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Minireview

Mechanisms by which pesticides affect insect immunity

R.R. James [a,*], J. Xu [b]

[a] USDA-ARS, Pollinating Insects Research Unit, Dept. Biology UMC 5310, Utah State University, Logan, UT 84322-5310, USA
[b] Utah State University, Department of Biology, 1410 N 800 E, North Logan, UT 84341, USA

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ABSTRACT

The current state of knowledge regarding the effect of pesticides on insect immunity is reviewed here. A basic understanding of these interactions is needed for several reasons, including to improve methods for controlling pest insects in agricultural settings, for controlling insect vectors of human diseases, and for reducing mortality in beneficial insects. Bees are particularly vulnerable to sublethal pesticide exposures because they gather nectar and pollen, concentrating environmental toxins in their nests in the process. Pesticides do have effects on immunity. Organophosphates and some botanicals have been found to impact hemocyte number, differentiation, and thus affect phagocytosis. The phenoloxidase cascade and malanization have also been shown to be affected by several insecticides. Many synthetic insecticides increase oxidative stress, and this could have severe impacts on the production of some antimicrobial peptides in insects, but research is needed to determine the actual effects. Pesticides can also affect grooming behaviors, rendering insects more susceptible to disease. Despite laboratory data documenting pesticide/pathogen interactions, little field data is available at the population level.

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1. Introduction

It is unquestionable that both pathogens and insecticides significantly affect insect populations, but questions often arise as to whether these two sources of mortality and poor health have interactive effects on each other. In particular, do pesticides affect insect immunity and the susceptibility of insects to infectious disease? The answer to this question is yes, sometimes, and the manner of this interaction is the topic of this review. Interactions between insecticides and pathogens has previously been investigated primarily on two fronts. On the one front, pest control strategies have been tested to determine whether the activity of microbial pesticides can be enhanced with certain insecticides (especially those chemicals least likely to cause environmental harm). On the other front, concerns have been raised as to whether sublethal doses of pesticides might render beneficial, non-target insects more

Abbreviations: AMPs, antimicrobial peptides; Imd, immune deficiency pathway; Jak-STAT, Janus kinase/signal transducers and activators of transcription; JH, juvenile hormone; PO, phenoloxidase; RNAi, ribonucleic acid interference; ROS, reactive oxygen species; SOD, superoxide dismutase; Toll, Toll pathway.

* Corresponding author. Fax: +1 435 797 0461.
E-mail addresses: Rosalind.James@ars.usda.gov (R.R. James), Junhuan.xu@usu.edu (J. Xu).

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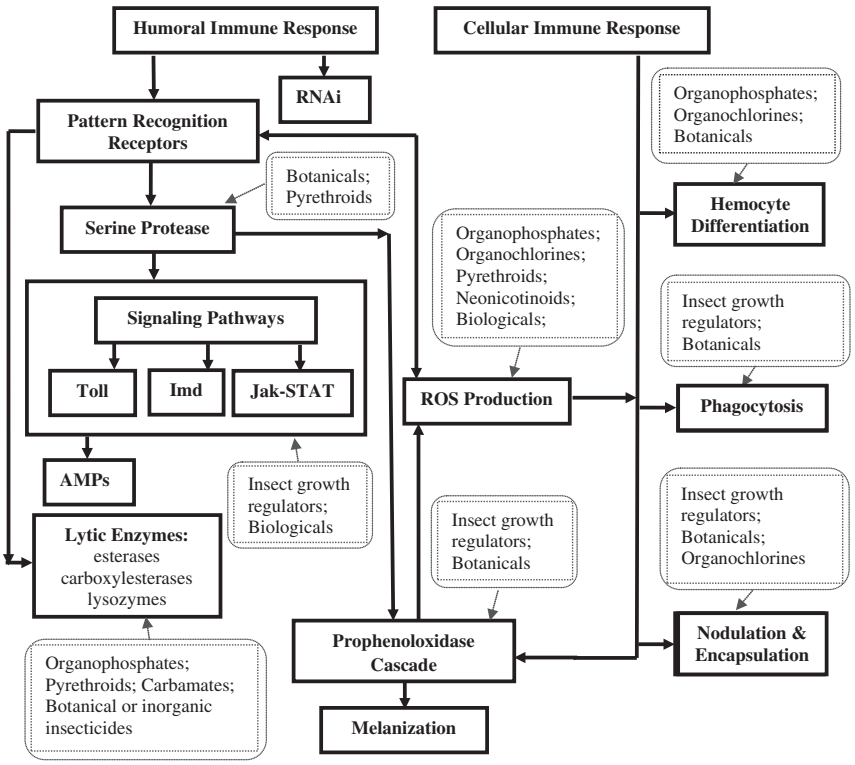

