

Previews

Whiteflies weaponize a plant defense via horizontal gene transfer

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Co-opting enemy weapons is a proven strategy in warfare. The war of nature is no different. In this issue of *Cell*, Xia and colleagues show how a major crop pest stole a plant phenolic glucoside malonyltransferase gene, allowing neutralization of a large class of plant defense compounds.

The Greek historian Polybius points to a single event that flipped control of the Mediterranean Sea from Carthage to Rome during the 23-year-long First Punic War: a Carthaginian quinquereme warship that ran aground in Roman waters. The Carthaginians produced quinqueremes, the best battleships of the era, built to allow five different levels of oars, as opposed to the Roman triremes that only had three (Polybius, 2010). By capturing the enemy's most technologically advanced weapon, the Romans turned the tide of war by unleashing 100 copies of the Carthaginian warships (Goldsworthy, 2000). In this issue of *Cell*, Xia et al. (2021) describe a similar twist of fate from nature. A plant protein used in the biosynthesis of anti-herbivore defensive chemicals was co-opted by a major crop pest through horizontal gene transfer (HGT) to gain access to diverse host plants.

The plant-herbivore co-evolutionary arms race (Ehrlich and Raven, 1964) is conceived of cycles of defense and counter-defense. Herbivore attack results in natural selection for novel plant defenses, especially secondary chemicals, to which herbivores are initially susceptible (Fraenkel, 1959). The plants, having escaped attack, gain a competitive edge over other plants and diversify across the landscape. However, herbivores quickly evolve countermeasures to overcome the novel plant defenses. In turn, the insects radiate on this new resource by evolving specialized resistance mechanisms.

Some herbivorous insects have even co-opted the very toxins that evolved to kill them, using the plant defenses as

weapons of their own. Monarch butterflies sequester heart poisons from milkweeds, for example (Reichstein et al., 1968). The genomics era has revealed even more intricate strategies used by herbivores to overcome host defenses. In a remarkable finding, Xia and colleagues have discovered that a sweet potato whitefly lineage stole a gene used by plants to detoxify xenobiotic molecules and synthesize defensive compounds. *Bemisia tabaci* (Gennadius) is a notorious plant pest capable of attacking over 600 plant species. The next time you are in a garden you might notice these tiny creatures, no larger than a snowflake, flitting about if a leaf or a stem is disturbed. Their fairy-like form belies a pest that not only causes damage by feeding on plant sap but is a vector for a multitude of plant viruses and causes major crop loss around the world (Gilbertson et al., 2015).

Xia and colleagues found that the secret to the success of *B. tabaci* lies in beating enemies at their own game through theft and co-option of a defensive weapon used by most plant lineages to modify and neutralize phenolic glucosides, one of the most common class of secondary compounds produced by plants. Phenolic glucosides can be found in plants as different as willows (*Salix* spp.) and tomatoes (*Solanum* spp.). Phenolic glucosides are, by and large, toxins that plants not only use but also often must defend themselves from as well. More specifically, plants use glucoside malonyltransferases to attach a malonyl group to phenolic glucosides, which can then be stored in vacuoles (Taguchi et al., 2010). Plants can resist herbicides in this way.

The authors find clear evidence that the *B. tabaci* gene *BtPMT1*, which encodes an enzyme with glucoside malonyltransferase activity, is not insectine in origin but likely traces its roots to a plant nuclear genome (Figure 1). The likely plant origin of the copy in *B. tabaci* is based on a phylogenetic analysis and homology of key domains between *B. tabaci*'s copy and those encoded in plant genomes. The theft occurred through an ancient HGT event (up to 86 million years ago), and, given the vast expanse of time, it is not surprising that the identity of the specific plant donor lineage remains unclear. An additional gene copy, *BtPMT2*, was also reported by the authors, but its function is not yet clear.

