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RESEARCH ARTICLE

Effect of Host Plants on Insecticide Susceptibility and Detoxification Enzymes Activity in *Spodoptera litura* Fabricius (Noctuidae: Lepidoptera)

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Abstract Susceptibility to two insecticides (profenophos and cypermethrin) as influenced by host plants viz., cauliflower, soybean and castor in comparison to artificial diet and changes in detoxification enzymes in tobacco caterpillar, *Spodoptera litura* were studied under laboratory. In comparison to larvae reared on artificial diet, those reared on cauliflower were tolerant to profenophos and cypermethrin by, 1.41 and 6.6 respectively, while the larvae reared on soybean showed 1.32 and 2.00-fold more tolerance to these insecticides. However, the larvae reared on castor were found to be more susceptible to profenophos than those reared on artificial diet. The host plants had a significant influence on levels of detoxification enzymes in *S. litura*. Elevated levels of carboxylesterase (20.72-fold) and cytochrome P450 mono-oxygenase (3.10-fold) were observed in larvae reared on cauliflower as compared to diet fed larvae. Activity of glutathione S-transferase (1.56-fold) was higher in larvae reared on soybean. Enhanced activity of detoxification enzymes in larvae of *S. litura* reared on different host plants could be correlated with insecticide susceptibility. Positive and significant ($p < 0.05$) correlation was observed between the detoxification enzyme (CarE and GST) activity in different host fed larvae and LD_{50} of profenophos ($r = 0.77$; $r = 0.93$). Activity of cytochrome P450 mono-oxygenase also had positive correlation with LD_{50} of cypermethin ($r = 0.98$). The present studies have shown that differential susceptibility of *S. litura* population could be correlated with the diet/host plants and levels of detoxifications enzymes like carboxylesterases, glutathione S-transferase and cytochrome P450 mono-oxygenase.

Keywords Detoxification enzyme · Insecticide · Larval diet · *Spodoptera litura* · Toxicity

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Introduction

Tobacco caterpillar, *Spodoptera litura* (Fab.) (Noctuidae: Lepidoptera) is a defoliator pest infesting more than 120 crop plants in India and worldwide [1–3]. In India, it causes serious economic damage to crops such as cauliflower, castor and soybean. Currently synthetic insecticides are widely employed for effective control of *S. litura*. Organophosphates and synthetic pyrethroids are widely used to manage this pest [4]. Often, control failures leading to insecticide resistance are reported in several field crops including cotton [1, 5]. The changes in susceptibility of field populations of *S. litura* have been attributed to enzymatic detoxification through over production of esterase, sequestration and oxidative metabolism [6]. The choice of insecticide, method and frequency of application were reported to play significant roles in imparting insecticide resistance [7, 8]. Besides, the host plant mediated physiological changes in insect pests also play a significant role in influencing sensitivity to insecticides [9, 10].

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The ingested plant secondary metabolites by the insects may also have some effects on pesticide detoxification [11]. The activation or inhibition of insect detoxification enzymes are induced by plant allelochemicals. However, induction of detoxification enzymes is influenced by several factors viz., plant nutrients, structure and distribution of secondary plant chemicals, developmental stages of insects as well as insecticide types [12]. The mechanism that insects employ to detoxify the plant secondary metabolites obtained from host plants may also be effective in detoxifying pesticides [13].

Among the xenobiotic detoxification enzymes, carboxylesterase (CarE), glutathione S-transeferase (GST) and cytochrome P450-dependent monooxygenase are involved in detoxification of OP and pyrethroids in majority of insects. CarEs are the major enzymes associated with hydrolysis and sequestration [14] while, GSTs are cytosolic enzymes which catalyze the conjugation of reduced glutathione to insecticides that renders resistance to OP compounds. An enhanced oxidative metabolism by monooxygenases is an important mechanism responsible for pyrethroid resistance [13].

Several studies have been carried out in the past to examine the host plants or diet influenced variation on the growth and development of *S. litura* [15]. However, investigation on host plant induced variation in the insecticide susceptibility and detoxifying enzyme activity is very limited. Considering the polyphogous feeding habits of *S. litura* on more than 120 diverse plant species [3] and reports on development of resistance to several insecticides [1, 5], it is imperative to study the host plants associated changes in the insecticide susceptibility and metabolic detoxification. It could be highly useful for the better understanding of insecticide resistance mechanism and for evolving successful management strategies for this pest.

