



Host suitability and diet mixing influence activities of detoxification enzymes in adult Japanese beetles



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ABSTRACT

Induction of cytochrome P450, glutathione S transferase (GST), and carboxylesterase (CoE) activity was measured in guts of the scarab *Popillia japonica* Newman, after consumption of single or mixed plant diets of previously ranked preferred (rose, Virginia creeper, crape myrtle and sassafras) or non-preferred hosts (boxelder, riverbirch and red oak). The goal of this study was to quantify activities of P450, GST and CoE enzymes in the midgut of adult *P. japonica* using multiple substrates in response to host plant suitability (preferred host vs non-preferred hosts), and single and mixed diets. Non-preferred hosts were only sparingly fed upon, and as a group induced higher activities of P450, GST and CoE than did preferred hosts. However, enzyme activities for some individual plant species were similar across categories of host suitability. Similarly, beetles tended to have greater enzyme activities after feeding on a mixture of plants compared to a single plant type, but mixing *per se* does not seem as important as the species represented in the mix. Induction of detoxification enzymes on non-preferred hosts, or when switching between hosts, may explain, in part, the perceived feeding preferences of this polyphagous insect. The potential consequences of induced enzyme activities on the ecology of adult Japanese beetles are discussed.

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1. Introduction

Plant chemical defenses can reduce growth, fecundity, or survival of non-adapted herbivores (Fraenkel, 1959; Krieger et al., 1971; Schoonhoven et al., 2005). Adapted herbivores are able to cope with plant toxins through various mechanisms; e.g., behavioral avoidance, sequestration, increased rates of excretion, or detoxification enzymes for biochemical metabolism (Dowd et al., 1983; Karban and Agrawal, 2002). Cytochrome P450 (P450), glutathione S transferase (GST) and carboxylesterase (CoE) are super-families of detoxification enzymes involved in insects' metabolism of plant secondary compounds (Feyereisen, 2005; Yu, 2008). These enzymes, are involved in phase I (P450, CoE) and phase II (GST) stages of xenobiotic metabolism in insects (Yu, 2008). Phase I metabolism generally reduces the toxicity and changes the functionality of lipophilic substrates and phase II functions to increase the solubility of toxic lipophilic substrates and hasten excretion. These enzymes also perform other physiological activities and housekeeping functions in insects, such as acting on endogenous substrates like hormones and lipids (Feyereisen, 2005; Yu, 2008; Ranson and Hemingway, 2005).

Elevated activities of detoxification enzymes have been linked with host plant utilization and diet heterogeneity (Brattsten, 1992; Ahmad, 1983; Snyder and Glendenning, 1996; Yu, 1989; Yu et al., 2003). For example, consumption of carrot, a non-preferred host plant, by the generalist caterpillar *Spodoptera eridania* induced higher P450 enzyme compared lima bean, a more favored host (Brattsten, 1992). *Bemisia tabaci* (B-biotype), a generalist whitefly, has significant variation in CoE, GST, and P450 activities among five host plants that varied in suitability (Xie et al., 2011). Caterpillars and certain hemipterans (e.g., aphids and whiteflies) are among the more common taxa used in empirical studies relating detoxification enzymes to diet, with fewer examples among adult insect life stages of coleopterans. Lepidopteran larvae and plant-feeding hemipterans (Krieger et al., 1971; Mullin, 1986; Rose, 1985) show increased activities of P450 and GST (Yu, 1982, 1983, 1984, 1996; Lee, 1991) upon feeding on non-preferred or less suitable host plants. When assayed using model substrates (Feyereisen, 2005), polyphagy among insect herbivores results in higher enzyme activity compared to monophagy (Krieger et al., 1971; Mullin, 1986; Ahmad, 1983; Yu, 1996). Higher enzyme activities may be induced by the diversity of plant toxins in phylogenetically dissimilar plants in mixed diets (Feyereisen, 2005). Selective or inducible enzyme systems, however, could provide generalist herbivores an ecological opportunity to utilize secondary plant compounds before expending metabolic costs for

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detoxification. Generalist herbivores are considered to benefit from polyphagy by having access to more plant nutrients (nutrient balance) to maximize fitness, escape predation from natural enemies, or diversification of chemical defenses acquired from multiple plant sources (toxin dilution) (Bernays, 1988; Bernays et al., 1994; Bernays and Minkenberg, 1997; Mason and Singer, 2015).

Adult Japanese beetles have more than 300 suitable plant species in 79 plant families (Fleming, 1972; Potter and Held, 2002). Dietary range and host preferences of adult Japanese beetles are well documented from historical field observations (Fleming, 1972; Held, 2004) and feeding trials (e.g., Keathley and Potter, 2008; Ladd, 1987, 1989), but relatively little is known about the underlying physiological responses such as induction of detoxification enzymes relative to host suitability or dietary mixing. Among plants within this host range, adult Japanese beetles prefer certain plants such as rose blooms and foliage of sassafras or Virginia creeper and consumption of these plants produce higher survival and greater fecundity (Held and Potter, 2004; Keathley and Potter, 2008; Ladd, 1987, 1989). Similarly, Japanese beetles that consume a dietary mixture of suitable hosts have improved fecundity and adult longevity (Held and Potter, 2004). The mechanism, toxin dilution or nutrient balance, to explain these apparent benefits of dietary mixing in Japanese beetles have not been well researched. Thus far, only Ahmad (1983) has suggested a link between enzyme activity, diet choice and dietary mixing in adult Japanese beetles. Midgut P450 activity in adult beetles is induced in response to feeding on three unrelated plants (broccoli, sassafras, and phlox) as single and mixed diets. Enzyme activities are lowest in unfed (starved) beetles, followed in magnitude by the single diets, which varied significantly with respect to one another. Polyphagy under lab or field condition induced the greatest enzyme activity. Those results support the hypothesis (Krieger et al., 1971; Mullin, 1986; Yu, 1989; Yu et al., 2003) that polyphagous species, because they encounter more chemically diverse plant toxins, tend to have inducible detoxification enzymes systems that have greater flexibility for metabolism of host plant toxins compared to specialists. Since Ahmad (1983) evaluated only P450 enzymes with a single substrate, it is not possible to determine the relative diversity of detoxification systems used by this polyphagous scarab.

