 10.5 mg/liter	Ingersoll et al. (1990)
			48 h acute toxicity test in San Joaquin River water (7 conc)	LC_{50}: 7.95 mg/liter	
		Selenate/selenite mixture (6:1)	48 h acute toxicity test in ASTM soft water (7 conc)	LC_{50}: 14.6 mg/liter	Ingersoll et al. (1990)
			48 h acute toxicity test in San Joaquin River water (7 conc)	LC_{50}: 9.34 mg/liter	
		Selenate/selenite mixture (6:1)	48 h acute toxicity test in ASTM soft water (7 conc)	LC_{50}: 14.3 mg/liter	
			30 d chronic testing (0, 750, 1,500, 3,000, 6,000 μg/liter Se)	Reduced % adult emergence at 6,050 μg Se/liter	
		Seleno-L-methionine	48 h acute toxicity test in San Joaquin River water (7 conc)	LC_{50}: 5.78 mg/liter	Ingersoll et al. (1990)
			48 h acute toxicity test in ASTM soft water (7 conc)	LC_{50}: 6.88 mg/liter	
		Selenite	Spiking with aqueous Se (Various experimental designs)	Larval mortality	Beaty and Hendricks (2001)
	Chironomus dilutus	Selenate	2nd instar (7–9 days old) in aqueous Se (4 μg/liter Se) for 10 d followed by clean water for 10 days	Larval survival > 85%	Franz et al. (2011)
		Selenite	2nd instar (7–9 days old) in aqueous Se (4 μg/liter Se) for 10 days followed by clean water for 10 days	Larval survival > 85%	Franz et al. (2011)
		Seleno-DL-methionine	2nd instar (7–9 days old) in aqueous Se (4 μg/liter Se) for 10 days followed by clean water for 10 days	Larval survival > 85%	Franz et al. (2011)
		Selenite	9–10 days old larvae exposed to waterborne SeNP[b] (5, 15, 50, 100, and 1,000 μg Se/liter) for 10 days	No effect on larval survival (> 80%)	Gallego-Gallegos et al. (2013)
			9–10 days old larvae fed spiked fish food SeNP[b] (nominal concentrations of 5, 15, 50, and 150, 500 μg Se/g d.w.) for 10 days	No effect on larval survival (> 80%)	
			9–10 days old larvae spiked selenized algae (*Scenedesmus* sp.) (nominal concentrations of 5, 15, 50, and 150 μg Se/g d.w.) for 10 days	No effect on larval survival (>80%)	

Table 1. Continued

Order	Species	Se Form	Testing method	Observations	Reference
	Megaselia scalaris	Selenate	Diet (0, 100, 200, 300, 400, and 500 µg/g) egg to adult	LC_{50}: 258 µg/g; Decreased larval survival (28% at 100 µg/g and 79% at 500 µg/g)	Jensen et al. (2005)
		Selenite	Diet (0, 100, 200, 300, 400, and 500 µg/g) egg to adult	LC_{50}: 392 µg/g; Decreased larval survival (19% at 100 µg/g and 58% at 500 µg/g)	Jensen et al. (2005)
		Seleno-L-methionine	Diet (0, 0.5, 5, 25, 50, and 100 µg/g) egg to adult	LC_{50}: 130 µg/g; Decreased larval survival (22% at 100 µg/g and 97% at 400 µg/g)	Jensen et al. (2005)
		Se-(methyl) selenocysteine hydrochloride	Diet (0, 0.5, 5, 25, 50, and 100, 200, 400, 800 µg/g) egg to adult	LC_{50}: 83 µg/g; Decreased larval survival (28% at 50 µg/g and 58% at 100 µg/g)	Jensen et al. (2005)
		Selenate	Diet flakes rehydrated (0, 100, 200, 300, 400, 500 µg/g) egg to adult or 35 d	LC_{50}: 260 µg/g Decreased larval survival 27% (100 µg/g) and 79% (500 µg/g); Decreased overall survival 28% (100 µg/g) and 79% (500 µg/g) No effect on egg survival No effect on survival of puparia	Jensen et al. (2006)
	Culex quinquefasciatus	Selenate	Solution (2, 4, 8, 16, 32 mg/liter) 2nd instar to adult	LC_{50}: 11 mg/liter at 14 days; Decreased larval survival at 8 mg/liter (27%) and at 16 mg/liter (83%)	Jensen et al. (2007)
	Ephydra cinerea	Selenate	Solution (10-20,000 µg/liter) 3rd instar for 24 h and 48 h	No effect on larval survival (>92% at 24 h and >88% at 48 h)	Rosetta and Knight (1995)
		Selenite	Solution (10-20,000 µg/liter) 3rd instar for 24 h and 48 h	No effect on larval survival (>92% at 24 h and >88% at 48 h)	Rosetta and Knight (1995)
		Seleno-DL-methionine	Solution (10-20,000 µg/liter) 3rd instar for 24 h and 48 h	No effect on larval survival (>92% at 24 h and >88% at 48 h)	Rosetta and Knight (1995)
Coleoptera	*Tenebrio molitor*	Selenite	Nutrient media (0.125, 0.25, 0.5, 1, 2% Se) 1 d old adults; 1 w in control then into treated until 28 days	0.125%: Progressive decreased survival from 7 to 28 days; survival (72%) vs control (99%) at 7 days 0.25%: Decrease in survival; survival slope about 12 insects/day from 7 to 14 days 0.5%: Survival curve slope 13.1 insects/d from 7 to 14 days 1% and 2%: 100% kill by 14 days	Hogan and Razniak (1991)
			Nutrient media (0.125, 0.25, 0.5, 1, 2% Se) 1 day old adults; 1 w in treated then into control until 28 days	0.125%: Decreased survival through 14 days, then less mortality 14 to 28 days; survival curve slope 8.6 insects/day for 7–14 days 0.25%: Survival curve slope 9.7 insects/day from 0 to 7 days then 3.3 insects/day from 7 to 14 days 0.5%: Survival curve slope 10.7 insects/day from 0 to 7 days and 0.85 insects/day from 7 to 14 days	

Table 1. Continued

Order	Species	Se Form	Testing method	Observations	Reference
		Selenate	Nutrient media (0.0125, 0.025, 0.05, 0.1%) 1 wk old adults on treated medium maintained at 4 and 25°C Nutrient media (0.0125, 0.025, 0.05, 0.1%) 1 wk old adults then transferred to control medium 12 days maintained at 4 and 25°C	4°C: Survival percentage curves steeper slopes; 100% kill by 24 days 25°C: Clear dose-dependent survival response; kill began ~12 days earlier than control; for 3 highest conc. kill progressive and abrupt between 6 and 24 days; 0.025% final deaths protracted to 48 days 4°C: No differences from groups that were maintained on treatment; slight shift to the right 25°C: Survival for control, 0.0125, and 0.025% groups are comparable	Audas et al. (1995)

aSelenized yeast product containing 2000 µg/g Se, equal to or greater than 98% organic form, primarily as SeMet.
bSelenium nanoparticles.

(2011) found minimal effects of selenate, selenite, and seleno-DL-methionine (4 µg/liter) on *Chironomus dilutus* Shobanov, Kiknadze & Butler larval survival after 10 days. Similarly, Gallego-Gallegos et al. (2013) exposed larvae to selenite in water, spiked fish food, and spiked algae at various concentrations without any significant effect on larval survival (>80%). Third instar brine fly, *Ephydra cinerea* Jones subjected to acute exposure of selenate, selenite, and seleno-DL-methionine for 24 and 48 h, still maintained larval survival of >92% and >88% for all forms, respectively (Rosetta and Knight 1995). Jensen et al. (2007) explored a medically relevant mosquito species, *Culex quinquefasciatus* Say. When larvae were exposed to aqueous selenate solutions, the LC_{50} was 11 mg/liter at 14 days. A 16 mg/liter solution provided 83% percent mortality. Based on larval mortality of aquatic Dipterans, inorganic and organic Se forms have been shown to exhibit a range of toxic effects that are as yet unpredictable across related species.

