

Chronic exposure to elevated levels of manganese and nickel is not harmful to a cosmopolitan detritivore, *Megaselia scalaris* (Diptera: Phoridae)

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Abstract Environmental contamination with metals such as manganese (Mn) and nickel (Ni) often results in elevated concentrations of these metals in plant tissues. At high concentrations, these metals are known to have detrimental effects on certain insect herbivores. Using laboratory bioassays and artificial diet, we investigated the development and survival of a cosmopolitan insect detritivore, *Megaselia scalaris* (Diptera: Phoridae), exposed to concentrations of Mn and Ni reaching 2 600 mg Mn/kg and 5 200 mg Ni/kg dry mass (dm) in artificial diet. Surprisingly, Ni and Mn at the concentrations tested did not harm this fly. Treatment groups from diets with 260–2 600 mg Mn/kg dm and 1 300–5 200 mg Ni/kg dm had significantly shorter larval development times, overall times to adult emergence, and both pupariation and pupal eclosion times compared to a control group. Wing length of females, a correlate of adult fitness, was also greater in metal treatment groups. Other measures including rate of egg hatch, percentage of emerging flies that were female, and wing length of male flies, were not significantly different in metal treatment groups. We conclude that *Megaselia scalaris* is tolerant of exceptionally high levels of Mn and Ni.

Key words detritivore, elemental defense, heavy metal, hyperaccumulator, pollution

Introduction

Manganese (Mn) and nickel (Ni) occur in soil both naturally and as anthropogenic contaminants. In serpentine soils, both metals may occur naturally at elevated levels (Alexander *et al.*, 2007). Although the level of natural Mn in soil ranges from 40–900 mg/kg, with an average of 330 mg Mn/kg, areas with anthropogenic contamination may contain soils with up to 7 000 mg Mn/kg (Barceloux, 1999a). Similarly, naturally occurring levels of Ni in soil range from 5–500 mg Ni/kg (Barceloux, 1999b), but concentrations at point sources for anthropogenic pollution, such as smelters, may be extraordinarily high, reaching

thousands of mg/kg (Barcan & Kovnatsky, 1998). Anthropogenic inputs of Mn and Ni are an increasing pollution problem (Alloway, 1990). Sources of Mn pollution include industrial metallurgy, fungicides, and anti-knock agents in gasoline (Gerber *et al.*, 2002), while Ni contamination commonly results from industrial metallurgy and the combustion of fossil fuels (Barceloux, 1999b). Although small amounts of both Mn and Ni are essential for animals, both metals have the potential to be toxic and carcinogenic at higher levels (Barceloux, 1999a,b).

Biomagnification (defined here as the presence of higher levels of a contaminant in an organism than in lower trophic levels) of Mn or Ni has not been found to occur, but bioaccumulation (defined here as the transfer of a contaminant from food or the environment to the organism, at any concentration) has been demonstrated (Mn: Kelley, 1914; Ni: Cataldo *et al.*, 1978). Plants and other organisms may acquire Mn or Ni and thereby become a contaminated food

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source for insect herbivores and detritivores feeding on dead plant or animal material.

Healthy plants may contain from 5–1 500 mg Mn/kg (Raven *et al.*, 1976), although 50 mg Mn/kg is a more typical value (Salisbury & Ross, 1978). Uncontaminated plants also contain concentrations of 1–10 mg Ni/kg (Reeves & Baker, 2000). In contaminated areas, plants may acquire elevated levels of Mn or Ni. Lytle *et al.* (1995) found that herbaceous terrestrial plants close (< 10 m) to a Utah roadway had around 100 mg Mn/kg compared to less than 10 mg Mn/kg in most plants not close to the roadway. Voorhees and Uresk (1990) found that rillscale (*Atriplex suckleyi*) contained up to 2 500 mg Mn/kg and up to 29 mg Ni/kg when grown on mine spoils. The amount of Ni taken up by plants is thought to be strongly correlated with the concentration of Ni in soil (Alegría *et al.*, 1991), up to a threshold concentration at which the metal becomes toxic to the plant. The toxic concentration for Ni is variable [e.g. 100 mg Ni/kg leaf dry mass (dm) (*Cyperus difformis*, Ewais, 1997), 42 mg Ni/kg shoot dm (*Vigna unguiculata*, Kopittke *et al.*, 2007)]. Manganese uptake and toxicity are also variable, and toxic concentrations may range from 160 to over 1 000 mg Mn/kg leaf dm (El-Jaoual & Cox, 1998).

