

Cotton treatment with methyl jasmonate at different growth stages reduces the population of sucking insect pests and marginally increases their associated predators

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Abstract

Methyl jasmonate (MEJA), a volatile organic compound, can induce plant defenses, thereby contributing to repelling insect pests and attracting their natural enemies. In 2013 and 2014, the influence of three exogenous MEJA doses (0.88, 1.76, and 3.55 mM) under field conditions was investigated on the abundance of the cotton pests *Thrips tabaci* Lindeman (Thysanoptera: Thripidae), *Empoasca decipiens* Paoli (Hemiptera: Cicadellidae), and *Aphis gossypii* Glover (Hemiptera: Aphididae), as well as of the predators *Coccinella septempunctata* L. (Coleoptera: Coccinellidae), *Aeolothrips intermedius* Bagnall (Thysanoptera: Aeolothripidae), and *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae). The MEJA treatments were performed at three cotton plant growth stages: 6–8 true leaves-early squaring, square bud, and boll forming. The abundances of *A. gossypii*, *T. tabaci*, and *E. decipiens* varied considerably among strata and growing seasons and between experimental years, but overall they were lower on MEJA-treated cotton plants than on control plants. The population density of *A. intermedius* and *C. septempunctata* did not differ between MEJA-treated and control plants, whereas the intermediate MEJA concentration had an attractive but inconsistent effect on *C. carnea*. Most of the insect pests and predators showed a preference for specific plant strata. The abundance of *T. tabaci* was higher in earlier plant growth stages, whereas *A. gossypii* and *E. decipiens* were more abundant in later growth stages. Our results demonstrate the deterrent effects of MEJA-induced cotton plants on sucking pests and suggest that MEJA could be exploited as a non-toxic pest management tool. Possible mechanisms underlying the effectiveness of MEJA-mediated cotton plant responses to insect pests are discussed.

KEYWORDS

cotton, elicitor, generalist predators, jasmonate, sucking insect pests, plant growth, *Thrips tabaci*, *Empoasca decipiens*, *Aphis gossypii*, *Coccinella septempunctata*, *Aeolothrips intermedius*, *Chrysoperla carnea*

INTRODUCTION

Cotton, *Gossypium hirsutum* L. (Malvaceae), is planted annually on approximately 500 000 ha in Turkey and constitutes a

significant cash crop (TUIK, 2019). Cotton plants suffer from damage by a wide range of economically important insect pests for most of the growing season in Turkey. Among important sucking insect pests are onion thrips, *Thrips tabaci*

Lindeman (Thysanoptera: Thripidae), leafhopper *Empoasca decipiens* Paoli (Hemiptera: Cicadellidae), and cotton aphid, *Aphis gossypii* Glover (Hemiptera: Aphididae).

Adults and larvae of *T. tabaci* rasp and pierce the surface of fresh cotton leaves and shoots. Their feeding in early plant growth stages is important, as the damaged plant parts grow over time and obtain silvery streaks, which could cause a delay in maturation and yield losses (Anonymous, 2008). *Aphis gossypii* feeds on the abaxial surface of host plant foliage, resulting in deformation of leaves and buds, which causes stunting (Leite et al., 2006). Development of fungi upon honeydew excretion by *A. gossypii* causes sooty mold formation, which lowers plants' photosynthetic capacity (Leite et al., 2006). *Empoasca decipiens* adults and larvae suck the sap from host leaves, inject their saliva, and lay their eggs into plant tissues (Raupach et al., 2002; Backus et al., 2005). A dynamic interaction between *E. decipiens* feeding and the specific response of host plants causes hopperburn disease, which is followed by curling, discoloration, and desiccation of leaves (Backus et al., 2005).

The presence of insect pests throughout the growing season can lead to the use of multiple insecticide treatments to prevent damage and yield losses. Alternative control strategies are required to reduce the use of insecticides, such as inducible plant resistance and natural enemies (Vet & Dicke, 1992; Choudhary et al., 2008). Plants, upon herbivore attack, release herbivore-induced plant volatiles (HIPVs), which play two main roles in plant defense: (1) repelling conspecifics of the herbivores, and (2) attracting their natural enemies (Dicke & van Loon, 2000). Such defense mechanisms can be triggered by exogenous treatments of synthetic elicitors such as methyl jasmonate (MEJA) (Williams et al., 2017; Bayram & TonĀ, 2018a). Compared with other jasmonate derivatives, MEJA is more active and volatile, especially when used exogenously (Beltrano et al., 1998; Horbowicz et al., 2009). Exogenous MEJA treatments induce defenses against herbivores in a wide range of plant taxa, including crop and non-crop plants (Rodriguez-Saona et al., 2001; Heijari et al., 2005; Erbilgin et al., 2006; Rohwer & Erwin, 2010; Tan et al., 2011; Williams et al., 2017). For example, MEJA-treated cotton, tomato, potato, soybean, and Indian mustard plants [*Brassica juncea* (L.) Czern] negatively affected the population growth of the aphids *A. gossypii*, *Myzus persicae* (Sulzer), *Macrosiphum euphorbiae* (Thomas), *Aphis glycines* Matsumura, and *Lipaphis erysimi* (Kaltenbach), respectively (Boughton et al., 2006; Brunissen et al., 2010; Koramutla et al., 2014; Selig et al., 2016; Williams et al., 2017). Additionally, MEJA plays a role in the induction of soybean plant responses to soybean thrips, *Neohydatothrips variabilis* (Beach) (Selig et al., 2016).

As inducible plant responses, volatile organic compounds (VOCs) play crucial roles for predators in locating suitable prey or hosts, on herbivore-infested host plants. For example, the predatory seven-spotted ladybird, *Coccinella septempunctata* L. (Coleoptera: Coccinellidae),

and the common green lacewing, *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae), employ VOCs released by elicitor- or herbivore-induced plants and traps loaded with such compounds in field conditions, and prefer these compounds over control arms in olfactometer studies (Zhu et al., 1999; Al Abassi et al., 2000; Zhu & Park, 2005; Yu et al., 2008, 2018; Williams et al., 2017; Bayram & TonĀ, 2018a,b; TonĀ et al., 2020). The compound MEJA serves as an indirect defense cue for ladybirds, e.g., MEJA-treated persimmon plants (*Diospyros kaki* L. fil.) were attractive to *Chilocorus kuwanae* Silvestri (Zhang et al., 2009). Also, wheat plants treated with various MEJA doses were attractive to a ladybird species community, the majority of which was represented by *C. septempunctata*, under field conditions (Bayram & TonĀ, 2018b). However, a recent study in cotton under field conditions showed that MEJA-treated plants did not affect a ladybird species community consisting of four coccinellid species, *C. septempunctata*, *Harmonia axyridis* (Pallas), *Hippodamia convergens* Guérin-Méneville, and *Coleomegilla maculata* (DeGeer) (Williams et al., 2017). Knowledge of the behavioral responses of cotton insect pests and their natural enemies to MEJA-treated host plants is scarce.

Most likely dependent on plant growth stage (plant phenology), temporal variation in abundance of cotton insect pests is a key component of the decision-making process in integrated pest management strategies (Visschers et al., 2019). Therefore, each cotton growth stage might require specific attention in terms of pest management practices. Thus, to control continuous populations of insect pests at subsequent growth stages, several exogenous elicitor treatments may be required (Williams et al., 2017; Bayram & TonĀ, 2018a,b; TonĀ et al., 2020). In addition, the feeding preference of insect pests and their natural enemies within a plant can affect the accurate quantification of insect population densities. This preference is dependent on morphological and phytochemical characteristics of the host plant leaves, due to differences in the plant's defensive profiles between young and old leaves (Gazola et al., 2019). Several studies have evaluated the within-plant distribution of insect pests and predators in cotton (Wilson & Gutierrez, 1980; Nibouche et al., 2004; Fernandes et al., 2012a,b; Reay-Jones et al., 2017). However, the behavioral responses of insect pests and their natural enemies to elicitor-induced cotton leaves at different strata (positions) remains unclear.

