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Plant to insect horizontal gene transfer: empowering whiteflies

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Abstract

Horizontal gene transfer (HGT) is a well-documented evolutionary driving phenomenon in prokaryotes and eukaryotes, but its impact on the plant kingdom has remained elusive. A recent study provides compelling evidences, which support that a plant-derived gene allows for the detoxification of plant defense metabolites in a polyphagous arthropod herbivore.

Keywords

Horizontal gene transfer; detoxification; malonyltransferase; phenolic glucosides; pest control

Main text

Originally described in the late 50's, horizontal gene transfer (HGT, see Glossary) is now largely documented and recognized as a motor-driving force of life evolution. In prokaryotes, HGT is uncontroversial and up to 80% of *E. coli* genes may result from HGT events that happened during its evolutionary history [1]. HGT is less prevalent in eukaryotes and may be responsible for only ~1% of their gene content but has often supported the colonization of extreme environments particularly for unicellular eukaryotes. In these cases, the DNA donor organism is always a fungus, a bacterium or a virus [2]. Multicellular eukaryotes also integrated HGT as an adaptation strategy, as illustrated by the production of carotenoids by aphids following a HGT from fungi [3]. Terrestrial plants benefited from a similar trend by using endosymbiotic gene transfer from organelles to the nuclei as a major evolutionary-shaping force of plant nuclear genomes [4] and by transferring nuclear genes to other plants [5]. Overall, DNA donors in known HGT events for eukaryotes are thus almost exclusively microorganisms, and evidence for horizontal transfer of functional plant derived genes to insects has been hitherto missing. In a groundbreaking study published in *Cell*, the first ever gene transfer from plant to insect has been very recently described [6]. Xia, Guo, Yang and colleagues indeed disclosed a functional HGT from an unknown donor plant conferring the capacity of an arthropod herbivore to feed on toxin-synthesizing plants.

As part of their arsenal, plants synthesize sophisticated specialized metabolites (toxins, see Glossary) such as phenolic glycosides with toxic properties against their herbivore aggressors. *In planta*, these specialized metabolites are managed by specific enzymes including malonyltransferases, which are also involved in the detoxification of many compounds such as xenobiotics/herbicides including naphtol glucosides [7] (**Fig. 1A**). Among the deadliest herbivore in contemporary agriculture, the *Bemisia tabaci* whitefly is a notorious supervector for 300 plant viruses on crops [8]. Albeit feeding

on a wide variety of plant species (500 species in 74 families, see [8]), little was known about the mechanism allowing this whitefly to cope with plant defense mechanisms [9] (**Fig. 1B**).

By mapping the *B. tabaci* genome, the authors identified a malonyltransferase encoding gene (*BtPMT1*), which is absent from another close whitefly. Interestingly, homology analyses also revealed that the closest homologues of the BtPMT1 protein were found in plants, while no homologs were identified in arthropods distinct from *B. tabaci*. Genomic analyses confirmed that *BtPMT1* is integrated into *B. tabaci* genome. PCR amplification also revealed that *BtPMT1* detection was independent from both *B. tabaci* strains and host plants demonstrating that *BtPMT1* is not a plant DNA contaminant and convincingly supporting the idea that the insect acquired this plant gene via HGT.

In a series of elegantly designed functional genetic approaches, the authors provide a body of evidence that strongly suggest that *BtPMT1* has conferred *B. tabaci* the capacity to feed on toxin-synthesizing plants. Firstly, they demonstrated that the recombinant BtPMT1 protein was able to malonylate a wide range of phenolic glucosides *in vitro*, and that acylated forms were far less toxic than native forms when added to the insect's diet. In addition, silencing of *BtPMT1* by dietary interference RNA (see Glossary) led to an increased insect mortality when fed with diets containing specific phenolic glycosides from tomato or after direct feeding on tomato plants. In their quest for answering the question whether *B. tabaci* metabolizes the plant's toxins, the authors further characterized the insect's honeydew (see Glossary) and detected the presence of malonylated forms of phenolic glycosides when insects were fed with individual toxins or on whole tomato plants. However, when the accumulation of BtPMT1 was silenced in the insect, the accumulation of the malonylated toxins strongly decreased together with the ability of the insect to survive. Interestingly, the authors also established that *BtPMT1* is highly expressed in the *B. tabaci*'s gut, in agreement with a function in plant toxin detoxification. Overall, since BtPMT1 is at least in part responsible for the wide host range of this polyphagous and deadly arthropod herbivore, targeting this gene could open new perspectives towards the improvement of plant resistance.

To validate this notion, the authors produced a tomato transgenic line expressing a hairpin construct with homology to *BtPMT1*. *In planta*, the hairpin RNA is processed by the silencing machinery to produce interfering RNAs inhibiting *BtPMT1* gene expression that will be ingested by the insect upon feeding. The authors first confirmed the downregulation of *BtPMT1* in *B. tabaci* fed on the transgenic line. Importantly, this silencing caused the death of almost 100% of the whiteflies 7 days after ingestion of transgenic plant leaves, without affecting the performance of other insects feeding on the same transgenic plants. This confirmed the specificity of the silencing effect and nicely suggests that this strategy could be used in the field to improve plant resistance against *B. tabaci*.

