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ORIGINAL PAPER

Effects of neonicotinoid seed treatment on maize anti-herbivore defenses vary across plant genotypes

Andreísa Fabri Lima[1] · Natalie M. Aguirre[2] · Geraldo Andrade Carvalho[1] · John M. Grunseich[3] · Anjel M. Helms[2,3] · Maria Fernanda G. V. Peñaflor[1]

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Abstract

Neonicotinoid seed treatment (NST) is a routine practice used worldwide to control insect pests in a variety of crops, including maize (*Zea mays mays* L.). However, previous work indicates that systemic insecticides can compromise plant defenses, counteracting efforts to control insect pests. The goal of this study was to evaluate the effect of thiamethoxam-neonicotinoid seed treatment on the resistance of two maize genotypes (B73 and MC 4050) against the major non-target pest, fall armyworm *Spodoptera frugiperda* (Lepidoptera: Noctuidae). In preference and performance assays, we evaluated the effect of NST on fall armyworm behavior and biology. We also determined the influence of NST on induced plant defenses, quantifying phytohormone levels and plant volatile emissions, in treatments with and without fall armyworm herbivory. NST did not affect caterpillar host preference, however it reduced caterpillar performance on the genotype B73 across both maize growth stages (V4 and V6). NST-treated B73 plants also had lower induced volatile production (V4 stage) compared to untreated herbivore-damage plants and lower constitutive salicylic acid (V6 stage). In contrast, MC 4050 was not affected by the insecticide, regardless of growth stage. In conclusion, we found that the effects of NST on maize defenses vary by plant genotype and growth stage, suggesting growers may need to tailor their selection of plant genotypes to avoid negative impacts of NST on plant resistance and ultimately pest control.

Keywords Fall armyworm · Phytohormones · Plant defense · *Spodoptera frugiperda* · Thiamethoxam · Volatiles

Introduction

Neonicotinoid insecticides are the most used pesticide worldwide for protecting crops against insect pests and are applied mainly through seed treatment (Jeschke et al. 2011; Douglas and Tooker 2015; Tooker et al. 2017). Neonicotinoid seed treatment (NST—e.g., active ingredients clothianidin, imidacloprid, or thiamethoxam) is a routine and prophylactic practice (Alford and Krupke 2017; Tooker et al. 2017), which aims to reduce pest damage in crops such as maize (*Zea mays mays* L.), soybean (*Glycine max* (Merr) L.) and cotton (*Gossypium* spp.) (Douglas and Tooker 2015), mainly against early season pests during crop establishment (Alford and Krupke 2017). Because they are soluble in water, neonicotinoid insecticides have the ability to translocate and spread throughout plant tissues (Jeschke and Nauen 2008; Bonmatin et al. 2015). Once ingested by insects, neonicotinoids act as a competitive modulator of the nicotinic acetylcholine receptor (nAChR), causing hyperactivity and collapse of the nervous system (Tomizawa and Casida 2005). They are usually used to suppress populations of sucking arthropods, such as aphids and leafhoppers (Oliveira et al. 2008; Magalhães et al. 2009; Krupke et al. 2017; Ding et al. 2018). Some characteristics that popularized the use of neonicotinoids are their systemic nature, efficiency at low doses, and relatively low toxicity to mammals (Elbert et al. 2008; Goulson 2013).

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✉ Maria Fernanda G. V. Peñaflor
fernanda.penaflor@ufla.br

[1] Department of Entomology, Lavras Federal University (UFLA), Aquenta Sol, Lavras, Minas Gerais 37200-900, Brazil

[2] Ecology and Evolutionary Biology Program, Texas A&M University, College Station, TX, USA

[3] Department of Entomology, Texas A&M University, College Station, TX, USA

However, despite their advantages, neonicotinoid insecticides can negatively affect beneficial insect populations and contribute to pest outbreaks. For example, neonicotinoids applied through seed treatment can cause lethal and sublethal effects on beneficial organisms that feed on plant resources such as pollen, floral and extrafloral nectar, and sap (Moscardini et al. 2014, 2015; Gontijo et al. 2014, 2018; Rundlöf et al. 2015; Sâmia et al. 2019; Wu et al. 2021). Additionally, beneficial insect populations, such as parasitoids and predators, can face second-hand exposure to the toxic effects of neonicotinoids by contacting untreated adjacent plants (Botías et al. 2016; Bredeson and Lundgren 2019), feeding on neonicotinoid-contaminated prey (Wanumen et al. 2016; Korenko et al. 2019), and from honeydew excreted by neonicotinoid-contaminated insects (Calvo-Agudo et al. 2019, 2021). NST can also cause complex and variable effects on primary and secondary plant metabolism. For instance, neonicotinoids can alter leaf photosynthetic pigments (Preetha and Stanley 2012; Macedo et al. 2013; Todorenko et al. 2021), increase root development, and improve yield even under water stress (Macedo and Castro 2011; Macedo et al. 2013; Endres et al. 2016). Additionally, neonicotinoids have also been associated with outbreaks of arthropod pests under various environmental conditions (Szczepaniec et al. 2011; Smith et al. 2013; Szczepaniec and Raupp 2013; Ruckert et al. 2018). A few studies have shown that neonicotinoid treatment can alter the plant's ability to defend itself against biotic factors due to changes in defense signaling pathways that modulate the synthesis of defensive metabolites against pathogens and insects (Ford et al. 2010; Szczepaniec et al. 2013; Zhou et al. 2019).

Jasmonic acid (JA), salicylic acid (SA) and ethylene are key phytohormones involved in modulation of plant defense signaling pathways (Pieterse et al. 2012). The phytohormone JA is generally responsible for modulating induced plant defenses against chewing herbivores, while SA is involved in modulating defenses against biotrophic pathogens and phloem-feeding herbivores (Thaler et al. 2010; Pieterse et al. 2012; Lazebnik et al. 2014). The SA signaling pathway often interacts antagonistically with the JA signaling pathway, leading to greater plant susceptibility to herbivores after activation of the SA pathway (Kawazu et al. 2012; Schweiger et al. 2014). It should be noted that neonicotinoids can interfere with SA and JA signaling, which seems to be responsible for the reduced resistance of neonicotinoid-treated plants to arthropod pests (Szczepaniec et al. 2013; Wulff et al. 2019). At the same time, activation of the SA signaling pathway makes neonicotinoid-treated plants more resistant to pathogens (Ford et al. 2010). Notably, systemic insecticides can also impact the release of plant volatile organic compounds (VOCs) (Zhou et al. 2019), which are responsible for plant defense and its interaction with the environment (Dudareva et al. 2013). These effects of NST on defense signaling pathways and differential expression of genes associated with defenses seem to depend on the plant species and neonicotinoid molecule (Szczepaniec et al. 2013; Wulff et al. 2019).

Maize is a crop of world economic and social importance (Shiferaw et al. 2011) and NST is widely used as a chemical control method. For example, in the US, most of the maize seeds are treated with neonicotinoid insecticides to control early season pest populations, such as aphids and leafhoppers (Douglas and Tooker 2015; Tooker et al. 2017). Fall armyworm [FAW; *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae)] is a major pest of maize in the Americas and has also recently spread in different geographic regions (reviewed by Kenis et al. 2022). Maize plants naturally possess metabolites with deterrent and toxic properties to caterpillars, such as benzoxazinoids, polyphenols and protein inhibitors (Wiseman et al. 1992; Pechan et al. 2000; Niemeyer 2009). However, intensive breeding has attenuated some of these direct defenses (Maag et al. 2015) and the control method is frequently carried out with resistant transgenic cultivars (*Bt* events) (Peralta and Palma 2017). NST is not recommended for this insect pest (AGROFIT 2021), but may affect the expression of plant defenses (Szczepaniec et al. 2013). Here, we evaluated the influence of NST on plant resistance to FAW, due to the need to obtain a better understanding of the influence of NST on plant resistance to pests.

We predicted that neonicotinoid seed treatment would decrease plant resistance against insect herbivores. Studying the effects of NST on a non-target maize pest allows us to detangle the direct insecticidal effect of NST on herbivores from the effect of NST on plant defense and resistance. The overall goal of this study was to evaluated the influence of NST on direct and indirect defense of two maize genotypes by evaluating the effects on FAW (performance and preference) and characterizing the constitutive and herbivore-induced plant volatile and phytohormones. This research highlights relevant information about the complexity of the relationship between insect, plant and chemical control.

Materials and methods

Plants, insects, and neonicotinoid seed treatment

We evaluated the effect of NST on two maize genotypes: the hybrid Masters Choice® 4050 (MC 4050) and the inbred B73. MC 4050 is a commercially available field maize genotype without NST that is grown in the United States. The B73 is a genotype widely used in studies, because its genome is well known (Schnable et al. 2009). First, the seeds were sterilized in a 10% hypochlorite solution for 10 min and rinsed in distilled water. Once the seeds were completely

dried, they were treated with the neonicotinoid insecticide thiamethoxam (Cruiser® 5FS, Syngenta) at 0.47 mg AI/kernel, following the maximum recommended concentration for the management of *Dalbulus maidis* (DeLong & Wolcott) (Hemiptera: Cicadellidae) in the maize crop in Brazil (AGROFIT 2021), where it is a major pest (Ribeiro and Canale 2021).

The seeds were individually planted in pots (10 × 10 × 9 cm) filled with commercial potting soil (BACCTO Premium Potting soil 85–15–10, Michigan Peat, TX, USA) and were kept in a climate-controlled room at 25 ± 3 °C, 40 ± 10% RH and 12:12 photoperiod (L: D) with broad-spectrum LED lighting (Fluence, TX, USA). The seedlings were watered whenever necessary with a minimum volume of water to prevent leaching of the insecticide. All experiments were conducted at the developmental stages V4 (25 days after planting and four fully-expanded leaves) and V6 (36 days after planting and six fully-expanded leaves) of seed-treated plants (treatment named NST) and seed-untreated plants (treatment named control) of MC 4050 and B73 under the same controlled conditions described above.

FAW caterpillars used in assays were obtained from eggs purchased from a commercial supplier (Benzon Research, Carlisle, PA, USA). In experiments using 4th instar FAW larvae, caterpillars were fed an artificial diet (Stonefly Heliothis Diet, Ward's Science, Rochester, NY, USA) and then transferred to feed on maize leaves for 24 h prior to the experiment.

Plant shoot growth

To assess whether neonicotinoid treatment affects plant shoot growth, we measured height (cm) and stem diameter (mm). Plant height was measured from the soil line to the insertion of the last expanded leaf. Two perpendicular stem diameters were measured using a digital micrometer (Pittsburgh®, Harbor Freight Tools, Camarillo, CA, United States) and an average diameter was reported. All measurements were carried out at the V4 and V6 stages of both genotypes with 24–28 replicates.

