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Table 3. Comparative soil analyses of Vanad Pass and other serpentine localities on the Great Dyke. Standard deviations are given where available.

Locality	% Ni total	% Cr total	Mg:Ca exchangeable
Noro[5]	0.66	0.01	3.25
Noro Chrome Mine[6]	0.55	12.5	
Vanad Pass (termite mounds)	0.67 ± 0.26	0.09 ± 0.10	3.12 ± 1.53
Mean from six serpentine localities on the Great Dyke[*5]	0.48 ± 0.26	0.14 ± 0.09	2.10 ± 1.20

*Localities include Noro, Kingston Hill, Tipperary Claims, Selukwe, Umvuma and Ngezi.

(Table 2) showed a percentage nitrogen similar to or slightly lower than that recorded for serpentine localities within the Barberton Greenstone Belt.[4] The results also showed high levels of chromium, magnesium and nickel. Soils are loamy, with low organic carbon and pH close to neutral (pH below 7 in the Barberton Greenstone Belt[4]). Total cation exchange capacity is similar to or slightly lower than that recorded for the Barberton Greenstone Belt.[4]

Results showed a total percentage of nickel in the termite mounds at Vanad Pass similar to Noro,[5] a locality near Vanad Pass, and higher than other serpentine localities on the Great Dyke (Table 3). The total percentage of chromium recorded from Vanad Pass is relatively low compared to other serpentine localities,[5] and much lower than at the Noro chrome mine.[6] The Mg:Ca ratio is very similar to that at Noro and higher than for the other serpentine localities. These results indicate that, with the exception of chromium, the termite mounds do not appear to be chemically ameliorated.

Conservation status

The extent of the distribution of *P. serpenticola* is estimated to be less than 100 km² (one locality is not precisely known); the species is known to exist at only three localities; there is some rate of decline due to the degradation of the habitat resulting from mining and grazing; and the number of mature individuals in existence is estimated to be fewer than 2500. The conservation status of *P. serpenticola* is thus endangered in terms of the new categories of the IUCN.[7]

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Host-switching does not circumvent the Ni-based defence of the Ni hyperaccumulator *Streptanthus polygaloides* (Brassicaceae)

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Elevated tissue concentrations of metals have been shown to defend metal-hyperaccumulating plants against both herbivores and pathogens. Tolerance of metal-based defences presents a challenge to herbivores, because heavy metals cannot be degraded or metabolized. One strategy that herbivores can employ to counter high-metal defences is dietary dilution, or host switching. Highly mobile herbivores are most likely to use this strategy, but less mobile lepidopteran larvae can also improve their performance on toxic hosts if early instar development occurs on more favourable hosts. We examined the effects of host switching on growth and survival of a generalist folivore. Specifically, we tested the hypothesis that early larval development on non-toxic hosts could improve larval performance of the beet armyworm, *Spodoptera exigua*, on high-Ni *Streptanthus polygaloides*, a Ni hyperaccumulator. Initial larval performance (weight gain) was lowest for insects switched to high-Ni hosts. Decreased initial larval performance was also noted for insects switched from lettuce to low-Ni *S. polygaloides*, but these larvae recovered quickly. Original host identity (lettuce or low-Ni *S. polygaloides*) did not affect subsequent larval performance. By day 8 of the feeding trials, all larvae switched to high-Ni hosts had died. We conclude that polyphagous *Spodoptera* larvae are unable to counter Ni-based defences via host switching.

Plants are protected from herbivory and disease by physical defences (e.g. spines, trichomes) and chemical defences (e.g. tannins, metals). Although most plant chemical defences are organic compounds, certain chemical defences use elements as active agents. Defensive elements include silicon,[1–3] calcium,[4,5] fluorine,[6] and heavy metals such as nickel,[7–10] copper[11] and zinc.[12] Elemental defences differ from organic defences in that the defensive agents are obtained from the soil instead of being synthesized from assimilated carbon.[8]

Plants that accumulate extremely high concentrations of heavy metals have been termed hyperaccumulators.[13] At least one function of this ability is plant defence; metal hyperaccumulators utilize sequestered metals to defend against herbivores and pathogens.[14] Elevated concentrations of metals in plant tissues have been shown to deter feeding,[12] delay larval development,[8,10] cause acute toxicity in certain insect herbivores[8–10] and to be toxic to some plant pathogens.[7]

