

Variability in host plant chemistry: behavioural responses and life-history parameters of the Colorado potato beetle (*Leptinotarsa decemlineata*)

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Summary. Many studies investigating effects of plant chemicals on herbivore performance have reported contradictory results, perhaps because of possible interaction between different chemicals. Also, a herbivore's performance is not necessarily consistent with its food or oviposition preference. Our aim was to investigate simultaneously antibiosis (larval growth and survival) and antixenosis (oviposition and feeding preferences) responses in herbivore to three plant chemicals, of which one is expected to have positive and two are expected to have negative effects. Antibiosis was measured by correlating the nitrogen and glycoalkaloid levels in host plants to the survival and adult size of *Leptinotarsa decemlineata*, by rearing larvae on whole plants of three potato varieties. Although host plants differed in their glycoalkaloid levels, survival rate and adult body size did not differ among beetles reared on different potato varieties. This suggests that beetles are quite robust for differences in both foliar α -chaconine and foliar α -solanine content. However, differences in antixenosis were found although they could not be directly predicted from the leaf chemistry. Females preferred to lay their eggs on the variety with high α -solanine content (Nevsky) towards which males showed a tendency to feeding preference. Overall, our results confirm that beetles are well adapted to the chemical defences of potato plants as potato varieties did not significantly affect beetle performance, but differences in oviposition preference may still result in major differences in the amount of damage inflicted on plants in the fields.

Key words. larval diet – glycoalkaloids – nitrogen – antibiosis resistance – antixenosis – Coleoptera – Chrysomelidae – *Leptinotarsa decemlineata* – *Solanum tuberosum*.

Introduction

The fitness of insect herbivores is crucially dependent on their diet, i.e. the quality of the plant they feed on (reviewed by Awmack & Leather 2002). Along with essential nutrients, which have a positive influence on insects such as nitrogen (e.g., Mattson 1980; Tabashnik 1982; Hare 1987; Clancy 1992; Hunt *et al.* 1992), plants have many characteristics that have detrimental effects on their herbivores. For example, plant secondary metabolites reduce the herbivore's performance (survival, development) and fitness since they have toxic, repellent, or digestibility-reducing properties (see for example Sinden *et al.* 1986). The effects of deterrents can be modified by nutrients. For example, above a certain level nitrogen can offset the negative effects of plant antifeedants (Hare 1987). Defensive chemicals might not only have a negative effect on the metabolism of insects (i.e. antibiosis) but also elicit a behavioural response by an insect (i.e. antixenosis). That is, herbivores themselves may exhibit hierarchies of preference between plant species and even consider some plants totally inedible and refuse to eat them (see for example Nylin & Janz 1993). While plants have a range of defence strategies affecting herbivore performance, herbivores are under selection pressure towards better resistance and/or tolerance to the defences employed by plants.

The Colorado potato beetle (*Leptinotarsa decemlineata* Say) (Coleoptera, Chrysomelidae) is a serious pest of potato worldwide. The potato plant is characterized by the presence of glycoalkaloids, such as α -solanine and α -chaconine which can disrupt cellular membranes and act as acetylcholinesterase inhibitors (Friedman & McDonald 1997). Hare (1987) determined the weight gain in 4th instar *L. decemlineata* larvae when they were reared on synthetic diet with α -solanine and α -chaconine for 24 hr. He found that both of these glycoalkaloids inhibit growth and retard development in a dose-dependent manner. Kowalski *et al.* (1999) reported contradictory results. They reared

L. decemlineata from egg to prepupal stage on an artificial diet and find no negative effect of α -solanine and α -chaconine on the growth or development. The discrepancy between these two experiments might suggest that effects of glycoalkaloids vary with the life-stage and/or the length of the exposure (single vs. all larval stages). Furthermore, glycoalkaloids can interact with other foliar compounds (e.g., proteins) ameliorating their harmful effects (Hare 1987). Therefore to acquire the complete picture of the reasons behind the performance differences of herbivores, we have to monitor all larval stages and take both nitrogen and glycoalkaloids into account. This was the aspect taken in the present study accompanied by behavioural analysis of *L. decemlineata*.