With the exception of some studies, such as Haimi and Matasniemi (2002), little is known regarding the impact of Mn and Ni on detritivores. The objective of the current study was to examine the chronic toxicity of Mn and Ni to a cosmopolitan detritivore, *Megaselia scalaris* (Diptera: Phoridae), using laboratory bioassays and artificial diet.

Materials and methods

Megaselia scalaris

The fly *Megaselia scalaris* (Loew) (Diptera: Phoridae), known as the scuttle fly, is a widely distributed species which has been reported feeding on a large variety of materials, most often decaying plant and animal material, but including living plants and animals, and more unusual food sources such as paint and boot polish (for a thorough review of published work on *M. scalaris* biology and diet breadth, see Disney, 2008). The *M. scalaris* laboratory colony used in all bioassays was established in 2001 from adult flies found infesting insect diet. The colony was maintained at 26°C with a photoperiod of 16:8 L:D and fed an alfalfa-based diet (similar to that used by Mandeville *et al.*, 1988). These flies have been used successfully for previous studies involving pollutants, and methods used here were adapted from those studies (Trumble & Jensen, 2004; Jensen *et al.*, 2005, 2006). Large numbers of eggs of standardized age were obtained for bioassays by placing

approximately 50 flies in 75-mL Petri dishes with control (uncontaminated) bioassay diet (Fisher's *Drosophila* diet, Fisher Scientific, Pittsburg, PA, USA) and allowing females to oviposit for 4 hours. This diet is a bright blue color and provides an excellent contrast to eggs, larvae and pupae. Flies were subsequently removed and eggs were transferred to bioassay treatments.

Survival and development bioassays

To create metal-contaminated food sources, commercially purchased Ni or Mn was dissolved in high performance liquid chromatography (HPLC) grade water, which was then used to hydrate the bioassay diet. Treatments included: control (0 mg/kg); 1 300, 2 600, and 5 200 mg Ni/kg dm; and 260, 1 300, and 2 600 mg Mn/kg dm. Concentrations were selected to represent levels reported from both contaminated plant tissue and contaminated soil. Nickel was added as nickel (II) chloride hydrate (CAS# 69098-15-3, $\text{NiCl}_2 \times \text{H}_2\text{O}$, 99.95%, Sigma-Aldrich, St. Louis, MO, USA), and Mn was added as manganese (II) chloride tetrahydrate (CAS# 13446-34-9, $\text{MnCl}_2 \cdot 4\text{H}_2\text{O}$, 98%, Sigma-Aldrich). The nickel chloride product obtained from Sigma-Aldrich had a published degree of hydration of 7–8, which was averaged to 7.5 to obtain a molecular weight of 264.6, which was used for calculations when preparing treatment solutions. Because both Mn and Ni may undergo a variety of reactions when dissolved in water or added to diet, including complexing with organic molecules, concentrations of both Ni and Mn are reported here as nominal concentration of elemental Ni or Mn per dry mass of diet. Concentrations of metals may be converted to mg/kg wet diet weight by multiplying by 0.278.

After mixing with treatment solution, diet was inserted into one-half of divided, 75-mL clear plastic Petri dishes. Because *M. scalaris* typically moves off the larval food for pupariation, the open side of the Petri dish provided a preferred pupariation site and facilitated counting of puparia. Twenty eggs were placed onto the surface of the diet in each Petri dish. After 24 h, unhatched eggs were counted and removed. Dishes were monitored daily and new puparia, newly eclosed adults, and sex of adults was recorded. Adults were preserved for wing-length measurements by freezing. Wing length was measured as an analogue for body size, a correlate of insect reproductive capacity (Honek, 1993) and therefore a predictor of fitness. Each treatment concentration was replicated eight times.

