Plants had to cope with pests as soon as they appeared on earth. There is excellent fossil evidence that insects were consuming plants by the Devonian, over 300 million years ago (LaBandeira, 2006). Natural selection no doubt favored resistant genotypes, a fact acknowledged indirectly by the earliest agriculturalists, who preferentially planted resistant crops. Much later, Gottfried Fraenkel (1959) pointed out that the basis of resistance to insects was likely to be chemical, a fact that had already been exploited for pest control at least since the 17th century. Ehrlich and Raven then pointed out that selection should also act on pests to overcome plant (chemical) defenses, resulting in reciprocal selection, or coevolution (Ehrlich and Raven, 1964). Detoxification mechanisms in animals had been studied for over 100 years by then, so by the 1970s we had a picture of plants producing chemical defenses that could be detoxified by insects, and selection on plants by insects for new chemistries.

Initially, plant resistance was assumed to be a fixed trait. However, in the 1970s it became apparent that plants play a more dynamic role in the plant–pest interaction, actively responding to pest attack. More recent work has revealed that not all pests elicit defense responses. Specialized behaviors like trenching and biochemical interference with signaling can subvert or prevent many plant defense responses. Many microbes and some insects can also manipulate host quality nutritionally. Because plants, microbes and animals share a range of signaling systems employed in intra- and inter-individual communication, there is ample evolutionary opportunity for evolution of the ability to manipulate each other. While this ability has been appreciated for a long time in plant–microbe interactions, it is only beginning to be demonstrated in plant–insect interactions. The 'stealthy' or manipulative insect represents yet another level of coevolutionary complexity.

This special issue of Journal of Insect Physiology examines some of the diverse ways in which insects interact and communicate with plants, and can manipulate their plant hosts to their own benefit. Examples of manipulation abound. Some of the clearest examples come from two of the most intimate plant–insect interactions, leaf mining and galling. Leaf miners feed between the upper and lower surfaces of leaves, often altering host development and quality while doing so. Galls are unique organs formed by plants in response to insect, nematode, or microbe signals, providing a favorable refuge and superior quality food source. The elicitors of these complex plant responses are unknown. Zhang et al. (2016) identify phytohormone changes in apple leaves attacked by a leaf miner that appear to be elicited by cytokinins provided by the insect. These changes alter the leaf's physiology to create a favorable nutritional environment. Favery et al. (2016) describe how root-knot nematodes cause plant roots to create a specialized nutritional structure called a 'giant cell'. They enumerate the changes in plant cellular functions that this process requires.

Gall formation by insects also involves changes in cell and tissue processes. Oliveira et al. (2016) trace these processes from recognition of 'reactive plant tissues' to development of specialized nutritional tissues for several gall ing insects and their hosts. They suggest that many of these processes may be regulated by changes in reactive oxygen species (ROS) known to be elicited by insect attack. At the same time, ROS also elicit plant defenses, are themselves toxic to insects and microbes, and may deplete oxygen inside plant tissues. Pécebouard and Casas (2016) evaluate the benefits and risks arising from gas composition to insects feeding inside structures they have created, and find predictive value in several features, including whether the plant recovers CO₂ from the insect and the insect's physical location in the plant tissues. Microbes are also sensitive to ROS, and many can suppress ROS production. Groen et al. (2016) show that the presence of ROS-suppressing bacteria can improve the quality of plant tissues for insects feeding in the same place. They describe a leaf-mining insect that can vector such a bacterium, and may inoculate plants with it to suppress plant defenses.

Sometimes plant manipulation by insects produces dramatic phenotypic change. Calderón-Cortés et al. (2016) describe a system in which adult beetles prune small branches from a tree. This releases buds and produces many nutritionally-superior juvenile shoots, which the beetles' offspring exploit. The authors describe ecosystem-wide impacts of this 'engineering' by an insect.

The elicitors or effectors involved in the creation of galls and other safe and nutritionally superior feeding sites for insects remain largely unknown. The search for clues is a very active research area. Guiguet et al. (2016) examine plant and animal immune responses, and find striking similarities between their early signal transduction pathways in terms of signal recognition. Together with what is known about signals used to manipulate their hosts by arthropods parasitic on animals, they suggest that herbivorous arthropods may exploit many of the same pathways. Giron et al. (2016) take a similar approach, surveying the types of responses insects can elicit in plants, and inferring from this the most likely signals insects may use.

Our more detailed understanding of plant–microbe interactions has stimulated interest in comparing them with plant–insect interactions. Kobayashi (2016) integrates what we know about the intimate molecular interactions between rice and the brown plant hopper. He concludes that resistance to this insect is monogenic and depends on interactions between virulence and avirulence genes. This interaction resembles plant–microbe interactions more than many plant–insect interactions. Zhao...
et al. (2016) take a detailed look at just such an interaction, involving wheat and the Hessian fly. Exploiting the Hessian fly genome sequences, they find a gene encoding a likely effector protein eliciting plant resistance against non-virulent flies, but which is silenced in flies that are virulent. This, too, is an apparent monogenic, “gene-for-gene” interaction. Another gene-for-gene interaction involving a galling insect is described at multiple levels by Bentur et al. (2016) The rice gall midge and its host exhibit a coevolutionary ‘arms race’ in which there is ongoing change in the plant’s resistance genes countered by shifts in the insect’s virulence genes. Bentur et al. highlight the continuing changes in molecular approaches used by this insect to overcome host resistance. The search for key resistance genes against galling insects is taken to the population level by Zinkgraf et al. (2016), studying the insect, focusing on target genes likely to provide a phenotypic basis for resistance. They find heritable variation in expression of two genes that may regulate formation of photosynthetic sinks, a function essential for galling aphid success. This interaction is likely to be polygenic.

Altogether, these studies make several things clear. First, there is a growing and bewildering array of ways in which plant parasites manipulate their hosts, from gene expression to chemistry to morphology. Second, many of the manipulations seen in plant–parasite interactions share elements with animal–parasite interactions. Third, we know much more about what happens when arthropods or nematodes manipulate host plants than we know about how this happens. The diversity of responses and of putative mechanisms described here suggests that one or a few processes are not likely to characterize all of these interactions. However, the availability of genomic resources and better analytical chemistry tools, coupled with comparisons among systems, is likely to advance our understanding of ‘stealthy’ and ‘manipulative’ plant pests more and more quickly.

References


Giron, D., Huguet, E., Stone, G.N., Body, M., 2016. Insect-induced effects on plants and possible effectors used by galling and leafmining insects to manipulate their host-plant. J. Insect Physiol. 84, 70–89.


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