METHYL JASMONATE AFFECTS POPULATION DENSITIES OF PHYTOPHAGOUS AND ENTOMOPHAGOUS INSECTS IN WHEAT

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Abstract. Methyl jasmonate (MEJA), a well-known herbivore-induced plant volatile, promotes plant defences against various stress factors. The aim of this study was to investigate the effects of different doses of exogenously applied MEJA on the population densities of wheat insect pests and their natural enemies by employing three sampling methods (direct visual sampling, sweep net, sticky traps) in 2012 and 2013 under semi-arid conditions. MEJA treatments had repellent effects on aphids (Hemiptera: Aphididae), phytophagous thrips species (Thysanoptera: Phlaeothripidae and Thripidae) and hoverfly species (Diptera: Syrphidae), whereas it was attractive to wheat stem sawflies (Hymenoptera: Cephidae), lady beetle species (Coleoptera: Coccinellidae) and *Collyria coxator* (Hymenoptera: Ichneumonidae). MEJA treatments had no effect on aphid parasitoids abundances (Hymenoptera: Braconidae). The experimental outcomes varied, depending on plant phenology and sampling method. MEJA treatment also led to reductions in wheat yield and plant height. MEJA treatment could be beneficial as a natural pest control tool when certain species are targeted.
Keywords: *semiochemical, predator, parasitoid, wheat insect pests, Triticum aestivum*

Introduction

Wheat, *Triticum aestivum* L., one of the most important food crops, confronts many stress factors, including insect pests and microbial diseases. Insect pests such as aphids (Hemiptera: Aphididae) and thrips species (Thysanoptera: Phlaeothripidae) reduce grain yield by piercing and sucking the contents of stems, leaves and spikes, while the larvae of wheat stem sawfly species cause decreased yield and grain number by disrupting sap flow as they tunnel into host stems. Therefore, these pests may cause substantial yield losses (Seddigh and Bandani, 2012; Larsson, 2005; Özberk et al., 2005). Extensive use of insecticides is the mainstay method to minimize yield losses, but these treatments are unsustainable and environmentally damaging. Moreover, insecticides are only partially effective against some of the pests e.g., wheat stem sawflies owing to their cryptic egg laying and life cycle. In addition, the natural enemies of these pests can also be harmed by insecticides, which is counterproductive to controlling the pest populations. Therefore, management of insect pests requires better methods.

Plants under herbivore attack release volatile organic plant compounds (VOCs) to minimize damage by settled attackers or to prevent impending dangers (Kessler and Baldwin, 2001; Tan et al., 2012). These herbivore-induced plant volatiles (HIPVs) are not only repellent to insect herbivores, but they also encourage the foraging behavior of natural enemies of the pests (Boughton et al., 2006; Moraes et al., 2009; Mandour et al., 2013). Among a large variety of HIPVs, the jasmonates seem to be key components of

plant defense systems (Lackman et al., 2011). Even though jasmonic acid (JA) is the most abundant volatile among the jasmonates, exogenous application of methyl jasmonate (MEJA) is generally more effective because of its greater volatility (Beltrano et al., 1998). Previous studies have demonstrated that MEJA induces plant defenses by increasing the activity of lipoxygenase and the production of C6-aldehydes, thus suppressing larval feeding by the hawkmoth *Manduca sexta* (Lepidoptera: Sphingidae) and the cabbage looper *Trichoplusia ni* (Lepidoptera: Noctuidae) (Avdiuskho et al., 1997). MEJA applications were also found to decrease the population growth of two phloem feeders, the green peach aphid *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) on tomato plants (*Lycopersicon esculentum*) and the potato aphid *Macrosiphum euphorbiae* on potato plants (*Solanum tuberosum*) (Boughton et al., 2006; Brunissen et al., 2010). Population growth of the soybean aphid *Aphis glycines* Matsumura (Hemiptera: Aphididae) and the soybean thrips *Neohydatothrips variabilis* (Beach) (Thysanoptera: Thripidae) was reduced by MEJA application (Selig et al., 2016). In addition, MEJA treatment contributes to plant defenses by attracting natural enemies of pests. For example, MEJA-treated persimmon plants (*Diospyros kaki*) were found to be attractive to the lady beetle *Chilocorus kuwanae* (Coleoptera: Coccinellidae) (Zhang et al., 2009). Furthermore, more parasitic wasps of the family Braconidae were attracted to MEJA-baited traps than unbaited traps in field trials (James, 2005). Another braconid, *Cotesia plutellae*, a larval parasitoid of *Plutella xylostella* (Lepidoptera: Yponomeutidae), preferred MEJA in Y-tube olfactometer tests (Ibrahim et al., 2005). Based on either single-dose studies of jasmonates or the targeting of single organisms under controlled conditions, the majority-opinion in the literature is that MEJA and other jasmonates are repellent to herbivores and attractant to their natural enemies (Birkett et al., 2000; Bruce et al., 2003; El-Wakeil et al., 2010; Dewhirst et al., 2012; El-Wakeil and Volkmar, 2012; Egger and Koschier, 2014). However, more studies of the effects of plant defense elicitors under field conditions are needed to elucidate whether they are useful tools for integrated pest management strategies.

Here, we investigated the influence of different MEJA doses on the population densities of wheat insect pests (aphids, thrips and wheat stem sawflies) and their natural enemies (aphid parasitoids, lady beetles, hoverflies and *Collyria coxator*) in two different plant growth stages. Population fluctuations were monitored by employing three different sampling methods, direct visual sampling, sweep-net sampling and colored (yellow and blue) sticky traps.

Materials and methods

Experimental design

Two years (2012 and 2013) of field experiments were conducted in a wheat field (*Triticum aestivum* L., cv. Pehlivan, the most commonly sown cultivar) established on alluvial soil under semi-arid climate conditions (Diyarbakir, Turkey 37°54'16"N; 40°16'46"E). Standard agronomic practices (e.g., fertilization) were made in our experimental plots. No pesticides were used in our experimental plots throughout of the study. The experimental system consisted of wheat plots established in a randomized complete block design. Each plot was 3×3 m^2 (4 replications) and 4×2 m^2 (3 replications) in 2012 and 2013, respectively. The distance between experimental plots and other cultivated or non-cultivated areas was at least 2 m.