The effect of treatment on percentage of eggs eclosing, percent pupariation, time to pupariation, percent of puparia eclosing, percent adult emergence, percent female, and wing length was analyzed using analysis of variance (ANOVA) followed by Tukey's honestly significant dif-

ference (HSD) post-hoc test as appropriate, with $P < 0.05$ (SAS Institute, 2002). Percentage data were arcsine transformed for analysis but were back-transformed for presentation. To evaluate potential differences in male and female developmental times, and the possible influence of metal treatment on the difference in development time of the sexes, time to adult emergence was analyzed using analysis of covariance (ANCOVA) (SAS Institute, 2002) with sex as the independent variable and metal treatment as the covariate. All values are reported as mean \pm standard error.

Results

The presence of Ni or Mn in the diet, at the concentrations tested, did not affect percentage of eggs hatched ($F_{6,56} = 1.03, P = 0.416$). However, there was a significant effect of metals on percentage of larvae forming puparia ($F_{6,56} = 5.07, P < 0.001$, Fig. 1) and time to pupariation ($F_{6,56} = 19.2, P < 0.001$, Fig. 2). The presence of metals increased the percentage of larvae pupariating in four of the six treatments and decreased the time to pupariation in all treatments.

All metal treatments significantly increased the percentage of the puparia formed that successfully eclosed ($F_{6,56} = 8.00, P < 0.001$, Fig. 3) as compared to controls. There was no significant difference among metal treatments, where percent puparial eclosion ranged from 88%–99%. The control treatment exhibited a significantly lower percent-

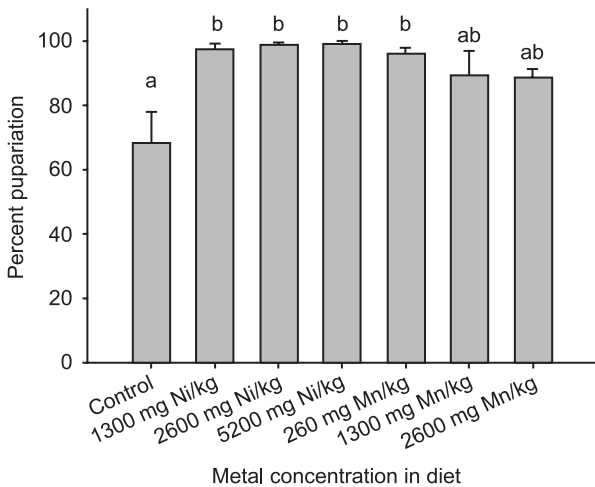


Fig. 1 Effect of Ni and Mn added to diet on percentage pupariation (\pm SE) of *Megaselia scalaris*. Concentrations given are per unit of dry mass. Different letters indicate a significant difference at the $P < 0.05$ level (ANOVA, Tukey’s HSD).

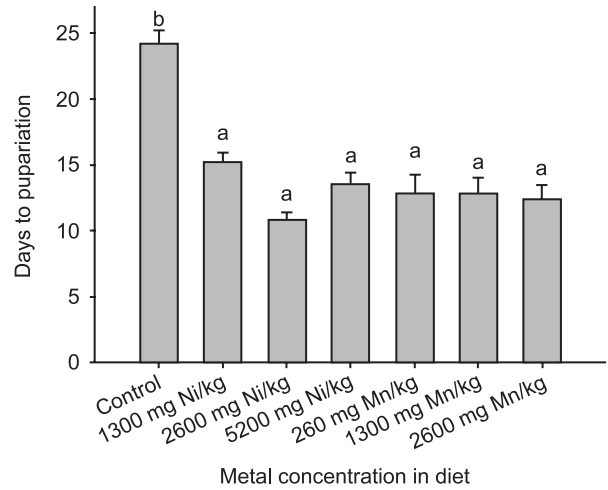


Fig. 2 Effect of Ni and Mn added to diet on time to pupariation (\pm SE) of *Megaselia scalaris*. Concentrations given are per unit of dry mass. Different letters indicate a significant difference at the $P < 0.05$ level (ANOVA, Tukey’s HSD).