The present study is aimed at determining the relationship of toxicity of two insecticides (profenophos and cypermethrin) to the larvae reared on four different diet regimes viz., cauliflower, castor, soybean leaves and on semi-synthetic diet, with the activities of xenobiotic detoxification enzymes.

Material and Methods

Larval Diet and Host Plants

A laboratory maintained population of *S. litura* on artificial diet was used in this study at Insecticide Toxicology Laboratory Division of Entomology, Indian Agricultural Research Institute, New Delhi, India. The neonates of *S. litura* were maintained on respective host plants cauliflower leaves, castor leaves, soybean leaves and an artificial diet without exposure to insecticides for three generations before the start of the experiment.

The ingredients of the artificial diet with necessary supplements were prepared as described by Gupta et al. [16] with slight modifications. The ingredients comprised of kidney bean powder (65 g), wheat bran (55 g), wheat germ(10 g), ascorbic acid (4 g), casein (3 g), yeast powder (25 g), methyl parahydroxybenzoate (0.4 g), sorbic acid (0.92 g), cholesterol (0.25 g), streptomycin sulphate (0.1 g), 35 % formaldehyde (2 ml) and 3 drops of multivitamin, ABDEC (Park-Davis India Ltd). The diets were prepared using standard protocols and the insect cultures were maintained at 27 ± 1 °C, 60–65 % RH and a photoperiod cycle of 12L:12D h.

Tender leaves of host plants were utilized for rearing. Five-day old larvae were transferred to rearing glass jar (30 × 20 × 7 cm) containing leaves of respective host plants, their petioles dipped in water to retain its turgidity. When the larvae exhibited gut purge and entered into non-feeding wandering stage, they were transferred to boxes containing saw dust for pupation. Pupae collected after 4–5 days were surface sterilized with 0.02 % sodium hypochlorite, after being washed with distilled water, wiped with soft tissue paper and kept in a jar containing sterile saw dust. The leaves of each host plant with their petiole dipped in water were provided for oviposition. Folded white paper was kept as substrate for egg laying to the diet reared female. Emerged adults were transferred to oviposition cages and fed with 20 % honey solution.

Chemicals

The insecticides used in this study were all technical grade material: profenophos from Syngenta India Ltd, Mumbai and cypermethrin from UPL. India Ltd, Mumbai. The following chemicals were obtained from Sigma: α-naphthyl acetate, 1-chloro-2, 4 dinitrobenzene (CDNB), reduced glutathione (GSH), sodium dithionite, Fast blue BB salt, bovine serum albumin (BSA) (Fraction V) and Coomassie brilliant blue G-250 dye (CBBG).

Insecticide Bioassay

To assess the acute toxicity, 7-day old (third instar) larvae of *S. litura* obtained from same egg mass were taken. Technical grade insecticides were dissolved individually in acetone, to yield a stock solution and required concentrations ranging from 0.001 to 0.09 % were prepared by serial dilution with the solvent. One µl of test solution was applied topically on the dorsum of the thorax of each larva using a Burkard micro applicator. Acetone alone was used as the control for each insecticide. Each treatment had a population of 30 larvae and it was replicated thrice. Treated

larvae were transferred to petri plates (11 × 9 cm) containing respective diet regiment. In each petri plate, five treated larvae were maintained and held in a chamber at 27 ± 1 °C. The larvae were checked at 24 and 48 h after treatment, and mortality was recorded and subjected to correction using Abbot's formula [17].

Carboxylesterase (CarE) Assay

Carboxylesterase activity was determined as described by Van Asperen [18] with slight modifications. Twenty, 7-day old larvae collected from each diet treatment were homogenized in 5 ml 0.1 M phosphate buffer (pH 7.4) containing 1 mM each of EDTA (ethylene diamine tetra acetic acid), PMSF (phenyl methyl sulfonyl fluoride), PTU (Phenyl thiourea) and 20 % glycerol and centrifuged at 10,000 rpm for 20 min at 4 °C. The supernatant obtained was used as the enzymatic source. The reaction mixture (40 µl of enzymatic source and 5.0 ml of 0.3 mM α-naphthyl acetate) was incubated for 20 min at room temperature in dark with occasional shaking, then 1.0 ml of mixture of fast blue B (1.0 % FB salt w/v in 0.04 M phosphate buffer, pH 6.8) and 5 % sodium dodecylsulfate (SDS) solution which was prepared using double distilled water were added at 2:5 ratio and incubated for 20 min at room temperature. Absorbance value (OD) at 590 nm was recorded with spectrophotometer (ECI, Hyderabad) against a blank made up from the buffer used, and the activity of α-NA towards esterase in different diet treatments were calculated from a standard curve.