We studied the effects of leaf chemistry (nitrogen and glycoalkaloid content) on behaviour (oviposition and feeding preference) and fitness (survival, development, and size of the insect herbivore) in *L. decemlineata* on different host plant varieties. Cultivated potato varieties have different levels of resistance to beetles that allows us to test the effects of leaf chemistry alone on herbivore performance using only one host plant (for example cf. Nylin & Janz 1993; Kagata & Ohgushi 2001). We reared beetles on potted potatoes (*Solanum tuberosum*) and used three cultivars, one of which was, according to field experiments, less attractive to the beetle than the others (Fasulati pers. obs.). The observed difference in abundance might be explained by differences in foliar nitrogen content, as shown in other varieties (Jansson & Smilowitz 1986), or by other plant characteristics. If nitrogen has positive and glycoalkaloids have negative effects, herbivores should select plants with high nitrogen and low glycoalkaloid content i.e. plants on which they and their progeny reach the largest body size. This is because natural selection should favour those individuals that prefer a host plant that optimizes their fitness (Thompson 1988; Jaenike & Holt 1991). As oviposition preference is not necessarily consistent with larval performance (e.g., Thompson 1988; Van Nouhuys *et al.* 2003; Martin *et al.* 2005), assessing both behavioural response and fitness performance concurrently gives us a holistic view of the interaction between the herbivore and the chemistry of its host plant.

Materials and methods

Study Species

The Colorado potato beetle (*L. decemlineata* S.) is an introduced defoliator of many cultivated crops of Solanaceae most importantly potato (*Solanum tuberosum*) (Solanales, Solanaceae) in Europe and the USA. Both larvae and adults feed exclusively on foliage, reducing crop productivity (Hare 1980). The beetles used in the experiment were descendants of adults collected from the St. Petersburg region (Russia) that had overwintered in the laboratory.

Potato Plants

We compared differences in resistance to beetles among three potato varieties (Nevsky, Hankkijan Timo, and Van Gogh). There are indications that Nevsky would not suffer as much from defoliation by beetles in the field in Russia as would the other varieties (pers. comm. Fasulati). It is not known whether low susceptibility is due to plant phenology or to host plant resistance to beetles.

The two other varieties are commonly cultivated in Finland and represent an early (Timo) and intermediate (Van Gogh) season potato crop. Their resistance to beetles has not previously been tested. Varieties were planted in pots (18 cm diameter, 3.5 l) filled with peat containing soil fertilizer (Puutarhan Y-lannos, Kemira; 8:4:14, N:P:K %), and grown in a greenhouse under natural lighting conditions, at 23 °C. If the light intensity dropped below 300 lux, the lights were switched on. The pots were placed on tables so that one of each variety stood side by side. During the course of the experiment, plants were watered as necessary. Plants were on average 21 days old at the beginning of the experiment.

Glycoalkaloid and Nitrogen Content

Since we were interested in the damage-induced responses of plants, leaf samples (N = 16 for each potato variety) for glycoalkaloid analysis were taken half-way through the experiment (on day 14). The sample taking was timed this way to ensure that, while none of the plants was completely defoliated, plants had had time to respond to feeding by larvae. Fully expanded leaves from each potato variety were collected, immediately freeze-dried for 24 h, and later analyzed for α -solanine and α -chaconine content. The glycoalkaloids were separated and quantified by high performance liquid chromatography following the method of Carman *et al.* (1986).

For nitrogen analysis, leaf samples were collected (using Leco FP-528 equipment; N = 16 for each potato variety) before larvae were introduced to assess the base nitrogen content of each plant.