Exogenous MEJA treatments

Plants were treated with MEJA (≥96% purity) (Sigma-Aldrich) twice in each year (2012 and 2013). The first and second treatments were performed at wheat growth stages GS-37th (flag leaf just visible, still rolled) and GS-59th (End of heading: inflorescence fully emerged) according to BBCH scale for cereals, respectively (Witzenberger et al., 1989; Lancashire et al., 1991). Three doses of MEJA (14.2 mM, 7.1 mM and 3.55 mM, of which the highest dose was applied by McEwen (2011) to cruciferous plants) were employed as the first treatment in year 1. However, we lowered the doses to 3.55 mM, 1.76 mM and 0.88 mM for all subsequent treatments (i.e. the second treatment of year 1 and both treatments of year 2) due to high phytotoxic effects observed one day after the first treatment of year 1. Silwet Gold (Chemtura) surfactant at a ratio of 10 ml per 100 L of water was added to each dose in all treatments. Plants in control plots were treated with distilled water and surfactant only. A hydraulic backpack sprayer was used to apply the treatments.

Sampling methods

Direct visual samplings

Presence of phytophagous and entomophagous insects was checked on all above-ground parts of ten plants. All biological forms, i.e. from egg to adult, were checked by using a 5× hand magnifier and recorded. Samplings were carried out 1 day prior to and 1, 3, 10 and 17 days after the MEJA treatments. There was a 4-day interval between the last sampling of the first treatment period and the first sampling of the second treatment period in both years.

Sweep-net samplings

A standard sampling net (R = 35 cm) was used to sweep samples from the experimental plots uniformly. The collected samples were put into clear plastic bags with a paper towel to reduce humidity and then labeled. The samples were transferred to the laboratory and put in a freezer (-20°C). All specimens were recorded afterward. Sweep-net sampling intervals were the same as those of the direct visual samplings.

Colored sticky trap samplings

Yellow and blue sticky traps (Kapar Organic, 20×25 cm) were placed in the middle of MEJA-treated and untreated control plots one week prior to the first samplings in both years to sample the population densities of flying wheat insect pests and their natural enemies. Data concerning the insects caught by the traps were recorded. The traps were cleaned with a wooden spatula and the insect-catching sticky substrate (Kapar Organic) was renewed when needed. The sampling intervals for the colored sticky traps were the same as those of the direct visual samplings, except that no samplings were conducted on day 1 after the treatments.

Effects of MEJA on agronomic properties

Seventy-five randomly chosen heads were collected from each plot in mid-June, at harvest time. Grains were extracted from the heads and separated from the glume by

hand. Grains were kept under laboratory conditions until weighed. In addition, the heights of 10 wheat plants per plot were measured at the the GS 92nd (over-ripe: grain very hard, cannot be dented by thumbnail) according to BBCH scale.

Statistical analysis

All log (n + 1) tranformed experimental data were checked for normality (Shapiro–Wilk's test) and homogeneity of variances (Levene's test) before analysis. To reveal effects of MEJA treatments on wheat insect pests and their natural enemies, data of each year and treatment periods were analyzed by fitting generalized linear mixed models (GLMM, lme4 package) with poisson error distribution (log link function) (Diggle et al., 2002, Bolker et al., 2009, Bates et al., 2015). MEJA doses were fixed factor whereas sampling dates were random factor for all cases. The fixed factor effects were tested using likelihood-ratio (LR) tests (p < 0.05). Tukey's post hoc tests were used to compare the means at the 95% confidence level (with the glht function of the multcomp package). The effects of MEJA treatment on plant height and yield were analyzed with one-way ANOVA. Means of all data were separated using the Tukey's multiple comparison test at the 95% confidence level. Insect taxa which did not respond to MEJA treatment in any treatment period or experimental year are not presented in the figures, but their statistical results are presented in *Table 1*. All statistical analyses were performed with R software, version 3.4.0 (R Core Team, 2017).

Results

Effects of different methyl jasmonate doses on some insect pests

Aphid species (Hemiptera: Aphididae)

There were two aphid species in our experimental area, *Sitobion avenae* (F.) and *Rhopalosiphum padi* (L.).

Direct visual samplings of apterous aphids: Generalized linear mixed model analysis revealed that the aphid densities in MEJA (0.88 mM and 3.55 mM)-treated wheat plots were lower than in control plots for the second treatment period and pooled whole season of year 1 ($\chi^2_{2012\text{-ST}}$ = 89.94, P < 0.001, $\chi^2_{2012\text{-whole}}$ = 87.10, P < 0.001; *Fig. 1A*). Data of the first treatment period of year 1 showed no significant differences among MEJA dose treatments (P > 0.05, *Table 1*). The population densities of aphid species on MEJA-treated and untreated plants were not different in the pooled whole-season and data of both treatment periods of year 2 (P > 0.05, *Table 1*).

Sweep-net sampling for apterous aphids: The population densities of apterous aphids swept from MEJA-treated and untreated control plants were not significantly different throughout the study. No apterous aphids were sampled in the first treatment period of year 2 (P > 0.05, *Table 1*).

Direct visual sampling of alate aphids: Data of whole season of year 1 demonstrated significant differences between the mean densities of alate aphids in MEJA-treated and control plants while alate aphid densities did not differ between treatments for first and second treatment periods ($\chi^2_{2012\text{-FT}}$ = 1.83, P = 0.607; $\chi^2_{2012\text{-ST}}$ = 4.15, P = 0.245; $\chi^2_{2012\text{-whole}}$ = 18.66, P < 0.001; *Fig. 1B*). However, there were no significant differences between alate aphids visually counted on plants between MEJA-treated plants and controls in year 2 (P > 0.05, *Table 1*). Furthermore, we did not encounter any alate aphid individuals on any experimental plants in the second treatment period of year 2.