The main aim of our study was to investigate the influence of three MEJA doses on the presence of sucking insect pests and their generalist predators in cotton under field conditions. Exogenous MEJA treatments were applied at three plant growth stages, to provide sustained defenses against insect pests throughout the growing season. Also, the abundance of insects on three plant strata was sampled, to reveal how pest and predator insects occur on plant strata in response to MEJA treatments.

MATERIAL AND METHODS

Field experiments

Cotton plants (*G. hirsutum* cv. Stoneville 468) were sown on 15 May 2013 and 20 May 2014 at the experimental farm of the Agriculture Faculty of Dicle University, Diyarbakır, Turkey (37°53'23"N, 40°16'33"E). Stoneville 468 is commercially available and widely cultivated in southeastern Turkey. A randomized complete block design included 16 plots with four treatments ($n = 4$). Each plot consisted of eight rows, and plots were 12 m long (70 cm space between rows, 20 cm space between plants). Each plot contained 460–500 plants. The distance between plots and blocks was at least 6 m. Three sides of the experimental area were cotton fields and the remaining side was a field path. The distance between the experimental area and the surrounding areas was at least 15 m.

A cotton drilling machine was employed for cultivation. Plots received an equal amount of fertilizer (160 kg ha⁻¹ nitrogen and 80 kg ha⁻¹ P₂O₅). Half of the nitrogen and all P₂O₅ was provided at the sowing stage, the second half of the nitrogen was supplied at the squaring stage (fruiting bud forming) as ammonium nitrate (Gübretaş, Istanbul, Turkey). There were no pesticide (i.e., insecticide, herbicide, and fungicide) treatments. Water was supplied to plot furrows when needed.

Methyl jasmonate treatments

Three doses of MEJA ($\geq 95\%$ purity; Sigma Aldrich, Burlington, MA, USA) were diluted in distilled water (D1 = 0.88 mM, D2 = 1.76 mM, and D3 = 3.55 mM) followed by adding 0.1 ml l⁻¹ of an aqueous surfactant (Silwet Gold, active ingredients: polyalkaleneoxide-heptamethyl trisiloxane and allyloxypolyethyleneglycol; Chemtura, Shelton, CT, USA) (Bayram & Tonğa, 2018a). The treatments were applied using a backpack sprayer (Matabi, Antzuola, Spain) with a cone nozzle (0.8 l per min). During treatments, all plants were covered as evenly as possible with the required amount of spray volume (200 l ha⁻¹). The control treatment (C) was distilled water with the same surfactant concentration. Three time-treatments were performed at three plant growth stages in both years. The first, second, and third treatments were applied at the plant growth stages: (1) 6–8 true leaves-early squaring (GS1: 28 June 2013 and 26 June 2014), (2) square bud stage (GS2: 20 July 2013 and 12 July 2014), and (3) boll forming stage (GS3: 16 August 2013 and 4 August 2014), respectively. Three MEJA treatments were applied based on previous studies suggesting that multiple exogenous jasmonate treatments are required in field conditions to sustain induced plant defense throughout the season (Williams et al., 2017; Bayram & Tonğa, 2018a,b; Tonğa et al., 2020).

Each plot received the same dose in all treatments. The mean temperature in June, July, and August was 26.2, 30.8, and 29.9 °C in 2013, and 26.0, 30.9, and 30.4 °C in 2014, whereas relative humidity was 32.3, 23.5, and 23.0% in 2013, and 33.6, 26.0, and 24.1% in 2014, respectively. Long-term representative mean precipitation in the study area is 8.0, 0.7, and 0.4 mm in June, July, and August, respectively. Climatic conditions were seasonally normal throughout the experiments. However, to mitigate possible negative effects of high temperatures and intense sunlight during midday and possible wind flow in the evening hours, MEJA treatments were performed at 17:00–18:00 hours.

Visual plant sampling procedure

Visual plant sampling was performed to avoid any possible mechanical damage by sampling tools such as sweepnet or D-vac, as defense mechanisms of mechanically induced plants could interfere with changes in settlement preference of insects and cause bias in sampling throughout the cotton growing season (Heil & Bueno, 2007). Five plants per plot were randomly selected and sampled visually. Because insect pests and associated natural enemies may prefer a distinct plant stratum for habituation, likely depending on the morphological and chemical characteristics of the leaves, one leaf from each stratum (lower, middle, and upper) was sampled to represent the insect population densities accurately, using a hand magnifier (5 \times). All biological stages of encountered insects were recorded. Uniform samplings were recorded between late afternoon and early evening (16:00–19:00 hours), as the optimum sampling time to minimize possible extreme variation in the activity and distribution of insects (Atakan, 2011). Plants were haphazardly chosen by zigzagging among rows. The outer plant rows in each plot were considered as a buffer zone and were not sampled.

Regular samplings were performed at weekly intervals starting in early June until the end of the third plant growth stage (late August) to monitor pest and predator insect abundances, plant growth stages, plant strata, and to decide the optimal treatment time of MEJA. All plots were resampled 1 day prior and 1, 2, 4, 7, and 14 days after MEJA treatments. Plants were 44 and 37 days old when the first sampling was performed in 2013 and 2014, respectively.

Statistical analysis

Data associated with the abundances of pest and predator insects for the three plant strata (lower, middle, and upper), plant growth stages (GS1, GS2, and GS3), and MEJA treatments (three doses) were checked for normality and homogeneity of variances with Shapiro-Wilk's test

and Levene's test, respectively ($\alpha = 0.05$). Because our data were longitudinal and did not meet assumptions of linear models, data of each year were separately analyzed fitting a generalized linear mixed model (GLMM, 'lme4' package) with Poisson error distribution (log link function) (Bates et al., 2015). Thus, we revealed the effects of factors involved in the model on insect abundance. In the initial model, MEJA dose, plant stratum, and plant growth stage were set as fixed factors, whereas sampling date was considered as a random factor (Bayram et al., 2007; Bayram & TonĀ, 2018a,b; TonĀ et al., 2020). Likelihood ratio (LR) tests were done for the effects of fixed factors ($\alpha = 0.05$). When the influence of plant growth stage or its interaction with other fixed factors was significant, data on relevant species were analyzed within the plant growth stage separately, considering MEJA dose, plant stratum, and their interaction as fixed factors, and sampling dates as random factors. Afterwards, MEJA doses, plant strata, and plant growth stages were compared with Tukey's post-hoc tests ($\alpha = 0.05$), employing the 'glht' function of the 'multcomp' package. All analyses were conducted using R v.3.6.1 (R Core Team, 2019).

RESULTS

In total, 12 insect species (four pests and eight predators) were recorded, belonging to five orders and 10 families. The abundances of insect species frequently found and in sufficient numbers were analyzed by GLMM, i.e., three pests (*A. gossypii*, *T. tabaci*, and *E. decipiens*) and three

predators [*Aeolothrips intermedius* Bagnall (Thysanoptera: Aeolothripidae), *C. carnea*, and *C. septempunctata*]. *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae), *Scymnus* spec. (Coleoptera: Coccinellidae), *Orius vicinus* (Ribaut) and *Orius niger* (Wolff) (Hemiptera: Anthocoridae), *Nabis pseudoferus* Remane (Hemiptera: Nabidae), and *Deraeocoris pallens* Reuter (Hemiptera: Miridae) were excluded from statistical evaluations due to their very low densities during experiments.