FAW preference assay

We evaluated whether NST influences preference (host-plant choice and leaf area consumed) of neonate FAW caterpillars (< 24 h post hatching) in dual-choice assays. The youngest completely developed leaf (either the fourth or sixth leaf) of the control and NST plants of the same genotype were placed inside a plastic Petri dish (diameter 140 mm × 15 mm height) and closed without damaging the plant (Fig. S1). Ten larvae were introduced in the center of the dish, which was sealed with Parafilm®. After 24 h, the number of larvae on each leaf was counted to assess host preference and the leaf fragments were excised and scanned to assess the feeding preference by the area consumed (mm^2) using the software ImageJ (O'Neal et al. 2002). The assay was performed in a completely randomized design, with eight replicates for each genotype and growth stage.

FAW performance assay

To evaluate FAW performance, we measured caterpillar mortality and the fresh weight gain (mg) of the surviving caterpillars after seven days of feeding on NST or control plants in a no-choice assay. Three neonate FAW were placed in a plastic Petri dish (diameter 100 mm × 15 mm height) with a leaf section of one of the treatments (NST or control) and closed and sealed as described above. We kept the leaf segments attached to the plant throughout the experiment and, whenever necessary, the dish was moved to a new leaf section to provide enough food supply for the caterpillars. We conducted 7–14 replicates with the two maize genotypes at the V4 and V6 stages, as described in the previous section.

Collection and analysis of plant volatiles

We characterized the constitutive and herbivore-induced plant volatile emissions from NST and control maize plants using a dynamic headspace sampling technique. For the FAW herbivore-damage treatments (control + FAW or NST + FAW), plants received a single fourth-instar caterpillar, which was starved for approximately 3 h. The youngest (either the fourth or sixth leaf) and the whorl leaf of each plant were individually enclosed inside nylon collection bags (Reynolds Consumer Products Inc., IL, USA), either with or without FAW. We sampled 8–12 NST and control plants at V4 and V6 stages for each maize genotype.

During the collections, filtered air was delivered into each collection bag at 0.7 L min^{-1} and pulled out of the bag through an adsorbent filter containing 60 mg of HaySep® Q (Hayes Separations, Inc., TX, USA) at 0.5 L min^{-1}. We collected volatiles during the photophase for the first 8 h after the onset of herbivory (10:00–18:00) as maize volatile emissions are produced rapidly following herbivory, typically within the first hours (Turlings et al. 1998). Volatiles were also collected from empty bags containing only air to control for background volatiles. After collections, volatile compounds were eluted from filters using 150 µL dichloromethane solvent. As an internal standard, 5 µL of a standard solution containing nonyl acetate (80 ng/µL) was added to each sample. The leaves were harvested, dried, and the dry mass of each repetition was recorded.

We analyzed the volatiles using an Agilent 7890B gas chromatograph and 5977B mass spectrometer with a splitless injector held at 250 °C and helium as the carrier gas. After sample injection (1 µL), the column (HP-5MS

30 m × 0.250 mm-ID, 0.25 µm film thickness, Agilent Technologies) was held at 40 °C for 5 min before the temperature was increased at 20 °C/min to 250 °C. Compounds were ionized by electron impact ionization at 70 eV and mass spectra were acquired by scanning from 40 to 300 m/z at 5.30 scans/s. The compound identities were tentatively determined by comparison with mass spectral libraries (NIST17, Adams2 [Allured Publishing Corporation]) and confirmed using authentic standards when possible. Compounds were quantified relative to the internal standard concentrations and calculated as ng g^{-1} dried leaf mass (Grunseich et al. 2020, 2021). We included a compound in the analysis only if it was detected in at least 50% of the samples.

Phytohormones

About 24 h of FAW feeding on maize plants, we sampled leaf tissue from the whorl of each plant (~ 100 mg tissue) to measure the levels of *cis*-JA (JA) and SA as indicators of plant defense response. The timing of phytohormone extraction differed from that of volatile sampling to induce a greater accumulation of phytohormones due to herbivory, increasing detectability in chromatographic analysis (Schmelz et al. 2003).The tissue was flash frozen in liquid nitrogen and stored at − 80 °C until analyzed. To quantify JA and SA, endogenous plant hormones were extracted and derivatized to methyl esters, which were isolated using vapor-phase extraction (Schmelz et al. 2004). These compounds were then analyzed by coupled GC/CI-MS using isobutane and selected ion monitoring (SIM). We quantified relative amounts of JA and SA by adding 100 ng dihydro-JA and labelled 2-hydroxy-benzoic acid, added as internal standards to each sample. Finally, we compared the retention times and spectra of our samples with standards of the pure compounds.

Data analyses

We carried out all data analyses using the software R version 4.0.3 (R CoreTeam 2022). The data were tested for normality and homogeneity of variances according to Shapiro–Wilk and Bartlett tests ($p < 0.05$), respectively. Whenever necessary, data were transformed with the Box-Cox method (Box and Cox 1964), using the function of the package MASS, or by square-root transformation. The plant parameters (height and diameter) and caterpillar mass gain were compared using Student's *t*-tests, while the consumed leaf area was analyzed using a paired *t*-test. The number of insects on each maize leaf (preference assay) and the FAW mortality (performance assay) were inferred using generalized linear models (GLM) (Nelder and Wedderburn 2000) with quasipoisson and quasibinomial distribution, respectively. The goodness of fit was evaluated using half-normal plots with a simulated envelope of hnp package (Moral et al. 2017). Data of volatile composition emitted by FAW herbivory and NST treatments were compared using permutational multivariate analysis of variance (PERMANOVA) calculated using the VEGAN package. Random forest analysis was used to identify compounds with the greatest contribution to variation among treatments. We also compared total volatile emission (sum of all detected volatiles), amounts of individual compounds and phytohormones using one-way ANOVA. For this, the GLM family with the best quality of fit was used and multiple comparisons tests were performed (Tukey's post hoc test, $p < 0.05$) in cases of significative differences.

Results

Plant shoot growth

Plant shoot height and stem diameter of B73 and MC 4050 were similar between NST and control maize plants at V4 and V6 stage (Table 1).

Table 1 Plant shoot height and diameter (means ± SE) of B73 and MC 4050 maize plants at V4 and V6 developmental stages. Height and diameter of the plants from neonicotinoid treatment (NST) did not differ from those of control (untreated plants) according to *t*-test

Treatment	Stage	B73		MC 4050	
		Height (cm)	Diameter (cm)	Height (cm)	Diameter (cm)
Control	V4	14.6 ± 0.3	5.0 ± 0.3	17.9 ± 0.6	5.3 ± 0.3
NST		14.5 ± 0.4	4.9 ± 0.3	19.0 ± 0.6	5.3 ± 0.3
p-value		0.809	0.744	0.216	0.864
Control	V6	20.9 ± 0.7	5.8 ± 0.3	30.0 ± 1.5	6.4 ± 0.4
NST		21.7 ± 1.0	5.8 ± 0.3	28.4 ± 1.7	6.2 ± 0.4
p-value		0.516	0.926	0.507	0.708

Preference assay

At the V4 stage, no significant differences were found in NST and control plants of both genotypes for leaf area consumed by FAW neonate larvae (Fig. 1A; B73: t = − 0.402, df = 7, $p = 0.699$; MC 4050: t = 1.012, df = 7, $p = 0.345$) or FAW host preference (Fig. 1B; B73: $F_{1, 14} = 0.389$, $p = 0.543$ and MC 4050: $F_{1, 14} = 2.572$, $p = 0.131$). On the other hand, at the V6 stage, more FAW caterpillars were found on control B73 than on NST B73 plants at the end of the assay (Fig. 1D; $F_{1, 14} = 5.289$, $p = 0.037$), although the leaf area consumed was similar in NST and control leaves of B73 (Fig. 1C; t = 1.843, df = 7, $p = 0.108$). Neonicotinoid treatment did not affect leaf area consumed (Fig. 1C; t = − 0.403, df = 7, $p = 0.699$) or host preference (Fig. 1D; $F_{1, 14} = 2.095$, $p = 0.169$) of FAW on MC 4050 plants at V6.

Performance assay

There was no lethal effect of NST compared to control plants after seven days of FAW feeding. These results were consistent for both maize genotypes at V4 (Fig. 2A; B73:

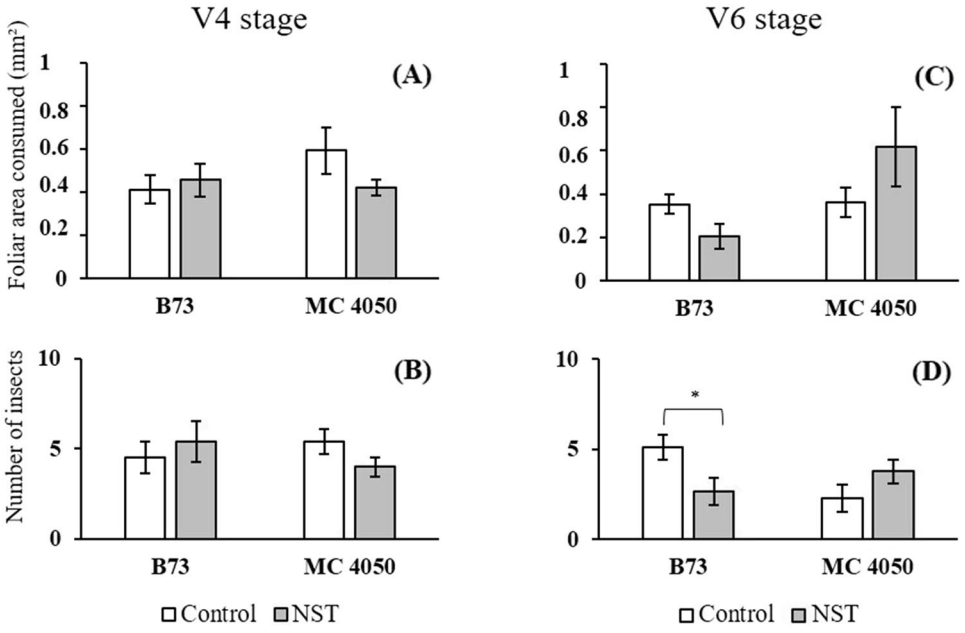

Fig. 1 Preference assay of *Spodoptera frugiperda* caterpillars fed on B73 and MC 4050 maize plants from control (untreated) and NST (neonicotinoid seed treatment) treatments at V4 and V6 developmental stages after 24 h of caging. Food preference was measured by foliar area consumed (mean ± SE) (**A**, **C**) and host preference as number of insects on each leaf segments (mean ± SE) (**B**, **D**). * Denotes statistical differences in number of caterpillars found in the control and NST plants.