Table 1. *Summary of the data analysis (GLMM) indicating the influence of methyl jasmonate (MEJA) treatments on some insect species sampled by different sampling methods (data pooled over sampling intervals within treatment periods and whole season). NI: no insect recorded (df = 3 for all cases)*

Pest insects	Year	Sampling method	First treatment		Second treatment		Whole season	
			χ^2	P	χ^2	P	χ^2	P
Apterous aphids	2012	Visual Sampling	3.52	0.317	89.94	<0.001	87.10	<0.001
		Sweep-net	0.86	0.833	6.76	0.079	5.56	0.134
	2013	Visual sampling	3.02	0.387	6.24	0.100	2.57	0.460
		Sweep-net	NI		2.72	0.435	5.13	0.162
Alate aphids	2012	Visual sampling	1.83	0.607	4.15	0.245	18.66	<0.001
		Sweep-net	2.34	0.504	3.77	0.286	5.53	0.136
		Yellow traps	2.02	0.567	0.46	0.925	1.53	0.675
	2013	Visual sampling	3.02	0.387	NI		0.02	0.999
		Sweep-net	2.92	0.403	4.12	0.248	5.21	0.156
		Yellow traps	12.16	0.006	19.98	<0.001	15.16	0.001
Thrips	2012	Visual sampling	3.30	0.346	1.81	0.612	1.63	0.651
		Sweep-net	17.67	<0.001	19.22	<0.001	31.50	<0.001
	2013	Visual sampling	3.02	0.387	1.01	0.796	0.08	0.993
		Sweep-net	1.97	0.577	1.81	0.612	2.74	0.433
Wheat stem sawflies	2012	Sweep-net	2.41	0.490	2.64	0.450	2.32	0.508
		Yellow traps	16.55	<0.001	44.33	<0.001	47.34	<0.001
		Blue traps	1.45	0.693	5.31	0.150	2.63	0.451
	2013	Sweep-net	2.44	0.485	1.45	0.693	2.80	0.423
		Yellow traps	5.08	0.165	1.53	0.673	0.39	0.940
		Blue traps	0.20	0.649	4.28	0.232	4.43	0.218
Natural enemies								
Aphid parasitoids	2012	Visual Sampling	0.32	0.954	1.53	0.673	1.80	0.614
		Sweep-net	1.28	0.733	5.68	0.128	4.89	0.179
		Yellow traps	0.42	0.934	1.65	0.646	0.39	0.941
	2013	Visual Sampling	2.66	0.445	3.02	0.388	0.03	0.998
		Sweep-net	1.29	0.729	1.81	0.612	3.62	0.305
		Yellow traps	0.40	0.938	1.53	0.673	0.39	0.940
Ladybirds	2012	Visual sampling	NI		20.95	<0.001	20.22	<0.001
		Sweep-net	3.15	0.367	4.65	0.198	5.27	0.152
		Yellow traps	1.44	0.694	13.92	0.003	12.31	0.006
		Blue traps	NI		1.53	0.673	1.40	0.704
	2013	Visual sampling	2.02	0.567	1.45	0.693	0.29	0.960
		Sweep-net	3.38	0.336	1.37	0.710	2.10	0.551
		Yellow traps	2.66	0.445	1.81	0.612	2.90	0.406
		Blue traps	NI		3.56	0.312	3.44	0.327
Syrphid flies	2012	Sweep-net	3.15	0.367	2.19	0.533	3.22	0.357
		Yellow traps	1.44	0.694	6.13	0.105	4.73	0.192
		Blue traps	6.72	0.081	23.09	<0.001	24.80	<0.001
	2013	Sweep-net	4.98	0.172	1.61	0.655	1.45	0.693
		Yellow traps	6.02	0.110	0.57	0.901	2.86	0.412
		Blue traps	6.65	0.083	2.19	0.530	3.84	0.278
C. coxator	2012	Sweep-net	10.64	0.013	0.88	0.827	10.07	0.017
		Yellow traps	13.19	0.004	29.64	<0.001	41.11	<0.001
		Blue traps	2.94	0.400	1.47	0.688	3.89	0.273
	2013	Sweep-net	5.77	0.123	0.57	0.901	6.12	0.105
		Yellow traps	27.37	<0.001	12.11	0.006	37.31	<0.001
		Blue traps	0.48	0.92	2.93	0.402	1.74	0.627

Sweep-net sampling for alate aphids: There were no significant effects of MEJA treatments on alate aphids collected by sweep-net sampling during the entire experiment ($P > 0.05$, *Table 1*).

Yellow sticky trap samplings for alate aphids: In both treatment periods and pooled whole-season data of year 1, the population densities of aphid species in MEJA-treated and untreated plants did not differ significantly ($P > 0.05$, *Table 1*). Evaluation of data of the first treatment period of year 2 demonstrated number of aphids caught on yellow traps were higher in 0.88 mM MEJA- treated plots than control plots ($\chi^2_{2013\text{-}FT} = 12.16$, $P = 0.006$). However, 1.76 mM MEJA- treated plots had lower number of alate aphids than control and 0.88mM MEJA- treated plants in both second treatment period and whole season of year 2 ($\chi^2_{2013\text{-}ST} = 19.98$, $P < 0.001$; $\chi^2_{2013\text{-}whole} = 15.16$, $P = 0.001$; *Fig. 1E*).

Phytophagous thrips species

Eleven phytophagous thrips species belonging to two families of Thysanoptera were recorded during the experiments. The numbers of *Haplanthrips tritici* (Kurdjumov), *H. aculeatus* (Fabricius) and *H. reuteri* (Karny) of family Phlaeothripidae were higher than those of *Frankliniella tenuicornis* (Uzel), *Thrips tabaci* (Lindeman), *Melanthrips pallidior* (Priesner), *T. angusticeps* (Uzel), *Kakothrips priesneri* (Pelikan), *Limothrips cerealium* (Haliday), *L. angulicornis* (Jablonowski) and *M. fuscus* (Sulzer) of family Thripidae.

Direct visual sampling of phytophagous thrips: There were no significant differences between the population densities of phytophagous thrips species sampled by direct counting on plants in pooled whole-season data and both treatment periods of both years ($P > 0.05$, *Table 1*).

Sweep-net sampling of phytophagous thrips: Evaluation of the first treatment period and whole season data of year 1 revealed that number of thrips in all MEJA treated plots were lower than control plots ($\chi^2_{2012\text{-}FT} = 17.67$, $P < 0.001$; $\chi^2_{2012\text{-}whole} = 31.50$, $P < 0.001$; *Fig 1C*). In addition, in year 1, MEJA-treated plants (0.88 mM) had lower population densities of pest thrips than control plants in the second treatment period ($\chi^2_{2012\text{-}ST} = 19.22$, $P < 0.001$; *Fig. 1C*). In contrast, in year 2, phytophagous thrips populations sampled by sweep-net from MEJA-treated and control plants did not differ significantly based on either pooled whole-season data or treatment periods ($P > 0.05$, *Table 1*).