Other dipterans that have been investigated include *Drosophila melanogaster* Meigen and the phorid, *Megaselia scalaris* (Loew). Newly emerged *D. melanogaster* flies were maintained on artificial media containing 10^{-8}–10^{-4} M selenocysteine (Martin-Romero et al. 2001). At the highest concentration, ≥90% mortality was observed by 35 days; however, the lowest 3 concentrations did not affect mortality. Two studies examined *M. scalaris* survival and development on a laboratory diet incorporating several forms of Se. Selenocysteine was the most toxic form, followed by seleno-L-methionine and selenate based on lethal concentrations in the *Drosophila* diet (Jensen et al. 2005). Subsequently, Jensen et al. (2006) compared the effects of selenate individually and in combinations with a sometimes co-occurring metal (methylmercury). They reported a comparable LC_{50} value to the 2005 study for selenate alone. Thus, in the relatively few studies that have tested insects over time, results appear to be consistent. Interestingly, there were no effects on the survival of pupae or eggs exposed to the treated diet.

Since plants bioaccumulate Se into their tissues, studies involving lepidopteran larvae potentially show the interaction between Se hyperaccumulators and herbivorous insects in contaminated environments (Bañuelos et al. 2002). *Spodoptera exigua* fed saltbush plants exposed to selenate for 30 days showed reduction in the mean time to mortality and mortality on treated plants (Trumble et al. 1998). Vickerman et al. (2002b) investigated the effect of irrigating alfalfa with selenium-contaminated water on the survival of *S. exigua*. They found reduced survival to pupal and adult stages when the insects fed on alfalfa plants that were irrigated at 0.20 g/ 60 liter of water. Selenate did not affect larval survival of a selenium-tolerant strain of diamondback moth, *Plutella xylostella* (L.), at an 80 mM dose on prince's plume (Freeman et al. 2006). In addition, the larval survival of the imported cabbageworm *Pieris rapae* (L.) was affected by 2 treated host plants (mustard and prince's plume) (Hanson et al. 2003, Freeman et al. 2006). In an artificial diet, selenite protected *Trichoplusia ni* (Hübner) from *Autographa californica* nucleopolyhedrovirus (Popham et al. 2005). Larvae fed on an untreated diet and then transferred to a treated diet showed an increased LC_{50} for the virus. This indicated that dietary Se increased the resistance of the larvae to the virus. The precise mechanism by which dietary Se increases resistance to nucleopolyhedrovirus has not been reported.

Due to the concerns of biotransfer across trophic levels, studies have sought to replicate the potential exposure of Se on insect predators. When the dragonfly *Sympetrum corruptum* (Hagen) nymphs were fed on selenium-exposed prey *C. quiquefasciatus*, there were no differences in predator survival compared to that of predators fed untreated prey (Jensen 2006). Similarly, in another

predator species, the spined soldier bug *Podisus maculiventris* (Say), survival was unaffected when they were fed *M. scalaris* larvae reared on diet containing 125 µg/g selenate (Jensen 2006). In contrast, Vickerman and Trumble (2003) observed 59% and 58% mortality in *P. maculiventris* when fed *S. exigua* larvae reared on a diet of 109 µg/g and 135 µg/g, respectively. Thus, despite similar concentrations of selenate fed to prey insects across these studies, variations in Se assimilation and availability between prey species appear to have substantial influence on the mortality experienced by a predator.

Parasitoids responses to Se have also been subject to investigation. *Cotesia marginiventris* Cresson, a parasitoid of noctuids, were allowed to parasitize *S. exigua* larvae fed on alfalfa plants irrigated with selenate (Vickerman et al. 2004). The authors observed no effect on the survival of pupae and adults. Although overall parasitoid fitness may have been reduced (see the next section), the authors concluded that use of alfalfa for Se phytoremediation would not eliminate populations of *C. marginiventris* or the ecosystem services they provide. Thus, at least in some agricultural systems, Se enhancement for pest suppression appears compatible with the use of biocontrol agents.

Studies on Coleoptera and Orthoptera have been limited. Hogan and Razniak (1991) investigated the effects of selenite on the yellow mealworm *Tenebrio molitor* L. fed treated nutrient media. The inorganic form decreased survivorship and had residual mortality effects on adults even when they were transferred onto control nutrient media after 1 wk. However, mortality progressively declined towards the latter part of the observation period. Audas et al. (1995) examined selenate ingestion on *T. molitor* and reported clear dose-dependent responses on survival when maintained on spiked nutrient media. Similar to results reported by Hogan and Razniak (1991), insects later transferred to control media after exposure also suffered decreased survival. The house cricket, *Acheta domesticus* (L.), fed mustard leaves from plants grown in selenate solution exhibited 100% mortality by 11 days (Freeman et al. 2007). Various field-collected orthopterans were fed desert princes' plume grown in 2 solutions of methyl-selenocysteine, 2 µM and 40 µM. The authors reported a 10% and 70% survival rate on the higher and lower solutions, respectively. Another study involving *A. domesticus* found that consumption of a selenite-spiked diet at 0.3 and 10 µmol Se/kg decreased survival compared to a dose of 1 µmol Se/kg (Ralston et al. 2006). Thus, while Se could cause mortality in most insect species from all major systematic groups tested and across all ecological categories examined (herbivores, predators, and parasitoids), predicting the outcome of specific forms of Se against a particular species or larger systematic groups is not yet possible given the limited data available.

Impact on Growth, Development, and Reproduction

Many toxicological studies include observations on the growth and development of test insects. From these studies, there is sufficient evidence to conclude that at sublethal doses, Se can disrupt normal physiological development and impact reproduction through reduced fecundity (Table 2). The sublethal effects of various forms of Se have been particularly well studied for the social insects *A. mellifera* (an important pollinator) and *L. humile* (an introduced ant species). Studies have documented sublethal developmental effects for inorganic and organic forms of Se: selenate, selenite, methylselenocysteine, and selenocystine. Hladun et al. (2013a) found reduced relative growth index (RGI) for all forms of Se when larvae were reared on a spiked artificial diet. However, there were

no effects on prepupal weight for all treatments. This suggested that the honeybee larvae that survived to pupation had to achieve a minimum weight before viability. For *L. humile*, de La Riva and Trumble (2016) tested selenate and found detrimental effects at the colony level in a 60-days exposure study. Brood surface area was reduced, and few capped cells and no pupae were observed. In addition, no brood was produced by the end of the experiments. *L. humile* fed selenate in a 25% sucrose solution produced fewer eggs, and the viability and development of the offspring were reduced as well (de La Riva and Trumble 2016).

Lepidopteran species have been extensively studied on the sublethal effects of Se on an artificial laboratory diet; *S. exigua* was the subject of most of the studies. In an artificial diet, both selenate and selenite reduced pupal weight at 12 µg/g (Trumble et al. 1998). In addition, time to pupation and adult emergence were delayed, and decreased relative growth rate (RGR) and RGI were also observed. However, the organic forms seemed to have a limited effect on development. Seleno-DL-methionine did not affect any developmental parameters, while seleno-DL-cystine only affected RGR (Trumble et al. 1998). Bañuelos et al. (2002) observed reduced growth when 1st instars were exposed to selenate by feeding on saltbush leaves. Vickerman and Trumble (2003) found no effect on the development of *S. exigua* on alfalfa plants irrigated at a lower dose of 0.0066 g/60 liter, while 0.20 g/60 liter had a significant impact on the stage at death and RGI. Popham et al. (2005) reported a dose-dependent response of reduced larval weight of cabbage looper *T. ni* from ranges 25–100 ppm of selenite in an artificial diet. In other experiments in the tested ranges of 0–20 ppm, larval growth lagged at the 2 highest concentrations (10 and 20 ppm) regardless of feeding procedure: entire larval stage on a treated diet or treated diet until 4th instar then transferred to untreated diet and vice versa. There were no effects on pupal weight except in the second protocol (treated diet then moved to untreated diet), where the 10 ppm Se group had a statistically higher mean pupal weight suggesting a benefit to a Se-supplemented diet (Popham et al. 2005). Lalitha et al. (1994) also documented a benefit of dietary Se in the rice moth *Corcyra cephalonica* (Stainton) reared on a wheat flour diet until the 4th instar. At 2 ppm selenite, larval weight increased by 100% and declined (30%) at a slightly higher concentration of 4 ppm, indicating a narrow range where Se may be beneficial. Popham and Shelby (2007) subjected *H. virescens* to 5 different treatments in an artificial diet: selenate, selenite, seleno-DL-cysteine, seleno-DL-methionine, and a selenized wheat product. Selenate did not affect time to pupation or emergence at rates 5 times more than those tested with selenite. Test insects exhibited a wide range of sublethal effects to the other forms of Se, including a decreased rate of development, reduced pupation, reduced pupal weight, and less adult emergence.

