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Research Article

Alterations in Plant Fatty Acid Composition Induced by Insect Herbivory and Elevated Carbon Dioxide: A Case Study on *Halyomorpha halys* (Stål, 1855) (Hemiptera: Pentatomidae)

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Abstract **–** In this study, the impact of brown marmorated stink bug *Halyomorpha halys* (Stål, 1855) (Hemiptera: Pentatomidae) feeding activity on the saturated and unsaturated fatty acid composition of pepper, tomato, and bean leaves was investigated under two different atmospheric carbon dioxide (CO_2) concentrations (600 ppm and 670 ppm). Leaf samples were collected from plants subjected to varying levels of insect feeding damage under controlled laboratory conditions and analyzed using gas chromatography. The results revealed that both *H. halys* herbivory and elevated CO_2 levels induced significant alterations in plant fatty acid profiles. Specifically, the levels of saturated fatty acids such as palmitic acid (16:0) and stearic acid (18:0) increased proportionally with the intensity of feeding damage, while the concentrations of unsaturated fatty acids such as linoleic acid (18:2 n6) and linolenic acid (18:3 n3) varied depending on CO_2 concentration and damage severity. These findings indicate that fatty acid metabolism plays a crucial role in plant defense mechanisms and is modulated by both biotic stress (insect herbivory) and abiotic stress (CO_2 application). This study contributes to the biochemical understanding of plant–insect interactions and provides foundational data for the development of future biological control strategies and climate change-related impact assessments.

Keywords – Halyomorpha halys, Saturated fatty acids, Unsaturated fatty acids, Plant–insect interaction, CO_2 application

I. INTRODUCTION

Halyomorpha halys (Stål, 1855) (Hemiptera: Pentatomidae), commonly known as the brown marmorated stink bug, is a pest species native to East Asia and has spread to many countries since 1998 [1,2]. Although it originates from Southeast Asia, *H. halys* has recently been reported in North America and Europe as well [6-8]. It was first detected in Istanbul and Artvin (Turkey) in 2017 and has since spread across the Black Sea region by 2020 [3-5].

H. halys is an occasional outbreak pest, particularly in fruit orchards. Damage to apples and pears was first reported in the United States in 2006. Once it establishes in orchards, *H. halys* rapidly becomes the dominant stink bug species. Unlike native stink bugs, it primarily targets tree fruits seasonally. It feeds heavily on peach, nectarine (*Prunus persica L.*), apple, and Asian pear (*Pyrus pyrifolia Nakai*). Feeding damage in stone fruits, especially peaches and nectarines, leads to sunken or pitted areas that may become cat-faced as the fruit matures. Feeding on apples and pears results in depressed spots and cork-like lesions on the flesh and can accelerate fruit deterioration. *H. halys* also has feeding and reproductive potential on small fruit crops such as blueberry (*Vaccinium spp.*), raspberry (*Rubus idaeus L.*), grape, and blackberry (*Rubus spp*.). However, the economic impact on these crops remains poorly understood. Ongoing research in the U.S. is focused on assessing its potential effects, spatial distribution, and seasonal abundance on small fruits [1,2]. In Turkey, this pest causes significant damage, especially in the Black Sea region, and its impact is expected to increase in the coming years due to climate change [3-9]. It is also known to cause considerable damage in vegetable crops [10].

The researchers focused on changes in pest populations and damage levels in response to CO_2 emission trends projected over the next 50 years in parallel with rising temperatures. Evaluating these findings in the context of plant–insect trophic relationships and biochemical changes in plant tissues is of critical importance. In particular, examining the relationship between insect damage severity and alterations in fatty acid composition under varying CO_2 conditions offers valuable insights for economic entomology [11].

Plants possess complex biochemical systems that help them respond to environmental stress factors. Among these systems, fatty acids play a central role. The ratio of saturated to unsaturated fatty acids directly influences the structural integrity of plant cells and their resistance to biotic stressors, especially insect herbivory [12].