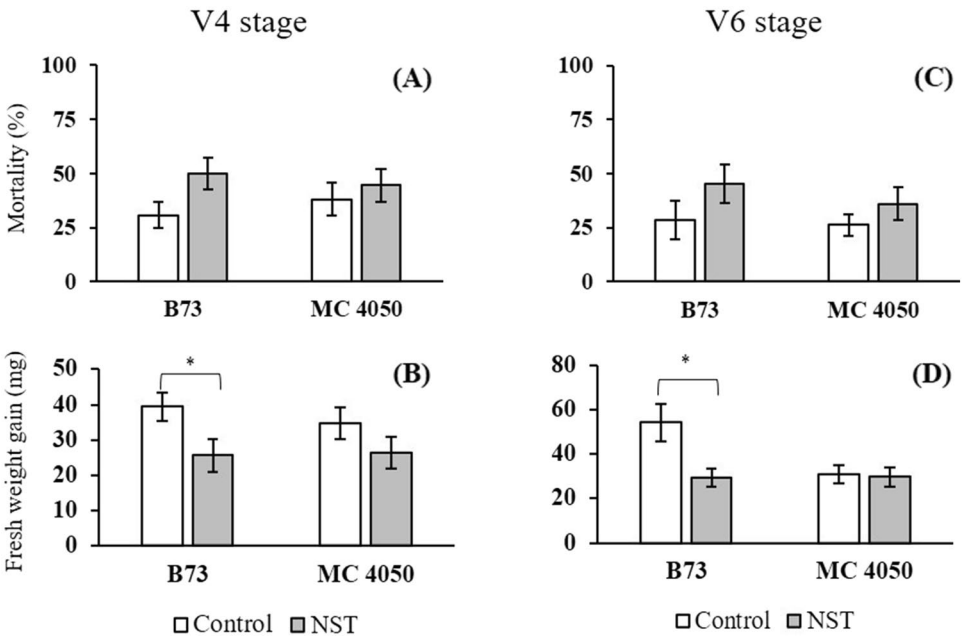

Fig. 2 *Spodoptera frugiperda* performance based on mortality (mean ± SE) (**A**, **C**) and fresh weight gain (mean ± SE) (**B**, **D**) found after seven days of feeding on maize plants (B73 and MC 4050 genotypes) at V4 and V6 developmental stages from control (untreated) and NST (neonicotinoid seed treatment) treatment. * Denotes significant differences in caterpillars fresh gain weight feeding on control and NST plants.

$F_{1, 21} = 4.036$, $p = 0.058$; MC 4050: $F_{1, 24} = 0.253$, $p = 0.619$) and V6 stages (Fig. 2C; B73: $F_{1, 19} = 1.647$, $p = 0.215$; MC 4050: $F_{1, 24} = 1.084$, $p = 0.308$). The surviving FAW caterpillars gained more weight when fed on control B73 than those fed on NST B73 plants at both growth stages (Fig. 2B; V4: t = 2.198, df = 17.464, $p = 0.042$; Fig. 2D; V6: t = 2.627, df = 8.738, $p = 0.028$). NST did not influence the weight gain of caterpillars fed on MC 4050 plants at either stage (Fig. 2B; V4: t = 1.299, df = 21.976, $p = 0.208$; Fig. 2D; V6: t = 0.208, df = 22.771, $p = 0.837$).

Plant volatiles

Overall, we observed interaction effects of neonicotinoid treatment and FAW herbivory on volatile emissions from the two maize genotypes across the V4 and V6 growth stages. Neonicotinoid treatment induced a distinct diurnal constitutive volatile blend in B73 plants at the V4 stage (Fig. 3A; PERMANOVA $F_{1, 43} = 3.694$, $R_2 = 0.079$, $p = 0.011$), but there was only a marginal effect of NST on the composition of herbivore-damaged volatile emissions in V4-stage of B73 plants (Fig. 3A; PERMANOVA $F_{1, 43} = 2.319$, $R_2 = 0.049$, $p = 0.065$). In contrast, for B73 plants at the V6 stage, multivariate analysis revealed significant differences only due to herbivore damage (Fig. 3C; PERMANOVA $F_{1, 42} = 4.055$, $R_2 = 0.091$, $p = 0.004$), but not by NST (Fig. 3C; PERMANOVA $F_{1, 42} = 0.474$, $R_2 = 0.011$, $p = 0.836$). Similarly, the volatile blend from MC 4050 plants was influenced solely by herbivore damage (Fig. 3B; V4: PERMANOVA $F_{1, 47} = 2.558$, $R_2 = 0.054$, $p = 0.030$; Fig. 3D; V6: PERMANOVA $F_{1, 46} = 2.438$, $R_2 = 0.051$, $p = 0.032$), but not neonicotinoid treatment (Fig. 3B; V4: PERMANOVA $F_{1, 47} = 0.407$, $R_2 = 0.009$, $p = 0.913$; Fig. 3D; V6: PERMANOVA $F_{1, 46} = 1.382$, $R_2 = 0.0291$, $p = 0.218$).

Random forest analysis revealed that the compounds that contributed most to the variation across treatments varied according to genotype and stage (Fig. S2). These compounds are highlighted (in bold) in the Table 2 and 3. In B73 plants, random forest identified eight compounds (Table 2). Undamaged NST plants emitted smaller amounts of nonanal and the aromatic benzyl acetate relative to undamaged control plants of B73 at V4 stage (Table 2; nonanal: $F_{3, 40} = 5.356$, $p = 0.001$; benzyl acetate: $F_{3, 40} = 10.916$, $p < 0.0001$). Six compounds were released in lower amounts

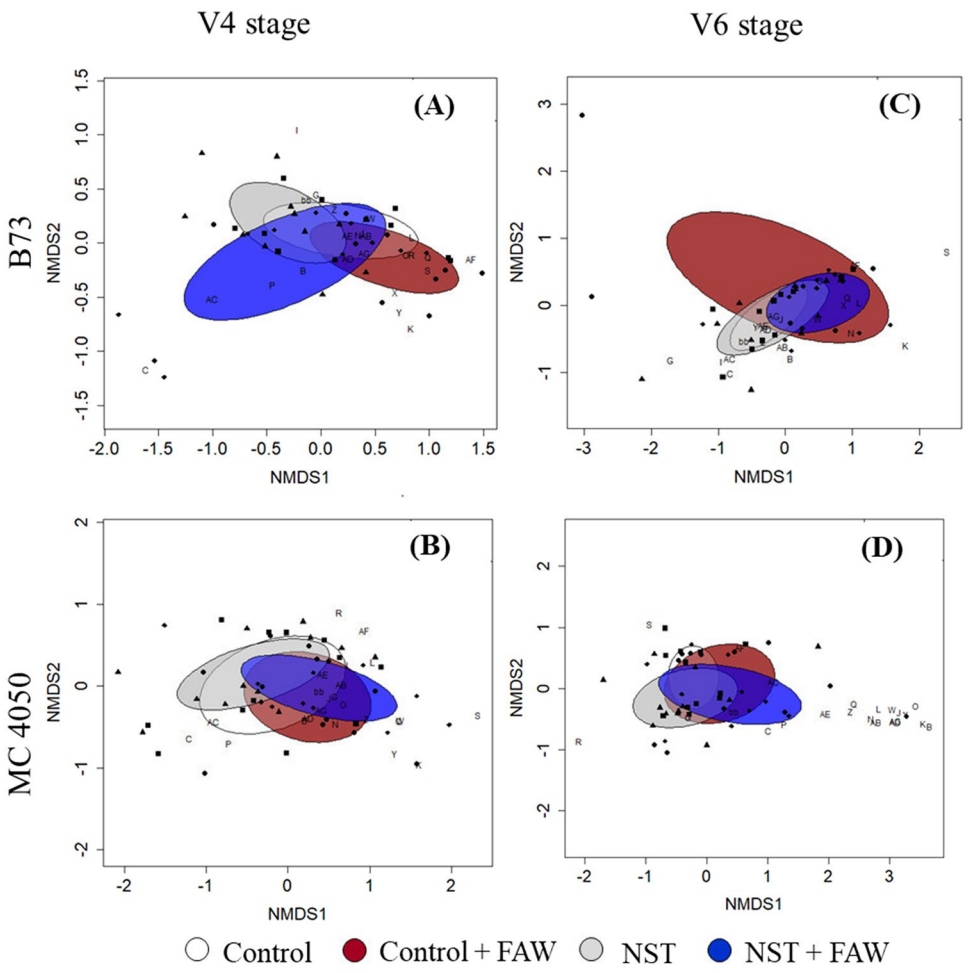

Fig. 3 Composition of diurnal constitutive and herbivore-induced plant volatile blends emitted by maize plants of B73 [V4 (**A**) and V6 (**C**)] and MC 4050 [V4 (**B**) and V6 (**D**)] after eight hours of volatile collections. Treatments: Control (untreated); Control + FAW (untreated + fall armyworm); NST (neonicotinoid seed treatment); and NST + FAW (neonicotinoid seed treatment + fall armyworm)

Table 2 B73 diurnal individual compound and total of volatile (means ng $g^{-1} \pm SE$) released by control (untreated); control + FAW (untreated + fall armyworm); NST (neonicotinoid seed treatment); and NST + FAW (neonicotinoid seed treatment + fall armyworm) treatments at V4 and V6 stage. Bold value indicates compounds that contributed most to the variation in each treatment according to random forest analysis. Different letters in the row indicate significant differences across treatment for individual compound and total by group according to an ANOVA followed by a Tukey's *post-hoc* test ($p < 0.05$)