Lepidopteran pest species showed similar effects on development when exposed to Se through host plant feeding. *Plutella xylostella* decreased larval weight gain on princes' plume watered at 8 mM selenate for 3 days (Freeman et al. 2006). *Pieris rapae* exhibited severe larval growth inhibition on mustard and princes' plume host plants watered with Se. Newly hatched larvae did not grow within 9 days of feeding on mustard (20 µM Se), and all died. In addition, 9-day-old larvae introduced to mustard plants lost 20% of their weight within the first day, while control larvae gained 30% during the same period (Hanson et al. 2003). Freeman et al. (2006) also observed decreased larval weight when *P. rapae* was fed with a treated princes' plume (80 mM Se). This lack of feeding and subsequent weight loss suggests that, at least in some systems, Se can act as an antifeedant or repellant.

Table 2. Impact of selenium on the growth, development, and reproduction of insects

Order	Species	Se Form	Testing method	Observations	References
Ephemeroptera	*Centroptilum triangulifer*	Selenous acid/Selenite	4–6 days old larvae (Periphyton exposed to 5, 10, 20 µg/liter for 7 or 9 days) Fed for 4.5–6 wk (until the emergence of subimagos)	Decrease in fecundity (most pronounced in 2 highest conc); Reduced adult body mass	Conley et al. (2009)
Orthoptera	*Acheta domesticus*	Selenate	Feeding *B. juncea* leaf grown in 20 µM solution	Weight reduction ~10% (nonchoice)	Freeman et al. (2007)
		Selenite	2 wk old crickets fed torula yeast-based diets (0.1, 0.3, 1, 3, 10 µmol Se/kg) for 5 wk	No effect on growth at any conc. vs 1 µmol Se/kg	Ralston et al. (2006)
	Various spp.	Selenate	*S. pinnata* grown in 40 µM (high) or 2 µM (low) solution	No molts produced in high 7DAE	Freeman et al. (2007)
Hemiptera	*Podisus maculiventris*	Selenate	Feeding *S. exigua* larvae reared on a diet 109 µg/g and 135 µg/g dry weight	Decreased developmental rate. Control nymphs achieved stadia 3, 4, 5, adult faster. About 20% less on both treatments vs fed control	Vickerman and Trumble (2003)
Hymenoptera	*Apis mellifera*	Selenate	Larva: artificial diet (0, 0.2, 0.4, 0.6, 1, 2 mg/liter)	No effect on prepupal weight at day 10. Reduced RGI[a]	Hladun et al. (2013a)
		Selenite	Larva: artificial diet (0, 0.2, 0.4, 0.6, 1, 2 mg/liter)	No effect on prepupal weight at day 10. Reduced RGI[a]	Hladun et al. (2013a)
		Methylseleno-cysteine	Larva: artificial diet (0, 4, 6, 7, 9, 10 mg/liter)	No effect on prepupal weight at day 10. Reduced RGI[a]	Hladun et al. (2013a)
		Selenocystine	Larva: artificial diet (0, 2, 4, 6, 8, 10 mg/liter)	No effect on prepupal weight at d 10. Reduced RGI[a]	Hladun et al. (2013a)
		Selenate	0.6 mg/kg Se in sugar syrup 6 mg/kg Se in pollen patty For 60 days	Reduced brood surface area. No effect on whole-colony weight, forager activity. Reduced total worker weight. Very few capped cells and no pupae. Consumed 42% less pollen patty vs control. Produced no brood by the end of experiment.	Hladun et al. (2016)
	Linepithema humile	Selenate	25% sucrose (0, 5, or 10 mg Se/ml)	Fewer eggs, viability and development of offspring affected	de La Riva and Trumble (2016)
	Cotesia marginiventris	Selenate	*S. exigua* larvae feeding on *M. sativa* irrigated with 3.3 mg/liter Se	Larval development and adult eclosion 2 days longer; no effects on time from pupation to adult; cocoons weighed 10% less	Vickerman et al. (2004)
Lepidoptera	*Spodoptera exigua*	Selenate	Larval artificial diet (5–7 conc)	Reduced pupal weight at 12 µg/g; increased time to pupation and time to adult emergence; decreased RGR[b] and RGI[a]	Trumble et al. (1998)
		Selenite	Larval artificial diet (5–7 conc)	Reduced pupal weight at 12 µg/g; increased time to pupation and time to adult emergence; decreased RGR,[b] and RGI[a]	Trumble et al. (1998)
		Seleno-DL-methionine	Larval artificial diet (5–7 conc)	No effect on pupal weight, developmental times, RGR,[b] and RGI[a]	Trumble et al. (1998)
		Seleno-DL-cystine	Larval artificial diet (5–7 conc)	No effect on pupal weight, developmental times, RGR[b]; decreased RGI[a]	Trumble et al. (1998)

Table 2. Continued

Order	Species	Se Form	Testing method	Observations	References
		Selenate	1st instar fed leaves collected from different *Atriplex* lines for 30 days (1 mg/liter with sulfate and chloride salts 90 days exposure)	Reduced growth	Bañuelos et al. (2002)
		Selenate	Feeding *M. sativa* irrigated with 0.0066 g/60 liter and 0.20 g/60 liter of water	Low: no effect on pupal weight, days to pupation, days to adult, stage at death, RGI[a] High: no effect on pupal weight, days to pupation, days to adult, but significant effect on stage at death and RGI[a]	Vickerman et al. (2002b)
	Trichoplusia ni	Selenite	Artificial diet (1–100 ppm)	No effect on larval weight (1–10 ppm), 40% reduction (25 ppm), 62% reduction (50 ppm), 75% reduction (100 ppm)	Popham et al. (2005)
			Artificial diet (0, 1, 5, 10, 20 ppm) i) Entire larval stage until pupation ii) Treated diet until early 4th instar then transferred to untreated diet iii) Untreated diet before the onset of 4th instar then transferred to treated diet	i) Lagged growth at 10 and 20 ppm; no effect on pupal weight ii) Lagged growth at 10 and 20 ppm; higher mean pupal weight at 10 ppm iii) Lagged growth at 10 and 20 ppm; no effect on pupal weight	Popham et al. (2005)
	Plutella xylostella Stanleyi	Selenate	Nonchoice bioassay: *S. pinnata* leaves watered with 80 mM Se for 3 days	No effect on larval weight gain	Freeman et al. (2006)
	Plutella xylostella G88	Selenate	Nonchoice bioassay: *S. pinnata* leaves watered with 80 mM Se for 3 days	Decrease in larval weight gain	Freeman et al. (2006)
	Pieris rapae	Selenate	Nonchoice bioassay: *B. juncea* watered with 20 µM Se i) Newly hatched larvae allowed to feed for 9 days ii) 9 days larvae allowed to feed for 2 days	i) No larval growth ii) Lost 20% of f. wt in the 1st day vs 30% gain in untreated control	Hanson et al. (2003)
		Selenate	Nonchoice bioassay: *S. pinnata* leaves watered with 80 mM Se for 3 days	Decrease in larval weight gain	Freeman et al. (2006)
	Corcyra cephalonica	Selenite	Wheat flour diet (0.5, 1, 2, 4 ppm) reared until 4th instar	100% increase in larval weight (2 ppm) and 30% decrease in larval weight (4 ppm); increase in weight was directly proportional to Se added up to 2 ppm	Lalitha et al. (1994)
	Heliothis virescens	Selenate	Artificial diet (1, 100, 200, 500 µg/g)	No effect on the rate of development (5–100 µg/g), pupation, emergence, and pupal weight	Popham and Shelby (2007)
		Selenite	Artificial diet (1, 5, 25, 50, 100 µg/g)	Decreased rate of development, pupation (28% at 100 µg/g), emergence (7% at 100 µg/g); Reduced pupal weight	Popham and Shelby (2007)
		Seleno-DL-cysteine	Artificial diet (1, 100, 200, 500 µg/g)	No effect on the rate of development (5–100 µg/g) and pupal weight; decreased rate of pupation and emergence	Popham and Shelby (2007)
		Seleno-DL-methionine	Artificial diet (1, 5, 25, 50, 100 µg/g)	Decreased rate of development, pupation (15% at 50 µg/g) and emergence; No effect on pupal weight	Popham and Shelby (2007)