More recent studies (reviews, Feyereisen, 2005; Ranson and Hemingway, 2005) suggest that polyphagous insects have greater diversities of genes encoding for different isoenzymes of detoxification enzymes with varying substrate specificity. Furthermore, insect herbivores irrespective of the host breath often deploy more than one detoxification enzyme system (Xie et al., 2011; Yang et al., 2001). Activities of GST and CoE, which may also facilitate metabolism of secondary plant chemicals and insecticides (Lee, 1991; Xie et al., 2011; Yu, 1996), have not been previously studied in *Popillia japonica*. Biochemical characterization remains a crucial first step in the study of detoxification enzymes, especially for insect species (i.e. Japanese beetles) whose genome or transcriptome is unavailable (Feyereisen, 2005). This study sought to quantify activities of P450, GST and CoE detoxification enzymes in the midgut of adult *P. japonica* using multiple substrates in response to host plant suitability (preferred host vs non-preferred hosts), and single and mixed diets. The work of Ahmad (1983) would predict greater enzyme activities for beetles consuming diets of non-preferred hosts and those with greater dietary heterogeneity.

2. Materials and methods

2.1. Source of insects and host plants

Adult beetles were collected from Town Creek Park in Auburn, AL, using traps (Pherocon® JB trap, Trécé, Adair, OK) baited with

a food lure (2-phenyl-ethyl propionate, eugenol, and geraniol; 3:7:3 ratio). Multiple host plants from different orders and families varying in relative suitability to *P. japonica* were used (Fleming, 1972, Table 1). Plant selections for these experiments were based on previous studies (e.g., Held and Potter, 2004; Keathley and Potter, 2008; Ladd, 1987, 1989) that have verified host preference and beetle performance in lab or field choice and rearing tests. Despite their generalist habit, beetle longevity and fecundity are generally greater when fed rose blooms or foliage from Virginia creeper, and sassafras relative to other suitable hosts (Fleming, 1972; Held, 2004). Foliage or flower petals were collected from plantings on the Auburn University campus <6 h before being used in each experiment. Leaves and flowers offered to the beetles were collected from at least four plants per species, and were examined visually to be disease free.

2.2. Reagents and supplies

Except where mentioned, all reagents and supplies were purchased from VWR Scientific and were of high grade and quality.

2.3. Feeding assays

Only active, apparently healthy beetles free of any morphological defects were used in experiments. For each trial, mixed sex beetles (25 per replicate), were held individually in 100 × 15 mm sterile polystyrene petri dishes with host plant's foliage or petals and allowed to feed for 24 h. Each dish contained a moistened filter paper (90 mm diameter) to prevent desiccation of the plant material. The feeding assays under each experiment were replicated four times. A 24 h feeding bout is sufficient for induction of P450, GST and CoE (Ahmad, 1983, unpublished data). Starved beetles (no food provided for 24 h) were used as controls because field-collected insects are mixed age and have unknown dietary histories. Starvation, which we reasoned would provide insight about baseline levels of each enzyme system, has been used to condition *P. japonica* before feeding assays (e.g., Held and Potter, 2004; Keathley and Potter, 2008; Ranger et al., 2010). Fed and starved beetles were maintained at 14:10 (L:D) photoperiod and 25–27 °C. Leaves or petals were provided without limit to each beetle during the trial.

The first experiment tested the effect of feeding on preferred and non-preferred host plants on beetles' enzymatic activity levels. Treatments included three preferred host plants, crape myrtle, rose, and sassafras, and three non-preferred but palatable host plants, red oak, boxelder, and river birch (Table 1). The second experiment compared activities of detoxification enzymes under short-term feeding bouts on single or multiple host plants. Virginia

Table 1

Japanese beetle's host plants of varying preference evaluated for induction of detoxification enzymes.

Species	Common name	Family	Plant part offered
<i>Preferred hosts</i>			
<i>Sassafras albidum</i>	Sassafras	Lauraceae	Foliage
<i>Lagerstroemia indica</i>	Crape myrtle	Lythraceae	Foliage
<i>Rosa x radazz 'knockout'</i>	Rose	Rosaceae	Petal
<i>Parthenocissus tricuspidata</i>	Virginia creeper	Vitaceae	Foliage
<i>Non-preferred hosts</i>			
<i>Quercus falcata</i>	Southern red oak	Fagaceae	Foliage
<i>Betula nigra</i>	River birch	Betulaceae	Foliage
<i>Acer negundo</i>	Boxelder	Sapindaceae	Foliage

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