ISSN 1067-4136, Russian Journal of Ecology, 2009, Vol. 40, No. 6, pp. 434–439. © Pleiades Publishing, Ltd., 2009.
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The Response of Gypsy Moth (*Lymantria dispar* L.) Larvae Infected with Nuclear Polyhedrosis Virus to Induced Resistance in Birch (*Betula pendula* Roth.)

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Received December 10, 2008

Abstract—The effects of birch resistance induced by its artificial defoliation on the development of gypsy moth larvae and their sensitivity to viral infection and on the state of the antioxidant and detoxification systems of the insect midgut were studied. The dynamics of larval body weight; larval mortality and its etiology; glutathione-S-transferase (GT), nonspecific esterase (NE), and catalase (CAT) activities; and the ratio between the concentrations of oxidized and reduced thiol-containing compounds (RSSR/RSH) were estimated. In larvae feeding on the leaves of a previously defoliated plant, body weight was decreased, NE was inhibited, and the RSSR/RSH ratio was increased.

Key words: host plant, defoliation, phytophage, insect resistance, nuclear polyhedrosis virus, detoxifying enzymes, antioxidant system.

DOI: 10.1134/S1067413609060095

Population control of various organisms, including insects, is one of the key problems in both ecology and plant protection. Defoliation or damage to foliage of perennial plants is known to induce rapid and delayed plant resistance, which decreases the viability of phytophagous insects (Haukioja, 2005a). The decrease in the photosynthesizing area of a plant triggers a cascade of biochemical reactions leading to an enhanced synthesis of inhibitors of serine proteases, polyphenol oxidases, NADP oxidases, peroxidases, etc., as well as altered concentrations of primary and secondary metabolites (allelochemicals) (Kaitaniemi, et al., 1998; Walling, 2000; Hukioja, 2005b).

The toxic effect of plant secondary metabolites on phytophages may cause uncontrollable increase in the production of reactive oxygen species (ROS) and, as a consequence, oxidative stress in insects (Peric-Mataruga et al., 1997; Barbehenn et al., 2005). ROS production in insects is controlled by enzymatic (superoxide dismutase, catalase (CAT), and enzymes of the ascorbate- and glutathione-dependent cycles) and nonenzymatic (thiol- and phenol-containing compounds) antioxidants (Felton and Summers, 1995; Wang et al., 2001; Krishnan and Kodrik, 2006). The cascade of reactions leading to ROS generation makes the food less preferential for the phytophage because of the increased toxicity and decreased quality (Kaitaniemi et al., 1998; Bakhvalov et al., 2002; Riipi et al., 2002). Woody plants may retain the induced resistance as long as four years after the damage (Neuvonen and Haukioja, 1991; Kaitaniemi et al., 1999), thereby restricting the insect population size.

Pioneering studies by Price et al. (1980) gave rise to analysis of the effect of food quality not only on phytophagous consumers but also on their predators and parasites, i.e., object of the next trophic level (Keating et al., 1990; Geervliet et al., 1994; Turlings et al., 1995; Gatehouse, 2002). However, studies in this field have not yet unambiguously answered the question as to the effect of the quality parameters of host plants on the parasites and predators of phytophages (Hunter and Shultz, 1993; Hoover et al., 1998; Lindroth et al., 1999; Bakhvalov et al., 2002; Gatehouse, 2002). It is known that phytophagous insects have developed a number of adaptations alleviating the deleterious effects of the protective responses of plants. Metabolic transformation of allelochemicals followed by their elimination from the insect body is one these adaptations (Tyshchenko, 1986). The detoxifying system of insects plays the key role in this process. Detoxifica-

tion of xenobiotics in insects involves microsomal monooxygenases, nonspecific esterases (NEs), and glutathione-S-transferases (GTs) (Roslavtseva, 1994). There is evidence that detoxifying enzymes may play an important role in insect pathology (Shiotsuki and Kato, 1996; Serebrov et al., 2001).

We studied the effect of artificial defoliation of birch (one year before the study) on the development of the gypsy moth and its sensitivity to viral infection, as well as on the activities of detoxifying antioxidant enzymes and the concentration of nonenzymatic antioxidants in the insect midgut.