Table 2. Continued

Order	Species	Se Form	Testing method	Observations	References
Diptera		Sel-Plex 2000[c]	Added into artificial diet (0, 1, 5, 25, and 50 μg/g)	Decreased rate of development, pupation (8% at 25 μg/g) and emergence (0% at 25 μg/g); No effect on pupal weight	Popham and Shelby (2007)
	Drosophila melanogaster	Selenite	Adult flies on artificial media for 14 days (combinations of 10^{-6} M Se or untreated) then transferred to untreated media to oviposit for 36 h	Viability of eggs >90% under all conditions; Decrease by 50% in the number of eggs when both sexes maintained on chemically defined medium without selenium vs when either males or females maintained on complete diet or diet supplemented with Se	Martin-Romero et al. (2001)
	Chironomus decorus	Various[d]	96 h feeding with 12 days old 4th instar on *R. maritima* substrate	Midges that bioaccumulated highest levels of Se had the greatest final mean weight than that of controls which had the lowest	Alaimo et al. (1994)
			14 days feeding with egg to pupation on *R. maritima* substrate	Decrease in mean midge weight as increase in Se	
		Selenate	4th instar (12–13 days) fed algal diet of *S. capricornutum* (0, 4, 10, 40 μg Se/liter) for 4 d	No effect on growth rate; reduced larval growth at 96 h (>1 μg Se/liter)	Malchow et al. (1995)
		Selenite	4th instar (12–13 days) fed algal diet of *S. capricornutum* (0, 10, 40 μg Se/liter) for 4 days	No effect on growth rate; reduced larval growth at 96 h (>1 μg Se/liter)	Malchow et al. (1995)
		Selenate/selenite mixture (6:1)	30 d chronic testing (0, 750, 1,500, 3,000, 6,000 μg/liter Se)	Increase in day of first emergence and emergence time ≥ 837 μg/liter	Ingersoll et al. (1990)
	Chironomus dilutus	Selenate	2nd instar (7–9 days old) in aqueous Se (4 μg/liter Se) for 10 days followed by clean water for 10 days	No effect on the growth rate, time of adult emergence, adult weight; Sex ratio (M:F) 1.11 vs 1.41 control	Franz et al. (2011)
		Selenite	2nd instar (7–9 days old) in aqueous Se (4 μg/liter Se) for 10 days followed by clean water for 10 days	No effect on the growth rate, time of adult emergence, adult weight; Sex ratio (M:F) 0.35 vs 1.41 control	Franz et al. (2011)
		Seleno-DL-methionine	2nd instar (7–9 days old) in aqueous Se (4 μg/liter Se) for 10 days followed by clean water for 10 days	Reduced growth rate at 10 days, but no effect at 20 days; no effect on time of adult emergence but met only 56% criterion of adult emergence vs 82% control; no effect on adult weight; Sex ratio (M:F) 0.87 vs 1.41 control	Franz et al. (2011)
		Selenite	9–10 days old larvae exposed to water-borne Se or SeNP[e] (5, 15, 50, 100, and 1,000 μg Se/liter) for 10 days	Reduced growth compared to control at highest conc. of nanoparticles SeNP[e] water-borne (overlying water Se): LOEC = 592 μg/L NOEC = 60.2 μg/L IC_{50} = 281 μg/g d.w. IC_{25} = 130 μg/g d.w. (whole-body Se): LOEC = 63.6 μg/liter NOEC = 45.7 μg/liter IC_{50} = 57.0 μg/g d.w. IC_{25} = 51.1 μg/g d.w.	Gallego-Gallegos et al. (2013)

Table 2. Continued

Order	Species	Se Form	Testing method	Observations	References
			9–10 days old larvae fed spiked fish food SeNP[a] (nominal concentrations of 5, 15, 50, and 150, 500 μg Se/g d.w.) for 10 days	Reduced growth compared to control at highest conc. of SeNP[a] dietary (food Se): LOEC = 784 μg/liter; NOEC = 219 μg/liter; IC_{50} = 398 μg/g d.w.; IC_{25} = 177 μg/g d.w. (whole-body Se): LOEC = 194 μg/liter; NOEC = 89.8 μg/g d.w.; IC_{50} = 96.2 μg/g d.w.; IC_{25} = 77.1 μg/g d.w.	
			9–10 days old larvae spiked selenized algae (*Scenedesmus* sp.) (nominal concentrations of 5, 15, 50, and 150 μg Se/g d.w.) for 10 days	No effect on larval growth	
Diptera	*Megaselia scalaris*	Selenate	Oviposition bioassay: *Drosophila* diet (0, 100, 200, 300, 400, and 500 μg/g) for 2 days; *Drosophila* diet (0, 100, 200, 300, 400, and 500 μg/g) egg to adult	No effect on egg hatching; Delay in larval development conc. as low as 100 μg/g; No effect on number of days to complete pupariation; No effect on number of days for females to emerge as compared to males; No females emerged at 500 μg/g	Jensen et al. (2005)
		Selenite	Oviposition bioassay: *Drosophila* diet (0, 100, 200, 300, 400, and 500 μg/g) for 2 days; *Drosophila* diet (0, 100, 200, 300, 400, and 500 μg/g) egg to adult	No effect on egg hatching; Delay in larval development conc. as low as 300 μg/g; No effect on number of days to complete pupariation; No effect in number of days for female to emerge as compared to males	Jensen et al. (2005)
		Seleno-L-methionine	Oviposition bioassay: *Drosophila* diet (0, 0.5, 5, 25, 50, and 100 μg/g) for 2 days; *Drosophila* diet (0, 0.5, 5, 25, 50, and 100 μg/g) egg to adult	No effect on egg hatching; Delay in larval development conc. as low as 50 μg/g; No effect on number of days to complete pupariation; Increase in number of days for female to emerge as compared to males at 25 μg/g	Jensen et al. (2005)
		Se-(methyl) selenocysteine hydrochloride	Oviposition bioassay: *Drosophila* diet (0, 0.5, 5, 25, 50, and 100 μg/g) for 2 days; *Drosophila* diet (0, 0.5, 5, 25, 50, and 100, 200, 400, 800 μg/g) egg to adult	Reduced egg hatchability only at highest conc. (100 μg/g); Delay in larval development conc. as low as 25 μg/g; no effect on number of days to complete pupariation; Increase in number of days for female to emerge as compared to males at 25 μg/g	Jensen et al. (2005)

Table 2. Continued

Order	Species	Se Form	Testing method	Observations	References
		Selenate	Diet flakes rehydrated (0, 100, 200, 300, 400, 500 ug/g) egg to adult or 35 days	Delays in larval developmental time as low as 100 ug/g; no effect on number of days required to complete pupariation	Jensen et al. (2006)
		Selenate	Diet flakes rehydrated (0, 100, 200, 300, 400, 500 ug/g) after 10 days number of larvae counted	No effect on fecundity (viable larvae per female)	Jensen et al. (2007)
	Culex quinquefasciatus	Selenate	Solutions (2, 4, 8, 16, 32 mg/liter) 2nd instar to adult	Relative growth index of all treatments was significantly different vs control from d 4 to experiment termination (as low as 2 mg/liter)	
	Ephydra cinerea	Selenate	Solutions (10–20,000 µg/liter) 3rd instar for 24 h and 48 h	No effect on larval weight changes and weight differences	Rosetta and Knight (1995)
		Selenite	Solutions (10–20,000 µg/L) 3rd instar for 24 h and 48 h	No effect on larval weight changes and weight differences	Rosetta and Knight (1995)
		Seleno-DL-methionine	Solutions (10–20,000 µg/liter) 3rd instar for 24 h and 48 h	No effect on larval weight changes and weight differences	Rosetta and Knight (1995)

[a] Relative growth index.
[b] Relative growth rate.
[c] Selenized yeast product containing 2000 µg/g Se, equal to or greater than 98% organic form, primarily as SeMet.
[d] Analysis of water-borne selenium levels where the substrate was collected.
[e] Selenium nanoparticles.