Wheat stem sawfly species

Throughout the experiments, two wheat stem sawfly (Hymenoptera: Cephidae) species were collected, of which *Cephus pygmaeus* (L.) was more prevalent than *Trachelus tabidus* (F.).

Sweep-net samplings of wheat stem sawfly species: Wheat stem sawfly population densities determined by sweep-net of MEJA-treated and untreated plants were not significantly different for either whole-season pooled data or between treatment periods in both years ($P > 0.05$, *Table 1*).

Yellow sticky trap samplings of wheat stem sawfly species: Yellow sticky trap sampling analysis revealed that the mean densities of wheat stem sawflies in MEJA-treated plants were significantly higher than in control plants in whole-season pooled

data, the first and the second treatment periods of year 1 ($\chi^2_{\text{2012-FT}}$ = 16.55, $P < 0.001$; $\chi^2_{\text{2012-ST}}$ = 44.33, $P < 0.001$; $\chi^2_{\text{2012-whole}}$ = 47.34; $P < 0.001$; *Fig. 1D*). In year 2, there were no significant differences between or among MEJA treatments and/or control plants in both whole-season pooled data and the treatment periods ($P > 0.05$, *Table 1*).

Blue sticky trap sampling of wheat stem sawfly species: The population densities of wheat stem sawflies in MEJA-treated and untreated control plants, as observed by blue sticky traps, did not differ significantly in both whole-season pooled data and the treatment periods of both years ($P > 0.05$, *Table 1*).
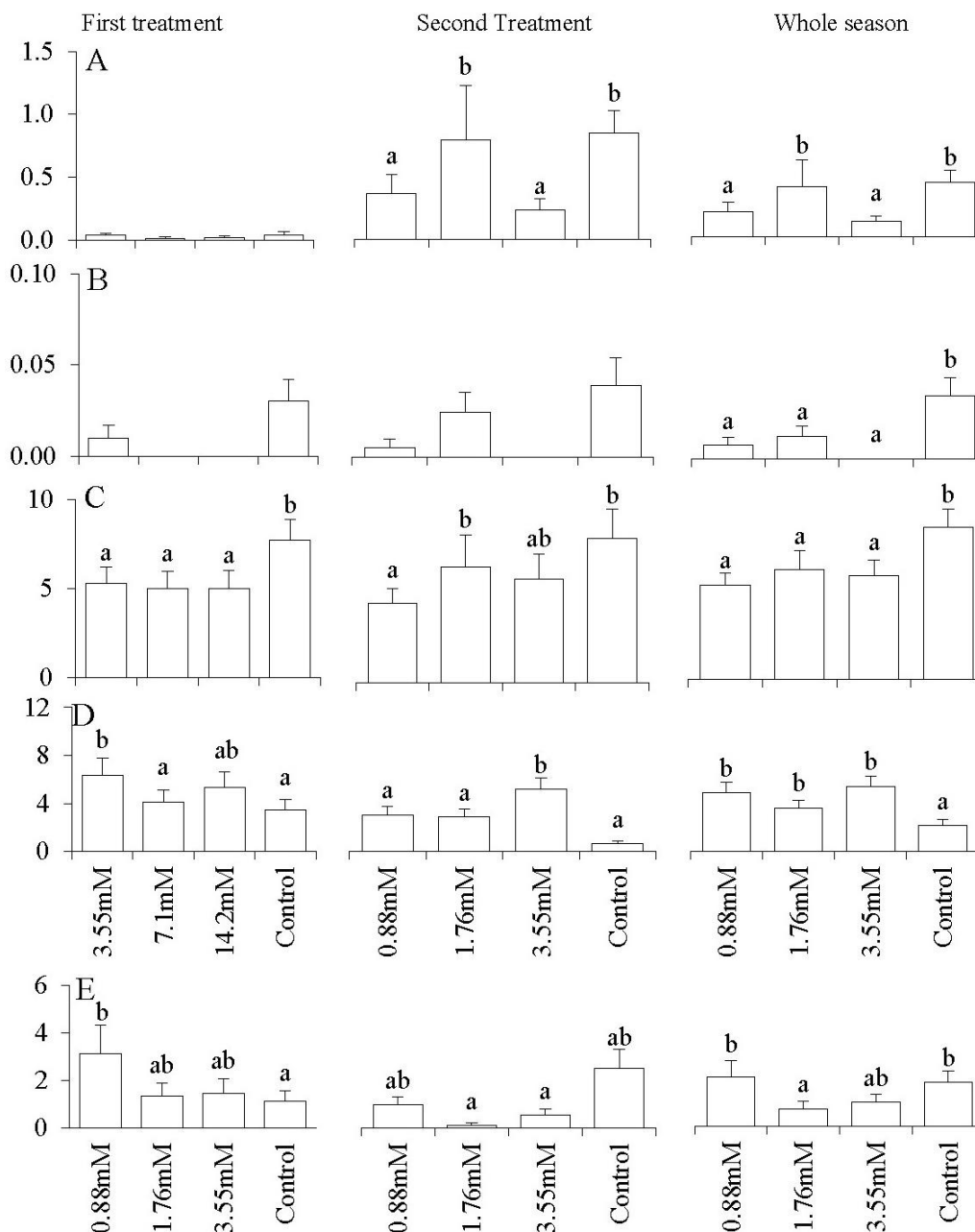
Figure 1. *Mean density (+SEM) of apterous aphids per plant in 2012 (A), alate aphids per plant in 2012 (B), pest thrips/ sweep-net in 2012 (C), wheat stem sawflies/ yellow traps in 2012 (D) and alate aphids/yellow traps in 2013 (E) in wheat plots treated with different methyl jasmonate doses for first-treatment and second-treatment periods and whole season (Means capped with different letters differ significantly, Tukey's multiple comparison test, P < 0.05)*

Effects of methyl jasmonate treatments on parasitoids and predators of wheat pests

Aphid parasitoids

Three braconid aphid parasitoids, *Aphidius ervi*, *Praon gallicum* (Stary) and *Binodoxys acalephae* (Marshall) were collected during our experiments, and *A. ervi* was the most prevalent species.

Direct visual samplings for aphid parasitoids: There were no differences in the population densities of aphid parasitoids in MEJA- treated and control plants in whole-season pooled data and the treatment periods of year 1 and year 2 ($P > 0.05$, *Table 1*).

