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DETOXICATION ACTIVITY IN THE GYPSY MOTH: EFFECTS OF HOST CO_2 AND NO_3^- AVAILABILITY

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Abstract—We investigated the effects of host species and resource (carbon dioxide, nitrate) availability on activity of detoxication enzymes in the gypsy moth, *Lymantria dispar*. Larvae were fed foliage from quaking aspen or sugar maple grown under ambient or elevated atmospheric CO_2, with low or high soil NO_3^- availability. Enzyme solutions were prepared from larval midguts and assayed for activity of cytochrome P-450 monooxygenase, esterase, glutathione transferase, and carbonyl reductase enzymes. Activity of each enzyme system was influenced by larval host species, CO_2 or NO_3^- availability, or an interaction of factors. Activity of all but glutathione transferases was highest in larvae reared on aspen. Elevated atmospheric CO_2 promoted all but transferase activity in larvae reared on aspen, but had little if any impact on enzyme activities of larvae reared on maple. High NO_3^- availability enhanced activity of most enzyme systems in gypsy moths fed high CO_2 foliage, but the effect was less consistent for insects fed ambient CO_2 foliage. This research shows that gypsy moths respond biochemically not only to interspecific differences in host chemistry, but also to resource-mediated, intraspecific changes in host chemistry. Such responses are likely to be important for the dynamics of plant–insect interactions as they occur now and as they will be altered by global atmospheric changes in the future.

Key Words—Carbonyl reductase, carbon dioxide, cytochrome P-450 monooxygenase, detoxication enzymes, esterase, global change, glutathione transferase, gypsy moth, *Lymantria dispar*, Lepidoptera, Lymantriidae, nitrate, phytochemistry, resource availability.

INTRODUCTION

Phytochemical variation *among* plant species is known to produce highly variable detoxication activity in insects (Yu et al., 1979; Yu, 1982; Lindroth,

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1989a,b). Changes in detoxication activity are generally attributed to differences in host allelochemical profiles (e.g., via induction and/or inhibition), although differences in nutrient content may also play a role (Lindroth, 1991). Such changes are of particular consequence to the nutritional ecology of generalist species such as the gypsy moth (*Lymantria dispar*), which may feed on multiple host species during larval development (Lance and Barbosa, 1982).

Phytochemical variation *within* plant species is also likely to effect changes in insect detoxication activity, although this possibility has received little attention by researchers. A host of environmental factors is known to alter individual plant chemistry and thereby to change insect performance (Denno and McClure, 1983; Mattson and Haack, 1987). Carbon–nutrient balance theory contends that such intraspecific variation results from differences in the relative availability of resources (e.g., carbon, nutrients) to plants (Bryant et al., 1983; Bazzaz et al., 1987; Tuomi et al., 1988). For example, environmental conditions that increase availability of carbon relative to nutrients may promote accumulation of carbon-based allelochemicals (Larsson et al., 1986; Bryant et al., 1987). Whether insect detoxication metabolism also changes in this context is poorly understood.

The purpose of this study was to evaluate the impact of host plant resource availability on insect detoxication capacity. We assessed the effects of carbon dioxide and nitrate availability on detoxication activity in gypsy moths fed quaking aspen (*Populus tremuloides*) and sugar maple (*Acer saccharum*).

We selected this experimental system for several reasons. First, larvae of the gypsy moth are highly polyphagous and are serious forest pests in the northeastern and, more recently, north central and eastern United States. Yet, apart from several studies of cytochrome P-450 monooxygenase enzymes (Ahmad, 1986; Sheppard and Friedman, 1989), little is known about host plant mediation of detoxication activity in this species. Second, both plant chemistry and larval detoxication capacity are known to influence host use by gypsy moths (Rossiter et al., 1988; Lindroth and Hemming, 1990; Lindroth et al., 1993; Hemming and Lindroth, unpublished data). Third, effects of carbon dioxide and CO_2 × nitrate interactions on trees are of increasing environmental importance, as atmospheric concentrations of CO_2 are expected to double by the latter half of the next century (Hansen, 1981; Gates et al., 1983) and to exert significant impacts on forest ecosystems (Eamus and Jarvis, 1989; Graham et al., 1990).