Insect pests

Thrips tabaci

Phytophagous thrips abundance on cotton plants was significantly affected by the factors MEJA dose, plant stratum, plant growth stage, and several of their interactions, in both study years (Table 1; Figure 1). When treated plant growth stages were evaluated separately, almost all effects of dose, plant stratum, and their interactions were significant (Table 1). Overall, the number of *T. tabaci* in MEJA-treated cotton plots was lower than in control plots throughout the study, except in GS3 in 2013. Pooled plant stratum data revealed the highest number of *T. tabaci* on upper cotton leaves and the lowest number on lower leaves. The lowest phytophagous thrips density was recorded in plots treated with the highest MEJA concentration (D3) in lower plant leaves in GS2 in 2013. The highest densities were recorded in GS1 in 2013 and in GS1 and GS2 in 2014 (Figure 1).

TABLE 1 Generalized linear mixed models (GLMM) for the influence of methyl jasmonate dose, plant stratum, treated plant growth stage, and their interactions on the abundance of *Thrips tabaci* in field plots of cotton plants with three time-treatments [at three plant growth stages: GS1 (6–8 true leaves-early squaring), GS2 (square bud), and GS3 (boll forming)] in 2013 and 2014

Treatment	Factors	d.f.	2013		2014	
			χ^2	P	χ^2	P
Overall	Dose (D)	3	138.94	<0.001	192.10	<0.001
	Stratum (S)	2	1012.82	<0.001	3283.93	<0.001
	Growth stage (GS)	2	32.56	<0.001	26.37	<0.001
	D*S	6	7.80	0.25	14.91	0.021
	D*GS	6	8.39	0.21	25.11	<0.001
	S*GS	4	34.57	<0.001	21.24	<0.001
	D*S*GS	12	28.74	0.004	39.69	<0.001
GS1	D	3	107.27	<0.001	33.86	<0.001
	S	2	614.65	<0.001	1337.66	<0.001
	D*S	6	8.65	0.19	25.28	<0.001
GS2	D	3	36.75	<0.001	160.44	<0.001
	S	2	365.73	<0.001	1477.88	<0.001
	D*S	6	21.54	0.001	19.14	0.003
GS3	D	3	3.37	0.33	22.54	<0.001
	S	2	67.59	<0.001	487.92	<0.001
	D*S	6	6.34	0.39	10.21	0.12

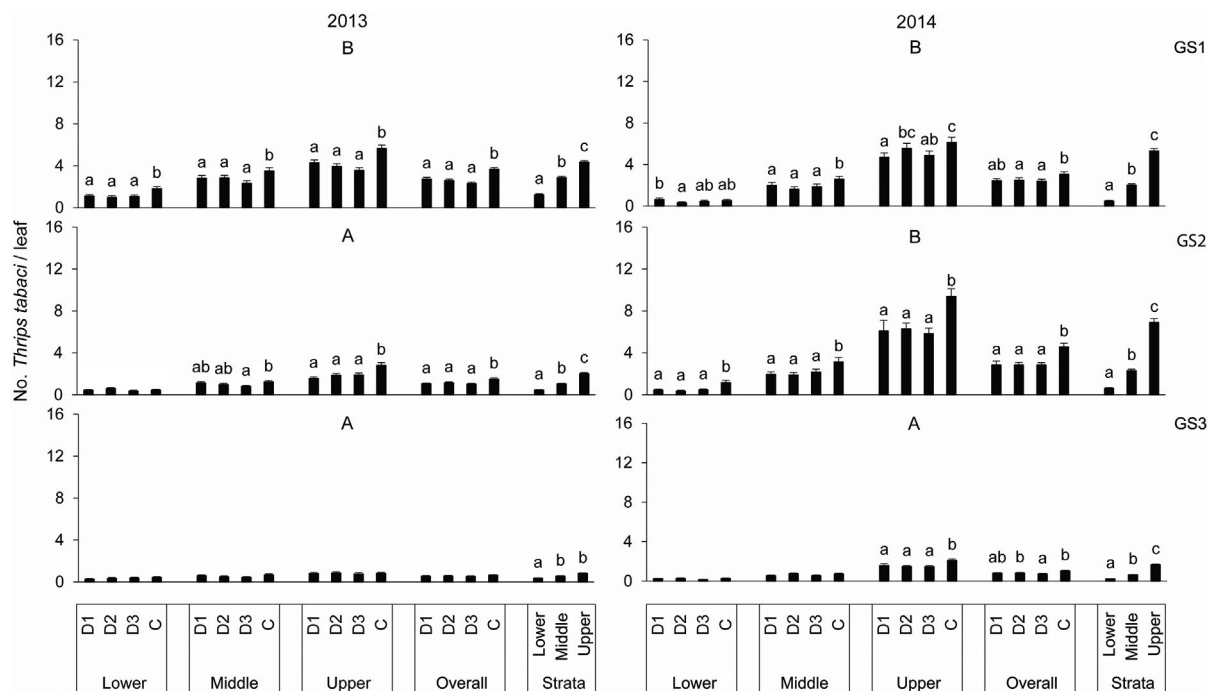


FIGURE 1 Mean (+ SE) number of *Thrips tabaci* on leaves of three strata (lower, middle, upper) of cotton plants of three growth stages (GS1: 6–8 true leaves-early squaring; GS2: square bud; GS3: boll forming) treated with three concentrations of methyl jasmonate (D1: 0.88 mM; D2 = 1.76 mM; D3 = 3.55 mM) or untreated (control, C) in field plots in 2013 and 2014. Means within each group of 3–4 treatments within a panel capped with different lowercase letters are significantly different (Tukey test: $P < 0.05$). Uppercase letters indicate significant differences between plant growth stages within a year (Tukey test: $P < 0.05$)

Empoasca decipiens

In 2013, the effects of all factors on the abundance of *E. decipiens* were significant, whereas in 2014 the influences of MEJA dose, plant stratum, and several interactions were significant (Table 2; Figure 2). When growth stages were evaluated separately, only plant stratum had significant effects in all growth stages in both years. The abundance of *E. decipiens* was variable among strata and growing seasons and between experimental years, but in general, leafhopper density in MEJA-treated cotton plants was lower than in the control plants. Lower plant strata hosted the highest leafhopper densities, and the lowest densities were present in the upper strata. In 2013 and 2014, the highest leafhopper densities were recorded in GS2 (Figure 2).

Aphis gossypii

The abundance of *A. gossypii* was significantly affected by all factors and their interactions in 2013, whereas in 2014 the effects of MEJA dose, plant stratum, plant growth stage, and dose \times plant stratum interaction were significant (Table 3; Figure 3). When growth stages were evaluated separately, dose, plant stratum, and their interaction had no significant effects in GS1 in both years and in GS2 in 2014, whereas the influences

of these variables were significant in GS2 in 2013 and in GS3 in both years. The abundance of *A. gossypii* was lower in MEJA-treated cotton plants than in untreated plants in 2013, but in 2014 MEJA treatment did not affect aphid abundance. In 2013, aphid abundance was highest in GS2 and GS3, and in 2014 it was highest in GS3 (Table 3; Figure 3).

Predators

Aeolothrips intermedius

The mean density of predatory thrips was differentially affected by MEJA dose, plant growth stage, and plant stratum in both years. In 2013, dose and plant stratum had no significant main effect on abundance, whereas plant growth stage and various interactions did have significant effects. In 2014, the effects of plant stratum, plant growth stage, and their interaction were significant (Table 4; Figure 4). Varying results also occurred when each plant growth stage was separately investigated. For example, dose significantly influenced *A. intermedius* abundance only in GS2 in 2013, plant stratum affected abundance in all plant growth stages except GS1 in 2013. In general, middle and upper leaves had a higher number of *A. intermedius* than lower leaves. The highest densities of *A. intermedius* were recorded in GS3 in 2013 and in GS2 in 2014 (Table 4; Figure 4).