Beetle Performance

We tested the effect of antibiosis by studying beetle performance on the different potato varieties. Egg masses were held on moist filter paper in a greenhouse at a natural photoperiod and a temperature of about 23 °C until they hatched. The 1st instar larvae of each female beetle (N = 16 females) were then divided equally among the three potato varieties placed randomly in a greenhouse (approved by the Plant Quarantine Office). We introduced 7 to 25 larvae to each potato plant which was then enclosed in an individual transparent plastic bag to prevent beetles escaping. The larvae were maintained on the caged potato plants until they developed into adults and thus they were allowed to pupate in the pot soil. We monitored larval-to-adult survival which was determined by dividing the total number of adults collected per plant by the number of larvae introduced. We further assessed beetle performance by measuring the length of the elytra of the newly emerged adults (N = 631), which is a reliable indicator of adult weight (Boman *et al.* unpublished data). There was no correlation between the number of larvae introduced to each plant and the chemical composition of the plant (α -solanine and α -chaconine) (r_s ranged from -0.44 to 0.39; P-values ranged from 0.092 to 0.881); moreover density did not negatively affect the survival of the larvae (Spearman, $r = 0.497$, $P < 0.001$, $N = 48$). Thus we used the family means for size as variables in the statistical analysis although beetle densities differed among families.

Oviposition Preference

To test potential differences in antixenosis, we tested whether female beetles (N = 23) show oviposition preference. Mated females that were dams of the offspring used in the beetle performance experiment were given a choice of leaves from two potato varieties (Hankkijan Timo and Nevsky). The potato leaves were placed in a petri dish (15 cm in diameter) and the beetle was given three sequential choices. We counted how many times an individual chose each potato variety for oviposition substrate.

Feeding Preference

To further test the antixenosis of different host plants, we measured beetles' feeding preferences in a separate experiment. The feeding

preferences of newly emerged adults (females: $N = 101$, males: $N = 75$) with no feeding experience as adults were tested by giving them a choice between leaf-cuts from three potato varieties (Nevsky, Hankkijan Timo, and Van Gogh). Size-standardized round-shaped leaf-discs (1.5 cm in diameter) were placed on a petri dish (15 cm in diameter) at equal distances from the centre. Beetles were individually released in the centre of the dish (to avoid bias associated with the position of a beetle relative to leaf-discs) and were allowed to make a choice between leaf-cuts. After the beetle had made a choice (i.e. started to eat a leaf), the choice was recorded and the leaf-disc was replaced with a new one. The experiment was repeated 3 times for each beetle. We counted how many times an individual chose each potato variety.

Statistical Analyses

To measure the differences in antibiosis between potato varieties, we performed an analysis of variance to determine whether beetles reared on different potato varieties differed significantly in adult size. We computed the mean elytra length for each family (sexes separately) within each host plant (hereafter: size) which was then used in subsequent analysis. Repeatability for the measurement of the elytra length was high ($R = 0.98$, $F_{19,40} = 147.774$, $P < 0.001$) and thus it was measured only once for each individual. In a two-way ANOVA, we used size (family means) as the dependent factor and potato variety and sex as fixed factors.

Larval-to-adult survival was calculated by dividing the total number of adults collected per plant by the number of larvae introduced and thus it is not sex specific. To test whether survival differed among potato varieties, a Friedman test was performed. We tested the influence of the foliar α -solanine, α -chaconine, and nitrogen content on adult size (family means) or survival by using a Spearman correlation. The potential differences in the foliar α -solanine, α -chaconine, and nitrogen content among potato varieties were compared by analysis of one-way ANOVA if data met the assumptions of parametrical tests; or by the Kruskal-Wallis test otherwise.

To test the antixenosis effects between Hankkijan Timo and Nevsky varieties, oviposition preference was tested with Wilcoxon signed ranks. Overall differences in feeding preference were tested with a Friedman test followed by a Wilcoxon signed ranks test to verify any significant differences between the two potato varieties. In pair-wise comparisons, all p -values are after sequential Bonferroni correction. To study whether feeding preference was affected by the host plant beetles fed on as larvae, a log-likelihood test was performed for the preference.

All analyses were performed using SPSS version 10.1 (SPSS, Inc., Chicago IL, USA). All P -values are two-tailed.