Many herbivores are able to counter plant chemical defences. Countering metal-based defences, however, presents a challenge to herbivores because heavy metals cannot be degraded or metabolized. Certain herbivores may avoid metal-based defences by selectively feeding on tissues with lower metal contents.[14] For instance, Ni and Zn have been shown to be concentrated in leaf epidermal cell walls of hyperaccumulators;[15,16] phloem parasites (e.g. aphids) may bypass this defence by feeding directly on cell or phloem sap.[17] Many polyphagous folivores, however, feed indiscriminately and cannot bypass metal sequestered in epidermal cells. To tolerate metal-based

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defences, these herbivores must rely on other mechanisms. Vertebrate folivores and highly mobile insect folivores can limit the adverse effects of plant toxins by feeding on a wide array of different plant species, thereby diluting the amounts of specific toxins in their diet. For 'sessile' folivores that cannot switch hosts, avoidance of toxin(s) must occur prior to feeding (e.g. oviposition on favourable hosts by adults).

Although not highly mobile, lepidopteran larvae are not always restricted to the hosts on which they are oviposited.[18] For the gypsy moth, *Lymantria dispar,* extensive host switching can occur during larval development.[19] For these larvae, switching occurs in both high- and low-density populations,[18] indicating that other factors (for instance, host quality or host phenology) dictate the dynamics of host switching. By switching hosts at least once, gypsy moth larvae can improve their growth rates.[20] Indeed, for these larvae, initial development on favourable hosts can improve subsequent larval performance (in particular growth rate and larval weight) on less suitable hosts.[20] Similar polyphagous larvae that feed on hyperaccumulators may be able to use this strategy to combat the toxicity of heavy metals.

Here, we examined the effects of host switching on the growth and survival of a generalist folivore. Specifically, we tested the hypothesis that early larval development on non-toxic hosts could improve larval performance of the beet armyworm, *Spodoptera exigua,* on high-Ni hosts. Neonate larvae were raised on hosts without metal-based defences and subsequently switched to new hosts, some containing hyperaccumulated Ni. The effects of the Ni-based defence on larval performance were examined along with the effects of host switching on the efficacy of that defence.

Materials and methods

Study species. The Ni hyperaccumulator, *Streptanthus polygaloides,* is an annual herb endemic to serpentine soils in the western foothills of the Sierra Nevada Mountains in California. For field-collected tissues, Ni concentrations >1000 μg g^{-1} have been reported for all plant parts (stems, roots, leaves, flowers, fruits and seeds).[21] Seeds for this experiment were collected from a population in the Red Hills Recreation Area, near Chinese Camp in Tuolomne County, California.[22] *Streptanthus polygaloides* plants were grown from seed in a greenhouse in Auburn, Lee County, Alabama. High-Ni plants (>2000 mg kg^{-1} dry weight) were raised on ProMix amended with anhydrous NiCl$_2$ (soil Ni concentration *c.* 800 mg kg^{-1} dry weight) and low-Ni plants (<100 mg kg^{-1} dry wt) were grown on unamended ProMix.

Spodoptera exigua (Hübner) (Lepidoptera: Noctuidae) is a generalist folivore with a broad host range.[23] Previous experiments have shown that *Spodoptera exigua* larvae cannot survive on a diet composed exclusively of high-Ni *S. polygaloides.*[8] Larvae for this experiment were obtained from a laboratory colony established from insects collected from Alabama cotton fields and maintained on an artificial diet[24] at 28°C with a light:dark period of 12 h:12 h.

Feeding trials. Neonate larvae were placed on either Romaine lettuce, *Lactuca sativa* (obtained from a local market), or low-Ni *S. polygaloides.* After 4 days larvae were switched to either lettuce, high-Ni *S. polygaloides,* or low-Ni *S. polygaloides,* resulting in six experimental treatments:

1. Initial lettuce, switched to high-Ni *S. polygaloides* (L to Sp+).
2. Initial lettuce, switched to low-Ni *S. polygaloides* (L to Sp–)
3. Initial lettuce, remaining with lettuce (L to L)
4. Initial low-Ni *S. polygaloides,* switched to high-Ni *S. polygaloides* (Sp– to Sp+)
5. Initial low-Ni *S. polygaloides,* remaining with low-Ni *S. poly-galoides* (Sp– to Sp–)
6. Initial low-Ni *S. polygaloides,* switched to lettuce (Sp– to L)

Larvae (12 per treatment) were placed individually into diet cups with leaf material from corresponding treatments and allowed to feed *ad libitum.* A small amount of agar was placed in the bottom of each cup to maintain high humidity, thus delaying leaf desiccation. Each larva was weighed on days 4, 8, and 12 of the experiment, and mortality or pupation was noted. High initial mortality (~100%) prohibited our including treatments in which neonate larvae were placed onto high-Ni *S. polygaloides.*

Statistical analysis. For feeding trials, the mean percentage of total body weight gained during a given time interval was used to create separate data sets. Excessive mortality of larvae switched to high-Ni *S. polygaloides* restricted most analyses to data collected for the 0–4 day interval. Data for the 8–12-day interval were not used because of high pupation rates. Owing to colony limitations, larvae initially placed onto lettuce were several days younger than those placed onto low-Ni *S. polygaloides.* To account for this variability, we used initial larval weight as a covariate during the analyses. Each dataset was analysed with a one-way analysis of covariance (ANCOVA).