METHODS AND MATERIALS

Insects and Diets. We obtained gypsy moth egg masses from USDA-APHIS, Otis Air National Guard Base, Massachusetts. Larvae were reared from egg hatch through the third stadium on standard wheat germ diet (ODell et al., 1985, but without the preservative methyl paraben) at 25°C, on a 15:9 hr light–

dark cycle. All insect rearing was conducted in the gypsy moth quarantine facility of the Department of Entomology, University of Wisconsin, Madison.

The experimental design was a 2 × 2 × 2 factorial, with two species of trees and two levels each of carbon dioxide and nitrate. We grew 1-year-old seedlings of quaking aspen and sugar maple in environmental control rooms at the University of Wisconsin Biotron under ambient (350 ppm) and elevated (650 ppm) atmospheric CO_2 (see Kinney and Lindroth, 1993, for additional experimental details). Within each room, half the trees were watered with low nitrate (1.25 mM) and half with high nitrate (7.5 mM) nutrient solution (1/2 strength Hoagland's). Foliage collected for insect feeding was pooled from several rooms at each level of CO_2 and NO_3^-. Leaves of an intermediate age were collected from aspen, which has indeterminate growth. Leaves from the first two leaf flushes were collected from maple.

Each experimental replicate consisted of 20–25 freshly molted fourth instars fed excised leaves from one of the experimental treatments. New leaves were provided every one to two days until larvae were mid-fifth instars (9–15 days, depending on development rate).

Enzyme Assays. Larval midguts (15–20) from each group were dissected into ice-cold potassium phosphate buffer (0.2 M, pH 7.8, with 1 mM EDTA) and ground in a Ten Broeck tissue homogenizer. We centrifuged the homogenates at 10,000 *g* (10 min) to remove cellular debris, and the resulting supernatants at 100,000 *g* (1 hr) to separate soluble and microsomal protein fractions. Microsomal pellets were resuspended in phosphate buffer containing 50% glycerol. Both enzyme fractions were flash-frozen in liquid nitrogen and stored at −70°C prior to assessing enzyme activity.

We determined protein concentrations of the solutions by the Bradford (1976) assay, using bovine serum albumin as a standard. Midgut preparations were then subjected to a suite of enzyme assays chosen to represent a broad range of detoxication activity. These tests included assays of cytochrome P-450-dependent monooxygenases (polysubstrate monooxygenases), esterases, glutathione transferases, and quinone reductases. All activities were quantified spectrophotometrically using a Perkin-Elmer Lambda 3B. Chemicals and reagents were obtained from Sigma Chemical Company (St. Louis, Missouri). The assays used were adapted from several sources; full descriptions are provided by Lindroth et al. (1990). A brief description of each assay follows.

In comparison to other Lepidoptera, P-450 monooxygenase activity in gypsy moths is very difficult to measure by many of the common catalytic assays, most likely because of exceptionally low activity (Lindroth, unpublished data; C. Sheppard, personal communication). Consequently, we used NADPH oxidation and cytochrome *c* reductase assays as indices of monooxygenase activity (Brattsten et al., 1980, 1984). Endogenous oxidation of NADPH by cytochrome P-450 was quantified as the decrease in absorbance at 340 nm over 90 sec.

Cytochrome *c* reductase is a redox flavoprotein coupled to cytochrome P-450, the terminal oxidase of the monooxygenase system. Reductase activity was measured by the rate of reduction of cytochrome *c* by NADPH, as indicated by the increase in absorbance at 550 nm over 60 sec. We caution that use of these assays as indices of cytochrome P-450 activity is not without problems. For the NADPH oxidation assay, other enzyme systems (e.g., tryptophan 2,3-dioxygenase) may contribute to NADPH oxidation. For the cytochrome *c* reductase assay, the ratio between reductase activity and P-450 activity can vary greatly, depending in part upon the particular P-450 isozymes and substrates involved. Our results should be interpreted accordingly.

Cytosolic general esterase activity was measured as the hydrolytic release of 1-naphthol from 1-naphthylacetate. Cytosolic glutathione-*S*-transferase activity was measured via halide substitution of reduced glutathione (GSH) onto the substrate 1-chloro-2,4-dinitrobenzene (CDNB). The conjugate GS-DNB absorbs light at 340 nm; enzyme activity is indicated by the increase in A_{340} over 60 sec. Enzymatic reduction of carbonyl compounds (specifically quinones) in cytosolic and microsomal fractions was measured by the juglone-dependent NADPH oxidation method (Yu, 1987). NADPH provides reducing equivalents for reduction of juglone (5-hydroxy-1,4-naphthoquinone); activity is detected as the decrease in A_{340} over 60 sec. The assay automatically corrects for endogenous NADPH oxidation (e.g., via P-450s) because enzymes and NADPH occur in both sample and reference cuvettes. Previous studies (e.g., Lindroth et al., 1990) documented that the NADPH oxidation observed in this assay is not catalyzed by cytochrome P-450 enzymes.