Results

Glycoalkaloid and Nitrogen Content

The amount of α -solanine and α -chaconine in leaves differed considerably among potato varieties (Kruskal-Wallis, α -solanine: $\lambda^2 = 17.528$, $df = 2$, $P < 0.001$; one-way ANOVA, α -chaconine: $F_{2,45} = 3.524$, $P = 0.038$; Fig. 1a). The highest foliage level of α -solanine was in Van Gogh and the lowest in Timo (Mann-Whitney, Timo vs. Nevsky: $Z = -2.827$, $P = 0.010$; Timo vs. Van Gogh: $Z = -3.882$, $P < 0.001$; Nevsky vs. Van Gogh: $Z = -1.771$, $P = 0.076$; P -values are after Bonferroni corrections). Foliar α -chaconine content was higher in Van Gogh than in Timo (LSD, $P = 0.017$) or in Nevsky foliage ($P = 0.047$), whereas Timo and Nevsky had equal amounts of α -chaconine ($P = 0.658$).

Potato varieties contained equal amounts of nitrogen measured as per cent of dry weight (one-way ANOVA: $F_{2,45} = 2.166$, $P = 0.126$). Foliar nitrogen levels (mean

Table 1 Spearman correlation between the α -solanine, α -chaconine, and nitrogen content and larval-to-adult survival. $N = 16$ families

Potato variety		Solanine	Chaconine	N-%
Timo	r	0.199	0.004	-0.196
	P	0.461	0.987	0.468
Nevsky	r	-0.298	-0.257	0.385
	P	0.262	0.337	0.141
Van Gogh	r	-0.434	-0.349	0.134
	P	0.093	0.185	0.621

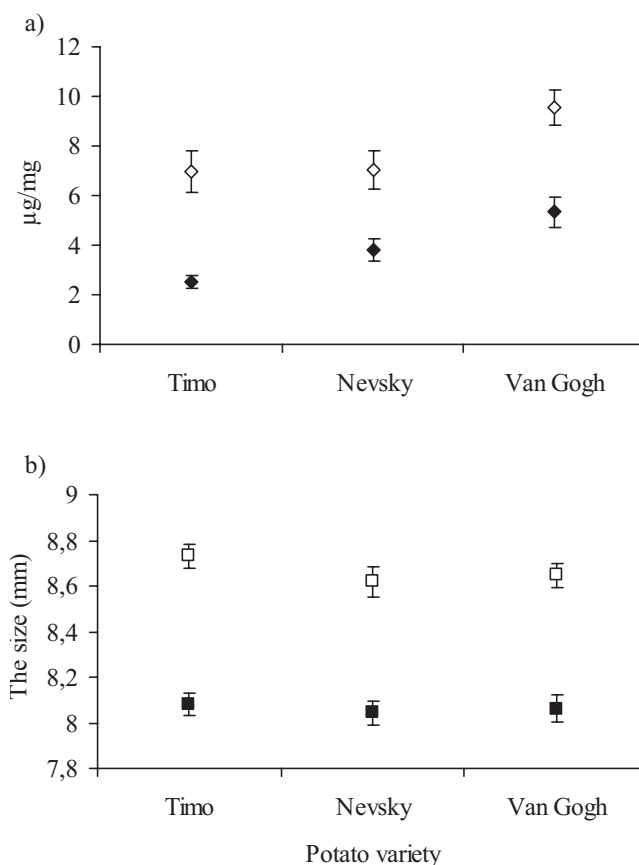


Fig. 1 a) The foliar α -solanine (filled diamonds) and α -chaconine (open diamonds) content of different potato varieties ($\mu\text{g}/\text{mg}$ dry weight, mean \pm SE; $N = 16$ in all varieties). **b)** The mean body size of female (open squares) and male (filled squares) beetles, with standard errors, fed on three different potato varieties (family $N = 15$ in all varieties). The size was measured by the length of the elytra ($\text{mm} \pm$ SE)

\pm SE) were 5.8 % (± 0.174) dry weight for Timo, 6.0 % (± 0.181) for Nevsky, and 5.5 % (± 0.094) for Van Gogh.