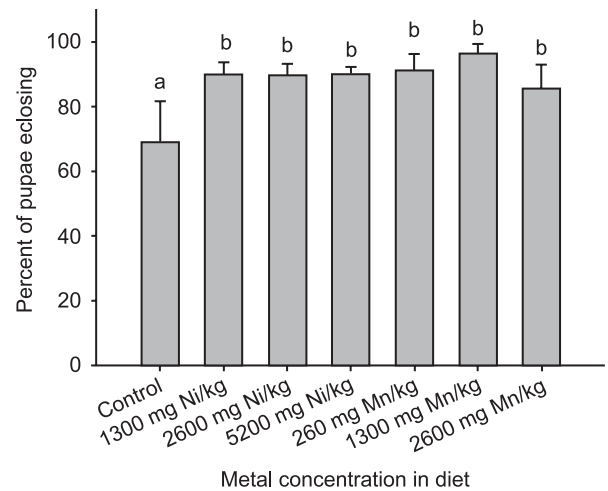


Fig. 3 Effect of Ni and Mn added to diet on the percentage of pupariated larvae that successfully eclosed as adults (\pm SE) of *Megaselia scalaris*. Concentrations given are per unit of dry mass. Different letters indicate a significant difference at the $P < 0.05$ level (ANOVA, Tukey’s HSD).

age of pupae eclosing ($68\% \pm 9.5\%$) relative to other treatments.

While sex did not have a significant effect on time to emergence ($F_{2,105} = 2.03, P = 0.157$), the time to adult emergence was significantly decreased by metal treatment ($F_{6,54} = 6.42, P < 0.001$, Fig. 4). Feeding on diets containing Ni or Mn caused adults to eclose significantly faster than controls in five of six metal treatments.

The percentage of flies that were female was not affected by either pollutant treatment ($F_{6,53} = 1.02$, $P = 0.423$). Wing length, a fitness correlate, was significantly increased by the metal treatments for females ($F_{6,52} = 3.12$, $P = 0.011$, Fig. 5), but not for males ($F_{6,50} = 1.31$, $P = 0.274$). Male flies in the control treatment had an average wing length of 1.64 ± 0.01 mm.

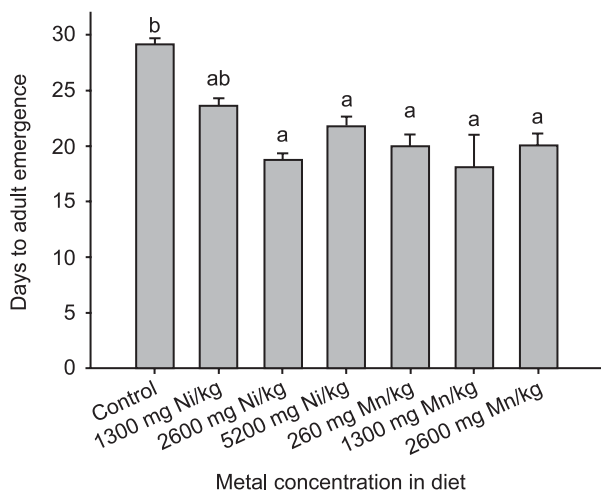


Fig. 4 Effect of Ni and Mn added to diet on time to adult emergence (\pm SE) of *Megaselia scalaris*. Concentrations given are per unit of dry mass. Different letters indicate a significant difference at the $P < 0.05$ level (ANOVA, Tukey's HSD).

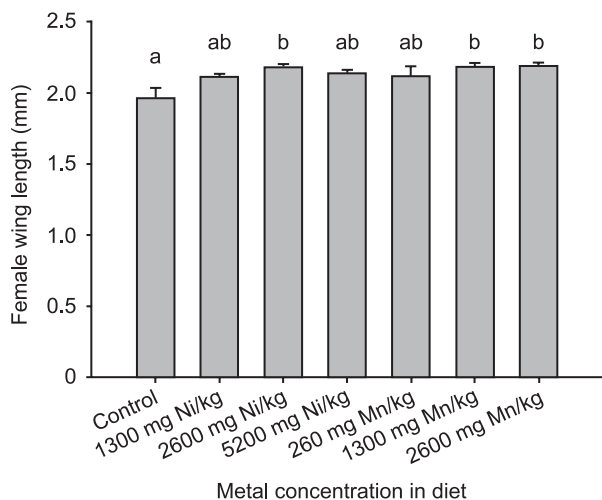


Fig. 5 Effect of Ni and Mn added to diet on female wing length (mm \pm SE) of *Megaselia scalaris*. Concentrations given are per unit of dry mass. Different letters indicate a significant difference at the $P < 0.05$ level (ANOVA, Tukey's HSD).

