

# New directions for improving crop resistance to insects by breeding for egg induced defence

Amanuel Tamiru<sup>1</sup>, Zeyaur R Khan<sup>1</sup> and Toby JA Bruce<sup>2</sup>



Plant defence responses to insect oviposition, including tritrophic interactions with natural enemies of herbivores, have rarely been targeted in crop breeding programmes. Emission of herbivore induced plant volatiles (HIPVs) that attract natural enemies early on at the egg-laying stage of herbivore attack could provide timely biological control of pests and deter subsequent oviposition. This is needed in an agroecological context where the third trophic level often does not keep pace with the growth rate of pests. Our very recent data, using maize as an example, show that herbivore egg induced volatile emission is very rare in commercial hybrids but common in farmer selected landraces. Strategies for crop genetic improvement to enhance such responses to insect attack are considered.

## Addresses

<sup>1</sup> ICIPE, PO Box 30772, Nairobi, Kenya

<sup>2</sup> Rothamsted Research, Harpenden, Herts AL5 2JQ, UK

Corresponding author: Bruce, Toby JA ([toby.bruce@rothamsted.ac.uk](mailto:toby.bruce@rothamsted.ac.uk))

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## Introduction

Wild plants have evolved intricate defence mechanisms against insect herbivores [1–3] over a period of 400 million years [4]. These depend partly on primary recognition of the insect mediated by specific herbivore-derived molecules, termed herbivore-associated molecular patterns or HAMPs [5,6,7]. Induced defence occurs after recognition of insect attack and includes ‘indirect defence’ entailing the emission of herbivore induced plant volatiles (HIPVs) that allow them to attract parasitoid and predator insects that are tuned in to these signals and use them when foraging for prey insects [8,9].

Several studies have shown that plants are able to even detect insect egg deposition (the earliest stage of herbivory) and respond by activating direct and indirect defences early before larvae hatch and cause damage by feeding (reviewed by [10]). This ‘early herbivore alert’

reduces the lag period for arrival of natural enemies. Parasitism of eggs by egg parasitoids reduces larval emergence and performance. Furthermore, emission of volatile cues attractive to larval parasitoids following egg deposition means that they are recruited in anticipation of larval emergence and parasitism can start before the larvae can cause much damage to the plant. Parasitoids are under selection pressure to respond to such cues and even distinguish between mechanical damage and those induced by the presence of their hosts as this enhances their foraging efficiency eventually improving their ecological fitness. Attraction of parasitoid wasps can improve biological control in open field environments, as already shown with intercrops [11]. Such indirect defence has perhaps been neglected as a potential trait for breeding increased crop resistance to insect pests. Breeding may have favoured ‘bottom-up’ rather than ‘top-down’ insect resistance [9]. In this paper we discuss genetic variation in crop responses to insect attack and strategies for crop genetic improvement to enhance such traits. To illustrate the concept we use our recent studies in maize with the stemborer *Chilo partellus* and its parasitoid *Cotesia sesamiae* because we have now found that insect egg induced volatile emission does exist in commercial hybrids meaning that there is a prospect of introgressing this trait into improved varieties.

## Fighting insects like a wild plant?

The impact of crop domestication on responses to insect attack was considered at the 15th Symposium on Insect–Plant Interactions (August 17–22, 2014; University of Neuchâtel, Switzerland). Plants subjected to artificial selection may have lost defence traits, used for protection against insects in nature, especially if crops are selected for yield in a pesticide treated background. Conversely, insect resistance may increase if breeders purposely select for insect resistance, although such breeding is often empirical and without characterisation of the underpinning mechanism. Palmgren *et al.* [12] hypothesised that traits allowing plants to withstand adverse environmental conditions have been lost while selecting for traits that made plants easier to harvest and/or resulted in higher yield. de Lange *et al.* [13] reviewed resistance to biotic stress in teosintes (wild maize species) which appear to have greater resistance against a number of pests than cultivated maize.

Wild plants or less domesticated landraces are a promising source of traits that could enable plants to withstand insect attack and other stressful conditions. Strategies

are required to identify resistance traits and introgress them into domesticated crop germplasm. Next generation sequencing (NGS) technologies being used to generate whole genome sequences for a wide range of crop species, when combined with precise phenotyping methods, can provide powerful and rapid tools for identifying the genetic basis of agriculturally important traits and for predicting the breeding value of individuals in a plant breeding population [14]. These approaches will greatly facilitate the identification of useful traits. However the phenotyping is often more time consuming than the genotyping [15].