Comparisons of individual treatment means were made using Fisher's protected least significant difference (PLSD) and orthogonal contrasts were used to make grouped means comparisons. Contingency table analysis determined the effects of treatment on larval mortality. Statistical comparisons were considered significant at $\alpha \leq 0.05$.

Results

High-Ni diets, regardless of original host, were fatal to *Spodoptera exigua* larvae. All larvae that were switched to high-Ni *S. polygaloides* died by day 8. Treatment significantly affected mortality ($\chi^2 = 61$, d.f. = 5, $P \leq 0.0001$). High-Ni *S. polygaloides* treatments were responsible for the observed effect (Fig. 1); highest and lowest total values for mortality of treatments not
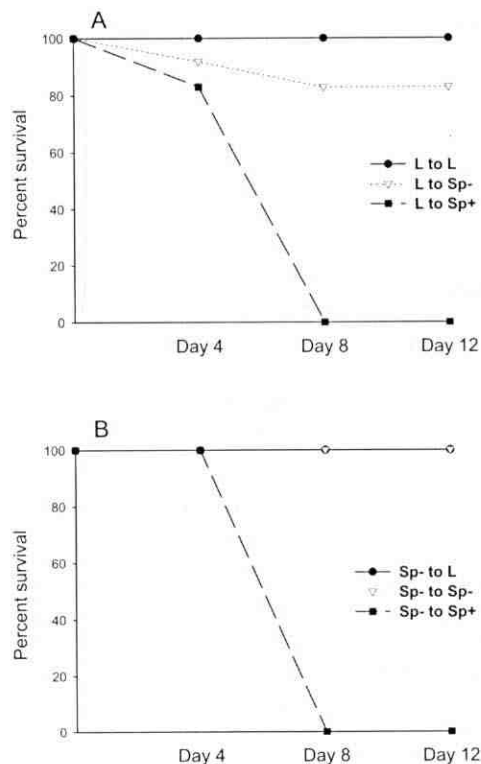

Fig. 1. Larval survival from days 0–12. **A**, lettuce as original host; **B**, low-Ni *Streptanthus polygaloides* as original host.
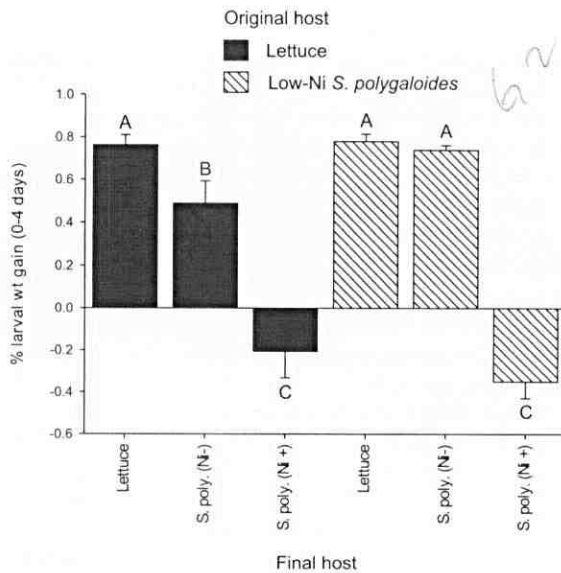
Fig. 2. Percentage larval weight change during days 0–4 of feeding trials (mean ± 1 s.e.). Solid bars, lettuce as original host; hatched bars, low-Ni *Streptanthus polygaloides* as original host.

Fig. 3. Percentage larval weight change during days 4–8 of feeding trials (mean ± 1 s.e.). Larvae switched to high-Ni *Streptanthus polygaloides* experienced 100% mortality by day 8. Solid bars, lettuce as original host; hatched bars, low-Ni *Streptanthus polygaloides* as original host.

involving high-Ni *S. polygaloides* were not significantly different ($\chi^2 = 2.4$, d.f. = 1, $P > 0.12$).