In summary, the work of Turling and Zhang groups thus described a new paradigm highlighting how an insect hijacked a plant gene to develop an effective strategy of plant toxin neutralization (**Fig. 1C**). As such, it will undoubtedly change our vision of the evolution of the arm race engaged between organisms and probably the way we can combat pests to decrease the effect of plant virus mediated by whiteflies. However, fundamental questions remain to be addressed. For instance, identification of the plant DNA donor obviously represents a thrilling quest. In addition, what could be the molecular mechanisms underlying the jump of a plant gene within an insect genome? A hint may come from the case of anti-freeze proteins (AFPs) that were acquired in the smelt fish by HGT from the Atlantic herring. Indeed, careful inspection of the genomic contexts neighboring AFPs revealed that smelt AFPs are flanked by transposable elements normally absent from this genome, but specific to the herring genome [10]. Plant genomes are very rich sources of transposable elements that may jump from their initial position in the genome under specific circumstances. It remains to be

determined whether the BtPMT1 loci in *B. tabaci* has neighboring sequences enriched in transposable elements. By then, based on this enlightening article, we can expect that new examples of plant gene piracy will be discovered in a near future.

Text box (glossary)

HGT: Horizontal gene transfer defines the movement of genetic material across the tree of life by other means than those employed in the case of parent to offspring genetic inheritance.

Dietary RNAi: allows for the specific knockdown of a gene by adding an *in vitro* synthesized double-stranded RNA to the regular laboratory diet (glucose and yeast extract) of whiteflies.

Specialized metabolites/toxins: Besides the core energy-producing metabolism, plants synthesize a number of compounds called specialized metabolites that regulate their interaction with environment. Plant specialized metabolites have thus numerous functions, including the defense against pest/herbivores as illustrated in the spotlighted article.

Honeydew: a number of sap-feeding arthropods excrete this carbohydrate-rich secretion that has a number of physio-ecological impacts.

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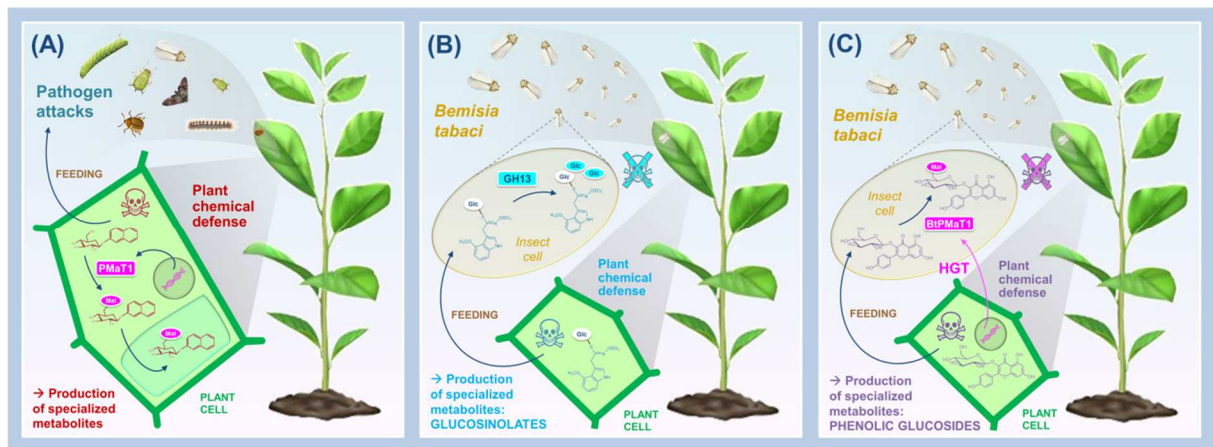


Figure 1. Whitefly acquired a plant detoxification gene that neutralizes plant toxins. (A) Plants produce specialized metabolites for fighting against pests. For instance, some plants such as Fabaceae accumulate in leaf cells phenolic glucosides that are toxic for many insect pathogens upon feeding. In planta, this type of compounds are metabolized by a malonylation catalyzed by PMaT1. **(B) Some insects have evolved molecular mechanisms to prevent plant metabolite toxicity.** Recently, whiteflies were found to detoxify the majority of the glucosinolates it ingests by the addition of glucose moieties through the activity of glycoside hydrolase family 13 (GH13) enzymes [9]. **(C) A plant to insect HGT event allows whiteflies to detoxify plant defense compounds.** Here, Xia and colleagues provide a new paradigm by demonstrating that *B. tabaci* has acquired a plant-derived gene to prevent toxicity of phenolic glucosides and continue to feed on their plant hosts [7].