HIPV emission is widespread in nature and lack of response to herbivory may be rare in wild plants [16]. It has been shown [17\*\*] that HIPV-silenced *Nicotiana attenuata* plants had reduced fitness due to increased herbivory by *Manduca* spp. resulting in a twofold decrease in bud and flower production. Furthermore, Zakir *et al.* [18] found a significant reduction in oviposition by *Spodoptera littoralis* on undamaged plants adjacent to herbivore-damaged cotton plants under both field and laboratory conditions. Heil [9\*\*] discussed use of HIPVs as tools in biocontrol and challenges faced in their application in agriculture. These include a lack of field studies, possible slower growth but increased damage by parasitised insects, attraction of hyperparasitoids or herbivores, lack of reward for attracted natural enemies and insufficient levels of natural enemies in the environment. These are important points that require further study, especially in outdoor field conditions and possible adjustment of agronomic practices, for example, conservation biocontrol to boost natural enemy populations and provide a suitable environmental context for the crops that ‘cry for help’.

Plant responses to insect oviposition can be direct as well: *C. partellus* egg deposition on maize plants that release HIPVs has recently been shown to have direct effects on the herbivores themselves [19] such that plants already with eggs had lower subsequent oviposition. HIPVs are known to have repellent effects on gravid female moths [20]. Once the plant recognises it is being attacked other defences such as induced antibiotic or anti-nutritive substances are also produced by plants which are responding [21]. Together, direct and indirect defences slow down the growth rate of the herbivore. Direct defences do this by reducing settlement and suitability of the plant as a host. Indirect defences increase mortality of the herbivore thus leading to a slower population build-up. Zakir *et al.* [18] found direct effects on oviposition behaviour in *S. littoralis* and Geiselhardt *et al.* [22] demonstrated that *Pieris brassicae* oviposition on *Arabidopsis thaliana* reduced subsequent feeding and growth rates of the larvae. Furthermore, Fatourous *et al.* [23] found synergistic effects of direct and indirect defences on herbivore egg survival in a wild crucifer.

### Egg induced defence against stemborer attack in maize

HIPV-mediated indirect defences following larval feeding are well known in maize (e.g. [13\*,24,25]). HIPV emission after oviposition of the stemborer *C. partellus* was recently discovered in certain maize landraces [26,27] but not in the commercial hybrids we examined initially. In the last two years, we screened for egg induced HIPV emission in a much wider range of maize germplasm (25 landraces, 30 hybrids and 22 inbred lines; Figure 1). This was to determine whether HIPV emission after stemborer oviposition could be found in improved, higher yielding maize varieties and to enable ongoing genome wide association studies (GWAS) [28] mapping single nucleotide polymorphisms (SNPs) linked to the egg induced indirect defence trait. We collected headspace samples of volatiles from plants with and without *C. partellus* eggs, analysing the volatiles by gas chromatography and exposed the parasitoid *C. sesamiae* to the volatiles in an olfactometer bioassay (Methods as in [26]). Plants were grown under insect free conditions; treated plants were caged overnight with five gravid naïve female stemborer moths and volatiles were then collected for 48 h. Egg hatch occurs five days after oviposition which meaning that the plants were only exposed to eggs and not to larvae.

We tested if gravid female *C. sesamiae* spent significantly more time in the olfactometer arms containing volatiles from plants exposed to egg deposition by *C. partellus* compared to arms with volatiles from unexposed plants or solvent control. Thirteen landraces were identified with the trait (Figure 1), whereas, out of 30 hybrid maize varieties tested, only two elicited significant attraction of female *C. sesamiae*. These were the CIMMYT line CKIR12001 and the commercial variety ‘SC Duma 43’, both of which strongly attracted parasitoids following oviposition ( $F_{2,37} = 9.47$ ,  $P = 0.0005$  and  $F_{2,33} = 9.47$ ,  $P < 0.001$ , respectively). Compounds that were induced included (*Z*)-3-hexen-1-ol, limonene, (*E*)-4,8-dimethyl-1,3,7-nonatriene (DMNT), methyl salicylate and (*E*)- $\beta$ -farnesene. The parental inbred lines of CKIR12001 were then tested and all three of them elicited parasitoid attraction. Female *C. sesamiae* were significantly attracted to HIPVs from maize inbredlines CML 442 ( $F_{2,37} = 21.84$ ;  $P < 0.001$ ); CML 312 ( $F_{2,37} = 16.60$ ,  $P < 0.0001$ ) and CKSBL10027 ( $F_{2,37} = 7.59$ ,  $P = 0.0017$ ) exposed to *C. partellus* egg deposition, compared with volatiles from unexposed plants and blank controls (Figure 1). These could provide a genetic resource for introgressing the trait into high yielding maize lines to increase indirect defence against stemborers.

Headspace samples from plants with and without eggs were analysed by GC. Comparison of volatile profiles revealed a close correspondence between any egg induced changes in the volatile profile and attraction

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