Plant–herbivore interactions: Thinking beyond larval growth and mortality

Rupesh R. Kariyat[2,4] and Scott L. Portman[3]

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Author Affiliations

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Author Affiliations

[2]Biocommunication and Entomology, Institute of Agricultural Sciences, Schmelzbergstrasse 9, ETH Zurich, Zurich 8092, Switzerland

[3]Montana State University, Western Triangle Agricultural Research Center, 9546 Old Shelby Road, Conrad, Montana 59425 USA

↵[4]Author for correspondence (e-mail: rupesh.kariyat@usys.ethz.ch)

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Plants provide food and habitat for numerous species of the animal kingdom. The multitude of resources that they provide is commonly thought to be one of the main reasons behind the remarkable adaptive radiation of terrestrial animals (Herrera, 2002). Because of their small size and specific feeding requirements, insect herbivores usually have a lifelong and more intimate association with their host plants than vertebrate herbivores (Strauss and Zangerl, 2002). Insect herbivores typically cause harm to plants by feeding on vegetative tissues, roots, fluids, flowers, or seeds, thus reducing the plants' fitness (Kareiva, 1999; Strauss and Zangerl, 2002). To limit herbivore damage, plants produce numerous antiherbivore chemicals that function as toxins, feeding deterrents, or antidigestive compounds (Chen, 2008). Ingestion of such chemicals causes phenotypic changes in the insects because they must expend valuable nutrient resources to neutralize and/or reduce the harmful effects from these compounds (Agrawal, 2001; Chen, 2008). Moreover, changes to insect behavior, morphology, physiological processes, or biochemical pathways, resulting from resource investment trade-offs, can also affect different insect performance traits associated with these systems (Saha et al., 2012).

The vast diversity of insect herbivore-plant relationships (Strauss and Zangerl, 2002) and large number of plant produced defense chemicals

(Chen, 2008) suggests that a multitude of phenotypic changes are occurring in insects that can impact different performance characteristics. However, most studies examining insect performance in relation to host plant differences measure effects on a limited number of traits, typically larval growth and mortality (Gols et al., 2008). Although larval growth parameters (e.g., body mass, growth rate) and mortality are indicative of how the insects are coping with their hosts' defenses and nutritional quality, these indices may not accurately predict changes to other important aspects of insect biology such as behavior, physiology, biochemistry, gene expression, or performance of later life stages (e.g., pupa or adult); consequently, larval growth and mortality may not be the only good estimators of the insect's overall fitness (Sears et al., 2012; Kariyat et al., 2013, 2014; Wilder et al., 2015). Although these measurements give us an excellent starting point to ask more detailed questions about other aspects of herbivore biology, measuring only differences in larval growth and/or mortality could limit the scope of ecologically relevant inferences we can make regarding plant–insect relationships. A more integrative approach to studying the effects of host plant defenses on insect herbivores would involve measuring a greater variety of insect performance traits and following these traits through different life stages (Bauerfeind and Fischer, 2013).

Studies on species interactions have benefitted greatly from the recent advancements in ecological genomics, providing us with the opportunity to discover the molecular and biochemical mechanisms responsible for changes in the interacting species, in this case, the host plant and insect herbivore (Zheng and Dicke, 2008). Interpreting "omics" data on plant–herbivore interactions, however, will require expertise in diverse fields such as physiology, biochemistry, behavior, and genetics (Strauss and Zangerl, 2002; Kariyat et al., 2012). Collaborative efforts across these fields can provide a more complete understanding of how changes to host plant chemistry affect various facets of insect biology, including, but not limited to performance characteristics. In a broader sense, this approach will help to improve our understanding of specific selection factors that influence the interactions of plants and insects.

Supporting this approach, two recent studies found that host plant effects on larval growth did not correspond with changes to insect behavior and physiology (Thaler et al., 2014; Portman et al., 2015). Both studies measured performance responses in Manduca sexta to differences in host plant quality, including measures of larval body mass. However, these studies also measured insect physiological performance variables; Thaler et al. (2014) measured the resting metabolic rates (RMR) of caterpillars, and Portman et al. (2015) measured flight metabolic rates of adult moths. Host plant quality was strongly related to larval body mass, but the effect of host plants on RMR was less apparent. In addition, the presence of a predator (Hemiptera: Pentitomidae) was associated with an increase in RMR for larvae that fed on low resistance plants, but not larvae fed on high resistance plants, indicating that other environmental factors play a significant role in altering herbivore responses to host plants (Thaler et al., 2014). Host plant differences affected adult body mass despite the lack of corresponding effects on larval body mass, suggesting that host plant differences can produce changes to the body composition of larvae that were not reflected in their body mass measurements (Portman et al., 2015). Furthermore, host plant quality did not affect the relative size of the adult's flight muscles, but host plant differences correlated with changes in the moths' mass adjusted fight metabolic rates, likely due to molecular modifications to their flight muscles. For Manduca sexta, host plant effects can vary across different life stages of the insect (Kariyat et al., 2013, 2014), and performance measurements such as larval body size do not always correlate with physiological performance measures such as RMR (Thaler et al., 2014) or flight muscle power output (Portman et al., 2015).