Group	Compound	V4				V6			
		Control	Control + FAW	NST	NST + FAW	Control	Control + FAW	NST	NST + FAW
Fatty acid derivates	Hexenal	58.9 ± 11.8	96.8 ± 40.0	79.9 ± 27.6	36.5 ± 8.2	**24.0 ± 5.9**	**40.5 ± 19.0**	**40.1 ± 16.5**	**96.8 ± 44.1**
	2-hexanol	59.9 ± 21.6	93.3 ± 39.2	139.8 ± 71.2	118.1 ± 42.2	95.3 ± 39.1	69.8 ± 35.8	65.8 ± 27.4	117.0 ± 64.8
	2-ethyl hexanal	28.4 ± 8.5	45.1 ± 22.3	18.7 ± 7.3	20.7 ± 10.2	6.5 ± 2.6	4.7 ± 3.0	8.5 ± 5.0	5.7 ± 1.9
	(*Z*)-3-hexenyl acetate	**23.8 ± 8.1 b**	**325.2 ± 213.1 a**	**10.5 ± 2.6 b**	**146.6 ± 54.1 a**	**14.8 ± 6.6 b**	**282.8 ± 220.6 a**	**11.7 ± 5.1 b**	**484.9 ± 280.4 a**
	Hexyl acetate	26.0 ± 10.1	21.8 ± 5.8	5.3 ± 1.6	8.5 ± 2.7	1.9 ± 0.7	7.0 ± 2.0	2.2 ± 0.9	8.7 ± 3.3
	Ethylhexyl acetate	223.3 ± 97.1	231.0 ± 139.5	19.3 ± 6.5	33.7 ± 14.4	–	–	–	–
	Nonanal	**93.1 ± 30.5 ab**	**186.0 ± 106.5 a**	**39.5 ± 10.6 c**	**52.0 ± 13.9 bc**	–	–	–	–
	Total	513.4 ± 105.1 b	999.2 ± 383.9 a	313.0 ± 107.3 b	416.1 ± 61.0 b	142.5 ± 47.0	404.8 ± 272.1	128.3 ± 49.7	713.1 ± 387.6
Terpenes	α-pinene	**70.4 ± 15.8 ab**	**116.0 ± 21.8 a**	**73.1 ± 21.5 ab**	**46.2 ± 12.5 b**	**37.8 ± 5.8**	**57.2 ± 17.4**	**53.6 ± 16.3**	**89.7 ± 29.1**
	β-pinene	83.5 ± 27.1	115.3 ± 50.0	70.1 ± 28.9	46.6 ± 15.3	21.4 ± 6.3	28.1 ± 16.8	31.3 ± 16.7	56.7 ± 33.5
	β-myrcene	103.0 ± 19.4	180.2 ± 38.5	64.9 ± 18.1	65.7 ± 17.0	56.2 ± 12.1	137.0 ± 31.5	84.1 ± 30.7	109.4 ± 26.7
	(*E*)-β-ocimene	**338.1 ± 90.6 ab**	**503.0 ± 130.5 a**	**203.8 ± 58.3 bc**	**141.8 ± 33.7 c**	**60.8 ± 17.4 b**	**179.2 ± 37.6 ab**	**85.9 ± 29.0 b**	**328.7 ± 153.3 a**
	Linalool	1070.9 ± 364.0	1597.1 ± 382.1	471.8 ± 117.6	625.9 ± 208.2	574.9 ± 210.8	1468.4 ± 405.9	779.9 ± 220.4	1315.1 ± 369.8
	DMNT	**971.9 ± 340.1 b**	**2228.5 ± 602.5 a**	**387.1 ± 90.6 b**	**663.2 ± 234.9 b**	**655.2 ± 228.9 c**	**1872.7 ± 446.2 ab**	**794.1 ± 198.8 bc**	**2288.9 ± 687.7 a**
	TMTT	553.7 ± 282.1	740.8 ± 320.0	106.0 ± 29.5	239.8 ± 106.1	507.4 ± 309.5	1098.7 ± 560.7	369.5 ± 97.7	949.5 ± 378.5
	(*E*)-β-caryophyllene	5.7 ± 1.5	9.7 ± 2.4	3.5 ± 0.8	3.7 ± 1.1	**0.6 ± 0.3 b**	**4.8 ± 0.9 a**	**3.7 ± 1.6 a**	**3.8 ± 1.4 a**
	(*E*)-α-bergamotene	**18.2 ± 5.4 b**	**56.6 ± 16.9 a**	**9.2 ± 2.9 b**	**15.9 ± 4.4 b**	23.9 ± 9.7	49.9 ± 18.0	30.1 ± 13.7	65.8 ± 20.4
	(*E*)-β-farnesene	**18.2 ± 5.2 b**	**68.1 ± 21.7 a**	**7.3 ± 2.7 b**	**15.0 ± 5.0 b**	27.6 ± 17.7	19.0 ± 8.3	38.2 ± 19.8	29.8 ± 13.8
	α-caryophyllene	3.4 ± 0.7	4.7 ± 0.7	2.1 ± 0.6	1.7 ± 0.4	1.5 ± 0.9	3.0 ± 1.0	2.0 ± 1.2	1.7 ± 0.8
	β-cubebene	36.1 ± 8.7	65.8 ± 19.5	25.1 ± 7.0	22.2 ± 5.6	6.7 ± 2.3	14.7 ± 6.2	22.8 ± 15.4	15.7 ± 9.3
	α-selinene	37.4 ± 5.7	60.9 ± 24.6	60.3 ± 23.3	57.2 ± 9.6	33.7 ± 10.1	37.5 ± 17.0	26.9 ± 9.5	54.7 ± 21.2
	δ-cadinene	40.7 ± 9.1	76.3 ± 16.9	26.8 ± 8.6	24.2 ± 6.4	28.9 ± 11.2	76.8 ± 22.1	42.2 ± 18.8	43.0 ± 12.1
	α-cubebene	32.2 ± 6.3	53.4 ± 9.8	21.7 ± 4.9	19.1 ± 4.4	17.4 ± 4.6	36.3 ± 9.7	26.3 ± 11.1	22.6 ± 6.3
	Unk sesq	34.3 ± 11.3	41.2 ± 9.0	16.7 ± 5.0	16.7 ± 4.9	**9.8 ± 2.4**	**29.1 ± 5.8**	**14.1 ± 4.6**	**16.1 ± 3.6**
	Total	3417.7 ± 1068.6 ab	5917.6 ± 1381.0 a	1549.5 ± 331.2 b	2004.9 ± 627.3 b	2063.8 ± 784.3 c	5112.4 ± 1374.6 ab	2404.7 ± 550.5 bc	5391.2 ± 1372.9 a
Aromatic	Benzyl acetate	**11.2 ± 6.3 b**	**60.0 ± 18.3 a**	**0.1 ± 0.1 c**	**39.2 ± 23.4 ab**	**6.1 ± 4.8 b**	**162.1 ± 105.4 a**	**62.7 ± 51.0 a**	**412.8 ± 313.4 a**
	Total	11.2 ± 6.3 b	60.0 ± 18.3 a	0.1 ± 0.1 c	39.2 ± 23.4 ab	6.1 ± 4.8 b	162.1 ± 105.4 a	62.7 ± 51.0 a	412.8 ± 313.4 a

by herbivore-damaged NST plants compared to the emission from herbivore-damaged control plants of the B73 genotype at V4 [Table 2: Nonanal ($F_{3, 40} = 5.356$, $p = 0.001$); α-pinene ($F_{3, 40} = 2.911$, $p = 0.046$); (*E*)-β-ocimene ($F_{3, 40} = 4.574$, $p = 0.008$); (3*E*)-4,8-dimethyl-1,3,7-nonatriene (DMNT) ($F_{3, 40} = 5.345$, $p = 0.003$); (*E*)-α-bergamotene ($F_{3, 40} = 6.042$, $p = 0.002$) and (*E*)-β-farnesene ($F_{3, 40} = 5.838$, $p = 0.001$)]. When considering the major compound groups, herbivore-damaged NST plants emitted a blend with reduced quantities of fatty acid derivates ($F_{3, 40} = 2.973$, $p = 0.043$) and terpenes ($F_{3, 40} = 4.396$, $p = 0.009$) relative to that emitted by herbivore-damaged control B73 plants at the V4 stage. These differences did not persist at the V6 stage of B73 plants, when only a marginal difference between treatments was observed for the total of fatty acids derivatives (Table 2; $F_{3, 38} = 2.452$, $p = 0.078$); however, herbivore-damaged control and herbivore-damaged NST emitted greater amounts of terpenes relative to respective undamaged treatments (Table 2; $F_{3, 38} = 3.291$, $p = 0.019$). Notably, undamaged NST plants of B73 emitted a blend containing greater amounts of (*E*)-β-caryophyllene ($F_{3, 38} = 3.754$, $p = 0.010$) and benzyl acetate ($F_{3, 38} = 3.140$, $p = 0.024$) than that of control B73 plants at V6 stage.

For MC 4050 plants at the V4 stage, herbivore-damaged NST and control plants emitted a similar blend of compounds, with greater production in herbivore-damaged than respective undamaged plants for fatty acid derivates ($F_{3, 44} = 4.586$, $p = 0.003$), aromatic compounds ($F_{3, 44} = 7.398$, $p < 0.0001$), and terpenes in NST plants ($F_{3, 44} = 3.207$, $p = 0.022$). On the other hand, for MC 4050 at the V6 stage, there was no difference in the total amounts released in each group among the treatments [fatty acids

Table 3 MC 4050 diurnal individual compound and total of volatile (means ng $g^{-1} \pm SE$) released by control (untreated); control + FAW (untreated + fall armyworm); NST (neonicotinoid seed treatment); and NST + FAW (neonicotinoid seed treatment + fall armyworm) treatments at V4 and V6 stage. Bold value indicates compounds that contributed most to the variation in each treatment according to random forest analysis. Different letters in the row indicate significant differences across treatment for individual compound and total by group according to an ANOVA followed by a Tukey's *post-hoc* test ($p < 0.05$)