Sweep-net samplings for aphid parasitoids: The population densities of aphid parasitoids in MEJA- treated and untreated plants determined by sweep-net samplings were not significantly different in both pooled seasonal data and the treatment periods throughout the study ($P > 0.05$, *Table 1*).

Yellow sticky trap sampling of aphid parasitoids: Yellow sticky trap sampling results demonstrated that the population densities of aphid parasitoids in MEJA-treated and untreated plants were not significantly different in both pooled whole season data and the treatment periods ($P > 0.05$, *Table 1*).

Lady beetles (Coleoptera: Coccinellidae)

Three predatory lady beetle (Coleoptera: Coccinellidae) species were recorded throughout our study, namely *Coccinella septempunctata*, *Adalia bipunctata* (L.) and *C. undecimpunctata* (L.), of which *C. septempunctata* was the most abundant.

Direct visual samplings of lady beetles: The population density of lady beetles in plants treated with 3.55 mM MEJA was higher than those in the other treatments and the controls for the second treatment period. Accordingly, the density of lady beetles directly sampled on plants treated with highest dose were higher than other treatments and control plots in whole-season pooled data, while no individual lady beetle was recorded in the first treatment period ($\chi^2_{2012\text{-ST}} = 20.95$, $P < 0.001$; $\chi^2_{2012\text{-whole}} = 20.22$, $P < 0.001$; *Fig. 2A*). MEJA treatments did not have any significant effect on the population densities of lady beetles in year 2 ($P > 0.05$, *Table 1*).

Sweep-net sampling of lady beetles: Throughout the study, there were no significant differences in population densities of lady beetles determined by sweep-net sampling between MEJA-treated and untreated control plants ($P > 0.05$, *Table 1*).

Yellow sticky trap sampling of lady beetles: The population densities of lady beetles caught on yellow sticky traps in treated and untreated plants did not differ significantly from one another in first treatment period of year 1 and second treatment period and whole-season pooled data of year 2 ($P > 0.05$, *Table 1*). However, number of lady beetles caught on yellow traps in 3.55 mM MEJA-treated plants were higher than control plots in the second application period and whole season pooled data of year 1 ($\chi^2_{2012\text{-ST}} = 13.92$, $P = 0.003$; $\chi^2_{2012\text{-whole}} = 12.31$, $P = 0.006$; *Fig. 2B*).

Blue sticky trap samplings of lady beetles: In the first treatment periods of both years, we did not encounter any lady beetle individuals on blue sticky traps. In the second treatment periods and whole season data of both experimental years, the differences between MEJA-treated and untreated control plants were not significant ($P > 0.05$, *Table 1*).

Hoverflies (Diptera: Syrphidae)

The hoverfly species collected consisted of four species, *Eupeodes corollae* (Fabricius), *Sphaerophoria scripta* (L.), *Melanostoma mellinum* (L.) and *S. turkmenica* (Bankowska). Of these species, *E. corollae* (F.) was the most prevalent.

Sweep-net samplings of hoverfly species: There were no significant differences in the numbers of hoverflies sampled from MEJA- treated and untreated control plants in both treatment periods and whole-season pooled data of both years ($P > 0.05$, *Table 1*).

Yellow sticky trap samplings of hoverflies: The population densities of hoverfly adults caught on yellow sticky traps were not significantly different between the MEJA-treated and control plants in both experimental years ($P > 0.05$, *Table 1*).

Blue sticky trap sampling of hoverflies: Data of the first treatment period of year 1 showed that there were no significant differences in the numbers of hoverfly adults caught on blue sticky traps between MEJA-treated and untreated plants (P > 0.05, *Table 1*). However, in the second application period, plants treated with 0.88 mM MEJA had a lower number of hoverflies compared to plants treated with other MEJA doses and control plants, which resulted in a significant reduction of the population density in 0.88 mM MEJA-treated plants over all treatments, including controls ($\chi^2_{2012\text{-}ST} = 23.09$, $P < 0.001$; $\chi^2_{2012\text{-}whole} = 24.80$, $P < 0.001$; *Fig. 2C*). In year 2, there were no differences between treatments in the whole-season data and the treatment periods ($P > 0.05$, *Table 1*).

A larval parasitoid of wheat stem sawfly species; Collyria coxator (Villers) (Hymenoptera: Ichneumonidae)

Sweep-net samplings of *C. coxator*: The population densities of *C. coxator* on the 14.2 mM MEJA-treated plants were higher than on the control plants in the first treatment period of year 1, which resulted in an increase of the *C. coxator* population density in plants treated with the highest MEJA dose over all treatments for the whole-season pooled data ($\chi^2_{2012\text{-}FT} = 10.64$, $P = 0.013$; $\chi^2_{2012\text{-}whole} = 10.07$, $P = 0.017$; *Fig. 2D*). However, there were no significant differences between the population densities of *C. coxator* in MEJA-treated and untreated control plants in the second treatment period of year 1 or in the pooled whole-season data and the treatment periods of year 2 ($P > 0.05$, *Table 1*).

Yellow sticky trap samplings of *C. coxator*: The population densities of *C. coxator*, as determined by yellow sticky traps, were significantly higher on MEJA-treated plants compared to control plants in both whole-season pooled data and the two treatment periods of both experimental years ($\chi^2_{2012\text{-}FT} = 13.19$, $P = 0.004$; $\chi^2_{2012\text{-}ST} = 29.64$, $P < 0.001$; $\chi^2_{2012\text{-}whole} = 41.11$, $P < 0.001$; $\chi^2_{2013\text{-}FT} = 27.37$, $P < 0.001$; $\chi^2_{2013\text{-}ST} = 12.11$, $P = 0.006$; $\chi^2_{2013\text{-}whole} = 37.31$, $P < 0.001$; *Fig. 2E* and *2F*).

Blue sticky trap samplings of *C. coxator*: *C. coxator* population densities, as determined by blue sticky traps, did not differ significantly between MEJA-treated and untreated control plants in both whole-season pooled data and the treatment periods of both years ($P > 0.05$, *Table 1*).