Glutathione S-transferase (GST) Assay

GST activity was measured using CDNB (1-chloro-2, 4-dinitrobenzene) as described by Habig et al. [19]. Larval homogenates were prepared using fresh 0.1 M phosphate buffer (pH 7.4) containing 1 mM each of EDTA, PMSF, PTU and 20 % glycerol. A reaction mixture of 2.77 ml phosphate buffer (100 mM, pH 6.5), 50 µl of 50 mM CDNB, 150 µl 50 mM reduced glutathione and 30 µl of enzyme solution was shaked gently followed by incubation for 2–3 min. Change in absorbance value (OD) was recorded for 5 min at 340 nm, and the GST activity (µmol $mg^{-1}min^{-1}$) was then calculated using extinction co-efficient 9.6 mM^{-1} cm^{-1}.

Cytochrome P450 Mono-oxygenase Assay

Twenty, 3rd instar larvae of *S. litura*, reared on different host plants were dissected in phosphate buffer (100 mM, pH 7.0) containing 1.5 % KCL. Larvae were placed individually in a dissection tray containing 10 ml of dissection buffer, with the dorsal side facing uppermost stretched and fixed by using fine pins through the head and posterior region. After careful dissection, the food bolus was completely removed from the gut portion. The mid-guts were transferred to 1 ml of freshly prepared homogenization buffer (100 mM, pH 7.0) containing 1 mM each of EDTA, PMSF, PTU and glycerol. The buffer containing the midguts was placed in an ice bucket and homogenized using homogenizer. The homogenates were transferred to 1.5 ml polypropylene tubes and centrifuged at 10,000 rpm for 20 min at 4 C. The supernatant was collected and the volume was brought up to 6 ml using cold homogenization buffer. Mono-oxygenase activity was estimated in a freshly prepared midgut homogenate using carbon monoxide different spectra, following reaction with sodium dithionite [20].

Protein Content Quantification

Protein content of homogenate was determined using the CBBG method as described by Bradford [21] with BSA as the standard. Absorbance at 595 nm was recorded in a spectrophotometer.

Data Analysis

Bioassay data were analysed for log probit fit regression using probit analysis software Indostat; LD_{50} and associated parameters were computed; mean values were separated using the least significant difference test (LSD). Failure of 95 % confident limit (CL) to overlap was used as the criteria for identifying significant differences among LD_{50} values for each insecticide Activities of CarE, GST and AChE among the different host reared larvae were analyzed using analysis of variance (ANOVA) and differences between treatments were tested using Tukey's test ($p < 0.05$).

Results and Discussion

Insecticide Bioassay

Tobacco caterpillar, *S. litura* larvae (7-day old) reared on four different host diets were bio-assayed with organophosphate-profenophos and synthetic pyrethroid-cypermethrin and log probit estimates are presented in Table 1. Among the treatments, larvae reared on cauliflower recorded the highest LD_{50} values of 0.310 and 0.330 ng/larvae for profenophos and cypermethrin, respectively. The LD_{50} values for profenophos were 0.180, 0.290 and 0.220 ng/larvae respectively for the larvae reared on castor, soybean and diet. The LD_{50} of cypermethrin was 0.060, 0.100 and 0.050 ng/larvae respectively for the larvae reared on castor, soybean and diet. The toxicity of each insecticide against larvae reared on different host plants was compared

Table 1 Susceptibility of *S. litura* larvae reared on different larval diets to insecticides