Considerable information describing the effects of organic and inorganic Se forms on chironomid development is available. These studies highlight the importance of the time of exposure to Se. For example, *C. decorus* larvae fed on selenium-contaminated widgeon grass (*Ruppia maritima* L.) in 96-h (4th instar) or 14-days (egg to pupation) feeding times reported contradicting sublethal effects (Alaimo et al. 1994). For 96-h exposures, controls had the lowest mean weight, while midges that accumulated the most Se had the highest mean weight. In contrast, in the 14-days experiment, higher Se accumulation decreased mean midge weight. The authors suggest that the differing results may be due to the prolonged exposure time. Malchow et al. (1995) also investigated *C. decorus* on a non-artificial diet of algae (*Selenastrum capricornutum* [Korshikov] Nygaard, Komárek) with selenate (0–40 µg/liter) and selenite (0–40 µg/liter). At higher concentrations, larval growth was reduced at 96 h. In addition, adult emergence was delayed when larvae were maintained at a 6:1 ratio of selenate and selenite (Ingersoll et al. 1990). Another chironomid species, *C. dilutus* was tested against selenate, selenite, and seleno-DL-methionine as larvae in aqueous solutions (4 µg Se/liter) (Franz et al. 2011). Both inorganic forms had no effect on the growth rate, time of adult emergence, or adult weight. On the other hand, seleno-DL-methionine reduced the growth rate during the first half of the experiment. Day 10 mean larval dry weight was 48% of the larval dry weight at day 20 versus 61% for control. In addition, adult emergence was only 56% for the seleno-DL-methionine compared to 82% in the control group. Interestingly, the male-to-female sex ratio was changed with a bias towards females with selenate, selenite, and seleno-DL-methionine. However, the effect was most drastic with selenite (0.35 Se vs. 1.41 control). This shift in sex ratio may suggest increased offspring in the next generation. Gallego-Gallegos et al. (2013) further examined the sublethal effects of selenite on *C. dilutus*. Nine to ten-day-old larvae exposed to water-borne Se, nanoparticles, or nanoparticles in fish food all had reduced growth at the highest concentrations. However, selenite in the form of spiked algae (*Scenedesmus* sp.) did not affect larval development. In a series of oviposition bioassays, the spiked diet did not affect *M. scalaris* egg hatching when subject to selenate, selenite, or seleno-DL-methionine at an exposure time of 2 days (Jensen et al. 2005). However, Se-(methyl)-selenocysteine hydrochloride reduced egg hatchability at the highest concentration tested (100 µg/g). Larval development was delayed for all Se forms when observed from egg to adult on the same concentrations for each compound. This delay was registered at 25, 50, 100, and 300 µg/g for selenocysteine, seleno-L-methionine, selenate, and selenite, respectively. No forms had any effect on the number of days to complete pupariation. There was an increase in the number of days for females to emerge compared to that of males in only both organic forms at 25 µg/g. Selenocysteine and seleno-L-methionine displayed the most negative sublethal effects compared to all other forms suggesting high toxicity with organic forms. Furthermore, Jensen et al. (2006) also observed comparable effects on development and no effect on fecundity when diet flakes were rehydrated with Se.

Selenium has been tested for developmental effects against a few other insect species. In a study designed to evaluate possible sex-specific effects of Se, male and female *D. melanogaster* were maintained separately on chemically defined media with or without selenite 10^{-6} M or complete media (Martin-Romero et al. 2001). After 14 days, they were combined and allowed to oviposit on untreated media for 36 h. Although the viability of eggs was not affected, the number of oviposited eggs decreased by 50% when both sexes were maintained on a chemically defined medium without Se versus all other treatments. This suggests that Se may benefit egg

production and/or fertilization. The common house mosquito, *C. quinquefasciatus* reared in solutions of selenate (2–32 mg/liter) resulted in a negatively affected RGI as low as 2 mg/liter from day 4 to experiment termination (Jensen et al. 2007). Rosetta and Knight (1995) found minimal effects of solutions of selenate, selenite, and seleno-DL-methionine on the brine fly, *E. cinerea*. No effect on larval weight changes and weight differences was observed at 10–20,000 µg/liter for 24 and 48 h. These results were similar to the minimal effects observed in *C. dilutus* (Franz et al. 2011).

Predatory insects exposed to Se through ingestion of their prey have shown that Se can transfer between upper trophic levels as well as between plants and herbivores. Vickerman and Trumble (2003) provided the spined soldier bug, *P. maculiventris* with treated *S. exigua* larvae as prey and observed a 20% reduction in weight compared to control predators and decreased developmental rates to reach various stadia. A parasitoid, *C. marginiventris*, was allowed to develop completely in *S. exigua* larvae fed alfalfa plants irrigated with 3.3 mg/L (Vickerman et al. 2004). Compared to controls, parasitoid larval growth and adult eclosion on selenium-contaminated prey were delayed by 2 days. However, no significant effects were seen on the time required from pupation to adult. Cocoons also weighed 10% less than that of the control. However, the authors were unable to determine whether the increased parasitoid developmental time was entirely related to the effects of Se on the parasitoid larvae or was due, in part, to the slowed development of the host. Previously we noted that the presence of Se did not always cause increased mortality of biocontrol agents. However, Se can have developmental effects other than mortality that will impact the fitness of natural enemies used in pest management programs. As a result, in those pest systems where selenium use is contemplated, additional research may be necessary to ascertain if selenium use is compatible with key biological control agents.

Minimal information is available on the effects of Se on development and reproduction for the orders of Ephemeroptera and Orthoptera. Conley et al. (2009) fed 4–6 days-old larvae of *Centroptilum triangulifer* (McDunnough) periphyton exposed to a mixture of selenious acid and selenite. Fecundity was reduced at the 2 highest concentrations of 10 and 20 µg/liter. In addition, the Se body burden was associated with reduced adult body mass; however, it was not linked to the decrease in fecundity. Freeman et al. (2007) found sublethal effects on *A. domesticus* and various orthopteran species. The weight of *A. domesticus* was reduced by 10% while the different orthopteran species produced no molts compared to 43 produced in the control group suggesting a delay in development. In contrast, Ralston et al. (2006) found no significant effect of a selenite-spiked diet on growth when 1.0 µmol Se/kg was compared to 0.1, 1, 3, or 10 µmol Se/kg. Thus, like other insect orders examined, the impact of Se was not consistent, and reliable predictions of the results of exposure are not yet possible.

Impact on Behavior and Other Effects

Selenium also caused behavioral effects leading to changes in consumption, preference, or avoidance of Se detected in food or substrate (Table 3). The complex nature of Se toxicity has warranted investigations to determine other effects Se may have on insects.

Hladun et al. (2012) conducted various experiments on *A. mellifera* to determine consumption responses to selenate and selenomethionine. Selenate at ranges from 0.6–6000 µg/mL in 1M sucrose produced no significant effects on proboscis extension reflex (PER) in an antennal response assay and total consumption in a proboscis response assay. However, in the sucrose response threshold

(SRT) assays, the authors observed a dose-dependent change in PER to increasing sucrose concentrations, lowering the overall PER for all Se treatments. In contrast, selenomethionine elicited more drastic behavioral changes. PER responses to antennal stimulation were significantly lower at 60 and 6000 µg/ml of Se in 1M sucrose. No differences in total consumption were noted in the proboscis response assays. Like selenate, there was a dose-dependent change in PER to increasing concentrations of sucrose where SRT occurred between 3 and 10% except for at 0.6 and 6 µg/ml where SRT was as high as 30%. Selenomethionine did not affect SRT. Burden et al. (2016) also observed no effect on PER in a sucrose responsiveness test for selenate and methylseleno-L-cysteine. Hladun et al. (2013a) found evidence for reduced consumption of 4 Se forms: selenate, selenite, methylselenocysteine, and selenocystine. Forager bees were treated with 19.2 µl of a 50% sucrose solution spiked with Se. The bees were given untreated sucrose solutions in the following days, and consumption was calculated. In a field setting, *A. mellifera* did not discriminate between selenate-treated floral resources even at moderately high concentrations, suggesting that these pollinators will not avoid Se during foraging (Quinn et al. 2011, Hladun et al. 2013b).