Statistical Analysis. Results were analyzed by three-way analysis of variance (ANOVA) to determine the effects of host species, CO_2 and NO_3^- levels, and their interactions on gypsy moth enzyme activities.

RESULTS

Indices of P-450 monooxygenase activity were significantly affected by host species, CO_2 and NO_3^- availability, and their interactions (Figure 1a). Rates of NADPH oxidation were 71% higher overall in larvae fed aspen than in those fed maple. High CO_2 levels increased oxidation activity 61% in larvae fed aspen but had no effect on larvae fed maple, as indicated by the significant species × carbon interaction term. High NO_3^- availability increased oxidase activity for insects fed high CO_2, but not ambient CO_2, foliage. Not surprisingly, treatment effects on cytochrome *c* reductase activity paralleled those on NADPH oxidation activity (Figure 1b). Activity was higher in larvae fed aspen than in those fed maple, increased with enhanced CO_2 availability to aspen but not maple, and increased with enhanced NO_3^- availability to trees grown under elevated CO_2.

The main effects of species, CO_2 and NO_3^- all significantly altered gypsy

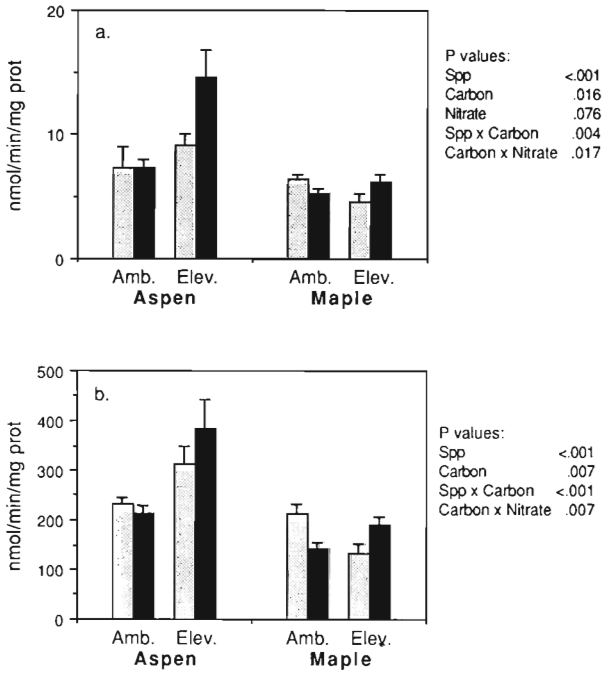

FIG. 1. Indices of cytochrome P-450 monooxygenase activity in gypsy moth larvae fed aspen and maple grown with low and high availability of CO_2 and NO_3^-. (a) NADPH oxidation activity; (b) cytochrome *c* reductase activity. Light- and dark-shaded bars represent low- and high-NO_3^- treatments, respectively. Vertical lines indicate 1 SE. Listed *P* values are from three-way ANOVAs; only values < 0.10 are shown.

moth esterase activities, but the magnitude of effect was large only for tree species (Figure 2). Larvae reared on aspen exhibited esterase activities 2.1-fold higher than those of larvae on maple. Activities increased for insects fed high CO_2 foliage, and more so for larvae on aspen than for those on maple. Improved host NO_3^- availability marginally increased (5–11%) insect esterase activity across all treatment combinations.

Glutathione transferase activities also responded to each of the main effects (Figure 3). Activities were 37% higher in larvae fed maple than in larvae fed aspen. Elevated CO_2 decreased transferase activity (37%) in larvae reared on aspen but had no effect in larvae reared on maple, as indicated by the significant interaction term. High NO_3^- availability promoted transferase activity (21–47%) in all treatment combinations.