Group	Compound	V4				V6			
		Control	Control + FAW	Neo	NST + FAW	Control	Control + FAW	NST	NST + FAW
Fatty acid derivates	Hexenal	**55.0 ± 19.6**	**79.3 ± 28.8**	**31.1 ± 6.1**	**79.6 ± 38.4**	35.0 ± 10.2	69.8 ± 38.9	40.4 ± 12.4	98.5 ± 30.0
	2-hexanol	103.2 ± 36. 8	131.4 ± 54.2	84.2 ± 27.6	105.2 ± 33.0	**94.2 ± 29.8**	**108.0 ± 45.9**	**135.6 ± 30.8**	**165.8 ± 44.1**
	2-ethyl hexanal	**14.8 ± 8.3**	**29.7 ± 11.0**	**10.7 ± 6.8**	**29.0 ± 18.7**	**5.7 ± 1.8**	**10.5 ± 6.7**	**7.4 ± 4.4**	**11.5 ± 4.2**
	(*Z*)-3-hexenyl acetate	**17.6 ± 4.8 b**	**656.5 ± 387.8 a**	**12.8 ± 3.4 b**	**404.7 ± 203.8 a**	**18.3 ± 5.1 b**	**319.2 ± 179.4 a**	**21.9 ± 7.0 b**	**534.9 ± 238.5 a**
	Hexyl acetate	12.6 ± 6.5	14.8 ± 4.8	12.0 ± 6.6	25.1 ± 11.9	**3.1 ± 0.8 bc**	**8.9 ± 2.9 a**	**2.3 ± 0.9 c**	**8.3 ± 2.6 ab**
	Ethylhexyl acetate	95.4 ± 46.0	47.0 ± 21.7	119.0 ± 74.3	85.9 ± 41.6	16.2 ± 7.8	107.0 ± 101.9	95.8 ± 89.0	15.8 ± 7.8
	Nonanal	**90.6 ± 51.2 ab**	**191.4 ± 62.1 a**	**38.5 ± 17.1 b**	**65.1 ± 11.0 b**	74.0 ± 28.9	143.8 ± 69.2	43.3 ± 19.1	47.8 ± 13.2
	Total	389.2 ± 109.7 bc	1150.1 ± 506.8 a	308.3 ± 80.6 c	794.6 ± 300.2 ab	246.5 ± 71.0	767.2 ± 364.6	346.7 ± 117.7	882.6 ± 299.6
Terpenes Terpenes	α-pinene	60.8 ± 22.0	49.6 ± 11.5	35.4 ± 10.7	107.5 ± 61.5	38.6 ± 11.4	102.4 ± 41.1	42.4 ± 7.4	112.8 ± 40.7
	β-pinene	**51.7 ± 15.5 ab**	**35.4 ± 6.8 b**	**41.7 ± 21.8 b**	**135.5 ± 86.5 a**	33.7 ± 15.5	98.1 ± 50.2	29.2 ± 7.2	112.4 ± 53.2
	β-myrcene	**31.3 ± 9.2**	**49.9 ± 17.2**	**22.8 ± 6.3**	**65.6 ± 19.7**	34.1 ± 9.5	30.9 ± 8.2	37.5 ± 19.6	34.9 ± 9.9
	(*E*)-β-ocimene	53.4 ± 23.8	90.4 ± 43.3	29.1 ± 7.9	72.3 ± 22.9	**26.7 ± 8.1**	**29.4 ± 13.6**	**44.5 ± 16.6**	**76.0 ± 35.0**
	Linalool	348.2 ± 128.5	468.7 ± 178.9	217.1 ± 62.8	644.2 ± 220.9	227.4 ± 50.5	228.9 ± 55.0	469.5 ± 359.0	226.5 ± 62.4
	DMNT	543.0 ± 222.78	1718.5 ± 894.6	285.2 ± 108.5	2055.9 ± 880.6	**304.2 ± 81.8**	**858.2 ± 388.8**	**635.4 ± 448.7**	**1211.1 ± 515.8**
	TMTT	423.4 ± 216.1	209.4 ± 64.3	391.9 ± 184.3	698.9 ± 326.3	**191.6 ± 62.7 ab**	**558.9 ± 288.0 a**	**522.2 ± 482.0 a**	**86.4 ± 21.9 b**
	(*E*)-β-caryophyllene	**20.2 ± 8.0 b**	**109.8 ± 45.4 a**	**18.2 ± 7.4 b**	**208.4 ± 83.0 a**	19.9 ± 4.7	41.1 ± 21.2	37.7 ± 24.2	45.1 ± 17.8
	(*E*)-β-farnesene	**44.3 ± 41.4 a**	**74.9 ± 41.8 a**	**2.0 ± 1.0 b**	**88.1 ± 40.0 a**	9.4 ± 3.9	62.9 ± 36.3	5.9 ± 2.7	27.7 ± 11.6
	α-caryophyllene	**2.4 ± 0.7 b**	**9.4 ± 3.5 a**	**2.1 ± 0.8 b**	**13.9 ± 5.0 a**	3.2 ± 0.7	3.2 ± 1.5	3.8 ± 1.5	4.1 ± 1.6
	β-cubebene	5.6 ± 1.9	8.0 ± 2.8	4.8 ± 2.4	13.3 ± 4.0	2.6 ± 0.9	2.3 ± 1.5	2.2 ± 0.8	4.1 ± 1.7
	α-selinene	58.6 ± 22.2	55.9 ± 15.1	34.5 ± 5.0	65.1 ± 14.7	**29.0 ± 7.7**	**59.0 ± 19.9**	**75.8 ± 26.1**	**69.2 ± 26.6**
	δ-cadinene	9.8 ± 3.7	21.2 ± 7.9	7.5 ± 1.9	24.3 ± 8.0	29.0 ± 12.6	21.4 ± 9.0	19.9 ± 3.9	38.4 ± 14.4
	α-cubebene	11.4 ± 2.7	16.9 ± 4.0	10.6 ± 3.1	28.4 ± 8.8	18.9 ± 5.1	16.7 ± 4.9	15.6 ± 2.5	21.5 ± 5.9
	Unk sesq	11.2 ± 4.0	19.7 ± 6.8	9.5 ± 2.4	30.6 ± 10.0	24.1 ± 8.4	18.5 ± 6.6	18.2 ± 3.2	37.1 ± 16.6
	Total	1675.3 ± 568.1 bc	2937.7 ± 1234.9 ab	1112.4 ± 377.6 c	4252.0 ± 1702.3 a	992.4 ± 193.9	2131.9 ± 705.6	1959.8 ± 1346.9	2107.3 ± 682.2
Aromatic	Benzyl acetate	14.3 ± 6.5	193.1 ± 115.5	24.6 ± 21.2	940.5 ± 560.6	108.8 ± 59.3	238.3 ± 150.4	143.9 ± 131.6	104.8 ± 62.0
	Total	14.3 ± 6.5 b	193.1 ± 115.5 a	24.6 ± 21.2 b	940.5 ± 560.6 a	108.8 ± 59.3	238.3 ± 150.4	143.9 ± 131.6	104.8 ± 62.0

derivates ($F_{3, 42} = 2.745$, $p = 0.055$), terpenes ($F_{3, 42} = 1.024$, $p = 0.392$), and aromatics ($F_{3, 42} = 0.287$, $p = 0.835$)]. The individual analysis of selected compounds in the random forest for MC 4050 at V4 stage (Fig. S2) revealed that NST suppressed the emission of nonanal released by herbivore-damaged plants (Table 3; $F_{3, 44} = 3.174$, $p = 0.023$) and (*E*)-β-farnesene of undamaged plants (Table 3; $F_{3, 44} = 3.539$, $p = 0.014$). At the same time, NST up-regulated the emission of β-pinene, which was 3.85 times higher in the blend of herbivore-damaged NST plants than of that emitted by herbivore-damaged control plants of MC 4050 at V4 stage (Table 3; $F_{3, 44} = 2.975$, $p = 0.030$). For MC 4050 plants at the V6 stage, NST suppressed the compound (3*E*, 7*E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene (TMTT) in the blend of herbivore-damaged volatiles (Table 3; $F_{3, 42} = 4.084$, $p = 0.007$). In addition, herbivore-damaged plants, irrespective of the neonicotinoid treatment, released greater amounts (*Z*)-3-hexenyl acetate (Table 3; $F_{3, 42} = 6.031$, $p = 0.002$) and hexyl acetate (Table 3; $F_{3, 42} = 3.441$, $p = 0.016$) relative to undamaged plants.

Phytohormones

SA levels in the two maize genotypes were not affected by neonicotinoid treatment or FAW damage at V4 (Fig. 4A; B73: $F_{3, 38} = 1.915$, $p = 0.144$; Fig. 4B; MC 4050: $F_{3, 40} = 1.649$, $p = 0.193$). However, at the V6 stage, the levels of SA were increased by herbivore damage in MC 4050 control and NST plants (Fig. 4D; $F_{3, 37} = 9.584$, $p < 0.0001$). While in B73, we observed that NST suppressed SA levels in undamaged plants (Fig. 4C; $F_{3, 34} = 2.929$, $p = 0.032$), but

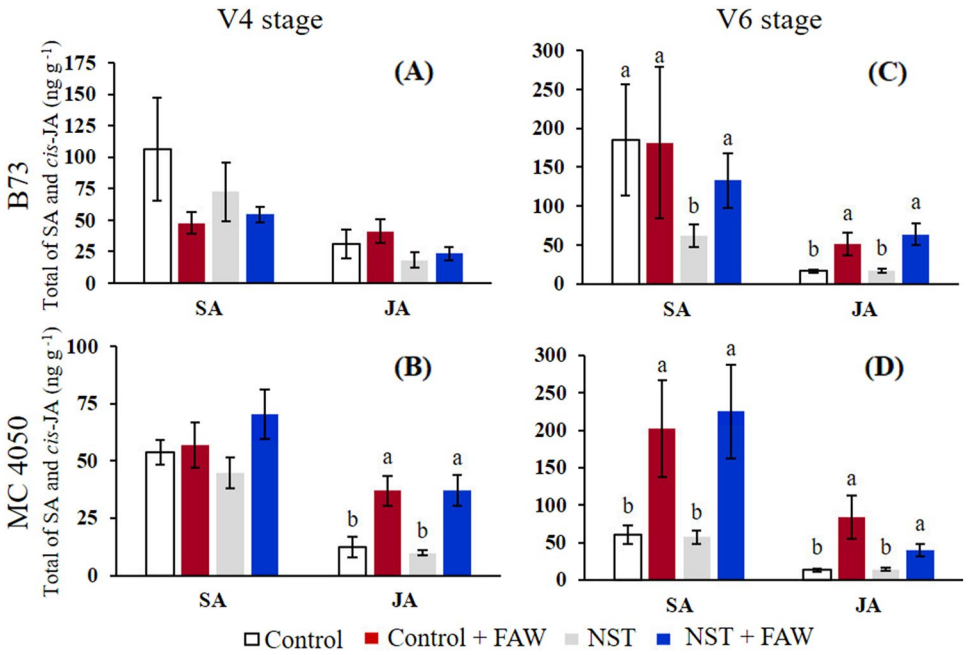

Fig. 4 Content of salicylic acid and *cis*-jasmonic acid (ng g^{-1}) of the treatments control (untreated); control + FAW (untreated + fall armyworm); NST (neonicotinoid seed treatment); and NST + FAW (neonicotinoid seed treatment + fall armyworm) in B73 and MC 4050 plants at V4 (**A**, **B** respectively) and V6 (**C**, **D** respectively). Lowercase letters indicate statistical difference between treatments according to GLM

NST and control plants were not different from each other when damaged (Fig. 4C).

Herbivore-damaged plants of MC 4050 genotype showed the highest amounts of JA at both growth stages, regardless of neonicotinoid treatment (Fig. 4B; $F_{3, 41} = 9.563$, $p < 0.0001$; Fig. 4D; $F_{3, 37} = 18.816$, $p < 0.0001$). On the other hand, in B73, JA levels were not affected by neonicotinoid or FAW damage at V4 (Fig. 4A; $F_{3, 37} = 1.842$, $p = 0.157$). However, the concentration of JA increased due to herbivore damage in B73 plants at the V6 stage (Fig. 4C; $F_{3, 37} = 14.704$, $p < 0.0001$).

Discussion

The few reports on neonicotinoid translocation and influence on plant physiology show varying effects depending on the plant species (Szczepaniec et al. 2013; Yang et al. 2018; Whalen et al. 2021). Here, we show that NST influences anti-herbivore plant defenses and plant defense signaling differently within the same plant species, as maize genotypes B73 and MC 4050 responded differently to thiamethoxam seed treatment. In B73 plants, NST negatively affected the behavior and biology (fresh weight gain) of FAW caterpillars, and suppressed the emission of herbivore-induced volatile compounds and constitutive levels of SA. In contrast, NST in the MC 4050 genotype did not affect plant resistance to FAW or herbivore-induced plant response, measured in terms of herbivore-induced plant volatiles and phytohormone levels.