TABLE 2 Generalized linear mixed models (GLMM) for the influence of methyl jasmonate dose, plant stratum, treated plant growth stage, and their interactions on the abundance of *Empoasca decipiens* in field plots of cotton plants with three time-treatments [at three plant growth stages: GS1 (6–8 true leaves-early squaring), GS2 (square bud), and GS3 (boll forming)] in 2013 and 2014

Treatment	Factors	d.f.	2013		2014	
			χ^2	P	χ^2	P
Overall	Dose (D)	3	39.54	<0.001	14.93	0.001
	Stratum (S)	2	1400.81	<0.001	241.72	<0.001
	Growth stage (GS)	2	24.01	<0.001	1.56	0.46
	D*S	6	15.99	0.013	8.20	0.22
	D*GS	6	25.23	<0.001	16.43	0.011
	S*GS	4	55.98	<0.001	128.08	<0.001
GS1	D	3	24.40	<0.001	7.41	0.059
	S	2	146.62	<0.001	38.21	<0.001
	D*S	6	34.83	<0.001	9.96	0.13
GS2	D	3	19.13	<0.001	9.12	0.027
	S	2	433.02	<0.001	160.78	<0.001
	D*S	6	23.83	<0.001	6.21	0.40
GS3	D	3	19.77	<0.001	16.43	<0.001
	S	2	880.22	<0.001	175.47	<0.001
	D*S	6	4.51	<0.001	8.16	0.23

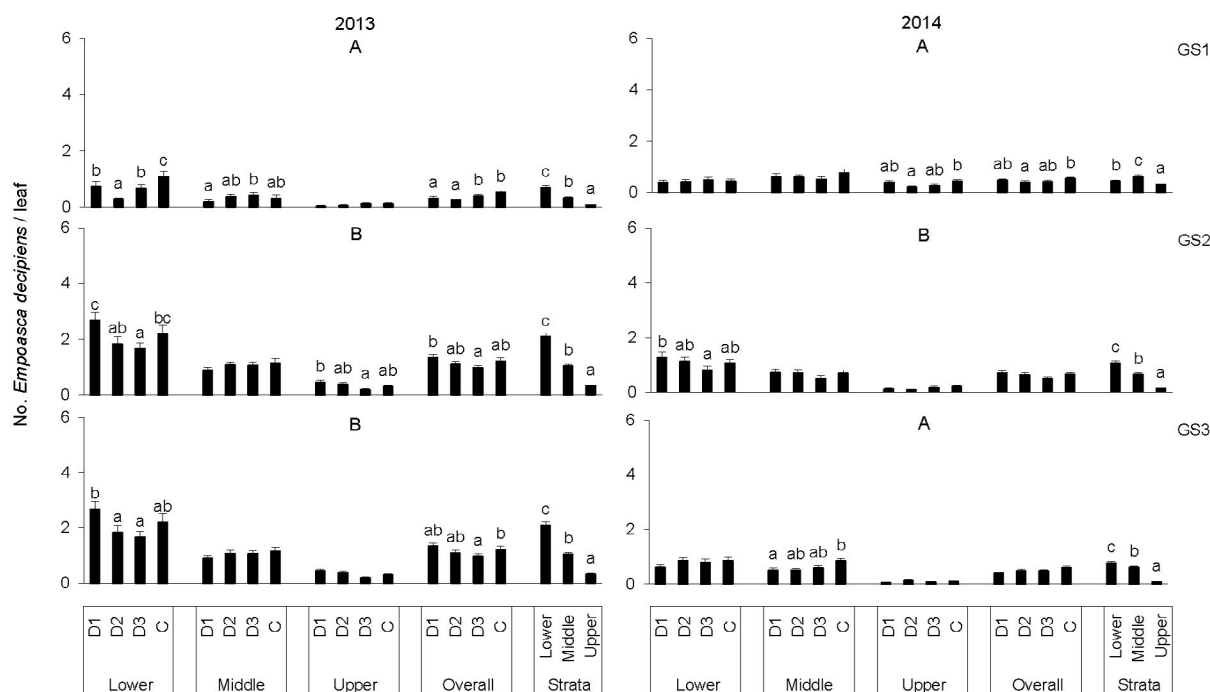
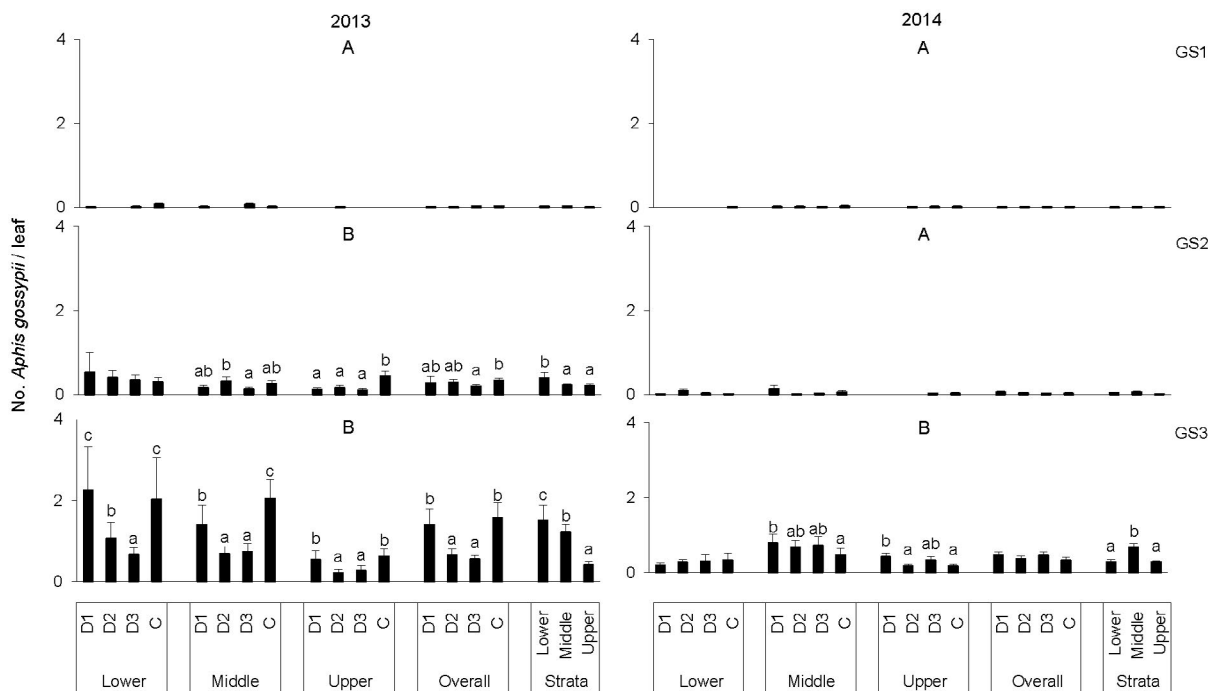


FIGURE 2 Mean (+ SE) number of *Empoasca decipiens* on leaves of three strata (lower, middle, upper) of cotton plants of three growth stages (GS1: 6–8 true leaves-early squaring; GS2: square bud; GS3: boll forming) treated with three concentrations of methyl jasmonate (D1: 0.88 mM; D2 = 1.76 mM; D3 = 3.55 mM) or untreated (control, C) in field plots in 2013 and 2014. Means within each group of 3–4 treatments within a panel capped with different lowercase letters are significantly different (Tukey test: $P < 0.05$). Uppercase letters indicate significant differences between plant growth stages within a year (Tukey test: $P < 0.05$)