Treatment also significantly affected percentage weight gain for the 0–4-day interval ($F = 13$, d.f. = 5, $P \leq 0.0001$, ANCOVA). A contrast showed that switching to a different host versus remaining on the same type of host reduced larval weight gain, although not significantly ($F = 3.0$, d.f. = 1, $P = 0.089$). Weight gains of *Spodoptera* larvae switched to high-Ni *S. polygaloides* were significantly lower than in all other treatments ($F = 16$, d.f. = 1, $P = 0.0002$,) (Fig. 2). These larvae, in fact, lost weight: –21% for L to Sp+ and –35% for Sp– to Sp+ treatments.

Larvae that remained on the same type of host (L to L and Sp– to Sp– treatments) did not differ significantly in percentage weight gain during the 0–4-day interval; >73% of day 4 biomass was gained during this interval for larvae remaining on lettuce or low-Ni *S. polygaloides*. Larvae remaining on lettuce had a higher percentage weight gain during the 0–4-day interval than larvae switched from lettuce to low-Ni *S. polygaloides* ($P = 0.012$, Fisher's PLSD). Percent weight gain of larvae remaining on low-Ni *S. polygaloides*, however, did not differ significantly from that of larvae switched from low-Ni *S. polygaloides* to lettuce ($P = 0.699$, Fisher's PLSD) for the same time interval. Although means of these two treatments (Sp– to Sp– and Sp– to L) did not differ from the L to L treatment, both means were significantly higher than that for the L to Sp– treatment ($P = 0.0197$ and $P = 0.0085$, respectively, Fisher's PLSD) (Fig. 3).

Because no larvae from either the L to Sp+ or Sp– to Sp+ treatments survived to day 8, only larval weights from the remaining treatments were analysed for the 4–8-day interval. Only larvae of the L to L and Sp– to Sp– treatments differed significantly in percentage weight gained for this time interval ($P = 0.0023$, Fisher's PLSD). Other treatment differences noted during the 0–4-day interval were not observed during the 4–8-day interval.

Discussion

Elevated Ni content in plant tissues can be acutely toxic to herbivores.[8–10] Still, no plant defence is inviolate, and some herbivores (such as aphids) can feed on hyperaccumulators.[17] Their apparent tolerance, however, is likely due to feeding strategies rather than specific detoxification mechanisms, although specific metal tolerance mechanisms exist.[25,26] Unlike carbon-
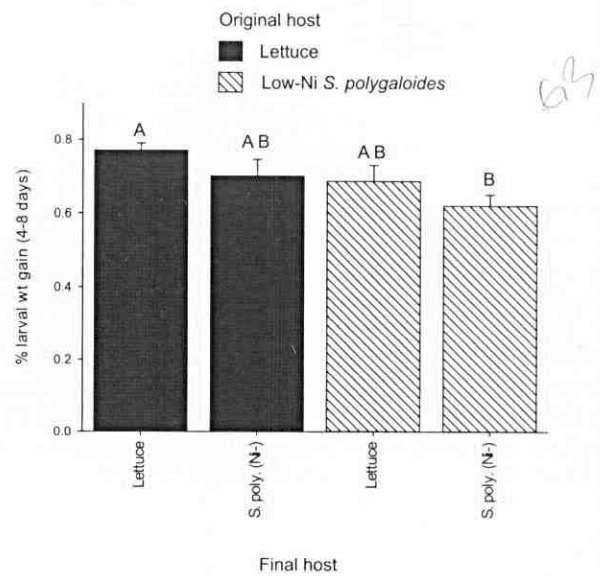
based defences, Ni cannot be degraded or transformed into a less toxic chemical.

Herbivores (actual and potential) of *S. polygaloides* and other Ni hyperaccumulators must possess ways to avoid or detoxify Ni if they are to survive the presence of high-Ni foliage in their diet. Avoidance of Ni-based defences can occur via deterrence or preferential feeding on low-Ni tissues. Detoxification methods include indiscriminate strategies, for example dietary dilution, and specific mechanisms, such as binding of metals in midgut epithelial cells.[26]

The best strategy for herbivore tolerance of plant chemical defences may be to avoid toxic plant tissues. Avoidance of metal-based defences ranges from complete non-consumption[12] to selective feeding on low-Ni tissues.[17] Pollard and Baker[12] showed that elevated foliar zinc in the Zn hyperaccumulator, *Thlaspi caerulescens*, completely deterred the feeding of *Pieris brassicae* larvae; these larvae refused diets of high-Zn foliage. Aphids, however, are not deterred by elevated levels of metal in plant tissues.[17] Indeed, aphids have been observed feeding on high-Ni *S. polygaloides* plants both in experiments[17] and naturally (Davis and Boyd, pers. obs.). Presumably, this behaviour is permitted by aphids' ability, via stylets, to tap directly into phloem fluid or cell sap, thus bypassing metals bound in cell walls. Still *et al.*[17] showed that even when aphids were forced to ingest high-Ni diets, their rapid rate of metabolism and excretion limited the toxic effects of Ni. Although both stylet penetration and rapid metabolism allows aphids to feed on hyperaccumulators, neither mechanism is specifically adapted for avoidance of metal-based defences.