In the case of *BtPMT1*, Xia and colleagues show that at least one function of this horizontally transferred glucoside malonyltransferase in the sweet potato whitefly is to neutralize diverse plant-derived phenolic glucosides. *BtPMT* is constitutively expressed across all developmental stages and tissues in *B. tabaci*. To determine the role of *BtPMT1* in detoxification of plant toxins, the authors profile the phenolic glucosides present in tomato plants, finding five phenolic glucosides to have particularly toxic effects against *B. tabaci*. The authors knocked down *BtPMT1* expression in whiteflies and then measured survival against isolated phenolic glucosides and the whole plant. Whitefly mortality was higher on the panel of phenolic glucosides and tomato plants when *BtPMT1* was knocked down. These results were corroborated with metabolic profiling of *B. tabaci* excretions. *B. tabaci* with knockdown of *BtPMT1* had lower amounts of the



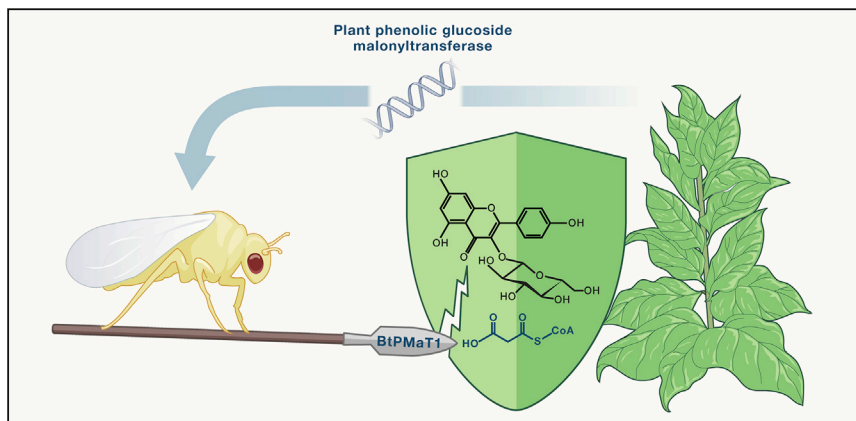


Figure 1. Horizontal gene transfer facilitates a host detoxification mechanism in *Bemisia tabaci*

Akin to the Romans during the First Punic War or the wisdom of third century BCE Chinese philosopher Han Fei of “attack[ing] your shield with your spear,” the horizontal transfer of a plant glucoside malonyltransferase into the ancestor of *Bemisia tabaci* allows this species to colonize a wide range of plant hosts. *B. tabaci* BtPMaT1 transfers a malonyl group onto the plant’s defensive phenolic glucoside molecule, neutralizing it.

“detoxified” malonylphenolic glucosides in their excretions than did the control, indicating the malonyl transfer activity as the detoxification mechanism. Co-option of a canonical plant enzyme by a generalist herbivore is a mechanism by which whiteflies can persist on diverse toxic host plant environments—600 different plant species armed with myriad phenolic toxins.

As Xia et al. point out, more work is needed to fully appreciate how a foreign gene is integrated into divergent gene regulatory networks. How pleiotropic is this gene or its paralog *BtPMaT2*? Can the donor lineage be ascertained with greater confidence?

The implications of this study by Xia and colleagues are broad. From a practical perspective, there is promise for delivering a hairpin RNA targeting *BtPMaT1* to whiteflies *in planta* as a means to con-

trol a global pest that contributes to major crop losses. More generally, the study reports one of the first instances of a plant-to-animal HGT event. Although we now take for granted that HGT events are the most important source of new genes in prokaryotes, biologists are just beginning to appreciate that HGT events have yielded eukaryotic innovations (Husnik and McCutcheon, 2018). Much adaptation proceeds through gradual improvement of native genes, but evolution can occur by leaps and bounds, almost overnight, through HGT events. Processes like reticulate evolution like hybridization, would surely have delighted Darwin.

The gilded age of evolutionary biology in which we find ourselves is revealing that the tree of eukaryotic life is better viewed as a grand, braided river of life. In this case, an ancestor of whiteflies

captured an essential gene used by plants to detoxify foreign molecules and create new defensive compounds. This HGT event opened the door to colonization of a great diversity of plant species, helping explain how generalist herbivores can be so successful.

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