TABLE 3 Generalized linear mixed models (GLMM) for the influence of methyl jasmonate dose, plant stratum, treated plant growth stage, and their interactions on the abundance of *Aphis gossypii* in field plots of cotton plants with three time-treatments [at three plant growth stages: GS1 (6–8 true leaves-early squaring), GS2 (square bud), and GS3 (boll forming)] in 2013 and 2014

Treatment	Factors	d.f.	2013		2014	
			χ^2	P	χ^2	P
Overall	Dose (D)	3	231.75	<0.001	51.95	<0.001
	Stratum (S)	2	269.51	<0.001	133.88	<0.001
	Growth stage (GS)	2	74.52	<0.001	133.21	<0.001
	D*S	6	41.32	<0.001	32.96	<0.001
	D*GS	6	55.59	<0.001	17.22	0.10
	S*GS	4	51.86	<0.001	12.34	0.19
	D*S*GS	12	31.23	0.001	8.84	0.72
GS1	D	3	3.73	0.29	0.591	0.90
	S	2	0.05	0.97	0.842	0.66
	D*S	6	5.06	0.54	0.862	0.99
GS2	D	3	12.38	0.006	7.77	0.10
	S	2	27.83	<0.001	0.95	0.81
	D*S	6	34.15	<0.001	9.37	0.15
GS3	D	3	209.15	<0.001	10.83	0.012
	S	2	220.88	<0.001	100.11	<0.001
	D*S	6	18.15	<0.001	22.97	<0.001

**FIGURE 3** Mean (+ SE) number of *Aphis gossypii* on leaves of three strata (lower, middle, upper) of cotton plants of three growth stages (GS1: 6–8 true leaves-early squaring; GS2: square bud; GS3: boll forming) treated with three concentrations of methyl jasmonate (D1: 0.88 mM; D2 = 1.76 mM; D3 = 3.55 mM) or untreated (control, C) in field plots in 2013 and 2014. Means within each group of 3–4 treatments within a panel capped with different lowercase letters are significantly different (Tukey test: $P < 0.05$). Uppercase letters indicate significant differences between plant growth stages within a year (Tukey test: $P < 0.05$)

Coccinella septempunctata

None of the factors affected *C. septempunctata* abundance in the overall pooled data for both years (Table 5; Figure 5). When

plant growth stages were evaluated separately, the single factor that significantly affected abundance was plant stratum in GS1 in 2013; upper and middle leaves had a higher number of *C. septempunctata* than lower leaves (Table 5; Figure 5).

TABLE 4 Generalized linear mixed models (GLMM) for the influence of methyl jasmonate dose, plant stratum, treated plant growth stage, and their interactions on the abundance of *Aeolothrips intermedius* in field plots of cotton plants with three time-treatments [at three plant growth stages: GS1 (6–8 true leaves-early squaring), GS2 (square bud), and GS3 (boll forming)] in 2013 and 2014

Treatment	Factors	d.f.	2013		2014	
			χ^2	P	χ^2	P
Overall	Dose (D)	3	0.51	0.92	0.79	0.85
	Stratum (S)	2	3.47	0.18	15.87	<0.001
	Growth stage (GS)	2	8.47	0.014	18.54	<0.001
	D*S	6	19.25	0.003	6.15	0.41
	D*GS	6	13.34	0.037	3.37	0.76
	S*GS	4	29.57	<0.001	10.05	0.039
	D*S*GS	12	14.14	0.29	5.80	0.93
GS1	D	3	4.91	0.18	2.43	0.49
	S	2	9.44	0.008	0.27	0.87
	D*S	6	13.43	0.036	2.01	0.92
GS2	D	3	11.04	0.011	0.32	0.96
	S	2	12.50	0.001	16.74	<0.001
	D*S	6	2.89	0.82	3.24	0.78
GS3	D	3	2.71	0.44	1.39	0.71
	S	2	15.33	<0.001	7.46	0.023
	D*S	6	17.41	0.007	6.51	0.37

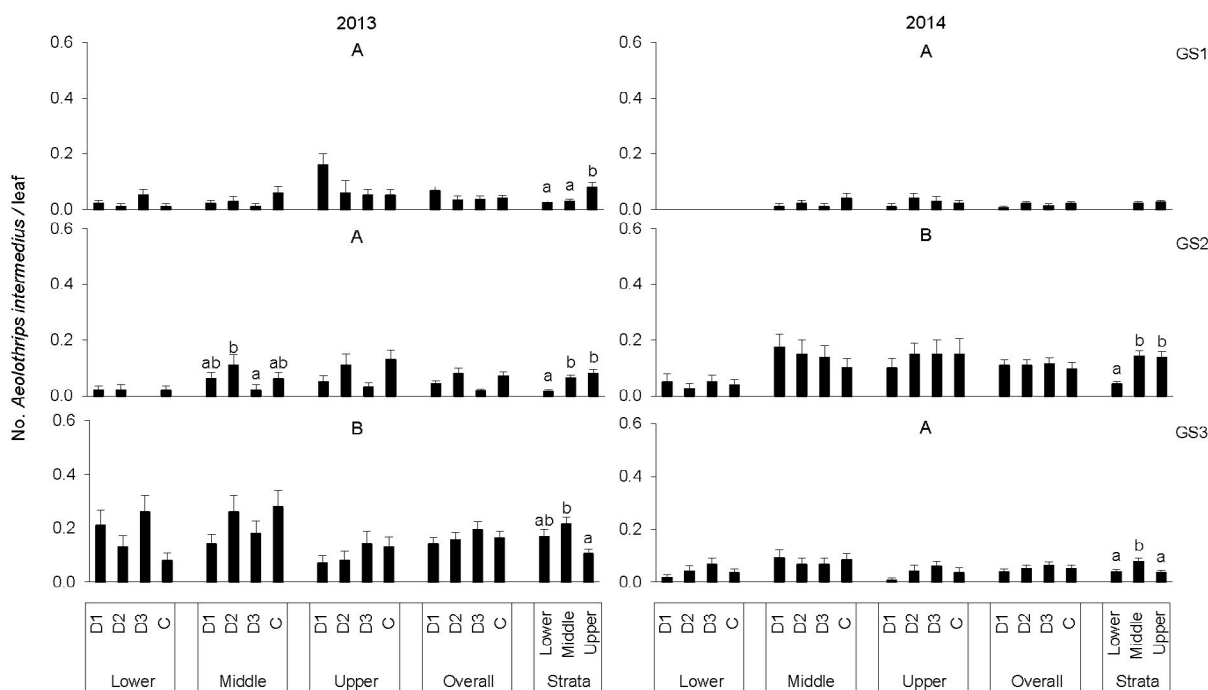


FIGURE 4 Mean (+ SE) number of *Aeolothrips intermedius* on leaves of three strata (lower, middle, upper) of cotton plants of three growth stages (GS1: 6–8 true leaves-early squaring; GS2: square bud; GS3: boll forming) treated with three concentrations of methyl jasmonate (D1: 0.88 mM; D2 = 1.76 mM; D3 = 3.55 mM) or untreated (control, C) in field plots in 2013 and 2014. Means within each group of 3–4 treatments within a panel capped with different lowercase letters are significantly different (Tukey test: $P < 0.05$). Uppercase letters indicate significant differences between plant growth stages within a year (Tukey test: $P < 0.05$)

TABLE 5 Generalized linear mixed models (GLMM) for the influence of methyl jasmonate dose, plant stratum, treated plant growth stage, and their interactions on the abundance of *Coccinella septempunctata* in field plots of cotton plants with three time-treatments [at three plant growth stages: GS1 (6–8 true leaves-early squaring), GS2 (square bud), and GS3 (boll forming)] in 2013 and 2014