Fatty acids are essential components of plant cell membranes and play a significant role in regulating membrane permeability, fluidity, and various metabolic pathways. Saturated fatty acids generally form more rigid and durable membrane structures, whereas unsaturated fatty acids provide greater fluidity. These structural differences can affect the plant's defensive responses to insect attacks. Some studies have shown that plants with higher levels of unsaturated fatty acids may be more attractive or susceptible to certain insect species, while plants with a higher proportion of saturated fatty acids tend to be less preferred by pests [13,14].

Understanding the relationship between fatty acid composition in plant tissues and insect herbivory is essential for both entomological and plant biochemical research. This knowledge is particularly valuable for developing pest-resistant crop varieties in agricultural production [15-18].

In this study, the saturated and unsaturated fatty acid profiles of different plant species subjected to feeding by *H. halys* were analyzed. Due to the ease of vegetable cultivation under laboratory conditions, vegetables were selected as model plants in pest interaction studies. Accordingly, pepper (Pe), tomato (T), and bean (Be) were selected as plant materials. The aim is to reveal how specific fatty acid compositions influence insect behavior and feeding preferences, and to provide foundational data for biological control strategies and assessments of pest damage under future climate change scenarios.

II. MATERIALS AND METHODS

In this study, plants grown under controlled laboratory conditions (Figure 1) were exposed to *H. halys* for 48 hours inside mesh cages to induce feeding damage. Due to the salivary secretions of *H. halys*, visible symptoms on the leaves were evaluated and categorized using a predefined damage scale. This categorization was based on the feeding damage descriptions and stylet morphology criteria established by Peiffer and Felton [19].

Figure 1. Cultivation of plants and carbon dioxide applications

The experimental plants included pepper (Pe), tomato (To), and bean (Be). Continuous CO_2 exposure was applied in parallel with increasing insect feeding intensity, and its effects on the biochemical structure of the plants were investigated. Feeding punctures on the leaves were examined and scored under a stereo binocular microscope. Based on the number of punctures, 10 leaf samples were grouped into four categories: 50, 100, 200, and 300 punctures. After 48 hours, leaf samples were excised using a scalpel and sealed in transparent plastic bags for biochemical analysis (Figure 2).

Figure 2. Classification and individual packaging of damaged plants

Additionally, to simulate artificial feeding damage on control plants, mechanical punctures were made using fine needles with a diameter comparable to the insect's stylet. These simulated damage samples were collected and grouped by plant type for subsequent analysis.

H. halys individuals released onto the plants were reared in a climate chamber maintained at 30 ± 1 °C, 65 ± 10% relative humidity, and a 16:8 h light/dark photoperiod. The main insect colony was established using adult *H. halys* specimens collected from hazelnut orchards in the Black Sea region, where the pest population is dense. On January 12–13, 2024, approximately 60 males and 60 female non-diapause adults were collected from provinces including Artvin, Samsun, and Trabzon. The insects were kept at room conditions for two days for acclimatization. Healthy individuals were then selected and placed into 12 separate rearing containers, each containing 10 individuals (5 males and 5 females).

Adults were housed in either circular container (25 cm in diameter × 9 cm in height) with ventilation holes (4–5 cm in diameter) or square plastic boxes (30 cm × 23 cm × 10 cm). Paper towels were placed inside the containers to provide additional surface area and egg-laying sites. Filter papers were inserted through holes in the container walls, with one end immersed in distilled water and the other end inside the container, to supply moisture. To ensure stable environmental conditions, each rearing unit was checked three times daily to monitor humidity and water access through the filter papers.

Dead insects were removed daily, and the male-to-female ratio was maintained at 1:1. Egg masses were manually organized to prevent damage by adults. Eggs were collected approximately one month after the initial adult capture and placed in smaller containers for hatching observation. The nymphs that emerged were fed primarily with carrots and soybeans until reaching adulthood, and these adult insects were used for experimental applications [16-18].