MATERIALS AND METHODS

Object. Experiments were performed on caterpillars of the gypsy moth *Lymantria dispar* L. (Lepidoptera: Lymantriidae) from a wild outbreaking population living in birch–aspen planting in Krasnozerskii raion of Novosibirsk oblast. The density of egg masses in the focus averaged 20 per tree; the defoliation rate of birch stands in the current season was 60–70%. The egg masses were collected in the first ten-day period of September and kept for one month at 4°C, for one month at –15°C, and then until the experiments at 4°C.

Defoliation of the host plant, rearing of insects, and their infection with the virus. For the experiment, we chose a young birch stand geographically isolated from the current outbreaks of gypsy moth where no substantial damage by phytophages had been observed before. Ten control and ten experimental trees aged 8–10 years were used in the experiment. The trees were selected randomly, except that the distance from the edge of the birch stand was no less than 10 m. The trees were mechanically defoliated during one day in the second half of June. The date of the artificial defoliation corresponded to the date of natural defoliation of trees of this species by insects in the Western Siberian forest–steppe zone. Trees from the same stand that were not defoliated served as a control group.

A year after defoliation, second-instar larvae were grown in hatcheries on cut-off shoots of defoliated and control plants at 25°C and a 16-h photoperiod. On day 7 after the start of the experiment (which corresponded to the third instar of the larvae), half the control caterpillars and half the experimental ones (reared on the leaves of birch trees defoliated a year before) were infected with nuclear polyhedrosis virus (NPV; a collection strain from the Laboratory of Insect Pathology of the Institute of Systematics and Ecology of Animals). For this purpose, a water suspension of virus polyhedrons with a concentration of 10^7 polyhedrons/ml was applied onto the surface of the leaves from the experimental and control trees by one-time spraying; the food was slightly dried at room temperature, and then the caterpillars were put onto it. The leaves were treated on a 50 × 50-cm frame using 50 ml of the suspension per frame. The amount of the shoots placed on the frame approximately corresponded to the density of the crown of a birch growing under natural conditions. The above NPV concentration corresponded to the LC_{50} for the given insect population. The food intended for control caterpillars was treated with 50 ml of distilled water.

To analyze the development of the larvae and the effect of NPV infection on them, we put the caterpillars into 19-dm^3 containers (50 caterpillars per variant, in triplicate). The mortality rate was estimated on day 14 after infection, which corresponded to 21 days from the start of feeding on the control and experimental leaves and during the entire larval stage. For biochemical studies, the caterpillars were grown individually in 200-cm^3 plastic containers (30 caterpillars per variant). Birch shoots treated with the NPV suspension were replaced for the first time when at least 75% of the leaf area had been eaten and; after that, the shoots from the control and experimental trees were replaced every day.

Estimation of the functional parameters of gypsy moth larvae. The average body weight of the caterpillars was determined by weighing them individually on an electronic balance to an accuracy of 0.01 g. The sensitivity of the caterpillars to the virus was estimated from their mortality rate after infection with the pathogen at a concentration equal to the LC_{50} (Bakhvalov et al., 1998). The insect mortality and its etiology were determined according to Weiser and Briggs (1971).

Estimation of biochemical parameters. All biochemical characteristics reflecting the state of the larvae were studied in fourth instar larvae three days after molting (Peric-Mataruga et al., 1997). An Agilent 8453 spectrophotometer (Germany) was used for the spectrophotometric analysis of reaction mixtures. The difference in the optical densities of the mixture before and after the reaction per minute per milligram of protein was taken to be the arbitrary unit of specific activity for all the enzymes studied.