Effects of methyl jasmonate doses on wheat agronomic properties

The mean weights of 75 heads collected from MEJA-treated plants were significantly lower compared to untreated control plants in year 1, whereas the year-2 experiments

showed no differences between or among treatments ($F_{2012} = 10.527$; d$f = 3$, 12; $P = 0.001$; $F_{2013} = 2.326$; d$f = 3$, 8; $P = 0.151$; *Fig. 3*).
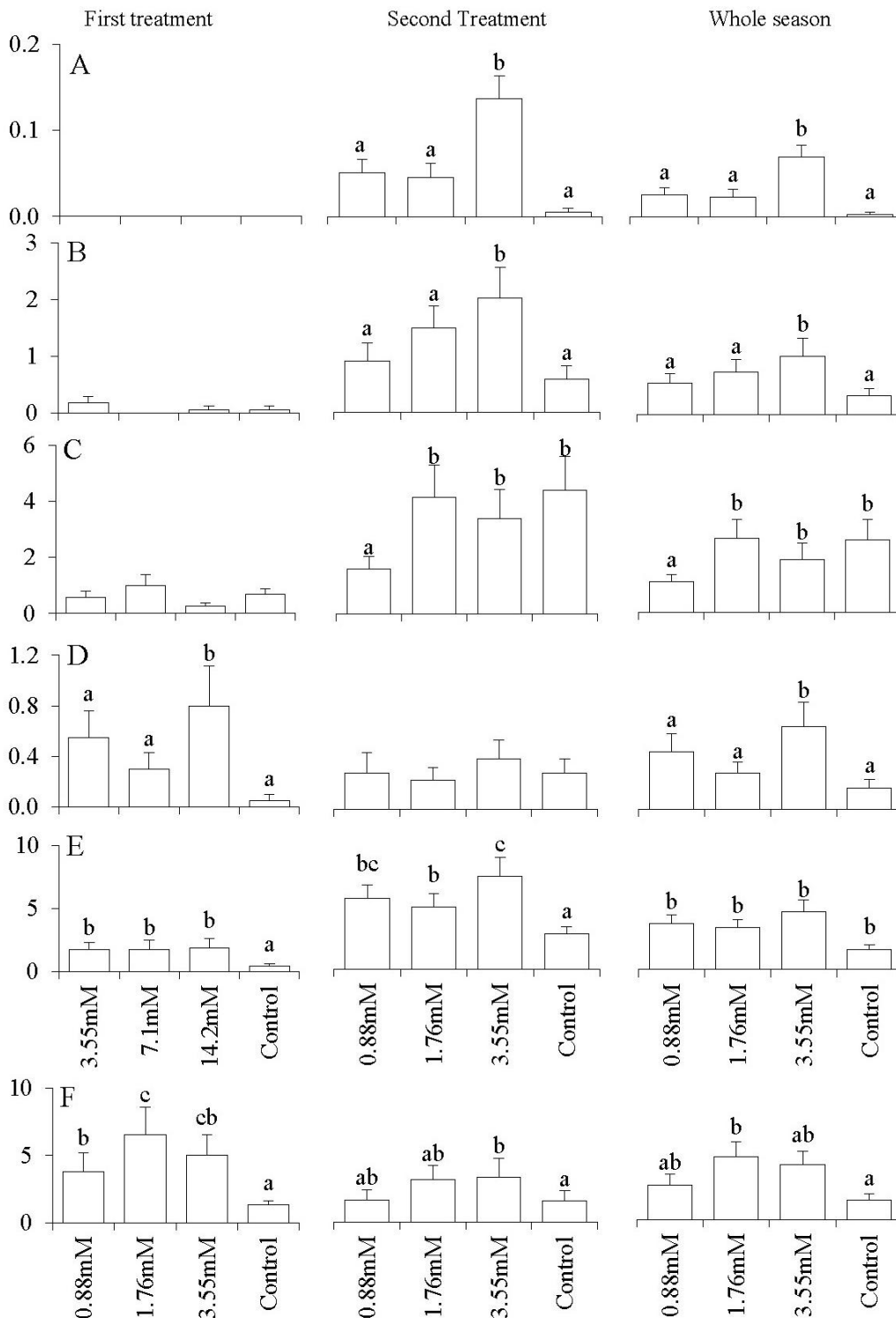

Figure 2. *Mean density (+SEM) of ladybeetles per plant in 2012 (A), ladybeetles/yellow traps in 2012 (B), hoverflies/blue traps in 2012 (C), C. coxator/sweep-net in 2012 (D), C. coxator/yellow traps in 2012 (E) and 2013 (F) in wheat plots treated with different methyl jasmonate doses for first-treatment and second-treatment periods and whole season (Means capped with different letters differ significantly, Tukey's multiple comparison test, P < 0.05)*
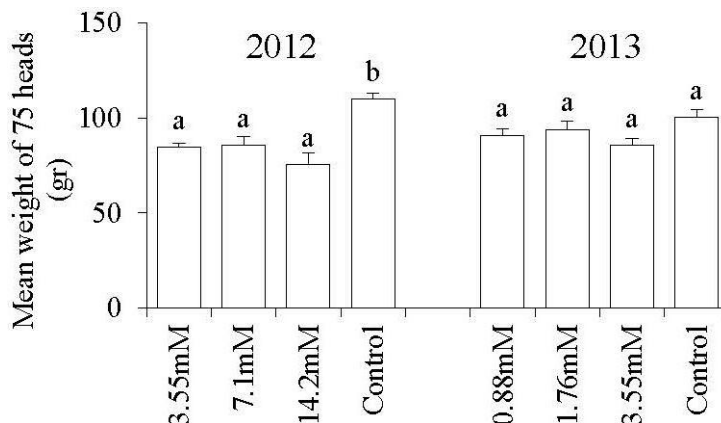
Figure 3. *Mean weight (+SEM) of 75 wheat heads from MEJA-treated and untreated control plants in 2012 (year 1) and 2013 (year 2). Means capped with different letters in the same year differ significantly (Tukey's test: P < 0.05)*

