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Minor effects of two elicitors of insect and pathogen resistance on volatile emissions and parasitism of *Spodoptera frugiperda* in Mexican maize fields

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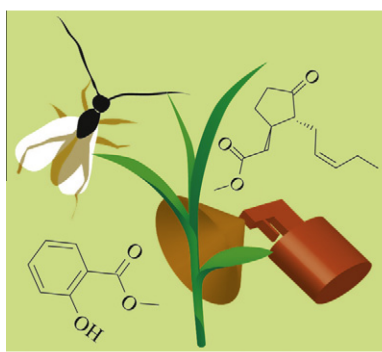
HIGHLIGHTS

- ▶ Elicitors can induce plant resistance against insects and pathogens.
- ▶ In maize field these elicitors also changed plant odor emissions.
- ▶ The changes have minor effects on herbivores and parasitoid presence.
- ▶ Elicitor treatment is compatible with biological control.

GRAPHICAL ABSTRACT



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ABSTRACT

Synthetic elicitors can be used to induce resistance in plants against pathogens and arthropod herbivores. Such compounds may also change the emission of herbivore-induced plant volatiles, which serve as important cues for parasitic wasps to locate their hosts. Therefore, the use of elicitors in the field may affect biological control of insect pests. To test this, we treated maize seedlings growing in a subtropical field in Mexico with methyl jasmonate (MeJA), an elicitor of defense responses against many insects, and benzo-(1,2,3)-thiadiazole-7-carbothioic acid S-methyl ester (BTH), an elicitor of resistance against certain pathogens. Volatile emission, herbivore infestation, pathogen infection, and plant performance (growth and grain yield) of treated and untreated maize plants were measured. Application of BTH slightly reduced volatile emission in maize, while MeJA increased the emission compared to control treatments. Despite the apparent changes in volatile emissions, the elicitor application did not consistently affect infestation by *Spodoptera frugiperda* larvae, the main insect pest found on the maize seedlings, and had only marginal effects on parasitism rates. Similarly, there were no treatment effects on infestation by other herbivores and pathogens. Results for the six replications that stretched over one summer and one winter season were highly variable, with parasitism rates and the species composition of the parasitoids differing significantly between seasons. This variability, as well as the severe biotic and abiotic stresses on young seedlings might explain why we measured only slight effects of elicitor application on pest incidence and biological control in this specific field study. Indeed, an additional field experiment under milder and more standardized conditions revealed that BTH induced significant resistance against *Bipolaris maydis*, a major pathogen in the experimental maize fields. Similar affects can be expected for herbivory and parasitism rates.

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1. Introduction

Plants attacked by arthropod herbivores respond by activating a number of defense mechanisms, including the emission of volatile organic compounds (VOCs) that attract predatory and parasitic arthropods (Dicke, 2009; Dicke et al., 1990; Turlings et al., 1990; Turlings and Wäckers, 2004). In maize, these herbivore-induced plant volatiles comprise mainly green leaf volatiles (GLVs), mono-, homo- and sesquiterpenes, as well as aromatic compounds (D'Alessandro et al., 2006; Hoballah and Turlings, 2005; Paré and Tumlinson, 1999). The emission of most herbivore-induced plant volatiles involves a number of well-understood metabolic pathways, such as the jasmonic acid (JA) pathway, the shikimic acid/tryptophan pathway, the mevalonate pathway, as well as the lipoxygenase (LOX) pathway (Paré and Tumlinson, 1999; Dudareva et al., 2004; Bruce and Pickett, 2007; Engelberth et al., 2007). Similarly, plants infected by fungi or bacteria respond with the activation of a number of defense mechanisms against these pathogens (van Loon et al., 2006; Walling, 2009), and in most cases this involves the plant hormone salicylic acid (SA) (Bari and Jones, 2009). Resistance against pathogens as well as defenses against insects can also be induced with synthetic versions of these elicitors or their derivatives (Heil and Walters, 2009; Walling, 2009). Besides increasing the direct defenses in the plants, such treatments may also enhance the volatile defense signals. For instance, spraying plants with methyl jasmonate (MeJA), a volatile derivative of JA, induces the emission of volatiles that are also induced by herbivore feeding (Degenhardt and Lincoln, 2006; Heil and Walters, 2009; Ozawa et al., 2008; Zhang et al., 2009). This can lead to increased parasitism of caterpillars as was observed by Thaler (1999) near tomato plants that she had treated with JA.

Pathogen resistance can be induced by the elicitor benzo-(1,2,3)-thiadiazole-7-carbothioic acid S-methyl ester (BTH), which mimics the effects of salicylic acid (SA) and results in a reduction of the impact of several pathogens in different plant species by inducing systemic acquired resistance (SAR) (Friedrich et al., 1996; Görlach et al., 1996), but see (Heidel and Baldwin, 2004). BTH is commercially applied in poaceous and solanaceous crops as well as sunflowers and grapevine as a preventive measure against pathogen growth (Goellner and Conrath, 2008; Perazzolli et al., 2008; Vallad and Goodman, 2004).