Interestingly, Se may impair the memory function of *A. mellifera* at sublethal doses of selenate and methylseleno-L-cysteine (Burden et al. 2016). An acute exposure as low as 18 ng reduced performance during a long-term recall test for both forms. These learning and memory impairments can severely impact colony success. Selenium may cause significant effects on the microbiome of Apidae (Rothman et al. 2019a, 2019b, 2020). When 0.6 mg/liter of selenate was provided in 50% sucrose solutions, *A. mellifera* experienced an altered microbiome composition over 7 days (Rothman et al. 2019b). In *Bombus impatiens* Cresson, selenate also altered microbiome composition and reduced core symbionts Exact Sequence Variants (ESVs) (Rothman et al. 2020). The microbiome may be a key component of bumble bee survival when exposed to Se, based on a study by Rothman et al. (2019a). Inoculated *B. impatiens* experienced a significant increase in mean survival when exposed to selenate in 40% sucrose. Surprisingly, the authors found a significant increase in alpha diversity of the bee microbiome while finding that some core symbiont ESVs decreased in proportional abundance.

The behavioral effects of Se were minimal in other hymenopterans. *Linepithema humile* did not show any preference toward untreated solutions over selenate, selenite, seleno-L-methionine, or methylselenocysteine in 10 or 30% sucrose solutions (de La Riva et al. 2014). Competition assays with *L. humile* and bi-colored pyramid ant, *Dorymyrmex bicolor* Wheeler, also revealed a minimal effect on behavior between these 2 species (de La Riva and Trumble 2016). There was no effect on the latency of bait discovery with the presence of a competitor or Se exposure for either species. However, *D. bicolor* did experience a slower time to bait discovery when Se exposure and presence of a competitor occurred in combination. Similarly, the parasitoid, *C. marginiventris*, displayed no attraction or repellency to organic Se volatiles in an olfactometer bioassay (Vickerman et al. 2004). This suggests that Se volatiles released by their caterpillar prey during feeding would not affect host location by the adult parasites. Of all the insect orders examined for behavioral responses to Se, the hymenopterans appeared to have the most reduced ability to detect or respond to Se in their environment. The inability to avoid Se can have significant implications for population fitness. For example, chronic exposure to Se in some hymenopterans (particularly honeybees) resulted in a "malaise" effect that greatly reduced foraging and led to the collapse of the hive (Hladun et al. 2016).

Table 3. Impact of selenium on behavior and other effects of insects

Order	Species	Se Form	Testing method	Observations	References
Odonata	*Sympetrum corruptum*	Selenate	Feeding *C. quinquefasciatus* 2nd instars reared in 15 µg/g; Grown in treated solution with treated prey and without	Increased feeding when in the treatment solution	Jensen (2006)
Blattodea	*Gromphadorhina portentosa*	Sodium hydrogen selenite	0.01 µmol Se solution (nonlethal dose)	Effect on enzymatic activity	Nakonieczny (1993)
Orthoptera	*Acheta domesticus*	Selenate	Feeding *B. juncea* leaf grown in 20 µM solution	5x more crickets preferred to feed on the untreated leaf (choice)	Freeman et al. (2007)
	Various spp.	Selenate	*S. pinnata* grown in 40 µM (high) or 2 µM (low) solution	Significantly less feeding on treated plants (choice) <10% feed on high vs ~70% low (7DAE)	Freeman et al. (2007)
			Field plot study *S. pinnata* pretreated for 8 w with high Se concentration (40 µM), and 4 low-Se plants (2 from each accession) pretreated for 8 w with 2 µM	Decreased feeding; final leaf areas was 5-fold higher for high-Se vs low-Se	Freeman et al. (2007)
Hemiptera	*Myzus persicae*	Selenate	Feeding *B. juncea* plants grown in 0, 1, 5, 10, or 20 µM solution (choice) Plants 0, 20, or 40 µM (choice)	7 times more aphid on control vs 1 µM Se, few if any at higher conc. ~100% aphids found on control 7DAE	Hanson et al. (2004) Hanson et al. (2004)
	Brevicoryne brassicae	Selenate	*R. sativus* (0, 0.51 mg, 1.53 Se/liter)	Decrease aphid numbers and aphid mummies No effect on leaf number or avg leaf damage	Hladun et al. (2013b)
Hymenoptera	*Apis mellifera*	Selenate	Antennal response assay, with PER[a] (0.6–6,000 mg/ml) in 1M sucrose + or – extension	PER[a] to antennal stimulation not significantly different than 1M sucrose, but higher than water at all conc.	Hladun et al. (2012)
			Proboscis response assay (0.6 µl) (0.6–6,000 mg/ml) in 1M sucrose + or – total consumption	No significant difference in consumption of droplet between 1M sucrose and any of 5 selenate conc.	
			Sucrose response threshold assay (24 h later fed 20 µl of treatment, then antennae stimulated with increasing sucrose solutions) (0.6–6,000 mg/ml) in 1M sucrose + or – extension Total consumption	Dose-dependent change in PER[a] to increasing conc. of sucrose (SRT at 3-10% except 60ug) at 2 h; Decrease in PER low as 17%; No interaction between sucrose antennal treatment and selenate feeding treatment; selenate feeding did not alter the sucrose response threshold of 3–10%	
			(0.6–6,000 mg/ml) in 1M sucrose	No effect at 24 h	
		Seleno-methionine	Antennal response assay, with PER[a] (0.6–6,000 mg/ml) in 1M sucrose + or – extension	PER[a] responses to antennal stimulation were significantly lower than 1M sucrose at 60, 6,000 µg, but higher than water at 4 lowest conc.	Hladun et al. (2012)
			Proboscis response assay (0.6 µl) (0.6–6,000 mg/ml) in 1M sucrose + or – total consump.	No significant difference in consumption of droplet between 1M sucrose and any of the 5 SeMet conc.	

Table 3. Continued

Order	Species	Se Form	Testing method	Observations	References
			Sucrose response threshold assay (24 hrs later fed 20 µl of treatment, then antennae stimulated with increasing sucrose solutions) (0.6–6,000 mg/ml) in 1M sucrose + or – extension	Dose-dependent change in PER[a] to increasing conc. of sucrose (3 and 10% except for 0.6 and 6 µg) at 2 h; SeMet feeding treatment did not have significant effect on SRT; Interaction of treatment feeding and sucrose antennal treatment was not significant	
			Total consumption (0.6–6,000 mg/ml) in 1M sucrose	No effect at 24 h	
		Selenate	Forager: 19.2 µl of 50% sucrose solution (0, 30, 60, 120, 240, 480 mg/liter) then 50% every day	Reduced volume consumed	Hladun et al. (2013a)
		Selenite	Forager: 19.2 µl of 50% sucrose solution (0, 30, 60, 120, 240, 480 mg/liter) then 50% every day	Reduced volume consumed	Hladun et al. (2013a)
		Methylseleno-cysteine	Forager: 19.2 µl of 50% sucrose solution (0, 104, 125, 150, 200, 250 mg/liter) then 50% every d	Reduced volume consumed	Hladun et al. (2013a)
		Selenocystine	Forager: 19.2 µl of 50% sucrose solution (0, 104, 125, 150, 200, 250 mg/liter) then 50% every day	Reduced volume consumed	Hladun et al. (2013a)
		Selenate	High vs low *B. juncea* plants (20 or 0 µM)	No effect on floral visitation	Quinn et al. (2011)
			High vs low *S. pinnata* plants (80 and 0 µM)	No effect on flora visitation	
		Selenate	*R. sativus* (0, 0.51 mg, 1.53 Se/liter)	No effect on pollinator visitation	Hladun et al. (2013b)
		Selenate	Fed 3 µl of 0.5 M sucrose + Se (0.6, 6, 60 mg/liter) 3 h prior to conditioning	No effect on PER[a] during sucrose responsiveness test; 1.8 ng before conditioning caused reduction in behavioral performance during conditioning; 18 ng caused reduction in performance during long-term recall test; No effect on short term recall tests	Burden et al. (2016)
			Fed 3 µl of 0.5 M sucrose + 6 mg/liter Se beginning of long-term recall test	No effect on either recall tests	
		Methylseleno-L-cysteine	Fed 3 µl of 0.5 M sucrose + Se (0.6, 6, 60 mg/L) 3 h prior to conditioning	No effect on PER[a] during sucrose responsiveness test; 18 ng caused reduction in performance during long-term recall test; no effect on short term recall tests	Burden et al. (2016)
			Fed 3 µl of 0.5 M sucrose + 6 mg/liter Se beginning of long-term recall test	No effect on either recall tests	
		Selenate	50% sucrose spiked with 0.6 mg/liter for 7 days	Altered microbiome	Rothman et al. (2019b)
	Bombus impatiens	Selenate	Microbiota-inoculated bees with 0.75 mg/liter selenate in 40% sucrose for 10 days	Increased bee survival (42%) for inoculated bees when exposed to Se	Rothman et al. (2019a)