The mean heights of MEJA-treated plants were found to be significantly shorter than those of control plants in both years ($F_{2012} = 137.859$, d$f = 3$, 156, $P < 0.001$; $F_{2013} = 106.402$, d$f = 3$, 116, $P < 0.001$; *Fig. 4*).
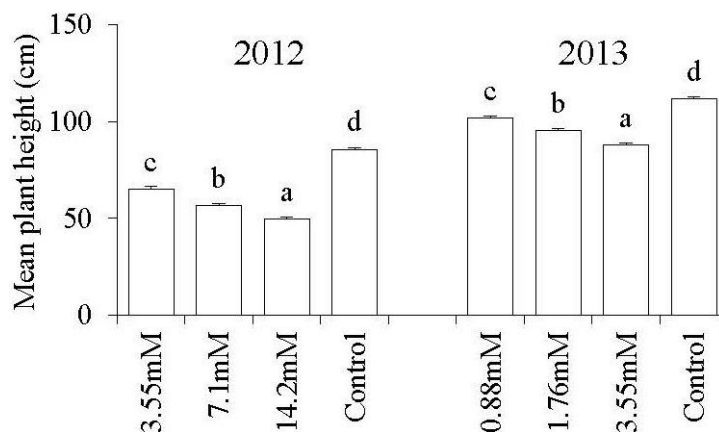
Figure 4. *Mean height (+SEM) of wheat plants from MEJA-treated and untreated plants in 2012 (year 1) and 2013 (year 2). Means capped with different letters in the same year differ significantly (Tukey's test: P < 0.05)*

Discussion

Results of the present study revealed that exogenous MEJA treatments had significant differential effects on both herbivores and their natural enemies in wheat.

Effects of different methyl jasmonate doses on some insect pests

Aphids

The population densities of apterous and alate aphids on MEJA-treated plants were significantly lower than those on control plants in both years, as assessed by direct visual counting, and the population densities of alate aphids determined by yellow sticky traps in MEJA-treated plants were lower than those of control plants in year 2.

However, the sweep-net method registered no differences in aphid densities among wheat plants, treated and untreated. Our results of direct visual sampling and yellow trap sampling are in agreement with results of several previous investigations. For example, the population growth of the mustard aphid *Lipaphis erysimi* on Indian mustard plants (*Brassica juncea*) was reduced by MEJA treatments (Koramutla et al., 2014). In addition, electronic penetration recording data suggested reduced feeding of apterous *R. padi* on MEJA-treated wheat seedlings, which led to a reduction in the population growth of this pest (Slesak et al., 2001). Another population growth test revealed potential population growth- and performance-suppressing effects of MEJA-treated tomato plants on the phloem feeder *M. persicae* (Boughton et al., 2006). Also, the number of *R. padi* settling on MEJA-treated barley (cv. Kara) was found to be lower than for unexposed plants during natural daylight (Glinwood et al., 2007). Further tests revealed that reproductive performance of the Russian wheat aphid *Diuraphis noxia* was lower on barley plants (cv. Makoei) whose parent seeds had been treated with MEJA (Taami and Dolatti, 2013).

Three main jasmonate derivatives — jasmonic acid (JA), *cis*-jasmone (CJ) and MEJA — are known to have repellent, deterrent and/or antixenotic effects on aphid species attacking cereals and cotton (Omer et al., 2001, Bruce et al., 2003; El-Wakeil et al., 2010; El-Wakeil and Volkmar, 2012). The mechanism behind this aphid resistance is multifold and may be due to: increased hydroxamic acid content and inhibition of trypsin activity in wheat; activation of resistance-related enzymes such as polyphenol oxidase and peroxidase in wheat, tomato and Indian mustard; and up-regulation of jasmonate biosynthetic genes in these plants (Slesak et al., 2001; Boughton et al., 2006; Cao et al., 2014; Koramutla et al., 2014). Wild-type *Arabidopsis* and a constitutively active jasmonate signaling mutant both repelled *M. persicae* when treated with MEJA (Ellis et al., 2002). However, despite advances in understanding the molecular mechanisms (e.g. in terms of enzymes, non-enzyme proteins and genes) by which exogenous jasmonate treatment deters aphids, much less is known about the effects of MEJA on aphids under natural conditions.

The significant repellent effects of MEJA on aphids, as detected by visual counting (2012) and yellow traps (2013), occurred in different years. Therefore, whether HIPV treatments encourage apterous aphids to produce alate aphids for 'take-off' remains obscure. Factors like colonization, wind, temperature, day length, light density, moisture, host plant growth stage and its quality are known to play roles in aphid migration (Parry, 2013). Further detailed studies are needed to understand whether HIPVs are one of the factors that induce aphids to migrate.

Phytophagous thrips

The population densities of thrips species on MEJA-treated plants were significantly lower than on control plants in both treatment periods of year 1, according to sweep-net samplings, whereas visual samplings did not reveal any significant difference. To our knowledge, this is the first record of how thrips populations on wheat plants are affected by MEJA treatment, while there is a growing body of evidence on the effects of JA and CJ on thrips populations. For example, JA was found to reduce the population density of thrips species, likely consisting of *H. tritici*, *H. aculeatus*, *L. denticornis*, *F. teucornis* and *T. angusticeps*, on wheat plants (El-Wakeil et al., 2010; El-Wakeil and Volkmar, 2012). Another study indicated that performance and preference of *F. occidentalis* was

restricted by JA application on *Arabidopsis* and *Brassica rapa* plants (Abe et al., 2009). MEJA and CJ were found to have deterrent effects on second instar larva of *F. occidentalis* on leaf dics of the bean *Faseolus vulgaris* in choice settlement assays (Egger and Koschier, 2014). In addition, the deterrent effects of jasmonates on feeding and oviposition by thrips were improved when combined with allylanisole (Egger et al., 2014). Jasmonates are also known to induce the formation of glandular trichomes, thus increasing the number of thrips entrapped by these plant-defense structures (Boughton et al., 2005). Furthermore, jasmonate-inducible defenses of tomato plants (i.e. proteinase inhibitors and polyphenol oxidase) were found to attenuate a community of herbivores, including a thrips species, *F. occidentalis* (Thaler et al., 2001). Apparently, jasmonate applications are responsible for inducing different defense mechanisms in plants and negatively affecting thrips performance and plant preference.

Wheat stem sawflies

MEJA may be a promising attractant for wheat stem sawfly adults, as their numbers were higher on MEJA-treated plants than on control plants, based on sampling by yellow sticky traps in our study, although data from the other sampling methods did not show significance. However, in our previous study, we found that the outcome of CJ on wheat stem sawflies is influenced by the sampling method, with more consistent results obtained from yellow sticky traps and indicating that CJ is repellent to wheat stem sawfly adults (Bayram and Tonğa, 2017). CJ-treated wheat plants release a group of HIPVs, one of which ((Z)-3-hexenyl acetate) repels the wheat stem sawfly *C. cinctus* at high doses while attracting it at lower concentrations (Piesik et al., 2008; Delaney et al., 2013). The same very high MEJA doses that we used in our study induced faster maturation of wheat plants in another study (Beltrano et al., 1998); therefore, in our field experiments, such faster growth may have limited the production of HIPVs like (Z)-3-hexenyl acetate, causing the compounds to remain at attractive (lower) concentrations after MEJA treatment. Nevertheless, such opposite results for chemicals belonging to the same biosynthetic pathway could be beneficial to "trap and kill" or "push-pull" pest management systems. In our studies, we did not assess oviposition-related parameters, e.g., eggs laid in each plant or the number of wheat stem sawfly females trapped. However, discovering the roles of HIPVs in the ovipositional behavior of wheat stem sawflies could help in developing these control strategies.

