Editorial overview: Pests and resistance: Social Networking: Studying the web of plant-insect interactions to improve host plant resistance

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Introduction

Insect pests are a major limitation on worldwide agricultural productivity, causing billions of dollars in crop losses annually; on maize alone, insects are estimated to cause approximately \$5.7 billion in annual yield losses (1). Moreover, these losses are in addition to even greater expenditures for pesticide applications and other management efforts, many of which have environmental as well as economic costs. In short, the need for strategies to control insect pests is obvious. One of the most effective, economical, and environmentally safe approaches to manage agricultural pests is to develop crop cultivars with improved levels of pest resistance. For example, the incorporation of resistance genes (R genes) into commercial wheat provides the most effective, efficient, and widely-used method of controlling the Hessian fly (*Mayetiola destructor*), one of the world's most damaging insect pests of cereals (2,3). However, the effectiveness of resistant cultivars tends to break down when they are deployed in a large area and over a long time, especially in regions in which the pest has high genetic diversity. Moreover, insect pressures on crops are changing rapidly as a result of climate change and new invasive species. Increasing temperatures, global trade, and severe weather are all expanding the geographic ranges of many insect pests (4); to illustrate this point, a thirty-year survey indicates that the number of aphid species in Europe is increasing, and that spring flights of aphids are occurring earlier in the growing season (5). Therefore, in the face of an increasing intensity and diversity of pest pressures, it is critical to identify an equally wide diversity of sources of insect resistance that can be utilized for crop protection. This effort, however, requires a greater fundamental knowledge of plant defenses, and an improved arsenal of tools for studying these defenses.

Current Questions in Plant Defense

Because of the practical importance of insect resistance to agriculture, the study of host plant defenses is a very active field. Recent research in this area is primarily focused on five central questions:

1. How do plants perceive and defend against insect herbivores?
2. What are the impacts of plant defenses on insect physiology?
3. How do insects evade or overcome plant responses?
4. How do abiotic environmental conditions as well as ecological interactions with other organisms influence the effectiveness of host plant defenses?
5. How can we best utilize our knowledge of plant-insect interactions in crop protection?

The focus of this issue is to review exciting recent progress in addressing these key questions, and to present current models for understanding the complex interplay among herbivorous insects, host plants, and their biotic and abiotic environment (Figure 1).

Common Themes

Plant perception of insect pests. Plants are able to detect the presence of herbivorous insects through perception of cues derived not only from damage caused by insect feeding, but also from insect oral secretions, eggs, or microbial associates of the insects. In this issue, Tamiru and coworkers (S2214-5745(15)00029-2)(6) provide an update on plant defense responses to insect oviposition, Schmelz (S2214-5745(15)00052-8) (7) reviews the state of knowledge on plant perception of insect oral

secretions, Huffaker (S2214-5745(15)00096-6) (8) discusses a novel class of damage-associated cues, and Stuart (S2214-5745(15)00028-0) (9) discusses the gene-for-gene interactions that govern R gene-mediated plant perception of insect pests. In addition, elicitation of plant defenses against herbivory by microbial associates and by wounding has recently been reviewed elsewhere (10-12). The picture that emerges from these analyses is that plant perception of insect herbivores strongly parallels plant perception of plant pathogens, and involves an arms race between plant pattern receptors and insect effector proteins (7,9, 13). The relationship between plant responses to insects and plant responses to pathogens is further strengthened by the fact that insects function as vectors of many plant pathogens, and that these pathogens can manipulate plant responses to favor transmission by insects (reviewed by Orlovskis and coworkers in this issue (S2214-5745(15)00057-7) (14).

Plant defenses and insect counter-defenses in an ecological context. In response to recognition of herbivores, plants produce a wide array of direct defenses that limit herbivory (15), as well as volatile organic compounds that act as indirect defenses by attracting predators and parasitoids and by priming defenses in nearby uninfested tissues (16). Many recent studies have examined the impacts of these defenses on herbivores, identified counter-adaptations in insects, and explored the ways in which other biotic and abiotic factors in the environment influence the efficacy of plant defenses. As reviewed by Howe and Herde (S2214-5745(15)00035-8) (15), many direct defenses in plants target the enzymatic functions or structural integrity of the insects' midgut; this makes sense because the midgut is the only interface between the insect and its host that lacks a protective exoskeleton, and also because the processes of digestion and absorption that occur in the midgut are critical to insect growth, reproduction, and survival. While some components of the insects' digestive system represent an Achilles heel and even contribute to the enzymatic activation of plant defense compounds, the insect gut is also a primary site of detoxification. Arthropods' close associations with microbes can aid in this process of adaptation to plant defenses, either through symbiotic partnerships or through horizontal gene transfer (7, 10, 14, 17). Moreover, some insects have developed cross-resistance to pesticides and plant defenses (15), which suggests that the environmental toxicants to which insects are exposed could influence their sensitivity to host plant resistance. Gish and coworkers (S2214-5745(15)00051-6) (16) also highlight the ways in which pollutants, climatic changes, and consequent changes in the species composition of insect communities could alter or disrupt volatile signaling and indirect defense. In short, the effectiveness of plant defenses depends upon the ecological context in which they occur, and the extent to which insect pests have developed counter-defenses.

