PROTECTIVE ACTION OF MIDGUT CATALASE IN LEPIDOPTERAN LARVAE AGAINST OXIDATIVE PLANT DEFENSES

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Abstract—Catalase activity was detected in the midgut tissues and regurgitate of several lepidopteran pests of the tomato plant. Greatest activity in the midgut was detected in larval Helicoverpa zea, followed by Spodoptera exigua, Manduca sexta, and Heliothis virescens. We present evidence that catalase, in addition to removing toxic hydrogen peroxide, may inhibit the oxidation of plant phenolics mediated by plant peroxidases. Small amounts of larval regurgitate significantly inhibited foliar peroxidase activity via removal of hydrogen peroxide. Treatment of foliage with purified catalase nearly eliminated peroxidase activity and was superior as a larval food source compared to untreated foliage. Tomato foliar peroxidases oxidize an array of endogenous compounds including caffeic acid, chlorogenic acid, rutin, coumaric acid, cinnamic acid, and guaiacol. The oxidized forms of these compounds are potent alkylators of dietary and/or cellular nucleophiles (e.g., thiol and amino functions of proteins, peptides, and amines). When tomato foliar protein was pretreated with peroxidase and chlorogenic acid and incorporated in artificial diet, larval growth was reduced compared to larvae fed untreated protein. Thus, the diminution of peroxidase activity and removal of hydrogen peroxide by catalase may represent an important adaptation to leaf-feeding. The secretion of catalase in salivary fluid during insect feeding is also suggested to be a potential mechanism for reducing hydrogen peroxide formation as an elicitor of inducible plant defenses.

Key Words—Helicoverpa zea, Heliothis virescens, Spodoptera exigua, Manduca sexta, Lycopersicon esculentum, Lepidoptera, Noctuidae, Sphing...
gidae, catalase, peroxidase, hydrogen peroxide, chlorogenic acid, plant phenolics, antioxidant defenses, insect–plant interactions.

INTRODUCTION

The presence of hydrogen peroxide in plant tissues may pose a significant impediment to the growth and survival of herbivores. Hydrogen peroxide is a powerful oxidant (Cadenas, 1989; Fridovich, 1989). The utilization and/or function of proteins, enzymes, and glutathione may be impaired due to oxidation of thiols and decarboxylation of amino acids by hydrogen peroxide (H$_2$O$_2$) (Slump and Schreuder, 1973; Berlett et al., 1990). In the presence of catalytic amounts of ferrous or manganese ions, H$_2$O$_2$ can degrade to form the hydroxy radical (HO·), the most powerful oxidant known (Fridovich, 1989; Cadenas, 1989; Yim et al., 1990). This radical can then react with DNA, membrane lipids, and other essential cellular components (Halliwell and Gutteridge, 1984; Fridovich, 1989).

In conjunction with plant peroxidases (POD), H$_2$O$_2$ catalyzes the oxidation of diphenols to o-quinones. The quinones are susceptible to attack by nucleophilic amino and thiol groups of proteins (Matheis and Whitaker, 1984a, 1987). The enzymatic oxidation of the diphenol chlorogenic acid to chlorogenoquinone by polyphenol oxidase has been shown to impair the growth of *Helicoverpa (=Heliothis) zea* and *Spodoptera exigua* (Felton et al., 1989).

Peroxidase with H$_2$O$_2$ can directly oxidize tyrosine residues of proteins, causing substantial cross-linking (Matheis and Whitaker, 1984b). Plant peroxidases have multiple oxidative activities with broad substrate specificity; an array of phytochemicals including simple monophenols (e.g., coumaric acid), alcohols (e.g., coniferyl alcohol), coumarins (e.g., esculetin), and dihydroxyphenols (e.g., chlorogenic acid) may be oxidized by peroxidase (Gaspar et al., 1982).

Furthermore, H$_2$O$_2$ and POD are known to catalyze the cross-linking of hydroxyproline-rich glycoproteins in cell walls that stabilize cell walls against pathogen invasion (van Huystee, 1987). Moreover, POD and H$_2$O$_2$ are involved in the formation of lignin (van Huystee, 1987). The role of these cell-wall strengthening reactions in impeding utilization of plant tissues by insect herbivores is largely unknown (Stamopoulos, 1988; Wainhouse et al., 1990). POD may also be involved in lipid peroxidation and the formation of reactive molecules such as linoleic hydroperoxide (Garner, 1984; Keppler and Novacky, 1987). Both the primary oxidative products, fatty acid hydroperoxides, and the secondary products, such as malondialdehyde, form addition products with nucleophilic groups of protein (Garner, 1984). These lipid oxidation products have been implicated as defense mechanisms against herbivores (Shukle and