Discussion

The presence of Ni or Mn in the diet, at the concentrations tested, did not affect the percentage of eggs that hatched. Thus, even though eggs have a known potential for absorbing liquid from the surface of the diet (Chapman, 1975) and thereby possibly acquiring Ni or Mn, either the eggs did not absorb appreciable concentrations of the metals or these metals did not have measurable effects on this life stage. Regardless, eggs laid on Ni- or Mn-contaminated food could be expected to hatch in normal numbers, at least up to the concentrations tested in this study.

While previous studies with hexavalent chromium (Trumble & Jensen, 2004; Jensen *et al.*, 2005) and methylmercury (Jensen *et al.*, 2006) found no effects on pupal eclosion, this study demonstrated that the presence of Ni or Mn in the diet significantly increased the eclosion rate of pupae, indicating that in some cases the pupal, as well as the larval, stadium may be affected by the presence of metals.

Sex did not have a significant effect on time to emergence. This finding is consistent with some earlier studies (Trumble & Jensen, 2004; Jensen *et al.*, 2005), but contrasts with other publications documenting that females required longer to emerge (Benner & Ostermeyer, 1980; Jensen *et al.*, 2005). The reason for this variability is not clear.

Although Mn and Ni are toxic to some invertebrates at levels as low as 400 mg Mn/kg (Kuperman *et al.*, 2004) and 20 mg Ni/kg (Coleman *et al.*, 2005), we found that concentrations of up to 2 600 mg Mn/kg and 5 200 mg Ni/kg were not toxic to *M. scalaris*, even when the effects of chronic exposure on developmental measures were evaluated. This result is surprising, as Heliövaara and Väisänen (1993) reported that the most common effects of pollutant metals on insects were a decrease in survival and an increase in larval developmental times. Our previous research on *M. scalaris* indicated that pollutants such as selenium and methylmercury caused increased larval developmental times (Jensen *et al.*, 2006), but only at concentrations above 100–300 mg Se/kg or when the metals were combined.

As is the case for other animals, Mn and Ni are essential trace nutrients in insects (Trager, 1953), although both metals also have demonstrated toxicity in some insect species. Generalist Lepidopteran larvae have been found to be sensitive to Mn and/or Ni when metals were added in artificial diets. Coleman *et al.* (2005) investigated the diamondback moth (*Plutella xylostella*) and found that Mn was toxic at levels greater than 1 370 mg/kg dm and Ni was toxic at levels greater than 20 mg/kg dm. Boyd and Martens (1994) found that 1 000 mg Ni/kg dm was acutely toxic to *Pieris rapae*. *Spodoptera exigua* exposed to Ni at 936 mg/kg dm experienced significantly more mortality than controls (Boyd & Moar, 1999). Some studies have examined the

sensitivity of predators to Ni. Boyd and Wall (2001) found that high-Ni prey (Mirid bugs, 770 mg Ni/kg dm) did not cause mortality for a mantid, a lacewing, or a Pholcid spider, but did cause mortality in *Misumena vatia*, a crab spider (Thomisidae).