Finally, carbonyl reductase activities also responded to host species and resource availability (Figure 4). Soluble reductase activity averaged slightly

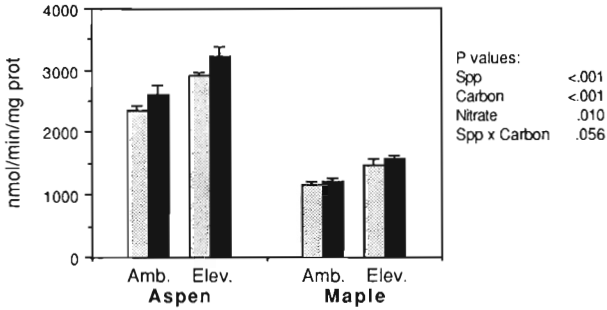

FIG. 2. Esterase activity in gypsy moth larvae fed aspen and maple grown with low and high availability of CO_2 and NO_3^-. See Figure 1 for description of figure components.

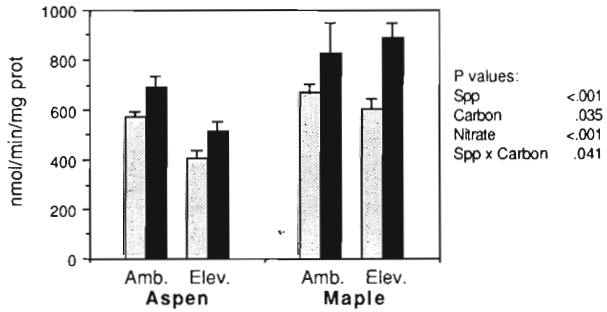

FIG. 3. Glutathione transferase activity in gypsy moth larvae fed aspen and maple grown with low and high availability of CO_2 and NO_3^-. See Figure 1 for description of figure components.

higher in larvae fed aspen than in larvae fed maple and was 25% higher in larvae fed elevated CO_2 foliage than in those fed ambient CO_2 foliage. The overall effect of high NO_3^- availability was a 16% increase in reductase activity. Treatment effects differed somewhat for microsomal reductase activities. Values were again higher in larvae fed aspen than in larvae fed maple, but the CO_2 effect was only significant for the former. We found no general NO_3^- effect but observed a $CO_2 \times NO_3^-$ interaction; high NO_3^- availability tended to reduce reductase activity in gypsy moths reared on low CO_2 leaves, but to increase activity in insects reared on high CO_2 leaves.

DISCUSSION

Our results show that gypsy moth larvae respond biochemically to changes in the chemical composition of their host plants, although specific cause-and-effect relationships cannot be ascertained from this study. (Increased activity of

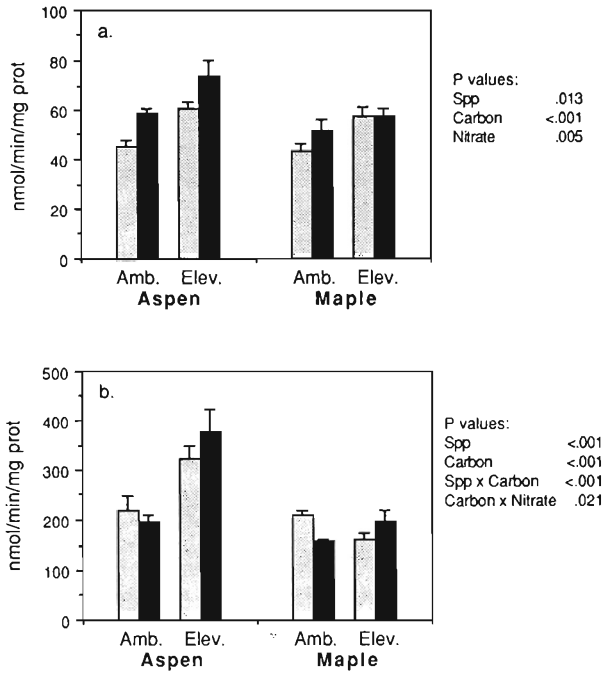

FIG. 4. Carbonyl reductase activity in gypsy moth larvae fed aspen and maple grown with low and high availability of CO_2 and NO_3^-. (a) Soluble enzyme fraction; (b) microsomal enzyme fraction. See Figure 1 for description of figure components.

an enzyme system may result from improved insect nutritional status or from consumption of inducing phytochemicals.)