The difference across maize genotypes is likely due to a large intraspecific genotypic and phenotypic variation intrinsic to the species (Degen et al. 2004; Stupar and Springer 2006; Chen et al. 2018; Luo et al. 2019). Importantly, we used an inbred (B73) and a commercial hybrid (MC 4050) in this study because both groups are known to have distinct homozygosis and traits (Gama and Hallauer 1977; Betrán et al. 2003; Yendrek et al. 2017; Hisse et al. 2019). Traits like plant growth rate, growth stage and physiological variations can affect the translocation of insecticides throughout the plants (Cloyd et al. 2011), and consequently their effects on the plant. Noticeably, MC 4050 plants were taller than B73 and this may have contributed to the lower effect of thiamethoxam on MC 4050. Fast growing plants might have lower concentrations of insecticides in leaf tissue, and higher concentration in the soil resulting from a dilution of relatively low soil insecticide and unavailability for plant absorption (Whalen et al. 2021). In maize, the effect of neonicotinoid on the plant seems to depend on the genotype and application technique. For example, when thiamethoxam was applied into the soil, a hybrid genotype showed reduced photosynthetic pigment content, hence being more susceptible to the insecticide than an inbred genotype (Todorenko et al. 2021). However, when applied via seed treatment, the amount of photosynthetic pigments were inversely proportional to the concentration of thiamethoxam in the maize hybrid (Macedo and Castro 2018).

FAW neonates consumed similar amounts of maize irrespective of NST treatment or the genotype or growth stage. This assay was performed for a short time interval (24 h), so it is possible that the food area consumed could change if a

longer time was given for larvae to settle on the treatments. However, we observed almost two-fold more FAW neonates on control plants than NST B73 plants at the V6 stage. Also, we demonstrate that FAW neonates gained more mass and performed better on control than NST B73 plants, corresponding to their capability of selecting better hosts (Rojas et al. 2018). Similarly, larvae of monarch butterflies also had lower weight, shorter body length, and longer duration of the first larval instar when fed on leaf segments treated with clothianidin (Pecenka and Lundgren 2015), which is a thiamethoxam metabolite (Nauen et al. 2003).

It was not expected that NST would negatively direct affect the biology of FAW since there is a rapid decrease in the concentration of neonicotinoid in the plant with the development and growth of maize (Myresiotis et al. 2015; Alford and Krupke 2017; Whalen et al. 2021) and it is not recommended for controlling the FAW (AGROFIT 2021). The lower weight of caterpillars feeding on NST plants of B73 may have at least two possible explanations. First, a feeding inhibition activity of the caterpillars by thiamethoxam, which is one of the sublethal effects caused by neonicotinoids (Barrania 2013; Sanchez-Bayo 2014; Uhl et al. 2015; Gontijo et al. 2018; Basley and Goulson 2018). In particular, for FAW, it has been shown that soybean seed treated with thiamethoxam reduced the leaf area consumed by caterpillars (Gontijo et al. 2018). A second explanation is an increase in energy demand for detoxification and coping with insecticide stress, as demonstrated for non-lepidopteran insects feeding on neonicotinoid-contaminated resources (Sawczyn et al. 2012; Uhl et al. 2015). In lepidopterans, the neonicotinoid imidacloprid acts on the nervous system of the late instar larvae and disrupts the pupae change for adults (Krishnan et al. 2021). However, the effects of neonicotinoids on biological and biochemical parameters of lepidopteran are diverse, complex, and may vary depending on the species of insect. For example, while thiamethoxam can reduce emergence, fecundity and fertility of *Spodoptera litura* (Fabricius) (Lepidoptera: Noctuidae) caused by changes in DNA and oxidative stress (Jameel et al. 2020), *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) larvae can rapidly eliminated thiamethoxam without toxicity to them (Fan and Shi 2017).

In general, previous studies have shown that neonicotinoids suppress the JA signaling pathway, resulting in greater plant susceptibility to arthropods (Szczepaniec et al. 2013; Wulff et al. 2019). Contrary to these findings, we found that thiamethoxam did not alter the levels of JA in undamaged or herbivore-damaged plants of either genotype at the V4 or V6 stage. However, thiamethoxam decreased the level of constitutive SA in NST plants by about three-fold in B73 at V6, although this effect was no longer detected in the plant upon FAW damage. Interestingly, at the V4 stage, we did not detect that NST influenced SA levels, similarly to what was observed after seed treatment with clothianidin in 4-week-old maize plants (Szczepaniec et al. 2013). The suppressive effect of thiamethoxam on the SA pathway was also found in soybean treated plants (Wulff et al. 2019). In contrast, studies have shown that neonicotinoid treatment activates the SA signaling pathway, as in *Arabidopsis thaliana* (Brassicaceae) and tomato (Ford et al. 2010; Szczepaniec et al. 2013). The suppression of SA may impact maize defense responses, in particular defense against biotrophic pathogens (Yuan et al. 2019), as well as other important plants parameters such as vegetative growth, photosynthesis, respiration and response to abiotic stress, which are regulated by SA (Vos et al. 2013). In our study, we did not measure quantities of plant metabolites with potential deterrent or toxic effect on *S. frugiperda*. However, overall, the changes in phytohormone levels caused by NST treatment in maize plants do not support that induced plant defenses led to a reduction in mass gain of FAW neonates that fed on B73 NST.

In our study, NST played an important role in changing plant volatile emissions, especially in B73 plants. Both B73 and MC 4050 plants released different volatiles blends across the treatments evaluated, which was expected due to the wide natural variability in maize volatile composition (Hoballah et al. 2002; Degen et al. 2004; Block et al. 2018; Yactayo-Chang et al. 2021). Thiamethoxam7 had a suppressive effect on volatile emissions of the B73 maize genotype at V4 stage, including compounds of varying groups, such as fatty acid derivates, terpenes, and aromatics. The suppression effect of volatile compounds caused by neonicotinoid was previously observed in tea plants sprayed with imidacloprid, which emitted lower amounts of the green leaf volatiles (Zhou et al. 2019). The suppression of constitutive and herbivore-induced plant volatiles caused by NST has potential implications for interactions among maize, herbivores, and natural enemies. For example, among the compounds suppressed, we notice that the fatty acid derivative nonanal was consistently suppressed at stage V4 in both maize genotypes in herbivore-damaged NST plants. This suppression may change the behavior of maize pests that are sensitive to nonanal, such as the Asian corn borer *Ostrinia furnacalis* (Guenée) (Lepidoptera: Crambidae), which is repelled by the compound (Huang et al. 2009). We observed that some terpenes linked with insect attraction or repellence were also affected by NST. For example, in B73 at V4, (*E*)-α-bergamotene was suppressed in the volatile blend emitted by herbivore-damaged NST plants, and this suppression may compromise the attraction of the FAW parasitoid *Cotesia marginiventris* (Cresson) (Hymenoptera: Braconidae) (Schnee et al. 2006) and may change the attractiveness to FAW females (Yactayo-Chang et al. 2021). On the other hand, NST B73 at V6 increased the amount of (*E*)-β-caryophyllene, which is correlated with increase attraction of *C. marginiventris* (Köllner et al. 2008). But, because it

is difficult to infer which changes in volatile blend would influence the recruitment of natural enemies, future studies should investigate whether the changes in maize volatile emission induced by NST are ecologically relevant for the third trophic level.

In summary, we found that the effects of neonicotinoid seed treatment on plant resistance against FAW and defense signaling are highly dependent on the plant genotype and growth stage. Both parameters have already been reported to influence the expression of maize genes that modulate defenses against FAW herbivory (Chuang et al. 2014). Another critical point that may have influenced the difference between the growth stages is the possible reduction in the insecticide concentration in the plant, which tends to decrease over time (Myresiotis et al. 2015; Alford and Krupke 2017; Whalen et al. 2021). Additional tests under field conditions are necessary to substantiate whether the changes in phytohormones and volatiles after thiamethoxam seed treatment can affect the maize defenses under realistic conditions of herbivore and pathogen infestation. From the pest management perspective, our results indicate that the side-effects of thiamethoxan on plant resistance against the fall armyworm can be avoided by using maize genotypes that are not affected by the insecticide.

Author contributions

AFL, MFGVP, GAC and AMH designed the experiment. AFL and NMA performed the bioassays. AFL and JMG analyzed the data. AMH led the volatile analyzes. AFL, MFGVP and AMH led the writing of the manuscript. Supervision by AMH, MFGVP and GAC. All authors read and approved the manuscript.

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Data availability All data are available from the corresponding author upon reasonable request.

Declarations

Competing interests The authors have no financial interests to disclose.

Ethics approval This study does not involve human participants or vertebrates, and it did not require ethical approval of the local Ethics Committee.

References

AGROFIT (2021) Sistema de agrotóxicos fitossanitários—ministério da Agricultura, Pecúaria e Abastecimento. http://agrofit.agricultura.gov.br/agrofit_cons/principal_agrofit_cons. Accessed 30 Mar 2021

Alford A, Krupke CH (2017) Translocation of the neonicotinoid seed treatment clothianidin in maize. PLoS ONE 12:0173836. https://doi.org/10.1371/journal.pone.0173836

Barrania AA (2013) Antifeedant, growth inhibtory and toxicity effects of chlorantraniliprole, thiamethoxam and novaluron against the cotton leaf worm, *Spodoptera littoralis* (Boisd) (Lepidoptera: noctuidae) in cotton fields. Egypt J Agric Res 91:903–911. https://doi.org/10.21608/ejar.2013.165357

Basley K, Goulson D (2018) Effects of field-relevant concentrations of clothianidin on larval development of the butterfly *Polyommatus icarus* (Lepidoptera, Lycaenidae). Environ Sci Technol 52:3990–3996. https://doi.org/10.1021/acs.est.8b00609

Betrán FJ, Beck D, Bänziger M, Edmeades GO (2003) Genetic analysis of inbred and hybrid grain yield under stress and bonstress environments in tropical maize. Crop Sci 43:807–817. https://doi.org/10.2135/cropsci2003.8070

Block AK, Hunter CT, Rering C et al (2018) Contrasting insect attraction and herbivore-induced plant volatile production in maize. Planta 248:105–116. https://doi.org/10.1007/s00425-018-2886-x

Bonmatin JM, Giorio C, Girolami V et al (2015) Environmental fate and exposure; neonicotinoids and fipronil. Environ Sci Pollut Res 22:35–67. https://doi.org/10.1007/s11356-014-3332-7

Botías C, David A, Hill EM, Goulson D (2016) Contamination of wild plants near neonicotinoid seed-treated crops, and implications for non-target insects. Sci Total Environ 566–567:269–278. https://doi.org/10.1016/j.scitotenv.2016.05.065

Box GEP, Cox DR (1964) An analysis of transformations. J R Stat Soc Ser B 26:211–243. https://doi.org/10.1111/j.2517-6161.1964.tb00553.x