Midgut homogenates were prepared as described (Dubovskiy et al., 2008). The GT activity was measured spectrophotometrically at 340 nm by the increase in the concentration of 5-(2,4-dinitrophenyl) glutathione, whose formation is catalyzed by GT (Habig et al., 1974). The NE activity was measured by a slightly modified method of van Asperen (1962). The reaction mixture containing 1 ml of 0.54 mM 1-naphthyl acetate in a phosphate buffer solution and 5 μl of a gut homogenate was incubated for 30 min in the dark at 30°C. After that, the reaction was stopped by adding 250 μl of a fixing solution (0.25% fast blue RR and 3.125% of sodium dodecyl sulfate in a phosphate buffer solution). The CAT activity was calculated from the rate of hydrogen peroxide decomposition measured spectrophotometrically at 240 nm (Wang et al., 2001). Measurement of the concentrations of thiol-containing compounds was based on the fact that they are oxidized by 5,5-dithio-bis-(2-nitrobenzoic acid) (Khramtsov et al., 1997). The optical density was mea-

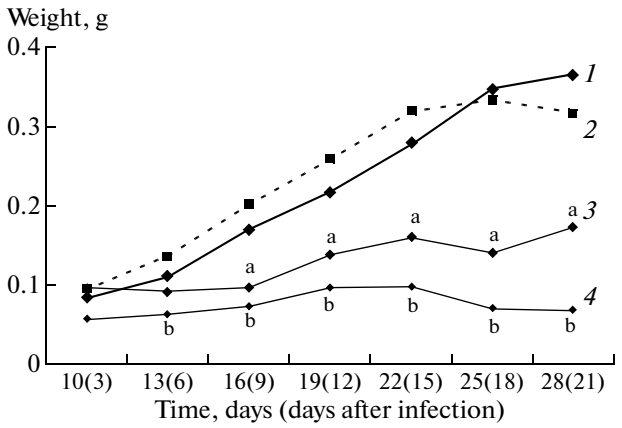

Fig. 1. Body weight dynamics in native and infected gypsy moth larvae: (*1*) control, (*2*) NPV-infected larvae feeding on leaves from intact trees, (*3*) intact larvae feeding on leaves from previously defoliated trees, and (*4*) infected larvae feeding on leaves from previously defoliated trees. The letters a and b indicate significant differences from the control variant and from all variants, respectively ($p \le 0.05$).

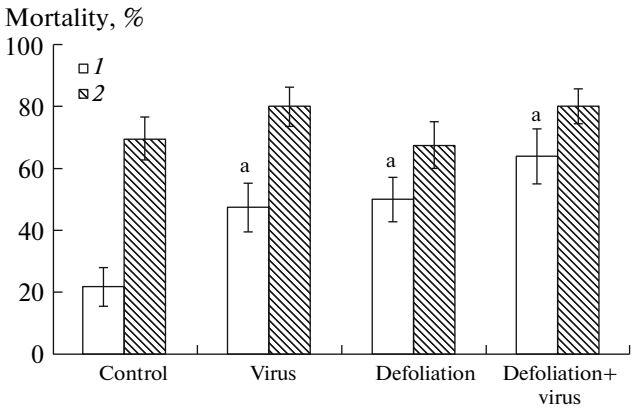

Fig. 2. Effect of birch defoliation on the total mortality of native and infected gypsy moth larvae: (*1*) mortality on day 14, (*2*) mortality throughout the larval stage. The letter a indicates significant differences from the control group ($p \le 0.05$).

sured at 412 nm using cisteine as a standard. The result was presented as the ratio between the concentrations of oxidized and reduced thiol-containing compounds (RSSR/RSH) (Dubovskiy et al., 2008). The protein content of the samples was measured according to Bradford with bovine serum albumin used as a standard.

Statistical analysis. The significance of differences between the mean weights of the larvae, enzyme activities, and concentrations of thiol-containing compounds in the groups compared were determined using ANOVA (Dospekhov, 1985). The insect mortality was evaluated using Abbot's equation (Gar, 1963).

RESULTS AND DISCUSSION

The body weight of intact larvae feeding on the leaves of the trees that had been previously defoliated became significantly lower than that of the control larvae on day 16 after they were placed on the leaves and remained so until the end of the experiment. The weight of NPV-infected larvae feeding on the leaves of damaged trees almost ceased to increase on day 6 after infection (Fig. 1). The weight of infected larvae feeding on the leaves of intact trees did not differ significantly from that of control larvae throughout the experiment (Fig. 1). Therefore, NPV infection had no effect on body weight gain in the larvae developing on the leaves of intact plants but considerably affected it if larvae developed on the leaves of damaged plants.

