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Impact of *Cameraria ohridella* infestation on the chemical composition of *Aesculus glabra* leaves in Dnipro city, Ukraine

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This study investigated changes in the metabolic profile of *Aesculus glabra* leaves in response to infestation by the horse chestnut leaf miner (*Cameraria ohridella*) in Dnipro city, Ukraine. Methanolic leaf extracts from uninfested and infested trees were analyzed using gas chromatography–mass spectrometry (GC–MS). Infestation by *C. ohridella* was associated with substantial metabolic restructuring, reflected by a marked reduction in the number of detected metabolites from 114 in uninfested leaves to 62 in infested leaves. The most pronounced changes were observed among carbohydrate-related compounds, indicating major alterations in carbon metabolism under herbivory stress. Increased relative abundances of sucrose, trehalose, mannobiose, catechin, and several fatty acid derivatives were detected in infested leaves, whereas multiple organic acids, terpenoid-related compounds, and sterols decreased in abundance or disappeared entirely. In addition, several metabolites, including quercetin, neophytadiene, monopalmitin, β-sitosterol, and hexatriacontane, were detected exclusively in infested leaves and may be associated with induced stress and defense responses. Conversely, compounds such as chlorogenic acid, α-linolenic acid, and β-tocopherol were detected only in uninfested leaves. The results demonstrate extensive metabolic reorganization of *A. glabra* leaves under *C. ohridella* infestation and highlight the potential role of specialized metabolites in herbivory-related stress responses.

Keywords: horse chestnut leaf miner; metabolic profile of leaf methanolic extract; *Aesculus glabra*.

Introduction

Aesculus glabra Willd. (Ohio buckeye) is a temperate deciduous tree species native to eastern North America, where it occurs in mesic forest ecosystems from Maine and Minnesota to Texas and Northern Georgia (Rudolf, 1974; Harris, 2003). Due to its ornamental and ecological characteristics, *A. glabra* has also been introduced into urban green spaces outside its native range, including cities of the Ukrainian Steppe zone. In urban ecosystems, woody plants contribute to environmental stabilization and improvement of microclimatic conditions, particularly under conditions of elevated anthropogenic pressure (Sturiale & Scuderi, 2019; Aslanoğlu et al., 2025).

Previous studies have demonstrated the diverse chemical composition of *A. glabra* tissues, including phenolic compounds, terpenoids, triterpenoid saponins, and other specialized metabolites (Aurada et al., 1984; Yuan et al., 2012; Oszmiański et al., 2015; Velazquez Cruz et al., 2024). Several metabolites identified in *A. glabra* have been associated with antioxidant and stress-related biological activity (Aurada et al., 1984; Yuan et al., 2012). Oszmiański et al. (2015) reported significant changes in the phenolic profile of *A. glabra* leaves affected by *Cameraria ohridella*, including alterations in flavan-3-ol composition. Woody plants growing in urban environments are frequently exposed to insect herbivores, which may substantially alter plant metabolism and reduce ornamental and physiological quality. One of the most widespread invasive pests affecting Aesculus species in Europe is the horse chestnut leaf miner *Cameraria ohridella* Deschka & Dimić, 1986 (Grabenweger et al., 2010; Shupranova et al., 2024). Feeding damage caused by this species disrupts leaf tissues and may induce changes in primary and secondary metabolism associated with plant stress responses (Kessler & Baldwin, 2002; Hartmann & Messier, 2008).

Plant responses to herbivory are frequently accompanied by alterations in carbohydrate metabolism, phenolic compounds, terpenoids, and lipid-derived metabolites involved in stress signaling and protective functions (Dixon & Paiva, 1995; Couée et al., 2006; Rolland et al., 2006; Heil & Ton, 2008; Kachroo & Kachroo, 2009; Erb & Kliebenstein, 2020; Divekar et al., 2022). Previous studies have shown that flavonoids and other phenolic compounds may participate in antioxidant protection and influence insect feeding behavior and survival (Harborne & Williams, 2000; Simmonds, 2001; Simmonds, 2003; Singh et al., 2021; Riddick, 2024). However, information regarding metabolic changes associated with leaf miner infestation in *A. glabra* leaves remains limited. Therefore, this study aimed to analyze the metabolic profiles of leaf extracts from *A. glabra* infested by *C. ohridella* under urban conditions in Dnipro city, with a focus on identifying metabolites associated with herbivory-related stress responses.

Materials and methods

The study was conducted in Dnipro city, located in the Ukrainian Northern Steppe zone. The research object was *A. glabra* (Fig. 1). Leaf samples were collected from trees growing in the Botanical Garden of Oles Honchar Dnipro National University. Species identification was performed by Dr. Iryna Ivanko. Herbarium specimens are deposited in the herbarium of the Institute of Biology of Oles

Honchar Dnipro National University. Leaf sampling was carried out in July 2023, when symptoms of *C. ohridella* infestation were well developed on *Aesculus* leaves. The studied trees were not treated with insecticides. Trees with similar morphological and biometric characteristics were selected for sampling. Two leaf categories were analyzed: i) leaves without visible signs of infestation (uninfested, U) and ii) leaves showing visible mines of *C. ohridella* (infested, CO).