Table 3. Continued

Order	Species	Se Form	Testing method	Observations	References
			60% sucrose spiked with 0.5 mg/liter for 4 days	Significant increase in the alpha diversity (as measured by the Shannon Diversity Index) off microbiome; ESVs[b] of some gut symbionts lower proportional abundance	Rothman et al. (2019a)
		Selenate	0.5 mg/liter into 60% sucrose for 4 days	Altered the composition of non-core bacteria; core symbiont ESVs[b] less abundant	Rothman et al. (2020)
	Linepithema humile	Selenate	Choice test 50 µg Se/ml in 10 or 30% sucrose (0,1, 2, 30, 60, 90, and 120 min)	No effect on choice	de La Riva et al. (2014)
		Selenite	Choice test 50 µg Se/ml in 10 or 30% sucrose (0,1, 2, 30, 60, 90, and 120 min)	No effect on choice	de La Riva et al. (2014)
		Seleno-L-methionine	Choice test 50 µg Se/ml in 10 or 30% sucrose (0,1, 2, 30, 60, 90, and 120 min)	No effect on choice	de La Riva et al. (2014)
		Methylseleno-cysteine	Choice test 50 µg Se/ml in 10 or 30% sucrose (0,1, 2, 30, 60, 90, and 120 min)	No effect on choice	de La Riva et al. (2014)
		Selenate	Competition assay with *D. bicolor*	No effect on latency of bait discovery	de La Riva and Trumble (2016)
			25% sucrose (0 or 5 mg Se/ml) 1 w exposure	No effect on competition behavior	
	Dorymyrmex bicolor	Selenate	Competition assay with D. bicolor Competition assay with *L. humile* 25% sucrose (0 or 5 mg Se/ml) 1 wk exposure	No effect on latency of bait discovery with Se alone, but slower time with Se and competitor; No effect on competition behavior	de La Riva and Trumble (2016)
	Cotesia marginiventris	Selenate	Olfactometer bioassay (Se irrigated *M. sativa* 3.3 mg/liter leaves *S. exigua* feeding damage and frass)	No Se-volatile-specific behavioral response	Vickerman et al. (2004)
Lepidoptera	*Spodoptera exigua*	Selenate	Choice test: Larval artificial diet (14.9, 18.5, 21.4, 24.8 µg/g) neonates or 3rd instar	Neonates and 3rd instars preferred control diet; decreased consumption	Vickerman and Trumble (1999)
		Selenite	Choice test: Larval artificial diet (4.8, 7.0, 9.1, 11.9 µg/g)	Neonates and 3rd instars preferred control diet; decreased consumption	Vickerman and Trumble (1999)
		Seleno-DL-cystine	Choice test: Larval artificial diet (9.0, 12.3, 15.2, 18.9 µg/g)	Neonates preferred the control diet, but 3rd instars had no preference; no effect on consumption	Vickerman and Trumble (1999)
		Seleno-DL-methionine	Choice test: Larval artificial diet (13.9, 17.8, 21.2, 25.1 µg/g)	Neonates had no preference except at 25.1 µg/g; 3rd instar had no preference; no effect on consumption	Vickerman and Trumble (1999)

Table 3. Continued

Order	Species	Se Form	Testing method	Observations	References
		Selenate	Food preference bioassay: *M. sativa* irrigated with 0.0066 g/60 liter and 0.20 g/60 liter of water (every half an hour for 5 h)	High: Neonates: no preference; 4th instars: preference for control only at time interval 3, no effect on consumption Low: Neonates: preference for control only at time interval 4; 4th instars: Preference for treated plants at time intervals 3, 5, 6, and 9; more consumption	Vickerman et al. (2002b)
			Oviposition preference bioassay: *M. sativa* irrigated with 0.0066 g/60 liter and 0.20 g/60 liter of water	Females preferred to oviposit on low Se treated plants over control; no preference between control and high Se plants	
	Trichoplusia ni	Selenate	Neonate larvae on *B. juncea* (1 mg/liter Se) for 14 d	Fewer pupae found on treated plants (14 vs 38 control)	Bañuelos et al. (2002)
		Selenite	Artificial diet (0, 5, 10 ppm) then infected with AcMNPV[c] i) Entire larval stage until pupation ii) Treated diet until early 4th instar then transferred to untreated diet iii) Untreated diet before the onset of 4th instar then transferred to treated diet	i) Increase in LC_{50} at 96 h of virus ii) Little effect on LC_{50} of virus iii) Increase in LC_{50} at 96 h of virus *LT_{50} decreased at higher viral concentrations in 5 ppm fed insects (averaged by dose for all Se regimes)	Popham et al. (2005)
	Plutella xylostella Stanleyi	Selenate	Choice bioassay: *S. pinnata* leaves watered with 80 mM Se vs untreated	No effect on larval preference	Freeman et al. (2006)
			Oviposition choice bioassay: *S. pinnata* plants watered with 80 mM Se vs untreated at 7 days	No effect on oviposition preference; 30 days after oviposition larvae completely eaten all plants	
	Plutella xylostella G88	Selenate	Choice bioassay: *S. pinnata* leaves watered with 80 mM Se vs untreated	Larval preference for untreated leaves	Freeman et al. (2006)
			Oviposition choice bioassay: *S. pinnata* plants watered with 80 mM Se vs untreated at 7 days	Oviposition preference for untreated leaves; 30 days after oviposition larvae fed less on treated plants	
	Pieris rapae	Selenate	Choice bioassay: *B. juncea* 20 µM selenate at 6 h	Larval preference for untreated leaves (*c*. 15-fold higher rate)	Hanson et al. (2003)
			Choice bioassay: *S. pinnata* leaves watered with 80 mM Se vs untreated	Larval preference for untreated leaves	Freeman et al. (2006)
			Oviposition choice bioassay: *S. pinnata* plants watered with 80 mM Se vs untreated at 7 days	Oviposition preference for untreated leaves; 30 days after oviposition larvae fed less on treated plants	
			Oviposition choice bioassay: *S. pinnata* plants watered with 80 mM Se vs untreated at 7 days	Oviposition preference for untreated leaves; 30 days after oviposition larvae fed less on treated plants	
Diptera	*Megaselia scalaris*	Selenate	Oviposition bioassay: *Drosophila* diet (0, 100, 200, 300, 400, and 500 µg/g) for 2 days	No oviposition preference	Jensen et al. (2005)
		Selenite	Oviposition bioassay: *Drosophila* diet (0, 100, 200, 300, 400, and 500 µg/g) for 2 days	No oviposition preference	Jensen et al. (2005)

Table 3. Continued

Order	Species	Se Form	Testing method	Observations	References
		Seleno-L-methionine	Oviposition bioassay: *Drosophila* diet (0, 0.5, 5, 25, 50, and 100 µg/g) for 2 days	No oviposition preference	Jensen et al. (2005)
		Se-(methyl) selenocysteine hydrochloride	Oviposition bioassay: *Drosophila* diet (0, 0.5, 5, 25, 50, and 100 µg/g) for 2 days	No oviposition preference	Jensen et al. (2005)
		Selenate	Oviposition preference: Diet (0, 100, 200, 300, 400, 500 µg/g) for 2 days	No oviposition preference between 50 µg/g vs control	Jensen et al. (2006)
	Culex quinquefasciatus	Selenate	Oviposition bioassay using experimental ponds (30 mg/liter Se) for 4 wk	No effect on the number of egg rafts	Jensen et al. (2007)
	Delia radicum	Selenate	*B. oleracea* var *italica* watered with 0.5 ml of 50 mg/liter Se in the field (2 growing seasons)	Increase in number of eggs laid on treated vs control for a single monitoring periods/dates during 1st generation (significant only at 2 dates)	Mechora et al. (2017)
Coleoptera	*Phyllotreta* spp.	Selenate	*B. oleracea* var *italica* watered with 0.5 ml of 50 mg/liter in field (2 growing seasons)	Increased damage on treated plants vs control (only 1 yr); Reduced number of pupae vs control both years (significant only 1 yr)	Mechora et al. (2017)

[a]Proboscis extension response.
[b]Exact Sequence Variants.
[c]*Autographa california* multiple nucleopolyhedrovirus.