Different groups of larvae did not differ from one another in the total mortality in the entire period from the start of the experiment to pupation ($p \ge 0.05$), this value varying from 67 to 80% (Fig. 2). However, the experimental and control groups differ in the mortality rate. For example, on the 14th day after infection, which is approximately equal to the incubation period of nuclear polyhedrosis virus, the mortality rates of infected caterpillars feeding on native and damaged birch shoots were two and three times higher, respectively, than in the control group (Fig. 2). On day 21 of feeding on the leaves of previously damaged plants (which corresponded to the 14th day after infection), the total mortality of uninfected larvae was two times higher than in the control group. Therefore, feeding on the leaves of damaged trees caused death of the larvae within a shorter period of time, the total mortality throughout the larval stage remaining the same as in the control group.

Although the experimental and control larvae did not differ significantly from each other in the total mortality, microscopic analysis showed that more larvae died from various infections, including nuclear polyhedrosis, in experimental groups compared to the control one (Fig. 3).

Spectrophotometric analysis of detoxifying enzymes in the larval midgut showed that NPV infection significantly decreased the GT activity irrespective of the quality of the leaves eaten (table). The NE activities in the larval midgut were inhibited in all experimental variants. The RSSR/RSH ratio was significantly increased in the midguts of both uninfected and infected larvae feeding on the leaves of damaged plants compared to native and infected larvae feeding on the leaves of intact plants.

The decrease in the body weight of the caterpillars feeding on the leaves of the trees that had been previously damaged indicates that insect resistance had been induced in the plants. This effect may have been mediated by a decrease in food consumption or a toxic effect of the leaves on the caterpillars. It is known that delayed insect resistance in deciduous woody plants is

often accounted for by a high phenol content of leaves (Kaitaniemi et al., 1998; Haukioja, 2005a, 2005b). Surprisingly, however, the induced insect resistance of trees did not increase the total mortality of insect larvae. Probably, gypsy moth caterpillars isolated from the population that reached the peak density have an increased sensitivity to various factors, as evidenced by the high mortality of control larvae. This may have masked the sensitivity to the induced insect resistance of birches. The absence of the effect of induced insect resistance of the host plant on the insect survival may be also explained age dependence of the sensitivity of caterpillars to the quality of the host plant. For example, caterpillars of many insects have been demonstrated to be more sensitive to secondary metabolites of plants immediately after hatching, compared to older instars (Zalucki et al., 2002). In our studies, only second-instar caterpillars began feeding on the leaves of damaged trees.

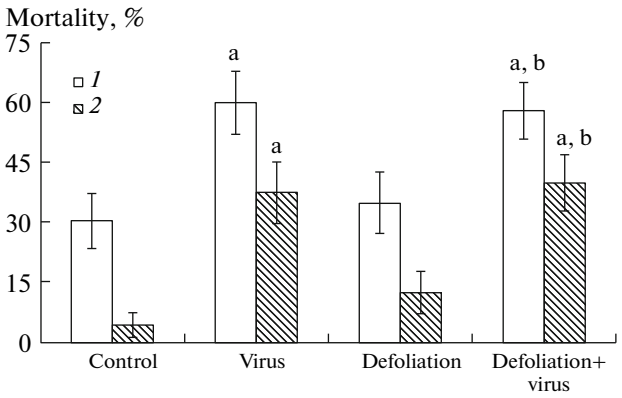

Fig. 3. Etiology of the mortality of intact and infected larvae feeding on trees of native and defoliated trees: (*1*) mortality from various infections, (*2*) mortality from nuclear polyhedrosis virus. The letters a and b indicate significant differences from the control variant and from the defoliation variant, respectively ($p \le 0.05$).