Detoxification mechanisms can be either generic (e.g. dietary dilution) or specific (e.g. metallothioneins). Some indiscriminate folivores of hyperaccumulators may limit Ni toxicity by consuming a mixed diet of high- and low-Ni foliage. Body mass and mobility, along with availability of dietary choices, are likely factors in determining the abilities of these herbivores to sufficiently dilute the toxic effects of Ni. Most vertebrate herbivores are polyphagous[27] and are unlikely to feed solely on hyperaccumulators. Extensive herbivory of *S. polygaloides*, presumably by vertebrates, however, has been observed in a recent field experiment (Boyd and Martens, unpubl. data,). Considerable herbivore damage has also been noted on individuals within a

natural serpentine population of the Ni hyperaccumulator *Thlaspi montanum* var. *montanum* (Davis and Boyd, pers. obs.). This evidence indicates that the broad diets of vertebrate herbivores, such as rodents and ungulates, sufficiently dilute the toxicity of Ni-based defences. Although lepidopteran larvae can switch hosts, they are not able to encounter the large number of different hosts that comprises the diets of most vertebrate herbivores.

Some herbivores possess specific metal detoxification mechanisms. The chilopod *Lithobius forficatus* accumulates dietary metals (e.g. Cd and Pb) in midgut epithelial cells.[26] Once sequestered, the metals are incorporated into insoluble granules, transported to the gut lumen, and excreted. Although metallothioneins (metal-binding proteins) are found in many organisms, their function in metal detoxification has not been fully explored for insect herbivores.[25] Certain *Spodoptera* species have specific detoxification strategies for plant chemical defences other than metals; *Spodoptera eridania* larvae utilize mixed-function oxidases that allow them to combat a wide range of chemical defences.[27] *Spodoptera exigua*, however, does not appear to be able to detoxify Ni-based defences. Previous experimentation with *Spodoptera exigua* larvae and *Streptanthus polygaloides* has demonstrated that neonate larvae cannot survive a diet of *Streptanthus polygaloides* foliage containing elevated Ni.[10] Similar results were found with neonate larvae of the white cabbage butterfly, *Pieris rapae*, and high-Ni foliage of the Ni hyperaccumulator, *Thlaspi montanum* var. *montanum*.[8] Our experiment shows that later instar *Spodoptera exigua* larvae also cannot detoxify Ni-based defences. In Boyd and Martens' study,[8] *P. rapae* adults were given a choice of high- and low-Ni plants, but were unable to discriminate between toxic and non-toxic hosts. In this instance, it appears that poor oviposition choices made by adults doom any resulting larvae. *Spodoptera exigua* possess limited mobility and cannot detoxify Ni-based defences once neonate larvae initiate consumption of high-Ni foliage.

Lepidopteran larvae can also counter plant defences by switching hosts at least once during larval development.[20] Stoyenhoff[20] demonstrated that gypsy moth larvae which initially fed on red oak or aspen foliage during early instars differed in their abilities to tolerate poorer quality foliage during later instars. Early feeding of larvae on red oak leaves improved subsequent larval performance on poorer hosts. Our study, however, shows that initial larval development of *Spodoptera exigua* on non-lethal diets does not alleviate the toxic effects of subsequent high-Ni dietary choices. For *Spodoptera exigua*, choosing high-Ni tissue, either as larvae or adults, is fatal.

Although Ni-based defences are acutely toxic to certain herbivores,[8–10] co-evolution of plant defences and herbivore counter-defences indicates that at least some herbivores should be able to tolerate otherwise toxic defences.[27] Herbivores that have frequently encountered hyperaccumulators over evolutionary time are more likely to have evolved specific metal detoxification mechanisms.

The novelty of hyperaccumulation (only a small percentage of serpentine flora comprises hyperaccumulators[28]), however, may have precluded the evolution of specific herbivore counter-defences for metal-based defences. Plant endemism is often high in serpentine communities,[29,30] however, and this geochemical isolation may be favourable for the evolution of distinctive plant–herbivore interactions.

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