Fig. 1. The effect of insecticides on insect immunity. Solid boxes and arrows represent a schematic of the insect immune system. Stippled boxes and arrows identify where pesticides have been documented to affect particular immune responses.

susceptible to disease, and this concern has most often been raised with regard to bees.

The effects of pesticides on mammalian immune systems have been reviewed previously (Vial et al., 1996; Blakley et al., 1999; Holsapple, 2002; Salazar et al., 2008), but the effect of these compounds on insect immunity has not. The distinction between mammals and insects is important because insects lack an adaptive immune system, or at least they do not have antibodies and T-type memory cells that occur in vertebrates (Schmidt et al., 2008). Insects rely on innate immune responses that are generally non-specific (although not all mechanisms are non-specific). Prior infections can make individuals more resistant to new infections, but as a result of a prolonged non-specific immune response (Pham and Schneider, 2008). Insect immunity is basically composed of three parts: (1) the cuticle, which presents physical and chemical barriers to the outside world of microbes, (2) humoral responses, and (3) cellular responses. Little to no research has been conducted to determine if the cuticle is affected by pesticides in a way that affects its immune defense function, and so this organ is not covered in this review, except briefly as it relates to pesticide effects on behavioral defenses.

Pesticides are more broadly known to affect the insect humoral and cellular immune responses. In the initial humoral response, pattern recognition proteins identify invading microbes (or other internal non-self objects) and initiate the synthesis of various of antimicrobial proteins (AMPs). AMPs include such compounds as cecropins, defensins, attacins, and dipteracins (Hetru et al., 1998) (Fig. 1). AMP production is regulated through signaling pathways, mainly the Toll, Imd, and Jak-STAT pathways (Hoffmann, 2003; Boderick et al., 2009) (Fig. 1). The cellular immune response consists of pathogen recognition followed by phagocytosis (for invading bacteria and viruses), nodulation (for large microbial pathogens, such as fungi and clusters of bacteria), and encapsulation (for multicellular parasites) (Franssens et al., 2006) (Fig. 1). Phagocytosis is typically accompanied by melanin production and melanization of nodules and capsules (Fig. 1). Melanin production can occur more rapidly than the production of antimicrobial peptides (AMPs), can lead to the formation of reactive oxidative species (ROS) that can contribute to killing pathogens and are regulated through the phenoloxidase (PO) cascade (Ragan et al., 2009) (Fig. 1). Thus, the humoral and cellular responses are not separate entities, but are interdependent defensive forces. Furthermore, this complex system involves detoxification mechanisms that are also utilized by insects to prevent damage from environmental toxins such as plant secondary compounds and fungal toxins, providing another avenue for interactive effects between pesticides and immunity.

Since many readers may not be familiar with the functioning of the insect immune system, in this review we give short descriptions of the different immune responses, followed by a review of published reports regarding pesticide effects on each response. Melanization is technically a humoral response, but since it is most often involved with the cellular response, we have included it as such. In addition to the humoral and cellular immune responses, we also include sections on oxidative stress and behavior, as these responses are areas where pesticides and pathogens interact in a manner that affects insect health, both negatively and positively. In the end, we discuss the current state of knowledge, identify important areas of research needed, and the implications this knowledge has not only for pest control, but also for honey bees and other beneficial insects.

2. The humoral immune response in insects

2.1. Overview

Humoral immunity can be either non-specific (i.e. the same compounds are released to control a variety of different pathogens) or