It is possible that the NE activities in the midgut of the larvae feeding on the leaves of previously defoliated trees were inhibited because of induced synthesis of a number of secondary metabolites in the leaves of the damaged plant. For example, food enriched with hydroxamic acid (2,4-dihydroxy-7-metoxy-1,4,-benzoxazin-3-one) inhibited NEs in the aphid *Rhopalosiphum padi* (Mukanganyama et al., 2003); therefore, the authors supposed that this secondary metabolite is bound with the serine-containing active center of esterases. The decrease in the body weight of the caterpillars feeding on the leaves of previously defoliated birches is likely to be partly caused by inhibition of NEs, which increases the susceptibility of the caterpillars to the effects of toxicants contained in the leaves.

It is difficult to explain the inhibitory effects of the virus on the GT and NE activities in the midgut of the phytophage. We did not find any published studies on the subject. Probably, this inhibition is related to destructive processes accompanying the replication of the virus in midgut cells.

The increased RSSR/RSH ratio in the caterpillars feeding on the leaves of previously defoliated trees may result from an increase in ROS production in the lumen of their midgut. This may also result from changes in the phenol composition of the foliage of previously defoliated plants, because many phenols have a prooxidant activity (Barbehenn et al., 2005). For example, "oxidative stress" in the midgut of *L. dispar* has been shown to accompany the switch from the preferable host plant (oak) to a less preferable one (locust) (Peric-Mataruga et al., 1997). The authors of this study believed that this was caused by higher alkaloid and flavonoid contents of the locust leaves. In our experiment, the prooxidative effect of secondary metabolites of plants may have resulted in damaging effects of ROS on both food components and the midgut epithelium and may have been the cause of the lower body weight of the larvae feeding on the leaves of previously defoliated birch trees.

Thus, we have found that total mechanical defoliation of birch induces insect resistance in the plants on the next year, which is expressed in a reduced body weight and increased mortality rate of the insect larvae. This may play a role in the natural regulation of the population dynamics of the gypsy moth. Probably, these changes in insect development are related to the effect of secondary metabolites of the plant on the

Effect of birch defoliation on the specific activities of some enzymes and the ratio between oxidized and reduced thiol-containing compounds in the midgut of native and infected fourth-instar *L. dispar* L. larvae

Variant	Specific enzyme activity, ΔD/(min mg protein) and the ratio between oxidized an reduced thiols			
	glutathione-S-transferase	nonspecific esterases	catalase	oxidized-to-reduced thiol ratio
Control	0.0336 ± 0.0102	0.4176 ± 0.1606	0.3207 ± 0.1493	1.30 ± 0.61
Virus	0.0255 ± 0.0106[a]	0.2364 ± 0.0863[a]	0.3892 ± 0.1126	1.09 ± 0.55
Defoliation	0.0271 ± 0.0028	0.2146 ± 0.0517[a]	0.3318 ± 0.2528	2.81 ± 0.24[a]
Defoliation + virus	0.0236 ± 0.0061[a]	0.2535 ± 0.0837[a]	0.3710 ± 0.1318	4.44 ± 2.57[a, b]

Note: The superscripts a and b indicate significant differences from the control group and the virus variant, respectively ($p \le 0.05$).

phyllophagous insect. This effect may also be mediated by NE inhibition in the caterpillar midgut and the prooxidant effect of secondary metabolites of the plant on components of the food and the midgut epithelium. These changes in the biochemical state of gypsy moths may alter their sensitivity to environmental factors. At the same time, the induced resistance of birch does not affect the sensitivity of the insect larvae to nuclear polyhedrosis virus or their mortality from latent viral infection. However, the effect of the qualitative composition of the food on the caterpillar sensitivity to the virus cannot be entirely excluded, because the plants were defoliated mechanically in our experiments, and its is known that the insect saliva triggers additional mechanisms of plant insect resistance in the damaged plant leaves, which may affect the insect sensitivity to pathogens (Baldwin et al., 1997).

ACKNOWLEDGMENTS

This study was supported by the Russian Foundation for basic Research (project nos. 07-04-00870-a and 06-04-49164-a), Kone Foundation, and International Association for the Promotion of Cooperation with Scientists from the New Independent States of the Former Soviet Union (project no. 06-1 000 014-5728).

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