Survival

Larval-to-adult survival did not differ among potato varieties (Friedman test: $\chi^2 = 0.246$, $df = 2$, $P = 0.884$, family $N = 16$). On Timo, Nevsky, and Van Gogh, 68.5 % (SE = 5.720), 70.4 % (SE = 6.693), and 70.6 % (SE = 6.439) of larvae survived to adulthood, respectively. Survival was

Table 2 Spearman correlation between the α -solanine, α -chaconine, and nitrogen content and the beetle adult size (family means). N = 15 families (larvae of one family died)

Sex	Potato variety		α -solanone	α -chaconine	N-%
♀	Timo	r	-0.182	-0.454	-0.329
		P	0.516	0.089	0.232
	Nevsky	r	0.082	-0.050	-0.436
		P	0.771	0.860	0.104
	Van Gogh	r	-0.607	0.050	0.275
		P	0.016	0.860	0.321
♂	Timo	r	-0.204	-0.357	-0.339
		P	0.426	0.191	0.216
	Nevsky	r	-0.161	-0.246	-0.293
		P	0.567	0.376	0.289
	Van Gogh	r	-0.250	-0.136	-0.021
		P	0.369	0.630	0.940

independent of foliar glycoalkaloid and nitrogen content (Table 1).

The Size of Adult Beetles

There was no significant interaction between host plant and sex on adult size (2-way ANOVA: $F_{2,84} = 0.274$, $P = 0.761$), indicating that both sexes reacted similarly to host plants. No marked antibiosis differences were found among varieties since larval diet did not affect the size of the adult beetle ($F_{2,84} = 0.936$, $P = 0.396$; Fig. 1b). This is somewhat surprising since different varieties clearly differed in their foliar glycoalkaloids. The fact that leaf chemistry did not correlate with adult size (Table 2) suggests that beetles may be relatively robust against plant secondary metabolites. Sexes, however, differed in size, females being larger than males ($F_{1,84} = 175.064$, $P < 0.001$).

To evaluate the effects of a possible competition, we plotted the body size (family means) against the number of larvae at the beginning of the experiment. Both the female and male body size correlated positively with beetle density (Spearman, females: $r = 0.430$, $P = 0.003$; males: $r = 0.313$, $P = 0.035$; family $N = 45$). This indicates that there was no competition between larvae that would have retarded the growing but on the contrary larvae grown in large group reached even the largest body size.

Oviposition Preference

In spite of the lack of antibiosis effects, adult female beetles ($N = 23$) slightly preferred Nevsky over Timo as an oviposition substrate (Wilcoxon signed ranks test: $Z = -2.118$, $P = 0.034$). On average, they chose Nevsky 1.91 times in 3 trials ($SE = 0.19$) and Timo only once ($SE = 0.19$). Thus some antixenosis differences were found between these varieties, although they were not consistent with what would be expected on the basis of leaf chemistry (Nevsky had the higher α -solanine level).

Feeding Preference

Adult females did not show feeding preference among potato varieties (Friedman: $\chi^2 = 3.379$, $df = 2$, $P = 0.185$,

$N = 101$) but male beetles did (Friedman: $\chi^2 = 6.710$, $df = 2$, $P = 0.035$, $N = 75$). The male preference for Nevsky over Timo was near significant after sequential Bonferroni correction, indicating a slight preference for Nevsky (Wilcoxon signed ranks test: Nevsky vs. Timo: $Z = -2.350$, $P = 0.057$). Other pair-wise comparisons were insignificant (Nevsky vs. Van Gogh: $Z = -1.282$, $P = 0.400$; Timo vs. Van Gogh: $Z = -1.165$, $P = 0.244$). The larval host plant did not affect the feeding preference of the same male as an adult (log-likelihood test: $\chi^2 = 4.323$, $df = 6$, $P = 0.633$). Thus feeding preference could not be explained by larval experience.