Bredeson MM, Lundgren JG (2019) Neonicotinoid insecticidal seed-treatment on corn contaminates interseeded cover crops intended as habitat for beneficial insects. Ecotoxicology 28:222–228. https://doi.org/10.1007/s10646-018-02015-9

Calvo-Agudo M, González-Cabrera J, Picó Y et al (2019) Neonicotinoids in excretion product of phloem-feeding insects kill beneficial insects. Proc Natl Acad Sci U S A 116:16817–16822. https://doi.org/10.1073/pnas.1904298116

Calvo-Agudo M, Dregni J, González-Cabrera J et al (2021) Neonicotinoids from coated seeds toxic for honeydew-feeding biological control agents. Environ Pollut 289:117813. https://doi.org/10.1016/j.envpol.2021.117813

Chen L, Zhang P, Fan Y et al (2018) Circular RNAs mediated by transposons are associated with transcriptomic and phenotypic variation in maize. New Phytol 217:1292–1306. https://doi.org/10.1111/nph.14901

Chuang WP, Ray S, Acevedo FE et al (2014) Herbivore cues from the fall armyworm (spodoptera frugiperda) larvae trigger direct defenses in maize. Mol Plant-Microbe Interact 27:461–470. https://doi.org/10.1094/MPMI-07-13-0193-R

Cloyd RA, Bethke JA, Cowles RS (2011) Systemic insecticides and their use in ornamental plant systems. Floric Ornam Biotechnol 5:1–9

de Ribeiro LP, Canale MC (2021) Cigarrinha-do-milho e o complexo de enfezamentos em Santa Catarina: panorama, patossistema e estratégias de manejo. Agropecuária Catarinense 34:22–25https://doi.org/10.52945/rac.v34i2.1144

Degen T, Dillmann C, Marion-Poll F, Turlings TCJ (2004) High genetic variability of herbivore-induced volatile emission within a broad range of maize inbred lines. Plant Physiol 135:1928–1938. https://doi.org/10.1104/pp.104.039891

Ding J, Li H, Zhang Z et al (2018) Thiamethoxam, clothianidin, and imidacloprid seed treatments effectively control thrips on corn under field conditions. J Insect Sci 18:1–8. https://doi.org/10.1093/jisesa/iey128

Douglas MR, Tooker JF (2015) Large-scale deployment of seed treatments has driven rapid increase in use of neonicotinoid insecticides and preemptive pest management in U.S. Field Crops Environ Sci Technol 49:5088–5097. https://doi.org/10.1021/es506141g

Dudareva N, Klempien A, Muhlemann JK, Kaplan I (2013) Biosynthesis, function and metabolic engineering of plant volatile organic compounds. New Phytol 198:16–32. https://doi.org/10.1111/nph.12145

Elbert A, Haas M, Springer B et al (2008) Applied aspects of neonicotinoid uses in crop protection. Pest Manag Sci 64:1099–1105. https://doi.org/10.1002/ps.1616

Endres L, Oliveira NG, Ferreira VM et al (2016) Morphological and physiological response of sugarcane under abiotic stress to neonicotinoid insecticides. Theor Exp Plant Physiol 28:347–355. https://doi.org/10.1007/s40626-016-0056-8

Fan Y, Shi X (2017) Characterization of the metabolic transformation of thiamethoxam to clothianidin in *Helicoverpa armigera* larvae by SPE combined UPLC–MS/MS and its relationship with the toxicity of thiamethoxam to *Helicoverpa armigera* larvae. J Chromatogr B 1061–1062:349–355. https://doi.org/10.1016/j.jchromb.2017.07.054

Ford KA, Casida JE, Chandran D et al (2010) Neonicotinoid insecticides induce salicylate-associated plant defense responses. Proc Natl Acad Sci U S A 107:17527–17532. https://doi.org/10.1073/pnas.1013020107

Gama EEG, Hallauer AR (1977) Relation between inbred and hybrid traits in maize. Crop Sci 17:703–706. https://doi.org/10.2135/cropsci1977.0011183X001700050007x

Gontijo PC, Moscardini VF, Michaud JP, Carvalho GA (2014) Non-target effects of chlorantraniliprole and thiamethoxam on *Chrysoperla carnea* when employed as sunflower seed treatments. J Pest Sci 87:711–719. https://doi.org/10.1007/s10340-014-0611-5

Gontijo PC, Abbade Neto DO, Oliveira RL et al (2018) Non-target impacts of soybean insecticidal seed treatments on the life history and behavior of *Podisus nigrispinus*, a predator of fall armyworm. Chemosphere 191:342–349. https://doi.org/10.1016/j.chemosphere.2017.10.062

Goulson D (2013) An overview of the environmental risks posed by neonicotinoid insecticides. J Appl Ecol 50:977–987. https://doi.org/10.1111/1365-2664.12111

Grunseich JM, Thompson MN, Hay AA et al (2020) Risky roots and careful herbivores : sustained herbivory by a root-feeding herbivore attenuates indirect plant defences. Funct Ecol 34:1779–1789. https://doi.org/10.1111/1365-2435.13627

Grunseich JM, Aguirre NM, Thompson MN et al (2021) Chemical cues from entomopathogenic nematodes vary across three species with different foraging strategies, triggering different behavioral responses in prey and competitors. J Chem Ecol 47:822–838. https://doi.org/10.1007/s10886-021-01304-8

Hisse IR, D'Andrea KE, Otegui ME (2019) Source-sink relations and kernel weight in maize inbred lines and hybrids: responses to contrasting nitrogen supply levels. F Crop Res 230:151–159. https://doi.org/10.1016/j.fcr.2018.10.011

Hoballah MEF, Tamò C, Turlings TCJ (2002) Differential attractiveness of induced odors emitted by eight maize varieties for the parasitoid *Cotesia marginiventris*: is quality or quantity important? J Chem Ecol 28:951–968. https://doi.org/10.1023/A:1015253600083

Huang C-H, Yan F-M, Byers JA et al (2009) Volatiles induced by the larvae of the Asian corn borer (*Ostrinia furnacalis*) in maize plants affect behavior of conspecific larvae and female adults. Insect Sci 16:311–320. https://doi.org/10.1111/j.1744-7917.2009.01257.x

Jameel M, Jamal K, Alam MF et al (2020) Interaction of thiamethoxam with DNA: hazardous effect on biochemical and biological parameters of the exposed organism. Chemosphere 254:126875. https://doi.org/10.1016/j.chemosphere.2020.126875

Jeschke P, Nauen R (2008) Neonicotinoids-from zero to hero in insecticide chemistry. Pest Manag Sci 64:1084–1098. https://doi.org/10.1002/ps.1631

Jeschke P, Nauen R, Schindler M, Elbert A (2011) Overview of the status and global strategy for neonicotinoids. J Agric Food Chem 59:2897–2908. https://doi.org/10.1021/jf101303g

Kawazu K, Mochizuki A, Sato Y et al (2012) Different expression profiles of jasmonic acid and salicylic acid inducible genes in the tomato plant against herbivores with various feeding modes. Arthropod Plant Interact 6:221–230. https://doi.org/10.1007/s11829-011-9174-z

Kenis M, Benelli G, Biondi A et al (2022) Invasiveness, biology, ecology, and management of the fall armyworm, *Spodoptera frugiperda*. Entomol Gen. https://doi.org/10.1127/entomologia/2022/1659

Köllner TG, Held M, Lenk C et al (2008) A maize (E)-β-caryophyllene synthase implicated in indirect defense responses against herbivores is not expressed in most American maize varieties. Plant Cell 20:482–494. https://doi.org/10.1105/tpc.107.051672

Korenko S, Saska P, Kysilková K et al (2019) Prey contaminated with neonicotinoids induces feeding deterrent behavior of a common farmland spider. Sci Rep 9:15895. https://doi.org/10.1038/s41598-019-52302-6

Krishnan N, Zhang Y, Aust ME et al (2021) Monarch butterfly (*Danaus plexippus*) life-stage risks from foliar and seed-treatment insecticides. Environ Toxicol Chem 40:1761–1777. https://doi.org/10.1002/etc.5016

Krupke CH, Alford AM, Cullen EM et al (2017) Assessing the value and pest management window provided by neonicotinoid seed treatments for management of soybean aphid (*Aphis glycines* Matsumura) in the Upper Midwestern United States. Pest Manag Sci 73:2184–2193. https://doi.org/10.1002/ps.4602

Lazebnik J, Frago E, Dicke M, van Loon JJA (2014) Phytohormone mediation of interactions between herbivores and plant pathogens. J Chem Ecol 40:730–741. https://doi.org/10.1007/s10886-014-0480-7

Luo Z, Han L, Qian J, Li L (2019) Circular RNAs exhibit extensive intraspecific variation in maize. Planta 250:69–78. https://doi.org/10.1007/s00425-019-03145-y

Maag D, Erb M, Bernal JS et al (2015) Maize domestication and anti-herbivore defences: leaf-specific dynamics during early ontogeny of maize and its wild ancestors. PLoS ONE 10:1–21. https://doi.org/10.1371/journal.pone.0135722

Macedo WR, de Castro Camago PR (2011) Thiamethoxam: molecule moderator of growth, metabolism and production of spring wheat. Pestic Biochem Physiol 100:299–304. https://doi.org/10.1016/j.pestbp.2011.05.003