Effects of methyl jasmonate treatments on parasitoids and predators of wheat pests

Aphid parasitoids

The population densities of aphid parasitoids sampled from different MEJA-treated wheat plants in this study were not significantly different from those of control plants. In a previous field experiment, MEJA-baited traps were found to be attractive to parasitoids from the family Braconidae (James, 2005). Electroantennogram studies revealed that the parasitic braconid wasp *Microplitis croceipes* responds to MEJA (Park et al., 2001). Testing of CJ on aphid parasitoids showed it to be an attractant. For example, in wind tunnel studies, *A. ervi* was attracted to vapor exposure of CJ-treated *Vicia faba* plants (Birkett et al., 2000). Moreover, plant defenses induced by CJ in *Arabidopsis* attracted *A. ervi*, a generalist aphid parasitoid, but had no influence on *Diaeretiella rapae*, a specialist aphid parasitoid (Bruce et al., 2008). Dewhirst et al.

(2012) found that HIPVs released from CJ-applied *Capsicum annum* plants were preferred by *A. ervi* and encouraged its foraging time. To our knowledge, the present study is the first report of aphid parasitoid responses to MEJA under field conditions. Our data are not in agreement with the above-mentioned CJ studies, but this could be due to the different jasmonate derivates investigated, the different species studied (host plant, insect pest, parasitoid), the phytotoxic effects of the MEJA doses, experiment type and/or ecological factors.

Lady beetles

Direct visual and yellow trap samplings showed that there were significant attractive effects of MEJA treatments on lady beetles, although these effects were not found based on sweep-net and blue sticky trap samplings. A previous study showed that persimmon plants infested with the herbivorous Japanese wax scale, *Ceroplastes japonicus* (Hemiptera: Coccidae), and persimmon plants treated with MEJA, released the terpenoid α-pinene, which was found to be a strong attractant to virgin female lady beetles of the species *Chilocorus kuwanae* (Coleoptera: Coccinellidae) (Zhang et al., 2009). In addition, an earlier study reported that CJ-impregrated filter papers were preferred over control arms by the seven-spotted lady beetle *C. septempunctata* in olfactometer studies (Birkett et al., 2000).

Hoverflies

The blue sticky trap sampling results in our study, but none of the other sampling methods we used, indicated an effect of MEJA on hoverflies (adults), suggesting a possible deterrent effect. In an earlier study, hoverflies did not positively respond to MEJA-baited traps in field tests (James, 2005). Thaler, (2002) found that JA-reduced aphid density was correlated with reduced numbers of hoverfly eggs, supporting the theory that hoverflies mostly employ visual cues to locate their hosts. Studies on the behavioral responses of *Episyrphus balteatus*, another hoverfly species, revealed that this hoverfly employs a composition of cues consisting of plant volatiles (i.e., green leaf volatiles and terpenoids) and a host pheromone(s) (Verheggen et al., 2008). Exogenous CJ application caused wheat plants to release volatiles such as (Z)-3-hexen-1-ol, which was found to contribute to host-plant locating and ovipositional behavior of the hoverflies (Verheggen et al., 2008; Delaney et al., 2013). A possible explanation is that the phytotoxic effects of MEJA may change both the chemical profile and the visual appearance of plants so that hoverflies may fail to locate their prey.

Collyria coxator

The population densities of *C. coxator*, a wheat stem sawfly larval parasitoid, were significantly higher in MEJA-treated wheat plants compared to control plants, according to both sweep-net and yellow sticky trap samplings. Our previous findings indicated that CJ is similarly attractive to *C. coxator* adults in field experiments (Bayram and Tonğa, 2017). The chemical ecology of *C. coxator* is not well-known. Thus, further investigations indicating how *C. coxator* adults respond either to jasmonates or to changes in the chemical profile of wheat after jasmonate treatment are highly suggested.

Agronomic properties

Results of our experiments revealed that MEJA applications significantly reduced wheat yield. Our findings confirm previous results by Beltrano et al. (1998). They reported that MEJA treatments accelerated wheat senescence and shortened the grain-filling period, resulting in reduced yield. Similar yield-decreasing effects of MEJA were also observed in rice (Kim et al., 2009a). However, the inflence of MEJA on plants can vary; for example, MEJA-treated rice and wheat plants under drought conditions had higher yields (Kim et al., 2009b; Anjum et al., 2016). Therefore, the effects of MEJA might be dependent on environmental conditions such as drought or MEJA dosage, where high doses are phytotoxic (Boughton et al., 2006; Anjum et al., 2016). We observed such phytotoxic effects in the present study, in that the heights of plants (the above-ground parts) treated with MEJA grew shorter than those of untreated control plants. These results are concordant with previous investigations in which it was found that MEJA treatments stunted the height of Scots pine (*Pinus sylvestris* L., Pinaceae) seedlings (Heijari et al., 2005).

Our results indicate that exogenously applied MEJA could act as a repellent against some piercing-sucking wheat pests (aphids and thrips) and as an attractant for wheat stem sawfly adults. In addition, some natural enemies of insect herbivores (lady beetles and *C. coxator*) were attracted to MEJA-treated plants whereas hoverflies were repelled and braconid aphid parasitoids were not affected either way. These results could be exploited to benefit integrated pest management programs, especially in push-pull strategies, when a certain pest is targeted. The effects of MEJA doses on different species varied depending on the plant growth stage. MEJA doses tested in our study had adverse effects on some agronomic features of wheat. Therefore, our results suggest that the roles of lower doses of MEJA in plant defense induction should be taken into consideration in future studies. Our study lacks of phytochemical analysis of wheat volatile chemical changes after MEJA treatment, so that further studies providing such data are needed to support our field-experiment findings.

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