Technological advances in studying plant-insect interactions. Genome sequences and functional genomics tools such as RNA interference (RNAi) are becoming increasingly available not only for a variety of plant species, but also for their associated insect pests, and this is enabling rapid advances in our understanding of plant-herbivore interactions (15). In addition, recent technological advances in high-throughput phenotyping (HTP) are overcoming the so-called 'phenotyping bottleneck' that limits our ability to decode genomes into 'phenomes'---or in other words, to predict the comprehensive phenotypic consequences of genotypic differences. As reviewed in this issue by Goggin and coworkers (18), HTP systems utilize automated image capture and analysis to characterize larger population sizes than were previously possible, and to enable the parallel, non-destructive measurement of multiple

traits, including certain physiologically important traits that lie beyond the visible spectrum. Together, advances in genomics and HTP have the potential to revolutionize the process of studying and breeding for insect resistance.

Applications and Future Prospects

The work reviewed in this special issue clearly demonstrates that plant-herbivore interactions are important models in which to study coevolution, multitrophic interactions, and physiological mechanisms of self-recognition and defense that long predate mammalian immunity. This work also has valuable applications for crop protection. Understanding how insects manipulate their hosts and evolve resistance to plant defenses can aid in developing improved strategies for pest management. For example, studies by Goggin et al. (S2214-5745(15)00029-2) on insect virulence against R genes suggest that pyramiding multiple R genes in a single cultivar could enhance the durability of resistance (9). Identifying effector proteins, detoxification enzymes, and other insect factors that facilitate the infestation process (7, 14) should also yield good targets for insect management, because disabling these factors through RNAi or other means could hinder the infestation process. The applications of RNAi for herbivore management have been reviewed recently (19-21). In addition, elucidating the signaling pathways and regulatory elements that control induction of host plant defenses could improve current approaches to genetic engineering of insect resistance (8). While insecticidal traits such as *Bacillus thuringiensis* toxins are typically expressed constitutively in genetically engineered crops, plants' native induced defenses provide a model for how to limit the fitness costs and non-target effects of defense by expressing defenses only when needed. Lastly, investigating the molecular and biochemical foundations of host plant defenses facilitates the improvement of these traits in crop plants. During crop domestication, traits that contribute to insect resistance are often diminished or lost as plants are subjected to artificial selection for higher yields. However, when traits that contribute to insect resistance are identified in crops, wild plants, or less domesticated landraces, these traits can be enhanced in elite germplasm through traditional breeding and genetic engineering (6). In closing, we expect exciting advances in the field of plant-insect interactions to continue; in fact, we predict that progress in identifying, characterizing, and selecting for insect resistance will accelerate dramatically in the near future as a result of advances in genomics and phenomics.

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Figure 1. Deciphering the interplay between plant feeders and plant defenses. Plants detect the presence of insect herbivores through perception of cues from the insects, their eggs, or their microbial associates, or through recognition of patterns of damage in the host plant (A). Insects' oral secretions and the phytopathogens they carry may promote or suppress this recognition process. Detection of herbivore-associated cues by plants triggers defensive signaling and the production of toxic allelochemicals, antinutritive proteins, and other barriers to herbivory (B). Many of these defenses target the insect gut, where the insect's own enzymes participate in both the activation and detoxification of plant defenses (C). Damaged plants also release volatile organic compounds that attract herbivores' natural enemies, and that may prime defenses in nearby foliage (D). This volatile signaling may be impacted by environmental conditions, including pollution (E). Video monitoring and other high-throughput phenotyping approaches (F) have great potential to facilitate the study of plant-insect interactions and the identification of plant genotypes with enhanced insect resistance.

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