In contrast, some lepidopteran larvae showed reduced feeding on the artificial diets containing Se, indicating that Se has a substantial repellent effect on those insects. Vickerman and Trumble (1999) provided beet armyworm neonates and 3rd instars with a choice between a control diet and a diet spiked with selenate, selenite, seleno-DL-cystine, or seleno-DL-methionine. The inorganic forms had the most repellent effect on neonates, and 3rd instars preferred the control diet over the treated diet. Furthermore, consumption of the treated diet was significantly reduced, showing evidence of antifeedant activity. On the other hand, the organic forms had variable responses where neonates displayed sensitivity to higher concentrations, but 3rd instars had no preference in choice studies. Vickerman et al. (2002b) observed varied responses when neonates and 4th instars were fed on alfalfa plants irrigated with selenate. At the higher concentration (0.20 g/60 liter), neonates had no preference for either untreated or treated plants, but 4th instars preferred treated plants at 4 of 10 observed time points. In addition, consumption increased on treated plants confirming that indicating that larvae would not always avoid selenium-containing host plant material. Other studies on *T. ni, P. xylostella,* and *P. rapae* revealed a similar preference for untreated plants over selenate-treated plants (Bañuelos et al. 2002, Hanson et al. 2003, Freeman et al. 2006). Thus, behavioral effects of Se such as repellency and food consumption not only vary between insect species, but also with the age of the insect at the time of exposure.

Oviposition preference for uncontaminated host plant material could reduce population-level effects and thereby minimize any negative outcome of Se exposure. However, the literature indicates ovipositional preference for low-selenium plants are not evident in all insect-plant systems. For example, *S. exigua* females preferred to oviposit on low-Se alfalfa plants over control plants but displayed no preference between high-Se and control plants (Vickerman et al. 2002b). Because the high rate of Se resulted in death of all the larvae, the authors concluded that these plants can potentially serve as a population 'sink' where pest larvae will be exposed to a lethal dose of Se. However, *P. xylostella* and *P. rapae* oviposited preferentially on untreated plants (Freeman et al. 2006). Further observation revealed that larvae fed less on the treated plants. In contrast, in the dipteran species, *M. scalaris*, showed no oviposition preference when presented with artificial diets spiked with selenate, selenite, seleno-methionine, or Se-(methyl)-selenocysteine hydrochloride (Jensen et al. 2005). Jensen et al. (2006) supported that *M. scalaris* has no oviposition preference for control diets even when the treated diet contained 500 µg/g of selenate, a concentration lethal to any larvae developing there. Similarly, *C. quinquefasciatus* also did not oviposit preferentially on experimental ponds with or without selenate (Jensen et al. 2007). Another dipteran, *Delia radicum* (L.) showed mixed results in the field where there were no differences in the number of eggs laid on traps next to selenium-treated or control plants on 11 of 13 sampling dates, but 2 of the sampling dates found more eggs near the treated plants (Mechora et al. 2017).

The orders Odonata, Orthoptera, Coleoptera, and Blattodea have comparatively limited literature available regarding sublethal effects on behavior. Most of the available studies measure feeding behavior. For example, a common dragonfly, *S. corruptum* increased feeding on *C. quinquefasciatus* when grown in a selenate solution compared to nymphs maintained in an untreated solution (Jensen 2006). Five times more *A. domesticus* preferred to feed on untreated mustard leaves than treated leaves grown in 20 µM of selenate solution (Freeman et al. 2007). A preference for untreated leaves was also observed for various Orthoptera species when given a choice of princes' plume leaves grown with or without methyl-selenocysteine.

In a field setting, herbivory by grasshoppers was variable when Se was present. Mechora et al. (2017) observed *Phyllotreta* spp. (Chevrolat in Dejean) of the family Chrysomelidae feeding damage on selenate-treated broccoli in the field. In 1 out of 2 growing seasons, there was increased damage on treated broccoli plants compared to control plants. However, fewer pupae were found on treated plants for both years (Mechora et al. 2017). Evidence suggests that aphid species can detect Se in host plants and thus avoid them. *M. persicae* preferred feeding on untreated *Brassica* plants. Seven times more aphids were observed on plants grown in selenate solutions as low as 1 µM (Hanson et al. 2004). At higher concentrations ≥5 µM, few, if any, aphids were found. Similarly, *Brevicoryne brassicae* (L.) numbers decreased on selenate-treated radish plants (Hladun et al. 2013b). The only study on a cockroach species was conducted by Nakonieczny (1993) on *Gromphadorhina portentosa* (Schaum). The author found reduced activities of several enzymes when treated at a sublethal dose of sodium hydrogen selenite.

Conclusion and Future Research Directions

This paper represents the most comprehensive review on the effects of Se on insects to date. The literature encompasses a wide variety of insects that have different life histories and ecological niches. The various ways that Se can affect survival, normal development and function, and behavior illustrate the complexity of Se as a toxicant. The effects vary depending on species, age of the insects, exposure method, the insect-plant system examined, and parameter studied. Although many of these studies investigated the effects of Se on insect mortality, growth, and physiology, the mode of action of Se on insects is remarkably variable. In fact, the variable responses between insect species and between plant-insect systems suggest that more than 1 mode of action may be active. Some of the studies reported in this review found Se exposure could alter the overall microbiome composition in bees, or that Se could replace sulfur in amino acids, resulting in non-functional proteins and enzymes. A recent study revealed that spider mites (*Tetranychus cinnabarinus* Boisduval) evolved adaptability for an increased rate of population growth and enhanced ability for Se metabolism after 40 generations of rearing on selenium-rich plants (Xu et al. 2021). Using gene expression and RNA interference approaches, the researchers found that a key GST gene (GSTd07) may be involved in Se metabolism. However, these mechanisms do not explain how Se kills some insects quite rapidly, or why some insects benefit from low to moderate concentrations. Clearly, elucidation of all potential modes of action will require considerable additional research and detailed studies are warranted to determine the effective concentrations and field performance against a wider range of beneficial and pest arthropods.

Nonetheless, a few generalizations can be made. For example, soil amendments with selenium for pest control should be avoided for plants (such as the Brassicaceae) that can transport selenium to flowers that are visited by honey bees. Even if immediate toxicity is not evident, the long-term effects on honey bee behavior and larval development should be avoided. In plants such as leafy vegetables (spinach, lettuce, celery, etc.), the use of selenium may be beneficial as long as foliar concentrations do not exceed maximum daily allowances. For ornamental plants or trees that are not insect pollinated, selenium applications for pest control appear valuable. In addition, insects that can be controlled using baits (such as ants) would be reasonable targets, particularly if the baits are formulated or presented in ways that minimize or eliminate human or companion animal exposure. Additional research with cockroaches, termites, and other urban pests is still needed, but the modes of action of selenium appear novel enough that this element may provide a rotational alternative for resistance management. The inability of most insects (at least those tested so far) to detect or behaviorally respond to toxic concentrations suggests that selenium has considerable potential for managing insect pests.

Author Contributions

John So (Conceptualization-Equal, Data curation-Lead, Formal analysis-Lead, Resources-Lead, Validation-Lead, Writing – original draft-Lead, Writing – review & editing-Equal), Dong-Hwan Choe (Supervision-Supporting, Validation-Supporting, Writing – review & editing-Supporting), Michael Rust (Supervision-Supporting, Validation-Supporting, Writing – original draft-Supporting, Writing – review & editing-Supporting), John Trumble (Conceptualization-Supporting, Validation-Supporting, Writing – original draft-Supporting, Writing – review & editing-Supporting), Chow-Yang Lee (Conceptualization-Equal, Data curation-Supporting, Funding acquisition-Lead, Methodology-Supporting, Project administration-Lead, Resources-Supporting, Supervision-Lead, Validation-Supporting, Writing – original draft-Supporting, Writing – review & editing-Equal)

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