Leaves were collected between 9:00 and 11:00 a.m. from the lower third of the southern side of the tree crown. Twenty leaves belonging to the same category were harvested using scissors and pooled to obtain one composite sample. In the case of infested leaves, only visually intact leaf tissue was sampled, while mined areas were excluded from the analysis. Leaf material was cut using a sterile scalpel and placed into paper bags. Disposable gloves were used throughout sampling, and all instruments were cleaned with ethanol between samples.

Fig. 1. Study species *Aesculus glabra* in Botanical Garden of Oles Honchar Dnipro National University, Dnipro city

For chemical analysis, leaf samples were air-dried and milled. Approximately 1 g of leaf powder was extracted with 8 mL of a methanol-chloroform mixture (1:1, v/v) for 48 hours at room temperature with occasional shaking. The extract was filtered through a 0.45 µm PTFE syringe filter and evaporated to dryness under vacuum. The dry residue was derivatized with 0.2 mL of N,O-bis(trimethylsilyl)trifluoroacetamide (BSTFA) containing 5% trimethylchlorosilane (TMS-Cl) by heating at 65 °C for 45 minutes. The derivatized samples were analyzed by gas chromatography-mass spectrometry (GC-MS) using a Shimadzu GCMS-QP2020 system (Kyoto, Japan). Separation was performed on a Restek Rxi-5ms capillary column (30 m × 0.25 mm × 0.25 µm; Crossbond® 5% diphenyl / 95% dimethylpolysiloxane). Helium (99.999%) was used as the carrier gas at a flow rate of 1.5 mL/min (89.5 kPa). The temperature program was as follows: initial temperature 50 °C, ramped at 10 °C/min to 300 °C, followed by an isothermal hold at 300 °C for 25 minutes. The injector and interface temperatures were set at 280 °C, and the ion source at 250 °C. A 1 µL aliquot was injected in splitless mode. Solvent cut-off time was 5 minutes, and total run time was 50 minutes.

Compound identification was based on mass spectral comparison with the NIST-14 mass spectral library. Analyses were performed in total ion current (TIC) mode, with a scan range of 20–900 m/z and electron ionization at 70 eV. The confidence level for compound identification ranged from 70% to 98%. All compounds were characterized as trimethylsilyl (TMS) derivatives. The identified groups of compounds included carbohydrates (CH), polyphenols (PPh), steroids (S), hydrocarbons (HC), and fatty acids (FA).

Metabolite data obtained by GC–MS analysis were processed semi-quantitatively using relative peak areas from chromatograms. Identified compounds were grouped according to their chemical classes and compared between uninfested and *C. ohridella*-infested *A. glabra* leaves based on their occurrence patterns and relative abundance. Changes in metabolite occurrence were visualized using Venn diagrams, whereas relative abundance shifts were presented as a heatmap. Chemical structures of selected metabolites were drawn using ChemDraw 19.0. Data processing and visualization were performed in R version 4.2.1.

Results

GC–MS analysis identified 114 compounds in methanolic extracts of uninfested *A. glabra* leaves and 62 compounds in leaves infested by *C. ohridella* (Table 1). The detected metabolites belonged to several major chemical classes, including carbohydrates, fatty acids, terpenoids, steroids, polyphenols, glycosides, organic acids, and amino acid derivatives.

Table 1
Changes in metabolite abundance in *Aesculus glabra* leaves in response to *Cameraria ohridella* infestation

