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Insects Co-opt Host Genes to Overcome Plant Defences

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EVALUATION OF



Whitefly hijacks a plant detoxification gene that neutralizes plant toxins.

Xia J *et al.*

<https://doi.org/10.1016/j.cell.2021.02.014>

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Insect pests of plants, such as whiteflies, cause immense economic damage both through direct feeding and by transmitting viruses. In a major breakthrough, a paper by Xia *et al.*¹ shows that some whiteflies have co-opted a gene from their plant host that has helped them neutralize a key component of the plant's defense. Plants produce a range of toxins as part of their defense against insect predation, and Xia *et al.*¹ show that, through a horizontal gene transfer (HGT) event from plant to insect, some whiteflies have acquired a gene whose original function was to protect the plants themselves from such damaging toxins through chemical modification that converts them to less harmful forms. Targeting of this gene in whiteflies using RNAi technology provided effective resistance in this ground-breaking study, which should lead others interested in crop protection to explore genes that have been transferred from plants to insects.

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Background

Insect pests of plants cause immense economic damage, and new strategies for effective crop protection are actively being sought². Herbivorous insects are often thought of as either generalists, which feed on a range of plant species, or specialists, which have a narrow host range. There has been much interest in how these different types of herbivores deal with plant defenses³. Plants mount a range of basal and inducible defenses against insects, including the effective production of toxic specialized metabolites⁴. Although many insects can detoxify plant defensive chemicals, known cases are mostly limited to specialist insect herbivores.

Bemisia tabaci (sweet potato whiteflies) are among the most damaging insect pests worldwide and are hard to control with conventional insecticides⁵. These highly polyphagous insects can feed on over 600 plant species and cause damage both from direct feeding and through the transmission of plant viruses. Given this broad host range, whiteflies are likely to have broad-spectrum resistance against defenses found in multiple host plants. Good progress has been made on how whiteflies manipulate the hosts' defense-signaling pathways to suppress some aspects of the plant defense response^{6,7} but little is known about how they avoid or inactivate plant toxins.

Main contributions and importance

The study by Xia *et al.* is an elegant demonstration of how a major insect pest manages to neutralize plant defenses¹. The study focuses on the sweet potato whitefly, *Bemisia tabaci* (Gennadius), and its interaction with tomato plants. The authors demonstrate that *B. tabaci* has a horizontally acquired plant gene, *BtPMT1*, that encodes a malonyltransferase. While a major function of these types of genes in plants is to protect against xenobiotic compounds, in some cases

they can also be used to protect the plants from their own toxic defense compounds⁸. For instance, tomato plants produce phenolic glycosides for insect defense and use malonyltransferases to malonylate these compounds, thereby allowing their detoxification and preventing damage to themselves.

HGT has been recognized for some time as an important mechanism for adaptation in microbial organisms, and there is growing evidence for a similar role in eukaryotes⁹. Whereas more than 140 HGT genes have been identified in whiteflies¹⁰, the vast majority are from microbial sources. Therefore, the identification of an acquired gene from plants in whiteflies—particularly one that allows detoxification of phenolic glycosides through malonyltransferase activity—is an astonishing finding. Whereas a few plant genes have been reported previously to be transferred to insects^{11,12}, their functions in the insects have not been elucidated, and the Xia *et al.* study is the first to demonstrate the beneficial effects of a plant-derived gene in an insect.

The authors applied a range of approaches to decipher the details underlying this plant-derived detoxification mechanism in *B. tabaci*, which potentially underpins a generalist feeding habit. They demonstrated, using an *in vitro* assay, that the BtPMT1 protein was able to malonylate 3 out of 11 phenolic glycosides tested. In another set of elegant experiments, the authors used transgenic tomato plants that expressed an RNAi construct that was able to effectively silence the *B. tabaci* gene upon whitefly feeding. They performed a whole-metabolome assay of the honeydew from the whiteflies feeding on the transgenic plants or wild-type controls and, among thousands of metabolites detected, there were 94 flavonoid glycosides and 4 flavonoid malonylglycoside compounds. Compared to whiteflies feeding on the wild-type plants, whiteflies feeding on transgenic plants had higher levels of 50 of the flavonoid glycosides, while the levels of

the 4 flavonoid malonylglycoside compounds were significantly lower.