Chemical	Host	d.f.	$\chi 2$	LD_{50} (ng/larvae)	Regression equation (Y)	Fudical limits	RS*
Profenophos	Castor	3	7.371	0.180	Y = 7.067 + 1.192 X	0.150–0.230	0.82
	Cauliflower	4	8.811	0.310	Y = 7.812 + 1.866 X	0.270–0.360	1.41
	Soybean	3	3.512	0.290	Y = 7.426 + 1.574 X	0.240–0.340	1.32
	Diet	3	1.622	0.220	Y = 6.830 + 1.101 X	0.170–0.280	1
Cypermethrin	Castor	3	2.180	0.060	Y = 7.624 + 1.163 X	0.040–0.070	1.20
	Cauliflower	4	8.638	0.330	Y = 6.799 + 1.217 X	0.250–0.440	6.60
	Soybean	3	7.542	0.100	Y = 6.351 + 0.680 X	0.070–0.150	2.00
	Diet	5	7.454	0.050	Y = 8.136 + 1.374 X	0.040–0.060	1

Y probit kill, *X* log dose, significant at $p = 0.05$

* Relative susceptibility to insecticides (RS) = LD_{50} of Larvae reared on various host diets/LD_{50} larvae reared on artificial diet

with larvae reared on artificial diet. *S. litura* fed on cauliflower and soybean showed 1.41 and 1.32 times more tolerance to profenophos as compared to diet reared larvae. Toxicity of profenophos was higher for the larvae fed on castor (LD_{50}-0.180 ng/larvae) but it was at par with that of the larvae reared on artificial diet. The larvae reared on cauliflower, soybean and castor showed 6.60, 2.00 and 1.20 times more tolerance to cypermethrin than those larvae reared on artificial diet. The order of susceptibility of *S. litura* larvae reared on four different host plants to profenophos was found as castor > Diet > soybean > cauliflower, while the order of susceptibility to cypermethrin was observed as diet > castor > soybean > cauliflower.

Plants defend themselves from the attack by herbivores through the allelochemicals and it has been well established that the plant secondary compounds influence the induction or detoxification of insecticidal compounds. The susceptibility of insects to insecticides is influenced to a greater extent by their host plants. Polyphagous pests like *S. litura* experience a wide array of secondary plant compounds under various food regimes, leading to differential activities on the detoxification enzymes and as such the susceptibility levels vary with different host plants.

The study clearly demonstrated that the host plants and diet fed by *S. litura* had a significant influence on the insect's response to insecticides. The susceptibility of *S. litura* to profenophos and cypermethrin was significantly higher on castor, soybean and artificial diet than on cauliflower. Xue et al. [8] demonstrated the differential susceptibility of *S. litura* larvae reared on tobacco, Chinese cabbage, cowpea and sweet potato to different groups of insecticides. Present results are in conformity with the several earlier studies on influence of host plants on susceptibility of *S. litura* and other polyphagous pests like *Heilcoverpa armigera* and other species [9–11]. This differential response of host plants to insecticides was attributed to the plant allelochemicals/secondary metabolites which could induce or decrease the activities of detoxifying enzymes [22]. However, toxicity level of profenophos and cypermethrin to *S. litura* fed on different host plants was not found to be consistent, as insecticide toxicity is influenced by many factors including stage of insects, feeding behavior, physiochemical properties of insecticides, and the method of testing. Feeding behaviour and stage of larvae combined with host plant influence on insecticidal susceptibility of *S. litura* larvae had earlier been demonstrated [23, 24].

Effect of Larval Diets on Larval Protein Content

Protein content of *S. litura* larvae fed with castor, cauliflower, soybean and artificial diet are present in Fig. 1. The total protein content of the third instar larvae was the highest in insects fed with artificial diet (102.65 mg/g) followed by feeding on cauliflower (97.52 mg/g), and soybean fed larvae (92.94 mg/g), while it was significantly lower in larvae fed with castor leaf (84.64 mg/g). All the treatments exhibited significant difference ($p < 0.05$) for protein content in *S. litura.* The difference in the level of protein, carbohydrate and lipid in *S. litura* larvae reared on various diets is related to organic constituents of host plants and diets that directly influence the biochemical constituents of the insects [25]. Similar trend has been observed in *H. armigera* with higher protein content on larvae reared on artificial diet as compared to those reared on cotton, pigeon pea and chickpea [26].