Of the three factors investigated (species, CO_2, and NO_3^-), plant species generally had the greatest modulating effect on gypsy moth detoxication activity. This is as expected, because qualitative and quantitative differences in chemical composition were greater between species than within species (Kinney and Lindroth, 1993). Insects reared on aspen had higher activities than insects reared on maple for all enzyme systems but glutathione transferase. Aspen foliage contained higher concentrations of carbohydrates, but lower levels of nitrogen and condensed tannins, than did maple (Kinney and Lindroth, 1993). Maple had appreciable amounts of ellagitannins and gallotannins, which do not occur in aspen. In contrast, aspen contained phenolic glycosides (salicortin and tremulacin), which do not occur in maple. The latter compounds may be responsible for the high esterase activity in larvae reared on aspen, although earlier research on induction of gypsy moth esterases by dietary phenolic glycosides

has given conflicting results (Lindroth and Hemming, 1990; Lindroth and Weisbrod, 1991).

Several researchers have suggested that metabolic adaptations to different host species may exact a cost in terms of food processing efficiencies and, ultimately, larval performance (Schoonhoven and Meerman, 1978; Scriber, 1981). Thus, gypsy moth larvae that frequently switch host species (true generalists) may exhibit reduced performance in comparison to monophagous larvae, even though the hosts may be similarly "nutritious." This possibility has not been experimentally investigated using natural diets, but Sheppard and Friedman (1990) documented significant switching effects on gypsy moth food conversion efficiencies using a combination of artificial and natural diets. Alternatively, mixed diets may be less metabolically costly than are single-species diets that require maintenance of high titers of multiple detoxication enzymes. Larvae reared on aspen, for example, exhibit high enzyme activities across the board and are much less efficient at converting digested food into body mass than are larvae reared on maple (Lindroth et al., 1993, Kinney and Lindroth, 1993).

Gypsy moth detoxication activity also responded to changes in host chemistry as mediated by resource availability. We found significant CO_2 and CO_2 interaction effects, and NO_3^- and NO_3^- interaction effects, for every enzyme system assayed. Elevated CO_2 led to an increase in activity of all but glutathione transferases in larvae fed aspen, whereas no such trend was observed in larvae fed maple. High NO_3^- availability promoted activity of most enzyme systems in larvae reared on high CO_2 aspen and maple leaves, but the effect was less consistent in larvae reared on ambient CO_2 leaves.

Foliage of trees grown under conditions that shifted the carbon–nutrient balance in favor of carbon (high CO_2 and/or low NO_3^-) generally had increased concentrations of starch and tannin compounds but decreased concentrations of nitrogen (Kinney and Lindroth, 1993). Because multiple leaf chemical characteristics changed in concert, we cannot attribute specific enzymatic responses to particular chemicals. Nevertheless, results of this and earlier studies suggest some possibilities. Aspen phenolic glycosides are most likely metabolized via esterases in gypsy moths (Lindroth and Hemming, 1990), and increased consumption rates of larvae fed high CO_2 foliage compared to ambient CO_2 foliage may have led to induction of this enzyme system. Changes in larval glutathione transferase activity can be explained in part by shifts in host nitrogen (protein) concentrations. Transferase activity requires glutathione, a tripeptide, for conjugation. Thus transferase activity is likely reduced in insects feeding on nitrogen-deficient diets, as has been documented for gypsy moths fed artificial diets (Lindroth et al., 1990). Indeed, correlation analysis of mean transferase activity versus mean foliar nitrogen content of trees in our study revealed a strong positive relationship ($r = 0.81$, $P = 0.014$, $N = 8$).

Modulation of insect detoxication capacity in response to changes in host phytochemistry has been accorded importance in the dynamics of plant–insect interactions. Mattson and Haack (1987), for example, proposed that drought-induced changes in plant chemistry improve insect detoxication capacity, thereby contributing to the onset of insect outbreaks. Empirical evidence of such metabolic responses, however, has been virtually nonexistent. Our study illustrates that insect detoxication metabolism does change in response to intraspecific changes in host chemistry, but more research is needed to elucidate the mechanisms and biological importance of such responses. For example, to what extent are changes in detoxication capacity an active defensive response to host allelochemicals versus a passive response to changes in insect nutritional status? Are these metabolic changes of a magnitude great enough to influence insect fitness, and thus the evolution and ecology of plant–animal interactions? And if so, how will they influence the dynamics of plant–insect associations under global atmospheric conditions anticipated for the future?

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