Treatment	Factors	d.f.	2013		2014	
			χ^2	P	χ^2	P
Overall	Dose (D)	3	12.22	0.20	7.39	0.69
	Stratum (S)	2	8.37	0.21	7.62	0.37
	Growth stage (GS)	2	15.51	0.050	2.04	0.99
	D*S	6	9.62	0.21	5.11	0.82
	D*GS	6	8.19	0.32	1.59	0.10
	S*GS	4	10.90	0.053	1.13	0.99
	D*S*GS	12	0.77	1.0	0.76	1.0
GS1	D	3	6.82	0.077	2.06	0.56
	S	2	21.29	<0.001	3.71	0.16
	D*S	6	6.04	0.42	2.08	0.91
GS2	D	3	3.70	0.30	1.45	0.69
	S	2	0.55	0.76	0.18	0.91
	D*S	6	0.82	0.99	3.27	0.77
GS3	D	3	2.48	0.48	0.001	1.0
	S	2	4.54	0.10	0.001	1.0
	D*S	6	0.04	1.0	0.001	1.0

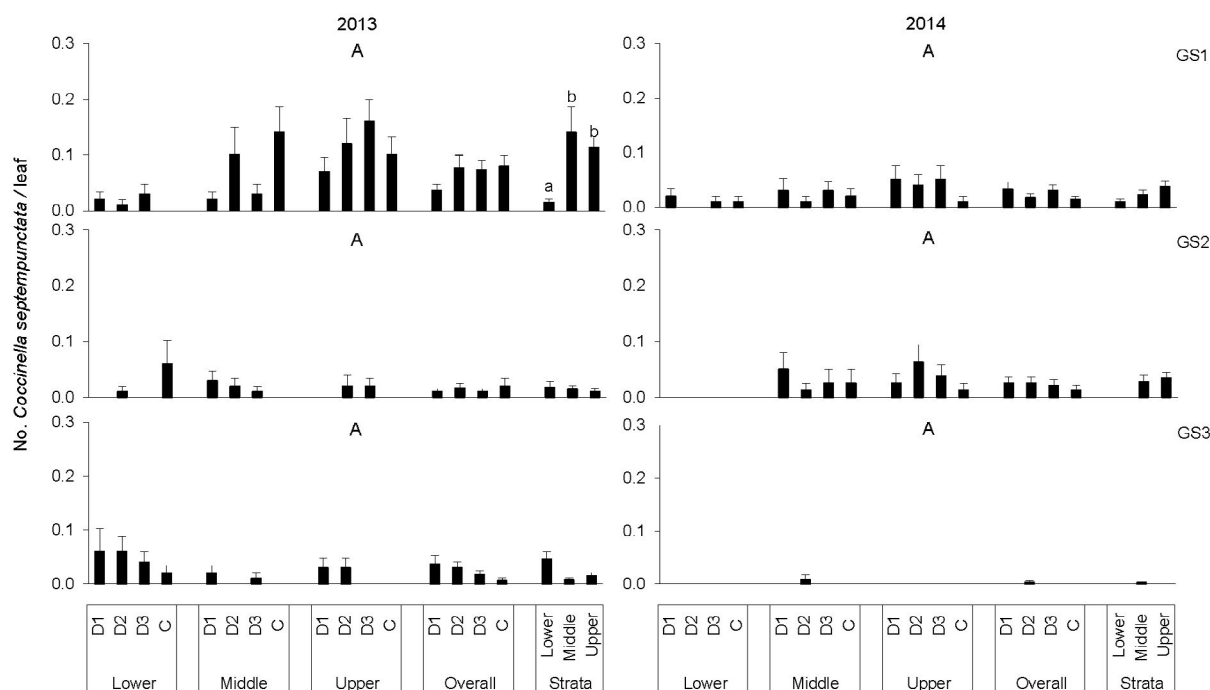


FIGURE 5 Mean (+ SE) number of *Coccinella septempunctata* on leaves of three strata (lower, middle, upper) of cotton plants of three growth stages (GS1: 6–8 true leaves-early squaring; GS2: square bud; GS3: boll forming) treated with three concentrations of methyl jasmonate (D1: 0.88 mM; D2 = 1.76 mM; D3 = 3.55 mM) or untreated (control, C) in field plots in 2013 and 2014. Means within each group of 3–4 treatments within a panel capped with different lowercase letters are significantly different (Tukey test: $P < 0.05$). Uppercase letters indicate significant differences between plant growth stages within a year (Tukey test: $P < 0.05$)

Chrysoperla carnea

In both years, *C. carnea* density was only affected not by plant growth stages, and by plant stratum in 2013; MEJA

dose or any of the factor interactions had no significant effect (Table 6; Figure 6). When plant growth stages were evaluated separately, *C. carnea* density changed with plant stratum in GS2 and GS3 in 2013, and in GS3 in 2014. A higher

TABLE 6 Generalized linear mixed models (GLMM) for the influence of methyl jasmonate dose, plant stratum, treated plant growth stage, and their interactions on the abundance of *Chrysoperla carnea* in field plots of cotton plants with three time-treatments [at three plant growth stages: GS1 (6–8 true leaves-early squaring), GS2 (square bud), and GS3 (boll forming)] in 2013 and 2014

Treatment	Factors	d.f.	2013		2014	
			χ^2	P	χ^2	P
Overall	Dose (D)	3	21.45	0.31	8.21	0.96
	Stratum (S)	2	83.73	<0.001	18.26	0.20
	Growth stage (GS)	2	108.61	<0.001	27.46	0.011
	D*S	6	6.91	0.86	5.31	0.92
	D*GS	6	12.29	0.42	7.14	0.79
	S*GS	4	12.42	0.26	7.42	0.59
	D*S*GS	12	2.73	0.10	1.78	1.0
GS1	D	3	0.44	0.93	3.26	0.51
	S	2	2.96	0.23	1.21	0.75
	D*S	6	0.159	0.10	1.83	0.93
GS2	D	3	8.36	0.039	2.84	0.42
	S	2	12.35	0.002	3.82	0.17
	D*S	6	4.04	0.67	1.21	0.98
GS3	D	3	6.08	0.11	1.16	0.76
	S	2	62.03	<0.001	14.32	<0.001
	D*S	6	2.84	0.83	2.94	0.82