Effects of Larval Diets on Carboxylesterase (CarE) Enzyme Activity

The CarE activity in *S. litura* larva reared on castor, cauliflower, soybean and diet were found to be 85.33, 254.80, 134.50 and 12.30 nmol $min^{-1}mg^{-1}$of protein, respectively (Table 2). In comparison to larvae reared on artificial diet, the CarE activity was significantly higher in the larvae fed with cauliflower (about 20.72-folds) followed by soybean (10.93-fold) and castor (6.94-fold). The

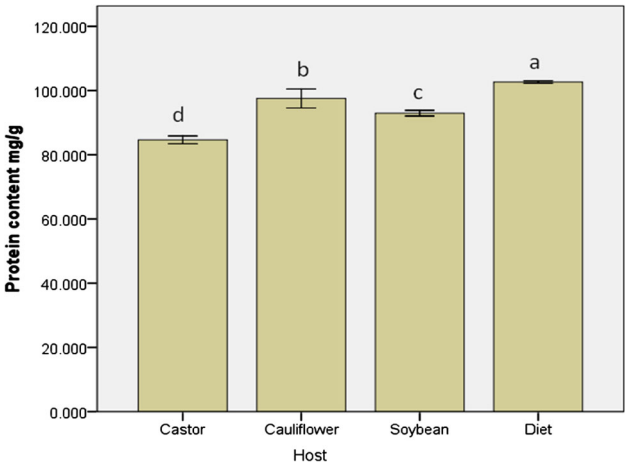

Fig. 1 Protein contents in *S. litura* fed on different diets. *Bars* with the different *letters* are significant at $p < 0.05$

activity of CarE in the three different hosts fed larvae was found to be cauliflower > soybean > castor > artificial diet. There was a strong positive correlation between the larvae reared on different regimens and LD_{50} values of the insecticides viz., profenophos ($r = 0.77$) and cypermethin ($r = 0.99$).

Detoxification enzyme CarE is an important determinant for the growth and survival in herbivores. Increase in CarE activity in *S. litura* larvae fed on cauliflower and soybean could be a plausible reason for more tolerance towards profenophos and cypermethrin. Elevated activity of CarE was found to be involved in insecticide resistance to organophosphate and synthetic pyrethroid [1, 5]. Several earlier works have confirmed in many lepidopteran species, that higher CarE activity was correlated with resistance to OP and pyrethroids. Similarly, there were reports on differences in CarE activity in insects fed with different hosts. Earlier it was found that the CarE activities of *S. litura* fed on tobacco and Chinese cabbage were greater than the activities of those that fed on sweet potato and cowpea [8]. Studies with *H. assulta* showed that differential activity of CarE on the larvae fed with chilli, pepper, tobacco and artificial diet had differential susceptibility to the insecticides tested [9]. Qualitative variation in CarE activity was observed as multiple esterases on *S. litura* larvae reared on tobacco and they were least susceptible to insecticides as compared to larvae fed on other hosts [27].

Effects of Larval Diets on Glutathione S-transferase (GST) Enzyme Activity

The activities of GST in the larva reared on four different diet regimes are given in Table 2. The GST activity of larvae reared on castor, cauliflower, soybean and diet was observed as 1322.20, 1912.34, 2658.20 and 1701.40 nmol $min^{-1}mg^{-1}$ of protein, respectively. The order of activity was as soybean > cauliflower > diet > castor. The larvae fed with soybean and cauliflower showed relatively 1.56 and 1.12 times more GST activity than the larvae which were fed on artificial diet. Positive correlation existed between the GST activity of different host reared larvae and median lethal concentration (LD_{50}) of profenophos ($r = 0.93$) and cypermethin ($r = 0.89$). Variation in GST profile in polyphagous herbivores fed on different host plants has been reported and it could influence the toxicity of insecticides [25]. Present study revealed that significantly higher GST activity was observed in the larvae fed with soybean and cauliflower was found to be more tolerant to profenophos.

As GSTs, enhance oxidative detoxification [9], the increased GST activity could be attributed to the less toxicity of profenophos and cypermethrin on *S. litura* reared on soybean and cauliflower. GST was found to be the major enzyme responsible for OP and pyrethroid resistance in insects [28]. Differential activities of GST on *S.litura* reared on different host plants have earlier been demonstrated. It was observed that the GST activity of *S. litura* larvae was highest when they fed on tobacco and Chinese cabbage than on cowpea [8].