Variation in host plant defenses can also impact other aspects of insect biology and life history such as diapause, reproduction, immunological response, and gene expression. Larvae of a generalist tortricid (Choristoneura rosaceana) were more likely to initiate diapause when they fed on low-quality host plants (red maple and black ash) compared with the high quality host plant (choke cherry; Hunter and McNeil, 1997). Corn leafhopper fecundity was reduced in females whose mothers were reared on low-quality wild-type (Zea spp.) vs. high-quality domesticated hosts (Zea mays; Dávila-Flores et al., 2013). Similarly, fecundity of Manduca sexta females was reduced when they were reared on wild devil's claw

(Proboscidea louisianica) compared with cultivated tobacco (Nicotiana tabacum; Diamond et al., 2010). Shikano et al. (2010) showed that cabbage looper (Trichoplusia ni) larvae that fed on cucumber plants (low-quality host) were more susceptible to infection with nucleopolyhedrovirus than larvae that fed on broccoli (high-quality host). In contrast, noctuid larvae (Heliothis virescens) were less susceptible to baculovirus infection after ingesting host plants that produced peroxidases because the peroxidases caused the larvae to shed more midgut epithelial cells (Hoover et al., 2000). On a molecular level, insect herbivores increase the synthesis of resistant isoforms of proteolytic enzymes in response to plant-produced protease inhibitors (Cloutier et al., 2000) and increase the activity of detoxification enzymes when fed on low-quality host plants (Saha et al., 2012). Flight muscle protein composition of Manduca sexta adults is altered when the larvae feed on high-quality vs. low-quality host plants (Portman et al., 2015). These studies illustrate that host plant variation affects insects in a multitude of ways, in addition to larval growth and survival. Hence, host plant-related changes to these often used indices (growth and mortality) may not provide complete and/or accurate predictions of herbivore performance or overall fitness (Sears et al., 2012; Thaler et al., 2014; Portman et al., 2015; Wilder et al., 2015).

The coevolution of plant defense and insect counter-defense mechanisms has given rise to countless complex interrelationships between plants and their associated insect herbivores (Agrawal et al., 2012; Strauss and Zangerl, 2002; Fig. 1). These interactions are further complicated by inter- and intraspecific variation in host plant chemistry (e.g., primary and secondary metabolites; Machado et al., 2015), and differences in herbivore feeding guilds (e.g., sucking and piercing vs. chewing, specialists vs. generalists; Leitner et al., 2005; Lankau, 2007). A more comprehensive understanding of host plant effects on insect herbivores is important because changes to performance traits that influence behavior, physiology, or gene expression (e.g., selective feeding, digestive metabolism, detoxification enzyme activity) can be critical factors that determine an insect's resistance or vulnerability to host plant defenses. Changes to performance traits that influence an insect's survival, mobility, or reproduction (e.g., immunological resistance, muscle function, egg or sperm production) can impact plant-insect population dynamics and colonization pressure of distant plant patches, which is particularly pertinent for predicting the movement of insect pests in agricultural landscapes or the spread of invasive insects and plants (Neubert and Parker, 2004). Lastly, identifying molecular mechanisms that underlie variations in the insect's response provides a powerful tool for determining which genes are being targeted by natural selection. Ultimately, expanding our notion of insect herbivore performance and fitness indices improves our ability to ask a wide range of evolutionary and ecological questions, thereby, gaining a better understanding of plant–insect interactions.

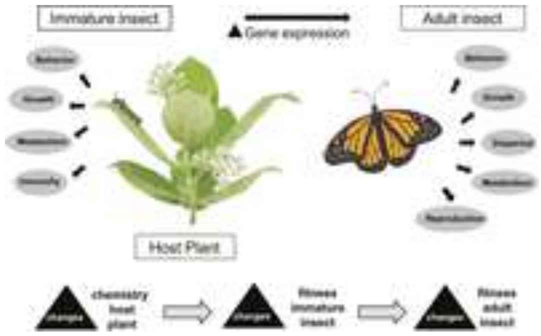

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FIGURE 1

Illustration of a cycle in which changes in the chemical profiles of a host plant can cause changes to the behavior and performance (e.g., growth, metabolism, immunity) of an immature holometabolous herbivorous insect. Changes to gene expression in early developmental stages cascade through metamorphosis to also produce changes to later development stages. Illustration: Sanil Sansar.

Next Section

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