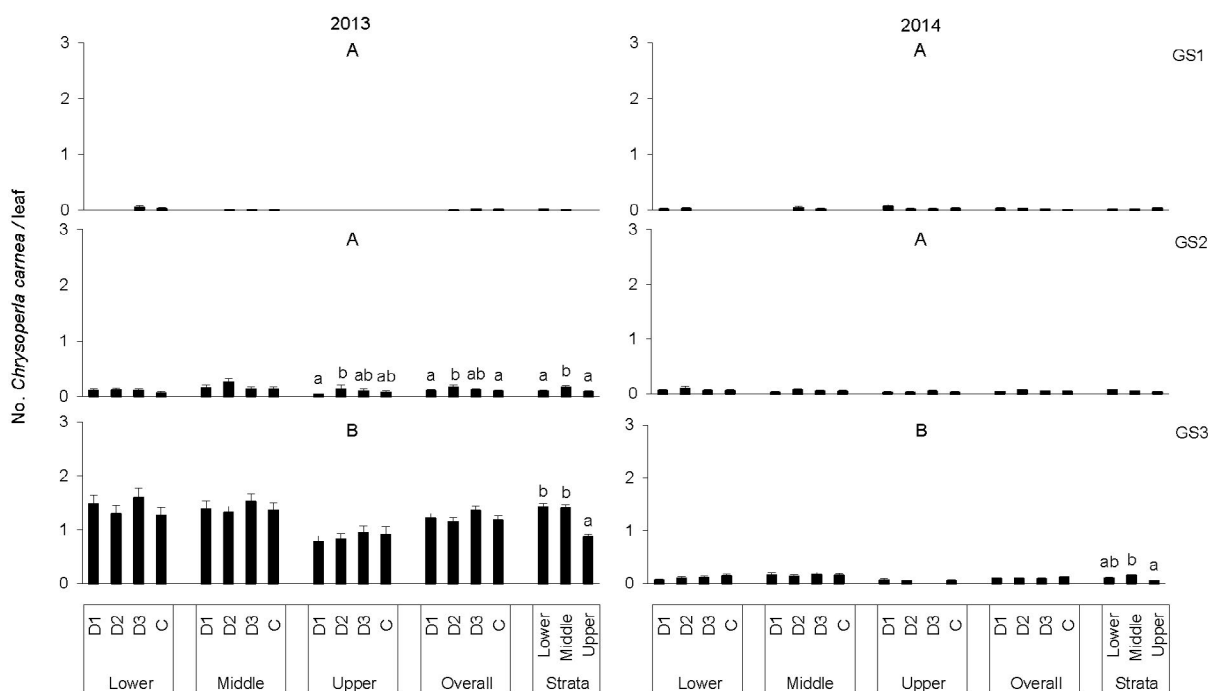


FIGURE 6 Mean (+ SE) number of *Chrysoperla carnea* on leaves of three strata (lower, middle, upper) of cotton plants of three growth stages (GS1: 6–8 true leaves-early squaring; GS2: square bud; GS3: boll forming) treated with three concentrations of methyl jasmonate (D1: 0.88 mM; D2 = 1.76 mM; D3 = 3.55 mM) or untreated (control, C) in field plots in 2013 and 2014. Means within each group of 3–4 treatments within a panel capped with different lowercase letters are significantly different (Tukey test: $P < 0.05$). Uppercase letters indicate significant differences between plant growth stages within a year (Tukey test: $P < 0.05$)

density was recorded in middle leaves compared to upper and lower leaves. The effect of MEJA dose on abundance was significant only in GS2 in 2013. Densities of *C. carnea* were higher in GS3 than in the other growth stages in both years (Table 6; Figure 6).

DISCUSSION

This study has demonstrated that the effects of MEJA treatment of cotton plants in the field, on some sucking insect pests and associated predators – with different within-plant distribution patterns – varied depending on dose, plant growth stage, and plant stratum in two years.

The MEJA doses reduced the abundance of *T. tabaci* in both years, with minor exceptions. In previous studies, MEJA-treated wheat and soybean plants were repellent to phytophagous thrips (Selig et al., 2016; Bayram & Tonča, 2018a). Playing distinct bio-activating roles in plants, jasmonic acid (JA) and *cis*-jasmonone (CJ) reduced the abundance of several thrips species in various host plants such as *Arabidopsis*, cotton, wheat, tomato, and *Brassica rapa* L. (Omer et al., 2001; Thaler et al., 2001; Abe et al., 2008, 2009; El-Wakeil et al., 2010; Bayram & Tonča, 2018b; Tonča et al., 2020). Similarly, laboratory experiments showed that CJ- and MEJA-treated faba bean plants and leaf discs had dose-dependent deterrent effects on feeding, oviposition, and settlement of the western flower thrips, *Frankliniella occidentalis* (Pergande) (Egger & Koschier, 2014; Egger et al., 2014, 2016). Suppressing the feeding and reducing the preference of thrips species, jasmonates are considered to have antixenotic effects, which are most probably provoked by VOCs (Pettersson et al., 1996; Omer et al., 2001). A previous study linked the induced plant defenses upon thrips herbivory and MEJA treatments, both of which increased the production of (*E*)-2-β-d-glucopyranosyloxy-4-methoxy cinnamic acid, a defensive compound of *Matricaria chamomilla* L. (Repčák & Suvák, 2013). Tamogami et al. (2012) showed that the production of jasmonoyl isoleucine and associated VOCs in the distal leaves of *Achyranthes bidentata* Bl. depends on the vascular transportation of MEJA. Exogenous MEJA treatments were also revealed to be responsible for 69% of JA-responsive genes expressed in *Arabidopsis* in response to *F. occidentalis* (de Vos et al., 2005). This might explain thrips herbivory and MEJA treatments induce similar plant defense responses. *Thrips tabaci* abundance was highest in GS1, followed by GS2 and GS3, respectively. In all plant growth stages, the upper plant strata harbored the highest number of *T. tabaci*, followed by the middle and the lower strata, respectively. Our results are concordant with previous efforts depicting within-plant variation in population patterns of cotton thrips. For example, the greatest number of thrips-infested cotton plants in early growth stages, as well as the highest number of thrips species, were recorded on the upper strata due to the suitability of fresh foliage (Parajulee et al., 2006; Atakan & Bayram, 2011; Reay-Jones et al., 2017).

Although varying considerably among plant strata and plant growth stages and between years, the abundance of *E. decipiens* on cotton plants was reduced by MEJA treatments in both years. Previously, we documented the decreasing effects of CJ-treated cotton plants on *E. decipiens* abundance (Tonča et al., 2020). There is evidence that jasmonate-mediated plant defense signaling prevents subsequent settlement of *Empoasca* species (Kallenbach et al., 2012). Herbivory and elicitor treatments may induce similar plant defenses, which affect conspecifics settlement. For example, *Cicadulina storeyi* China-infested maize plants emit a bouquet of VOCs, several of which are also released by MEJA-treated cotton plants (Rodriguez-Saona et al., 2001; Oluwafemi et al., 2011; Williams et al., 2017). Further evaluation of these compounds showed that VOCs such as methyl salicylate (MESA), (*E*)-β-farnesene, (*E*)-caryophyllene, and (*E,E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene (TMTT) were less preferred by *C. storeyi* in Y-tube olfactometer studies (Oluwafemi et al., 2011). However, some choice tests revealed that (*Z*)-3-hexenyl acetate (Z3HA) and (*E*)-4,8-dimethyl-1,3,7-nonatriene (DMNT) were preferred by *Empoasca onukii* Matsuda and that Z3HA was preferred by *Empoasca vitis* (Gothe) (Cai et al., 2017; Xin et al., 2017). These varying results suggest species-specific behavioral responses of leafhopper species to plant volatiles. Further, in our study, lower strata harbored the highest abundance of leafhoppers throughout the study, except for GS1 in 2014, suggesting that leafhoppers prefer larger and older leaves for habituation. As a significant ecological factor, intense sunshine during long-lasting summer days could cause a higher leafhopper preference for lower host plant leaves (Simwat & Gill, 1992).

The abundance of *A. gossypii* in MEJA-treated cotton plots was similar to that in control plots in GS1 in both years and in GS2 in 2014. In 2013 in GS2, overall data revealed that only the highest MEJA dose caused a lower *A. gossypii* abundance compared to control, whereas in GS3, both the intermediate and the highest MEJA dose reduced the density of the pest. Those two MEJA concentrations caused a consistently lower density of *A. gossypii* in all plant strata in 2013 in GS3. In 2014 in GS3, the number of *A. gossypii* in MEJA-treated plots was not lower than in control plots. In previous olfactometer bioassays, *A. gossypii* spent more time in the presence of headspace VOC samples from healthy cotton plants compared to clean air and less time in the presence of VOC samples from cotton plants infested with conspecifics (Hegde et al., 2011). In the same study, gas chromatography-mass spectrometry analysis revealed a higher release of four compounds upon *A. gossypii* infestation: MESA, Z3HA, TMTT, and DMNT, the first three of which were individually less preferred by *A. gossypii* in olfactometer tests. Previous greenhouse studies revealed greater emissions of Z3HA, TMTT, and DMNT upon MEJA treatments (Rodriguez-Saona et al., 2001; Williams et al., 2017). The increased emissions of such volatiles may be involved in cotton defense against *A. gossypii*. Sampling of various plant strata did not reveal a consistent within-plant distribution pattern for *A. gossypii*.