Effects of Larval Diets on Cytochrome P450 Mono-oxygenase Activity

The cytochrome P450 mono-oxygenase activity estimated in the larvae fed with four different diets are presented in Table 2. The level of Cyt P450 mono-oxygenase was 4.09,

Table 2 Activity of CarE, GST and Cyt450 mono-oxygenase enzymes in *S. litura* larvae reared on different host plants

Host	CarE (nmol/min/mg of protein) (±SE)[a]	Relative activity	GST(nmol/min/mg of protein) (±SE)[a]	Relative activity[*]	Cytochrome P450 mono-oxygenase (nmol/min/mg of protein) (±SE)[a]	Relative activity
Castor	85.33 ± 0.218^{c}	6.94	1322.20 ± 110^{b}	0.78	4.09 ± 0.29^{bc}	1.32
Cauliflower	254.80 ± 1.472^{a}	20.72	1912.34 ± 447^{ab}	1.12	9.62 ± 0.69^{a}	3.10
Soybean	134.50 ± 0.223^{b}	10.93	2658.20 ± 145^{a}	1.56	5.22 ± 0.54^{b}	1.68
Diet	12.30 ± 0.218^{d}	1.00	1701.40 ± 238^{b}	1.00	3.11 ± 0.77^{c}	1.00

[a] Values in the same column followed by the same letters are not significantly different at $p = 0.05$

[*] Relative activity = Activity of CarE or GST or Cyt P450 mono-oxygenase in different host plants fed larvae/Activity of CarE or GST or Cyt P450 mono-oxygenase in larvae fed on artificial diet

9.62, 5.22 and 3.11 nmol $min^{-1}mg^{-1}$ of protein on the castor, cauliflower, soybean and artificial diet reared *S. litura* respectively. The larvae that fed on cauliflower exhibited greater activity and it was 3.10 times higher as compared to the larvae grown on diet. While, the larvae bred on soybean and castor showed relatively 1.68 and 1.32 times more mono-oxygenase activity than those reared with the diet.

The cytochrome P450 mono-oxygenase are the major metabolic enzymes causing pesticide detoxification in insect systems [20] and enhanced activity of mono-oxygenase in pyrethroid resistance has also been reported [12, 13]. The order of mono-oxygenase activity in three different host fed larvae was found as cauliflower > soybean > castor > artificial diet.

In the present study, cypermethrin was found to be highly toxic to the larvae reared on artificial diet followed by soybean, whereas larvae fed on cauliflower and castor were found to be least susceptible. The highest mono-oxygenase activity in cauliflower fed larvae of *S. litura* synchronized with the highest LD_{50} value and hence tolerance to cypermethrin. Correlation analysis revealed a strong positive correlation ($r = 0.98$) between the mono-oxygenase activity in different host reared larvae and susceptibility to cypermethrin. The differential activity of mono-oxygenase in *S. litura* and larvae response to insecticides could be attributed due to nutritional composition of host plants. Under various food regimes, the differential activity of P450 mono-oxygenase in *S. litura* was demonstrated by Karthi et al. [10].The results are in conformity to the earlier reports [13, 29]

Conclusion

The present investigation gives an insight to the mechanisms of host-pest interaction with induction of detoxification enzymes and insecticidal susceptibility in *S. litura*. Development of insecticidal tolerance and diverse response of insects to insecticides were found to be associated with host plant induction of detoxifying enzymes. The susceptibility level of *S. litura* larvae reared on four different host plants or diets found to have a relation with activities of detoxification enzymes. The importance of detoxification enzyme induction and toxicity alteration in *S. litura* by different host plants, on which they fed, should be taken into account while framing pest management strategies. Proper understanding of this mechanism will set novel targets for pest management which will be helpful in overcoming insecticidal tolerance. Thus, there is need to modify the amount of insecticides applied in field as host plants play important role in imparting tolerance against insecticides while considering the immunity developed by insects against insecticides. However, host plant allelochemicals and insect cuticle enzymes also need to be considered because they are associated with the induction and absorption of toxic compounds. Further, studies on host-herbivore interaction at molecular level would give better understanding of host plant genes and associated factors, involved in detoxification enzyme metabolic pathway.

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