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Review

Plant latex and other exudates as plant defense systems: Roles of various defense chemicals and proteins contained therein

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ABSTRACT

Plant latex and other exudates are saps that are exuded from the points of plant damage caused either mechanically or by insect herbivory. Although many (ca. 10%) of plant species exude latex or exudates, and although the defensive roles of plant latex against herbivorous insects have long been suggested by several studies, the detailed roles and functions of various latex ingredients, proteins and chemicals, in anti-herbivore plant defenses have not been well documented despite the wide occurrence of latex in the plant kingdom. Recently, however, substantial progress has been made. Several latex proteins, including cysteine proteases and chitin-related proteins, have been shown to play important defensive roles against insect herbivory. In the mulberry (*Morus* spp.)–silkworm (*Bombyx mori*) interaction, an old and well-known model system of plant–insect interaction, plant latex and its ingredients – sugar-mimic alkaloids and defense protein MLX56 – are found to play key roles. Complicated molecular interactions between Apocynaceae species and its specialist herbivores, in which cardenolides and defense proteins in latex play key roles, are becoming more and more evident. Emerging observations suggested that plant latex, analogous to animal venom, is a treasury of useful defense proteins and chemicals that has evolved through interspecific interactions. On the other hand, specialist herbivores developed sophisticated adaptations, either molecular, physiological, or behavioral, against latex-borne defenses. The existence of various adaptations in specialist herbivores itself is evidence that latex and its ingredients function as defenses at least against generalists. Here, we review molecular and structural mechanisms, ecological roles, and evolutionary aspects of plant latex as a general defense against insect herbivory and we discuss, from recent studies, the unique characteristics of latex-borne defense systems as transport systems of defense substances are discussed based on recent studies.

Contents

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1. Introduction

Plant latex is a sap, typically a white sap, that is stored in the tissue called laticifer and that is exuded from a point of damage in plant tissues immediately after insect herbivory (see Figs. 1A, 2A, and 6A). More than 20,000 species from over 40 families of angiosperm plants exude latex (Lewinsohn, 1991), which is 8.9% of all angiosperm plants. The figure increases to 35,000 species when conifers and resin-exuding plants are included (Farrell et al., 1991). Latex contains a variety of chemicals and proteins, such as various terpenoids, alkaloids, rubber, and cardenolides as well as various proteins and enzymes such as proteases, chitinases, and glucosidases (see Section 4). In regard to latex's role, there have been several hypotheses, such as excretion of waste metabolites, coverage of damaged tissue, defense against herbivores, and defense against pathogens. Among these hypotheses, there is a lot of evidence to support the defensive roles against herbivores and pathogens, especially herbivores (Farrell et al., 1991). The earliest experimental observation was by Kniep, a German scientist, in the early 20th century (Kniep, 1905). He observed that Euphorbiaceae plant individuals whose leaves had been artificially damaged and that had no more exuded latex were damaged by slugs in outdoor conditions, whereas intact individuals with latex were not damaged (Kniep, 1905). More than a half century later, Dussourd and Eisner found that several specialist insects feeding on milkweeds have developed a vein-cutting behavior that can inactivate laticifer and stop the exudation of latex (Dussourd and Eisner, 1987). They also observed that the mandibles of beetles (*Tetraopes* spp.) were trapped and glued by latex when milkweed latex was artificially placed on the mandibles (Dussourd and Eisner, 1987). Also, under natural feeding conditions, the mandibles of caterpillars that attempted to eat leaves, or the whole bodies of aphids that walked on plant surfaces became trapped by the latex of *Lactuca* species (Asteraceae) (Dussourd, 1993, 1995). Further, a large percentage of newly hatched monarch butterfly larvae (*Danaus plexippus*) were found trapped by milkweed latex (Zalucki and Brower, 1992; Zalucki et al., 2001a,b). These results suggested that plant latex, which is often sticky, defends plants against herbivorous insects by trapping and immobilizing them. On the other hand, some chemical ingredients in latex, such as morphine, an alkaloid, from poppy latex and cardenolides from milkweed latex, show apparent toxicity against animals, including insects. In these cases, such toxic chemicals are suggested to have defensive roles (Farrell et al., 1991). However, the roles of most of the remaining latex ingredients, especially various latex proteins, remain unknown. Also, not all latex and/or exudates are sticky enough to trap insects, such as the latex of mulberry trees, *Morus* spp. (Konno, unpublished data). Recently, a couple of findings have shown that various latex ingredients, notably latex proteins, play key defensive roles against insect herbivory (Konno et al., 2004, 2006; Wasano et al., 2009; Ramos et al., 2007, 2010). In this review, I present emerging observations that suggest the importance of latex ingredients – chemicals and proteins – in plant–insect interactions. Then, based on these observations, I discuss various aspects and characteristics of latex-borne defense and other canalicular defenses.