The abundance of *A. intermedius* was not affected by MEJA doses when data were pooled for plant growth stages. When growth stages were evaluated separately, the number of *A. intermedius* was higher in plants treated with the intermediate MEJA concentration than with the highest MEJA concentration when middle leaves were evaluated in GS2 in 2013. In a previous study, we did not obtain any significant outcomes for *A. intermedius* when wheat plants were treated with MEJA and CJ due to a very low incidence (Bayram & TonĀ, 2018a,b). However, in another study, a higher number of *A. intermedius* was recorded in CJ-treated cotton plots (100 g ha⁻¹) when compared with lower doses and control plots (TonĀ et al., 2020). As there is lack of knowledge on the chemical ecology of *A. intermedius*, behavioral and electroantennogram responses of *A. intermedius* to either sap-sucking prey- or elicitor-induced plants should be studied. The within-plant distribution of *A. intermedius* varied depending on the plant growth stage. The predator showed inconsistent dispersion patterns throughout the study with a tendency towards upper plant parts. This tendency is most probably provoked by the presence of the prey species, as a higher number of *T. tabaci* were recorded in the upper strata. Similarly, the higher colonization of the predatory bug *O. niger* on the upper leaves and flowers of cotton was related to the higher abundance of *F. occidentalis* in these plant parts (Atakan & Bayram, 2011).

In the present study, the population density of *C. septempunctata* did not differ between MEJA-treated and untreated cotton plants. Our results are in concordance with a previous study that revealed that MEJA-treated cotton plants had no effect on the abundance of a ladybird community consisting of four species under field conditions (Williams et al., 2017). Similarly, CJ-treated cotton plants also had no effect on *C. septempunctata* under field conditions (TonĀ et al., 2020). In previous studies, we found that MEJA- and CJ-induced wheat plants were attractive to a ladybird population represented by *C. septempunctata*, *Coccinella undecimpunctata* L., and *Adalia bipunctata* (L.) (Bayram & TonĀ, 2018a,b). Therefore, ladybird species may show different responses to the jasmonate-induced defense mechanisms of specific host plants. The abundance of ladybirds was not affected by plant growth stages in either year. Similarly, ladybird abundance was not influenced by plant strata, except in GS1 in 2013, in which middle and upper strata had a higher number of ladybirds than lower strata. The very low population density of ladybirds could also explain why clear evidence for the effects of MEJA doses, plant strata, and growth stages was not recorded.

The MEJA treatments did not affect the population density of *C. carnea* throughout the two years, except in GS2 in 2013, in which plants treated with the intermediate MEJA concentration had a higher number of *C. carnea* than plants treated with the lowest MEJA concentration and control treatments. Research on the behavioral responses of *C. carnea* to jasmonate-treated cotton plants is scarce. As mentioned above, MEJA-treated cotton plants release

a number of VOCs (Rodriguez-Saona et al., 2001; Williams et al., 2017). Research in a Y-tube olfactometer revealed that *C. carnea* spent more time in the Z3HA-treated arm than in the control arm (Reddy et al., 2002). This VOC could possibly play a role in the attraction of *C. carnea* to MEJA-treated cotton plants. However, these results are not conclusive, as field experiments reported that Z3HA-treated traps were not attractive (Zhu et al., 2005). The upper cotton strata harbored a lower number of *C. carnea* when compared to the middle strata, whereas the results varied for the lower leaves. We assume this variation occurred due to the presence of soft-bodied host insects such as aphids, or entomophagous insects that may pose a threat to pre-imaginal stages of *C. carnea*. In both years, the highest population densities were recorded in GS3.

Overall, MEJA treatments could be a promising alternative pest management tool against *T. tabaci*, *E. decipiens*, and *A. gossypii*, as MEJA-treated cotton plants were repellent to these pests and were (inconsistently) attractive to an important generalist predator, *C. carnea*. The effectiveness of MEJA-treated cotton plants on repelling insect pests and attracting their natural enemies varied depending on plant growth stage, plant strata, and experimental year. Induced plants emit numerous VOCs that may affect insect responses, either individually or as a blend in various concentrations (Bruce et al., 2005; Bruce & Pickett, 2011). Despite the fact that VOCs were not analyzed in this study, our data on insect abundance indicate MEJA-mediated repellency to insect pests, consistent with previous studies. Our findings could be explained by linking the increasing emission of VOCs with insect repellency, as was reported in previous studies. Therefore, future studies should address cotton plant volatile emission upon herbivory or elicitor treatments under field conditions. The reduction in the number of insect pests may be attributed to various plant defense mechanisms triggered by elicitor treatments other than repellency (Stout, 2007, 2014). For example, polyphenol oxidases, crucial substances in plant resistance to herbivore attacks, occur in many plant taxa and could be activated either upon cell ruptures or elicitor treatments, thereby influencing herbivore growth by several modes of action, including antibiosis (Bhonwong et al., 2009). Furthermore, host plants under herbivore attack or treated with elicitors may attract natural enemies as an indirect defense mechanism (Zhu & Park, 2005).

The abundances of the predator species *C. septempunctata* and *A. intermedius* on cotton plants were not influenced by MEJA treatments, which could be associated with the presence of a complex chemical environment containing host-derived cues that masked MEJA-induced host plant odors for the predators. A low number of predators within the experimental areas in this study may also potentially contribute to the lack of predator responses to treatments (Williams et al., 2017). Due to the marginal attraction of *C. carnea* to MEJA-treated cotton plants, we assume the reductions in pest insect density in the treated plots were most probably caused by induced direct

defenses (antixenosis or antibiosis) rather than indirect defenses. Our results confirmed that the population density of insects could change across plant strata and plant growth stages, each species having a distinct distribution pattern. For example, *T. tabaci* consistently preferred upper (fresh) plant leaves followed by middle and lower leaves, whereas *E. decipiens* chose lower (larger) cotton leaves followed by middle and upper leaves. Even though all insects were present on all plant strata, the tendency of preference differed. Further studies could investigate possible mechanisms involved in host plant habituation of insect pests, i.e., whether competition exists. Testing behavioral responses of each species to VOCs collected from leaves, buds, and flowers from various plant strata could lead to an explanation of such distribution patterns and plant strata-dependent preference by insects. In addition, we did not observe any phytotoxicity or negative effects of MEJA treatments on cotton plants, whereas growth- and yield-associated components should be assessed in future studies.

This study shows promising deterrent effects of MEJA treatments on sucking insect pests with different temporal distribution patterns on cotton, suggesting possible sustained induced plant defenses via multi-treatments for non-toxic pest management programs.

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AUTHOR CONTRIBUTIONS

Adil Tonğa: Conceptualization (supporting); Data curation (lead); Formal analysis (lead); Investigation (equal); Methodology (equal); Resources (supporting); Software (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review & editing (lead). Kadri Şeker: Investigation (equal). Suna Çakmak: Investigation (equal). Mefhar Gültekin Temiz: Investigation (equal); Methodology (equal); Resources (supporting). Ahmet Bayram: Conceptualization (lead); Data curation (supporting); Formal analysis (supporting); Investigation (equal); Methodology (lead); Project administration (lead); Resources (lead); Supervision (lead); Validation (equal); Writing – original draft (supporting); Writing – review & editing (supporting).

DATA AVAILABILITY STATEMENT

Author elects to not share data.

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