Lipid extraction from the damaged leaf samples was performed using the method described by Hara and Radin (1978) [20], employing a hexane: isopropanol mixture (3:2, v/v). For each sample, 1 g of plant tissue was homogenized in 10 mL of the solvent mixture for 30 seconds. The homogenate was centrifuged at 4500 rpm for 10 minutes, and the supernatant was collected for fatty acid analysis. The supernatant was transferred to large capped test tubes.

To prepare fatty acid methyl esters (FAMEs), the lipid extract in the hexane/isopropanol phase was transferred into leak-proof 25 mL glass tubes. Then, 5 mL of 2% methanolic sulfuric acid was added. The mixture was incubated at 55 °C for 15 hours in a drying oven, then cooled to room temperature. Subsequently, 5 mL of 5%

sodium chloride was added and mixed thoroughly (Figure 3). The FAMEs formed in the tubes were extracted with 5 mL hexane and then washed with 5 mL of 2% $KHCO_3$ solution. After phase separation, the hexane layer containing the methyl esters was evaporated under nitrogen at 45 °C. The residue was re-dissolved in 1 mL of hexane and transferred into capped 2 mL autosampler vials for gas chromatographic analysis [20-22].

Figure 3. Sample preparation for analysis

After conversion to methyl esters, the fatty acids were analyzed using a Shimadzu GC-2010 Plus gas chromatograph equipped with a capillary column (Rtx 2330, USA) of 30 m length, 0.25 mm inner diameter, and 25 µm film thickness. The analysis was performed with the column oven programmed from 138 °C to 218 °C, injection temperature set at 245 °C, and detector temperature at 290 °C. Helium was used as the carrier gas. Prior to the sample analyses, standard mixtures of FAMEs were injected to determine the retention times of individual fatty acids. Sample injections were then carried out based on this calibration, and the fatty acid compositions were determined accordingly.

III. RESULTS AND DISCUSSIONS

The results for saturated and unsaturated fatty acid percentages (%) are presented in Table 1 and Table 2. In these tables, samples are labeled according to the number of feeding punctures, such as control pepper without feeding (PeC) and pepper with 50 punctures (Pe50). Similar naming conventions were used for tomato (T) and bean (Be) samples based on feeding intensity. Table 1 shows the percentage values of saturated fatty acids under different CO_2 treatments.

Under the applied CO_2 concentrations (600 ppm and 670 ppm), the percentages of saturated fatty acids in pepper, tomato, and bean leaves are shown in Table 1, while unsaturated fatty acids are detailed in Table 2. According to the data, the detected saturated fatty acids include myristic acid (14:0), palmitic acid (16:0), heptadecanoic acid (17:0), stearic acid (18:0), and arachidic acid (20:0). For example, the proportion of palmitic acid (16:0) in pepper leaves showed similar values under both 600 ppm and 670 ppm CO_2 treatments. The highest level of 16:0 was recorded in the Be300 group exposed to 600 ppm CO_2.

It was observed that the feeding damage itself had a greater effect on increasing fatty acid concentrations than the CO_2 concentration. This suggests that plants increase their fatty acid levels as part of a defensive metabolic response to herbivore attack.

Table 1. Saturated fatty acids (%)

	Sample	14:0	16:0	17:0	18:0	20:0	Σ saturated fatty acid
600 ppm	PeC	0.30	23.65	0.36	3.35	0.34	28.00