Similarly, soil organisms have been examined for sensitivity to Mn and/or Ni. Kuperman *et al.* (2004) surveyed soil organisms' sensitivities to Mn. The three species tested were *Enchytraeus crypticus* (Oligochaeta, $EC_{50} = 386$ mg Mn/kg), *Eisenia fetida* (Oligochaeta, $EC_{50} = 1\,970$ mg Mn/kg), and *Folsomia candida* (Collembola, juvenile $EC_{50} = 1\,663$ mg Mn/kg). On the basis of their bioassays, Kuperman *et al.* (2004) recommended a limit of 445 mg Mn/kg in soil when remediating contaminated sites. Scott-Fordsmand *et al.* (1999) found the LC_{50} of Ni for Collembola, in a 3-week bioassay, to be 800–900 mg/kg dm in soil. In contrast, Jaworska and Gorczyca (2002) found that Mn was beneficial rather than harmful to entomopathic nematodes, when Mn was dissolved in water at a concentration of 400 mg/L. This concentration of Mn significantly decreased entomopathic nematode mortality as compared to a control. In a study of decomposers, Haimi and Matasniemi (2002) found that in a coniferous forest with 460 mg Ni/kg (250 mg exchangeable Ni/kg) in soil, the soil microarthropod community was significantly altered as compared to a control area.

Some plants have adapted to living in areas with high soil metal concentrations by acquiring exceptionally high levels of metals in their tissues. These plants have been designated as accumulators or hyperaccumulators, with an Mn accumulator being a plant with more than 2 000 mg Mn/kg, an Mn hyperaccumulator being a plant with more than 10 000 mg Mn/kg, and an Ni hyperaccumulator being a plant containing more than 1 000 mg Ni/kg dm (Reeves & Baker, 2000). Although there are only about 13 recorded species of Mn hyperaccumulators, Ni hyperaccumulators are more abundant (318 recorded species) (Brooks, 1998; Reeves & Baker, 2000). Martens and Boyd (1994) hypothesized that hyperaccumulation of metals may provide a defense against herbivores. Coleman *et al.* (2005) extended the hypothesis to include a defensive function for accumulators that contain even lower levels of metals in their foliage. Evidence for these ideas, termed the elemental defense hypothesis, is reviewed by Boyd (2007).

Clearly, most of the insects previously studied are sensitive to levels of Mn and Ni that did not harm *M. scalaris*. Indeed, *M. scalaris* may be one of a few organisms, other than metal-adapted specialists such as *Melanotrichus boydi* (Hemiptera: Miridae) (Wall & Boyd, 2006) and a *Stenoscepa* sp. (Boyd *et al.*, 2007), capable of overcoming an elemental defense to feed on Mn-accumulating (> 2 000 mg Mn/kg) or Ni-hyperaccumulating (> 1 000 mg Ni/kg) plants. Generalist detritivores such as *M. scalaris* feed on a wide

variety of plant and animal matter in varying stages of decay and therefore must be able to tolerate a wide variety of components in their food.

Many minerals, such as Se, Ni and Mn, are considered essential-toxic, meaning that although low levels are essential for growth and survival, too much can be lethal (e.g. Daniels, 1996). In our experiments, all concentrations of Mn and Ni in the diets increased various measures of *M. scalaris* fitness (time to pupariation, percent pupariation, percent eclosion of pupae, time to adult emergence, or wing length of female flies). While these findings seem to suggest that these metal concentrations are above the essential threshold but below a toxic threshold, an alternate explanation is that these insects were able to utilize as much Mn or Ni as they needed, then excrete or detoxify the rest. Whether these levels of Mn and Ni were not toxic or if negative effects were avoided through detoxification, both Mn and Ni were clearly not harmful to *M. scalaris* at the levels tested.

Trumble and Jensen (2004) found that hexavalent chromium was toxic to *M. scalaris* at levels above 500 mg CrVI/kg. Although toxicity data are not available to compare the chromium susceptibility of *M. scalaris* with that of other organisms, the toxicity of Se ($LC_{50} = 260$ mg/kg selenate; Jensen *et al.*, 2006) to *M. scalaris* is much lower than that for the herbivore *Spodoptera exigua* ($LC_{50} < 50$ mg/kg selenate; Trumble *et al.*, 1998). These studies as well as the findings reported in this paper suggest that *M. scalaris* may be more tolerant of pollutants than many other invertebrates.

Megaselia scalaris is known to feed on an exceptional range of foods (Disney, 2008). This ability to utilize extremely diverse resources is perhaps aided by *M. scalaris*' having an extreme metal tolerance. Additional research is necessary to discover the physiological or behavioral mechanisms responsible for the tolerance of *M. scalaris* to Mn and Ni.

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