In many plant species there is crosstalk between the SA and the JA pathways, where the increased activity of one pathway diminishes the activity of the other (Kunkel and Brooks, 2002). Hence, the application of an elicitor to induce one of these two pathways might result in a suppression of other defense mechanisms depending on the interactions between the pathways (Beckers and Spoel, 2006; Thaler et al., 2002a,b; Walters and Heil, 2007). There are exceptions (Boughton et al., 2006), but in general, herbivorous insects perform better on plants with an activated SA pathway (Rayapuram and Baldwin, 2007; Smith et al., 2009; Taylor et al., 2004; Thaler et al., 2002a,b). However, this may be different if indirect defense signals and tritrophic interactions are also taken into account. In fact, a recent study (Rostás and Turlings, 2008) shows that treatment with BTH not only increases resistance to the pathogenic fungus *Setosphaeria turcica* in maize, but also strongly enhances the attractiveness to the parasitoid *Microplitis rufiventris* (Kokujev) (Hymenoptera: Braconidae) if the treated plants are subsequently infested with hosts of the parasitoid, the larvae of *Spodoptera littoralis* Boisduval (Lepidoptera: Noctuidae). Ongoing experiments indicate that other parasitoid species also show increased attraction to BTH-treated maize plants (I. Sobhy, personal communication).

Hence, induction of pathogen resistance may affect the emission of volatile compounds, and thereby indirectly enhance resistance against herbivores via the third trophic level. The aim of the current study was to assess whether treating maize plants with BTH or MeJA affects the plants' direct and indirect defenses against important pest species under realistic field conditions. Direct effects can be through the induced production of defense compounds or volatiles that repel the pests, whereas indirect effects would be the enhanced attraction of natural enemies of herbivores. To study this, four experiments were conducted at different time-points over the year in maize fields in the subtropical lowlands of Mexico to determine the effects of elicitors on volatile emission of maize plants, herbivory, parasitism, and plant performance.

2. Material and methods

2.1. Maize fields

Seven field experiments with *Zea mays* (cv Tuxpeño Sequía) planted on six dates were conducted at the International Wheat and Maize Improvement Center (CIMMYT) experimental station near Agua Fría, Puebla State, Mexico (20°26′56.93″N, 97°38′23.98″W, 98 masl). Two fields were planted in summer 2008 (replicate 1 on 9 June 2008 and replicate 2 on 16 June 2008) and four fields in winter 2009 (replicate 3 on 6 February 2009, replicate 4 on 9 February 2009, replicate 5 on 11 February 2009 and replicate 6 on 13 February 2009). A seventh field was planted on 6 February 2009 to evaluate the treatment effects on disease resistance and kernel production. The fields were planted in 31 rows of 25 m, with 20 cm distance between plants within the rows and 70 cm distance between rows (Fig. 1). They were regularly irrigated with sprinklers 2–4 days after sowing, and with occasional flooding from V2 developmental stage (collar of the second leaf visible) onward (Çakir, 2004). Neither seeds nor plants were treated with insecticides until the end of the experimental period. Each field was divided into plots that were used for the different treatments.

2.2. Treatment of plants with elicitors

Four types of treatments (two elicitors and corresponding control sprays) were applied to plots of four meters length and four rows wide that were evenly distributed in the field. One meter on each

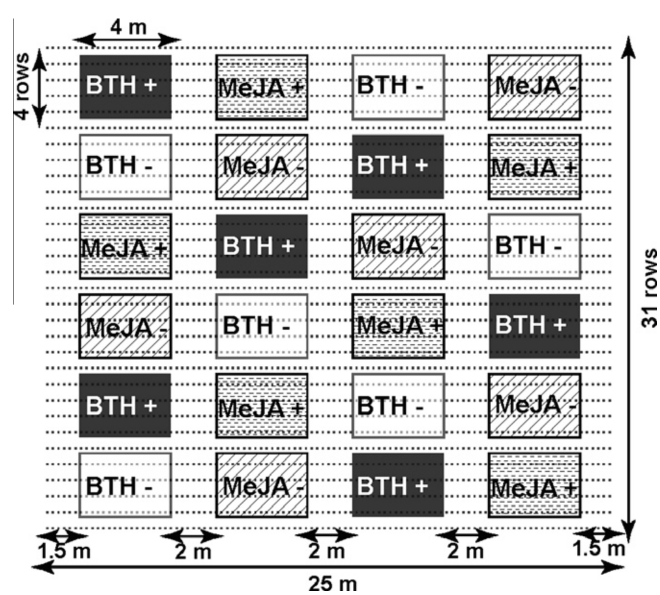

Fig. 1. Design of the field experiments. The field was 25 m × 21.5 m (31 rows 0.7 m) wide. Each plot was 4 m × 4 rows, represented by a square. Dots represent the maize plants. On each side of the field, 1.5 m was left untreated. Between plots, 2 m and 1 row was left untreated. The treatments (BTH+, BTH−, MeJA+ and MeJA−) were applied to young maize seedlings in evenly distributed plots. This treatment was applied on different fields on six occasions throughout the year.