Macedo WR, de Castro Camago PR (2018) Thiamethoxam altera o conteúdo de pigmentos fotossintetizantes e biomassa de milho:

análise em casa-de-vegetação e no campo. Rev Ciência Agrícola 16:34. https://doi.org/10.28998/rca.v16i2.4389
Macedo WR, Araújo DK, de Castro Camago PR (2013) Unravelling the physiologic and metabolic action of thiamethoxam on rice plants. Pestic Biochem Physiol 107:244–249. https://doi.org/10.1016/j.pestbp.2013.08.001
Magalhães LC, Hunt TE, Siegfried BD (2009) Efficacy of neonicotinoid seed treatments to reduce soybean aphid populations under field and controlled conditions in Nebraska. J Econ Entomol 102:187–195. https://doi.org/10.1603/029.102.0127
Moral RA, Hinde J, Demétrio CGB (2017) Half-normal plots and overdispersed models in R : the HNP package. J Stat Softw 81:1–23. https://doi.org/10.18637/jss.v081.i10
Moscardini VF, Gontijo PC, Michaud JP, Carvalho GA (2014) Sublethal effects of chlorantraniliprole and thiamethoxam seed treatments when *Lysiphlebus testaceipes* feed on sunflower extrafloral nectar. Biocontrol 59:503–511. https://doi.org/10.1007/s10526-014-9588-5
Moscardini VF, Gontijo PC, Michaud JP, Carvalho GA (2015) Sublethal effects of insecticide seed treatments on two nearctic lady beetles (Coleoptera: Coccinellidae). Ecotoxicology 24:1152–1161. https://doi.org/10.1007/s10646-015-1462-4
Myresiotis CK, Vryzas Z, Papadopoulou-Mourkidou E (2015) Effect of specific plant-growth-promoting rhizobacteria (PGPR) on growth and uptake of neonicotinoid insecticide thiamethoxam in corn (*Zea mays* L.) seedlings. Pest Manag Sci 71:1258–1266. https://doi.org/10.1002/ps.3919
Nauen R, Ebbinghaus-Kintscher U, Salgado VL, Kaussmann M (2003) Thiamethoxam is a neonicotinoid precursor converted to clothianidin in insects and plants. Pestic Biochem Physiol 76:55–69. https://doi.org/10.1016/S0048-3575(03)00065-8
Nelder JA, Wedderburn WM (2000) Generalized linear models. In: handbook of statistical analyses using stata, Fourth Edition. Chapman and Hall/CRC, pp 370–384
Niemeyer HM (2009) Hydroxamic acids derived from 2-Hydroxy-2 H -1,4-Benzoxazin-3(4 H)-one: key defense chemicals of cereals. J Agric Food Chem 57:1677–1696. https://doi.org/10.1021/jf8034034
O'Neal ME, Landis DA, Isaacs R (2002) An inexpensive, accurate method for measuring leaf area and defoliation through digital image analysis. J Econ Entomol 95:1190–1194. https://doi.org/10.1603/0022-0493-95.6.1190
Oliveira CM, Oliveira E, Canuto M, Cruz I (2008) Eficiência de inseticidas em tratamento de sementes de milho no controle da cigarrinha *Dalbulus maidis* (Hemiptera: Cicadellidae) em viveiro telado. Ciência Rural 38:231–235
Pecenka JR, Lundgren JG (2015) Non-target effects of clothianidin on monarch butterflies. Sci Nat. https://doi.org/10.1007/s00114-015-1270-y
Pechan T, Ye L, Chang Y et al (2000) A unique 33-kD cysteine proteinase accumulates in response to larval feeding in maize genotypes resistant to fall armyworm and other Lepidoptera. Plant Cell 12:1031–1040. https://doi.org/10.1105/tpc.12.7.1031
Peralta C, Palma L (2017) Is the insect world overcoming the efficacy of *Bacillus thuringiensis*? Toxins (basel) 9:1–5. https://doi.org/10.3390/toxins9010039
Pieterse CMJ, Van Der Does D, Zamioudis C et al (2012) Hormonal modulation of plant immunity. Annu Rev Cell Dev Biol 28:489–521. https://doi.org/10.1146/annurev-cellbio-092910-154055
Preetha G, Stanley J (2012) Influence of neonicotinoid insecticides on the plant growth attributes of cotton and okra. J Plant Nutr 35:1234–1245. https://doi.org/10.1080/01904167.2012.676134
R CoreTeam (2022) R: A language and environment for statistical computing
Ruckert A, Allen LN, Ramirez RA (2018) Combinations of plant water-stress and neonicotinoids can lead to secondary outbreaks of banks grass mite (*Oligonychus pratensis* Banks). PLoS ONE 13:e0191536. https://doi.org/10.1371/journal.pone.0191536
Rundlöf M, Andersson GKS, Bommarco R et al (2015) Seed coating with a neonicotinoid insecticide negatively affects wild bees. Nature 521:77–80. https://doi.org/10.1038/nature14420
Sâmia RR, Gontijo PC, Oliveira RL, Carvalho GA (2019) Sublethal and transgenerational effects of thiamethoxam applied to cotton seed on *Chrysoperla externa* and *Harmonia axyridis*. Pest Manag Sci 75:694–701. https://doi.org/10.1002/ps.5166
Sanchez-Bayo F (2014) The trouble with neonicotinoids. Science 346:806–807. https://doi.org/10.1126/science.1259159
Schmelz EA, Alborn HT, Banchio E, Tumlinson JH (2003) Quantitative relationships between induced jasmonic acid levels and volatile emission in *Zea mays* during *Spodoptera exigua* herbivory. Planta 216:665–673. https://doi.org/10.1007/s00425-002-0898-y
Schmelz EA, Engelberth J, Tumlinson JH et al (2004) The use of vapor phase extraction in metabolic profiling of phytohormones and other metabolites. Plant J 39:790–808. https://doi.org/10.1111/j.1365-313X.2004.02168.x
Schnable PS, Ware D, Fulton RS et al (2009) The B73 maize genome: complexity, diversity, and dynamics. Science 326:1112–1115. https://doi.org/10.1126/science.1178534
Schnee C, Köllner TG, Held M et al (2006) The products of a single maize sesquiterpene synthase form a volatile defense signal that attracts natural enemies of maize herbivores. Proc Natl Acad Sci U S A 103:1129–1134. https://doi.org/10.1073/pnas.0508027103
Schweiger R, Heise A-M, Persicke M, Müller C (2014) Interactions between the jasmonic and salicylic acid pathway modulate the plant metabolome and affect herbivores of different feeding types. Plant Cell Environ 37:1574–1585. https://doi.org/10.1111/pce.12257
Shiferaw B, Prasanna BM, Hellin J, Bänziger M (2011) Crops that feed the world 6. Past successes and future challenges to the role played by maize in global food security. Food Secur 3:307–327. https://doi.org/10.1007/s12571-011-0140-5
Smith JF, Catchot AL, Musser FR, Gore J (2013) Effects of aldicarb and neonicotinoid seed treatments on twospotted spider mite on cotton. J Econ Entomol 106:807–815. https://doi.org/10.1603/EC10125
Stupar RM, Springer NM (2006) Cis-transcriptional variation in maize inbred lines B73 and Mo17 leads to additive expression patterns in the F1 hybrid. Genetics 173:2199–2210. https://doi.org/10.1534/genetics.106.060699
Szczepaniec A, Raupp MJ (2013) Direct and indirect effects of imidacloprid on fecundity and abundance of *Eurytetranychus buxi* (Acari: Tetranychidae) on boxwoods. Exp Appl Acarol 59:307–318. https://doi.org/10.1007/s10493-012-9614-1
Szczepaniec A, Creary SF, Laskowski KL et al (2011) Neonicotinoid insecticide imidacloprid causes outbreaks of spider mites on elm trees in urban landscapes. PLoS ONE 6:e20018. https://doi.org/10.1371/journal.pone.0020018
Szczepaniec A, Raupp MJ, Parker RD et al (2013) Neonicotinoid insecticides alter induced defenses and increase susceptibility to spider mites in distantly related crop plants. PLoS ONE 8:e62620. https://doi.org/10.1371/journal.pone.0062620
Thaler JS, Agrawal AA, Halitschke R (2010) Salicylate-mediated interactions between pathogens and herbivores. Ecology 91:1075–1082. https://doi.org/10.1890/08-2347.1
Todorenko DA, Hao J, Slatinskaya OV et al (2021) Effect of thiamethoxam on photosynthetic pigments and primary photosynthetic reactions in two maize genotypes (*Zea mays*). Funct Plant Biol 48:994. https://doi.org/10.1071/FP21134
Tomizawa M, Casida JE (2005) Neonicotinoid insecticide toxicology: mechanisms of selective action. Annu Rev Pharmacol Toxicol 45:247–268. https://doi.org/10.1146/annurev.pharmtox.45.120403.095930

Tooker JF, Douglas MR, Krupke CH (2017) Neonicotinoid seed treatments: limitations and compatibility with integrated pest management. Agric Environ Lett. https://doi.org/10.2134/ael2017.08.0026

Turlings TCJ, Lengwiler UB, Bernasconi ML, Wechsler D (1998) Timing of induced volatile emissions in maize seedlings. Planta 207:146–152. https://doi.org/10.1007/s004250050466

Uhl P, Bucher R, Schäfer RB, Entling MH (2015) Sublethal effects of imidacloprid on interactions in a tritrophic system of non-target species. Chemosphere 132:152–158. https://doi.org/10.1016/j.chemosphere.2015.03.027

Vos IA, Pieterse CMJ, Van Wees SCM (2013) Costs and benefits of hormone-regulated plant defences. Plant Pathol 62:43–55. https://doi.org/10.1111/ppa.12105

Wanumen AC, Sánchez-Ramos I, Viñuela E et al (2016) Impact of feeding on contaminated prey on the life parameters of *Nesidiocoris tenuis* (Hemiptera: Miridae) adults. J Insect Sci 16:103. https://doi.org/10.1093/jisesa/iew084

Whalen A, Catchot AL, Gore J et al (2021) Temporal profile of neonicotinoid concentrations in cotton, corn, and soybean resulting from insecticidal seed treatments. Agronomy 11:1200. https://doi.org/10.3390/agronomy11061200

Wiseman BR, Snook ME, Isenhour DJ et al (1992) Relationship between growth of corn earworm and fall armyworm larvae (Lepidoptera: Noctuidae) and Maysin concentration in corn silks. J Econ Entomol 85:2473–2477. https://doi.org/10.1093/jee/85.6.2473

Wu C, Zhang H, He M et al (2021) Toxicity of neonicotinoid insecticides on key non-target natural predator the larvae of *Coccinella septempunctata* in environmental. Environ Technol Innov 23:101523. https://doi.org/10.1016/j.eti.2021.101523

Wulff J, Kiani M, Regan K et al (2019) Neonicotinoid insecticides alter the transcriptome of soybean and decrease plant resistance. Int J Mol Sci 20:783. https://doi.org/10.3390/ijms20030783

Yactayo-Chang JP, Mendoza J, Willms SD et al (2021) *Zea mays* volatiles that influence oviposition and feeding behaviors of *Spodoptera frugiperda*. J Chem Ecol 47:799–809. https://doi.org/10.1007/s10886-021-01302-w

Yang D, Avelar SAG, Taylor AG (2018) Systemic seed treatment uptake during imbibition by corn and soybean. Crop Sci 58:2063–2070. https://doi.org/10.2135/cropsci2018.01.0004

Yendrek CR, Erice G, Montes CM et al (2017) Elevated ozone reduces photosynthetic carbon gain by accelerating leaf senescence of inbred and hybrid maize in a genotype-specific manner. Plant Cell Environ 40:3088–3100. https://doi.org/10.1111/pce.13075

Yuan W, Jiang T, Du K et al (2019) Maize phenylalanine ammonia-lyases contribute to resistance to *Sugarcane mosaic virus* infection, most likely through positive regulation of salicylic acid accumulation. Mol Plant Pathol 20:1365–1378. https://doi.org/10.1111/mpp.12817

Zhou Q, Cheng X, Wang S et al (2019) Effects of chemical insecticide imidacloprid on the release of C6 green leaf volatiles in tea plants (*Camellia sinensis*). Sci Rep 9:1–6. https://doi.org/10.1038/s41598-018-36556-0