Discussion

Although the three potato varieties clearly differed in their glycoalkaloid content, these differences did not cause antibiosis as the performance (size, survival) of *L. decemlineata* was not affected by larval host. This indicates that Colorado potato beetles are quite robust on the relative differences in glycoalkaloid content of their host plant foliage. Our result is consistent with an experiment where beetles were reared on an artificial diet containing α -chaconine and α -solanine in the amounts found in potato foliage and beetles grew larger than beetles reared on a no-glycoalkaloid diet (Kowalski *et al.* 1999). Our and Kowalski's results contrast with those of Hare (1987) who reported decreasing larval (4th instar) growth with increasing glycoalkaloid concentration. This difference might be due to differences in responses of the different life stages to glycoalkaloids. We reared beetles from 1st instar larvae to adulthood and Kowalski from egg to prepupal stage while Hare recorded the growth of 4th instar larvae after 24 hr.

Contrary to our expectation, foliar nitrogen content affected neither adult size nor larval-to-adult survival. This result was unexpected since nitrogen is essential for normal insect growth (Mattson 1980) and hence it would be expected to have a positive effect on beetle performance (see for example Tabashnik 1982; Hare 1987; Hunt *et al.* 1992). This lack of effect could be the result of behavioural responses of the herbivores as it has shown that low nitrogen content in their host plant increases both food consumption (Slansky & Feeny 1977; Tabashnik 1982; Obermaier & Zwölfer 1999; Lavoie & Oberhauser 2004)

and the efficiency of nitrogen use in order to maintain an adequate rate of nitrogen accumulation (Slansky & Feeny 1977; Tabashnik 1982). Individuals also compensate by concentrating their feeding on the most nitrogen rich parts of plants (Obermaier & Zwölfer 1999). These mechanisms to cope with inadequate nitrogen would also mask the effects of nitrogen content. Alternatively and probably more likely, the lack of effect could be result from relatively minor differences in nitrogen content between potato plants accompanied by relatively high nitrogen content which did not allow performance differences to manifest themselves.

Although we did not find antibiosis differences, some antixenosis differences were detected. Females preferred Nevsky as their oviposition substrate although they did not show any feeding preference when offered different potato varieties simultaneously. In contrast, male beetles tended to prefer the potato variety Nevsky, a preference which was independent of their feeding history as larvae. Minor preference differences accompanied by similar performance success on different potato varieties suggest that selection acting on host and food plant choice is rather weak. Despite this weak selection, these observed oviposition and feeding preference differences may explain field observations of potato varieties suffering different defoliation levels by beetles. Therefore, susceptibility to feeding damage might reflect differences in antixenosis more than in antibiosis. Antixenosis might be based on simple chemical cues or on the surface properties of leaves rather than on the foliar alkaloids (Harrison 1987) and, thus, the preferences might not have adaptive significance. However, our results show the importance of studying the behaviour and performance of herbivores in combination when assessing resistance mechanisms.

Taken as a whole, size-at-emergence of *L. decemlineata* did not vary with larval host and was not apparently mediated by any of the leaf chemicals measured. It is not entirely surprising that glycoalkaloids did not have negative effects on *L. decemlineata* since it is a specialist herbivore, feeding on species of Solanaceae. Specialist herbivores in general are well-adapted to the chemical defences of their host plant and can even perform better on a diet containing high levels of secondary plant metabolites (e.g., Bowers & Puttick 1988; Harvey *et al.* 2005). However, our results are noteworthy because they reflect the capacity of *L. decemlineata* to respond to new selection pressures. Although it has rather recently moved from a wild host to the cultivated potato and it has faced many potato varieties with varying levels of leaf chemicals while expanding its range into novel areas, it has been able to adapt to grow on them.

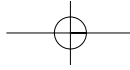
Our results underline the importance of measuring several plant characteristics and more than one component of herbivore performance simultaneously in order to get a broader picture of plant resistance. For example, observed differences in antixenosis may cause significant variation in feeding damages among cultivated crops in the field although there would be only marginal variation in plant resistance. However, these minor differences in antixenosis should not be the only bases for successful pest management strategy.

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