The potential of RNAi for the control of whiteflies is an active research area (see 13). The Xia *et al.* study demonstrates that an RNAi approach targeting the *BtPMT1* gene can provide highly effective resistance in a field-simulation scenario, although full field-based studies still need to be performed. Whilst not a silver bullet, the importance of this finding is two-fold. Firstly, it provides another tool in the armory for whitefly control, which, based on the preliminary studies conducted by Xia *et al.*, is likely to have a high degree of specificity. Secondly, given the hurdles for getting HGT from a plant to an insect—from integration and expression to selection in the host—such genes are likely to be good RNAi targets. Consequently, this ground-breaking study is likely to lead to many other similar approaches to look for and then capitalize on genes that have been transferred from plant hosts to their insect pests, to help engineer insect resistance.

Open questions

While the Xia *et al.* study was quite comprehensive, it opens up a number of interesting questions. No evidence is given as to whether the phenolic glycosides are found in the phloem, which is the target tissue for whitefly feeding. However, there is evidence from other plants for these phenolic compounds to be found in the phloem (see 14). Furthermore, their presence in whitefly honeydew demonstrates that these compounds are being ingested and makes the tomato phloem the most likely source.

Another question is how an insect obtains genes from a plant. While it is possible that it was a direct HGT event from a yet to be identified donor plant to the whitefly, this is not a common system of direct transfer and less likely from a phloem feeder, since this

tissue is low in nucleic acids. It therefore seems more likely that an intermediate organism, such as a virus or bacterial pathogen, may have been involved. There are a number of viruses that interact with both whiteflies and plants, and some even replicate in both insects and plants, making these good candidates for assisting in gene transfer. Testing of this hypothesis needs to wait for the original plant donor of the gene to whiteflies to be identified.

The enzymatic activity of *BtPMT1* needs to be further characterized, as it was striking that only 4 of the 96 phenolic glycosides identified in the honeydew were malonylated. Does the protein have any other functions, and what about the second gene, *BtPMT2*, that was identified in the study but not characterized further? Related to this is the question of which gene was transferred first and subsequently duplicated to undergo neofunctionalization or whether both genes were transferred at once.

While the results of the RNAi experiments are promising for whitefly control, these experiments need to be extended to field conditions and different environments/crops. Further analysis of the specificity of this approach to insects is needed. It also remains to be seen how long it will take for whiteflies to develop resistance to RNAi. This could happen quickly if an RNAi construct is heavily used as a single whitefly protection strategy in the field, and the sensible way forward will be to incorporate the RNAi/*BtPMT1* approach as part of integrated pest management program.

More generally, it remains to be seen how common this sort of strategy is for insect pests. Although targeted detoxification of defensive plant metabolites is frequently observed in specialist insect herbivores, *BtMAT1* has multiple substrates that are present in a variety of plant species. Given the ability of the


BtPMT1 to detoxify a range of phenolic glycosides, it may be a class of detoxification enzymes that is more relevant to generalists that can infest many types of plants. An intriguing possibility is that this gene was acquired by whiteflies while still more a specialist than a generalist, and that the gene helped precipitate the evolution of whiteflies to a more generalist lifestyle.

Conclusion

The discovery of a gene in whiteflies that came from a plant, and its pivotal role in detoxifying defensive compounds ingested by the whiteflies upon plant feeding, is a major contribution to the field of

plant-pest interactions and the control of insect pests. Going forward, it provides a good strategy to look in a more focused manner for evidence of HGT happening in this fashion and then targeting these genes for pest control. Such a strategy is likely to give a high degree of specificity and thereby not harm beneficial insects. Moreover, given that horizontally transferred genes are likely to be under a relatively high level of selection in the insects, this may provide a more durable option than many other targets. The results of this paper have highlighted the value of well-annotated insect genomes and the need to generate more such insect genomes to better capitalize on these findings.

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