	Pe50	1.58	24.68	0.42	4.14	0.31	31.13
	Pe100	2.09	21.25	0.18	7.63	0.15	31.15
	Pe200	1.78	24.24	0.40	8.18	0.33	34.93
	Pe300	1.07	34.67	nd	10.26	0.50	46.49
	TC	0.26	16.09	nd	5.71	0.60	22.66
	T50	0.46	28.00	nd	9.62		38.08
	T100	0.98	27.15	nd	9.27	0.61	38.01
	T200	0.54	8.85	nd	7.12		16.51
	T300	0.63	11.99	nd	5.81		18.43
	BeC	0.48	23.11	0.31	4.78	0.35	29.03
	Be50	0.44	23.39	nd	5.17	0.25	29.25
	Be100	0.62	22.64	nd	6.11	0.33	29.70
	Be200	0.78	24.97	nd	6.90	0.36	33.01
	Be300	0.72	23.60	0.22	4.35	0.33	29.22
670 ppm CO_2	PeC	0.23	22.47		4.50	0.40	27.60
	Pe50	0.33	22.53	0.31	4.45	0.38	28.01
	Pe100	0.47	23.19	0.20	5.26	0.37	29.49
	Pe200	0.47	21.90	0.11	4.05	0.36	26.89
	Pe300	0.69	21.70	0.14	4.91	0.39	27.82
	TC	0.33	21.99		5.11		27.43
	T50	0.37	23.78		5.96		30.11
	T100	0.32	20.47		5.72	0.50	27.01
	T200	0.23	24.53		6.47	0.46	31.68
	T300	0.34	24.33		5.96	0.49	31.11
	BeC	0.48	23.21		6.58	0.28	30.54
	Be50	0.69	21.11	0.37	4.44		26.60
	Be100	0.33	21.52	0.54	4.83	0.26	27.47
	Be200	0.73	20.03	0.70	4.98		26.44
	Be300	1.08	22.61	0.35	5.20	0.38	29.60

The final product of fatty acid biosynthesis in plants is palmitic acid (16-carbon). Palmitic acid is the end product of the enzyme known as fatty acid synthase (FAS). Through the catalytic activity of elongase enzymes, longer-chain saturated fatty acids such as stearic acid (18:0), arachidic acid (20:0), behenic acid (22:0), and lignoceric acid (24:0) can be synthesized from 16:0. In Table 1, an increase in palmitic acid levels was observed in the Pe100 and Pe300 groups (under 600 ppm CO_2) compared to the control group (PeC). This suggests that this CO_2 concentration may positively influence FAS activity. Moreover, the increase in stearic acid (18:0) levels in the Pe100, Pe200, and Pe300 groups also indicates enhanced elongase enzyme activity. These increases in individual saturated fatty acids contributed to the rise in total saturated fatty acid content.
In the tomato group (T), compared to the control (TC), increases in palmitic acid, stearic acid, and total

saturated fatty acids were observed at the T50 and T100 concentrations. These results indicate enhanced activity of both FAS and elongase enzymes at these levels. However, at T200 and T300 concentrations, a negative effect on these enzymes was observed.

In the bean group (Be), no significant differences in palmitic acid levels were detected between the control (BeC) and treatment groups. However, stearic acid levels increased at the Be50, Be100, and Be200 concentrations. The rise in 18:0 levels at Be200 was also reflected in the total saturated fatty acid content. As these results indicate, varying CO_2 concentrations influenced the substrates and products associated with fatty acid metabolism, particularly through changes in the activity of FAS, elongase, and stearoyl-CoA desaturase enzymes.

In tomato leaves, saturated fatty acid levels were slightly higher in the 670 ppm CO_2 groups than in the 600 ppm CO_2 groups. In contrast, slightly lower levels were observed in bean leaves under 670 ppm CO_2. Stearic acid (18:0) was consistently found at lower levels in pepper, tomato, and bean leaves treated with 670 ppm CO_2 compared to those treated with 600 ppm CO_2. The lowest concentration of 18:0 was recorded in the group (600 ppm CO_2, no feeding). Heptadecanoic acid (17:0) was not detected in tomato leaf samples.

Although minor variations were observed among the 670 ppm CO_2 treatment groups, no significant differences were noted within each treatment set. Overall, increases in CO_2 concentration did not lead to major changes in saturated fatty acid profiles in relation to *H. halys* feeding damage.

Unsaturated fatty acids and their components (%) are expressed in Table 2. The unsaturated fatty acids, cis-10-pentadecanoic acid (15:1), palmitoleic acid (16:1 n7), cis-10-heptadecanoic acid (17:1), trans-elaidic acid (18:1 n9 t), cis-oleic acid (18:1 n9 c), vaccenic acid (18:1 n11), cis-linoleic acid (18:2 n6 c), and gamma-linolenic acid (18:3 n6) were identified. The concentration of 16:1 n7 was found to be slightly higher in pepper, tomato, and bean leaves treated with 600 ppm CO_2 compared to those treated with 670 ppm CO_2. Conversely, 18:1 n9 c levels were slightly lower in the 600 ppm CO_2-treated plants than in those exposed to 670 ppm. Similarly, 18:2 n6 c and 18:3 n6 were also detected in slightly lower concentrations in plants treated with 600 ppm CO_2. Among all unsaturated fatty acids identified, 18:3 n6 had the highest concentration, followed by 18:2 n6 c.

In the context of plant fatty acid metabolism, the major unsaturated fatty acids are palmitoleic acid (16:1 n-7), oleic acid (18:1 n-9), linoleic acid (18:2 n-6), and linolenic acid (18:3 n-3). Palmitoleic acid is synthesized from 16:0 by the enzyme known as stearoyl-CoA desaturase (Δ9 desaturase), while oleic acid is synthesized from 18:0. The Δ12 desaturase enzyme, found only in plants, introduces a double bond between carbon atoms 12 and 13 in 18:1 n-9, producing linoleic acid (18:2 Δ9,12). The Δ15 desaturase enzyme, also plant-specific, converts linoleic acid (18:2 Δ9,12) into linolenic acid (18:3 Δ9,12,15) by adding a double bond between carbons 15 and 16.

The most abundant unsaturated fatty acids in plants are 18:1 n-9 (oleic acid), 18:2 n-6 (linoleic acid), and 18:3 n-3 (linolenic acid). Oleic acid is synthesized by Δ9 desaturase; an enzyme presents in all organisms including plants. Linoleic acid (18:2 n-6) and linolenic acid (18:3 n-3) are polyunsaturated fatty acids (PUFAs) synthesized exclusively by plants. Linoleic acid is formed via Δ12 desaturase, which uses 18:1 n-9 as a substrate and introduces a double bond between carbons 12 and 13. Similarly, 18:3 n-3 is synthesized by Δ15 desaturase using 18:2 n-6 as a substrate, introducing a double bond between carbons 15 and 16.

From this biochemical perspective, experimental results showed an increase in 18:1 n-9 and 18:2 n-6 concentrations in the group depending on the CO_2 concentration applied. However, a decrease was observed in 18:3 n-3. These patterns suggest increased Δ9 desaturase activity for 18:1 n-9 and increased Δ12 desaturase activity for 18:2 n-6. The decrease in 18:3 n-3 levels may be attributed to reduced Δ15 desaturase activity. Overall, fatty acid metabolism appeared to be influenced by both piercing-sucking herbivory and increased atmospheric CO_2 concentrations.

Table 2. Unsaturated fatty acids (%)

	Samples	15:1	16:1 n7	17:1	18:1 n9 t	18:1 n9c	18:1 n11	18:2 n6	18:3 n3	Σunsaturated fatty acid
600 ppm CO_2	PeC	2.12	1.47	0.27	6.25	5.82	0.34	12.82	42.92	72.00
	Pe50	1.97	1.52	0.41	0.18	14.81	0.49	14.55	34.94	68.87
	Pe100	0.84	2.59	0.23	0.19	25.58	0.54	22.77	16.66	68.86
	Pe200	1.30	1.96	0.35	0.24	22.62	0.43	16.30	22.31	65.07

	Pe300	2.73	2.10	0.25	0.26	13.43	0.69	11.63	22.42	53.51
	TC	1.97	0.77	0.25	0.15	19.62	0.30	38.43	16.11	77.34
	T50	1.68	1.58	0.32	0.19	11.51	0.79	15.26	30.91	61.92
	T100	1.28	2.35	0.34	0.19	14.27	0.84	15.69	27.38	61.99
	T200	1.85	2.14	0.91	0.66	40.76	0.79	20.28	16.90	83.49
	T300	2.47	3.28	0.83	0.61	48.10	0.84	21.95	14.33	91.57
	BeC	1.36	2.08	0.12	0.19	9.53	0.32	11.96	45.54	70.97
	Be50	1.78	2.03	0.11	0.33	11.77	0.45	12.45	41.95	70.75
	Be100	1.91	2.08	0.13	0.21	8.90	0.69	9.92	46.59	70.30
	Be200	3.49		0.11	1.00	8.69	0.52	12.57	40.73	66.99
	Be300	2.11	1.13	0.13	0.17	9.76	0.29	11.02	46.18	70.78
	PeC	1.75	0.91	0.40	4.16	11.09	0.32	15.79	38.00	72.41
	Pe50	1.70	0.92	0.31	3.81	9.96	0.27	16.25	38.78	71.99
	Pe100	1.41	0.95	0.23	2.48	14.81	0.27	19.46	31.18	70.51
	Pe200	1.51	1.15	0.18	3.17	17.61	0.49	19.32	29.68	73.11
	Pe300	1.27	1.76	0.27	2.85	19.22	0.33	18.46	28.35	72.18
	TC	1.07	1.39	0.26	3.88	16.03		22.99	26.95	72.57
	T50	1.40	1.56	0.37	0.31	16.41	0.41	22.45	26.98	69.89
	T100	1.32	1.25	0.42	4.17	18.33	0.46	23.38	23.65	72.99
	T200	1.69	1.68	0.37	5.17	11.76	0.34	16.45	31.23	68.32
	T300	1.42	1.65	0.42	4.73	15.32	0.50	17.63	27.63	68.89
	BeC	3.26	1.21	0.32	0.40	7.91	0.39	10.92	45.06	69.46
	Be50	2.10	1.83	0.18	0.25	5.06	0.24	10.22	54.01	73.40
	Be100	2.25	1.81	0.37	0.24	5.13	0.26	9.69	53.29	72.54
	Be200	2.33	1.38	0.58	0.25	5.98	0.24	11.81	51.01	73.56
	Be300		0.94	0.39	0.24	6.82	0.26	12.58	49.18	70.40

670 ppm CO_2

IV. CONCLUSIONS

This study demonstrated that *H. halys* infestation and different atmospheric CO_2 concentrations significantly affect the saturated and unsaturated fatty acid profiles in pepper, tomato, and bean plants. The results indicate that plants respond biochemically to both abiotic and biotic (insect herbivory) stressors. In particular, changes in fatty acid composition appear to be part of the plant's defensive strategy. These results offer valuable insight for the development of pest-resistant crop varieties, a better understanding of plant physiological responses, and sustainable agricultural practices in the context of climate change.

This research indicates that both biotic and abiotic stressors—namely *H. halys* herbivory and elevated atmospheric CO_2 levels—induce significant modifications in the fatty acid composition of pepper, tomato, and bean leaves. The observed increase in saturated fatty acids, particularly palmitic and stearic acids, in response to intensified feeding damage highlights the potential defensive role of these compounds in mitigating herbivore attack. Meanwhile, the fluctuating levels of unsaturated fatty acids, such as linoleic and linolenic acids, suggest a complex regulatory mechanism influenced by both environmental CO_2 conditions and the severity of insect herbivory. These changes reflect a dynamic adjustment in plant lipid metabolism, underscoring its importance in stress response.

These findings contribute valuable insights into the biochemical interactions between plants and insect herbivores under changing environmental conditions. The study not only enhances our understanding of plant defense strategies at the molecular level but also provides a foundation for developing sustainable pest management approaches. Moreover, the results are relevant for assessing the broader ecological implications of climate change on crop resilience and pest dynamics. Future research should focus on the underlying genetic and enzymatic controls of fatty acid biosynthesis in response to combined stresses, paving the way for breeding or engineering stress-resilient crop varieties.

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