Compound	Uninfested, %	Infested, %	Trend
N-Formylglycine	0.36 ± 0.03*	0.48 ± 0.03	increase
L-Valine	0.43 ± 0.03	0.50 ± 0.03	increase
Nonanoic acid	1.93 ± 0.09	2.49 ± 0.12	increase
Palmitic acid	2.54 ± 0.12	2.95 ± 0.14	increase
Stearic acid	1.00 ± 0.05	1.29 ± 0.06	increase
Glycerol monostearate	0.87 ± 0.05	1.17 ± 0.06	increase
Catechin	5.32 ± 0.24	8.60 ± 0.38	increase
Fructofuranose	0.88 ± 0.04	1.20 ± 0.06	increase
Sucrose	9.51 ± 0.41	12.00 ± 0.55	increase
Trehalose	0.38 ± 0.03	1.67 ± 0.08	increase
Lactose	0.10 ± 0.01	0.64 ± 0.04	increase
Mannobiose	0.90 ± 0.04	2.17 ± 0.10	increase
Thymol-glucoside	1.98 ± 0.09	2.27 ± 0.10	increase
Malic acid	0.61 ± 0.04	0.15 ± 0.02	decrease
Citric acid	0.72 ± 0.04	0.17 ± 0.02	decrease
Ascorbic acid	1.16 ± 0.07	0.25 ± 0.02	decrease
Quinic acid	1.67 ± 0.08	0.55 ± 0.03	decrease
Phytol	0.43 ± 0.03	0.22 ± 0.02	decrease
Squalene	1.25 ± 0.06	0.96 ± 0.05	decrease
β-Amyrin	1.15 ± 0.06	0.73 ± 0.04	decrease
α-Amyrin	0.92 ± 0.05	0.65 ± 0.04	decrease
Lupeol	0.82 ± 0.04	0.59 ± 0.03	decrease
Stigmasterol	0.96 ± 0.05	0.62 ± 0.03	decrease
Arabinofuranose	0.31 ± 0.03	0.12 ± 0.01	decrease
Ribofuranose	0.44 ± 0.03	0.22 ± 0.02	decrease
Lyxofuranose	4.85 ± 0.22	3.23 ± 0.15	decrease
Glucose	1.34 ± 0.06	0.34 ± 0.03	decrease
Talofuranose	1.73 ± 0.08	0.23 ± 0.02	decrease
Xylopyranose	0.76 ± 0.04	0.40 ± 0.03	decrease
Pinitol	6.50 ± 0.28	4.92 ± 0.22	decrease
Oleic acid	0.00	0.40 ± 0.03	appeared
Monopalmitin	0.00	1.05 ± 0.05	appeared
Monomyristin	0.00	0.32 ± 0.03	appeared
Neophytadiene	0.00	1.66 ± 0.08	appeared
Hexatriacontane	0.00	5.84 ± 0.26	appeared
β-Sitosterol	0.00	1.56 ± 0.07	appeared
Quercetin	0.00	1.97 ± 0.09	appeared
Arbutin	0.00	0.43 ± 0.03	appeared
Oxalic acid	0.46 ± 0.03	0.00	disappeared
Fumaric acid	0.18 ± 0.02	0.00	disappeared
α-Linolenic acid	1.67 ± 0.08	0.00	disappeared
Chlorogenic acid	2.99 ± 0.14	0.00	disappeared
Ribose	0.18 ± 0.02	0.00	disappeared
Galactose	0.81 ± 0.04	0.00	disappeared
Maltose	0.86 ± 0.04	0.00	disappeared
Tocopherol (β)	0.56 ± 0.03	0.00	disappeared
Benzoic acid	0.25 ± 0.02	0.21 ± 0.02	no change
Cyclohexaneacetic acid	0.13 ± 0.02	0.11 ± 0.01	no change
Myristic acid	0.21 ± 0.02	0.21 ± 0.02	no change
Stigmastanol	0.32 ± 0.03	0.31 ± 0.03	no change
Arabinose	0.20 ± 0.02	0.23 ± 0.02	no change
Tocopherol (α)	5.10 ± 0.23	5.26 ± 0.24	no change
Tocopherol (γ)	0.20 ± 0.02	0.19 ± 0.02	no change

Notes: values are presented as relative peak area (%) obtained by GC–MS semi-quantitative profiling; data are presented as mean ± analytical uncertainty.

The most pronounced reduction was observed among carbohydrate metabolites, where the number of detected compounds markedly decreased in infested leaves. Terpenoid- and steroid-related metabolites were represented by fewer identified compounds, whereas the

number of detected fatty acids slightly increased. Increased relative abundances in infested leaves were observed for metabolites such as catechin, sucrose, trehalose, mannobiose, nonanoic acid, palmitic acid, and stearic acid. In contrast, infested leaves exhibited lower relative abundances of several organic acids, terpenoid-related compounds, and sterols. Several compounds were detected exclusively in infested leaves, including oleic acid, monopalmitin, monomyristin, neophytadiene, hexatriacontane, β-sitosterol, quercetin, and arbutin. Conversely, oxalic acid, fumaric acid, α-linolenic acid, chlorogenic acid, ribose, galactose, maltose, and β-tocopherol were detected only in uninfested leaves.

Figure 2 illustrates the distribution of shared and unique metabolites between uninfested and *C. ohridella*-infested *A. glabra* leaves across four metabolite groups. In all metabolite groups, shared compounds constituted the largest proportion of detected metabolites or were comparable to the number of unique compounds.

Carbohydrates showed the largest overlap between leaf categories, with 14 metabolites detected in both uninfested and infested leaves. In addition, three carbohydrate compounds were detected exclusively in uninfested leaves, whereas one compound was specific to infested leaves. In the lipid group, nine metabolites were common to both uninfested and infested leaves, whereas two compounds were detected only in uninfested leaves and four only in infested leaves. Polyphenols exhibited an equal distribution of unique and shared metabolites, with one compound unique to uninfested leaves, one shared by both leaf categories, and one detected only in infested leaves. Within the terpene group, five metabolites were shared by both uninfested and infested leaves, whereas one terpene compound was detected exclusively in infested leaves. No terpene compounds unique to uninfested leaves were detected. The heatmap revealed distinct metabolite-specific patterns associated with *C. ohridella* infestation (Fig. 3). Infested leaves were characterized by increased levels of several carbohydrates, fatty acids, lipids, and phenolic compounds, whereas reduced abundances were observed for multiple organic acids, terpenoids, and sterols.

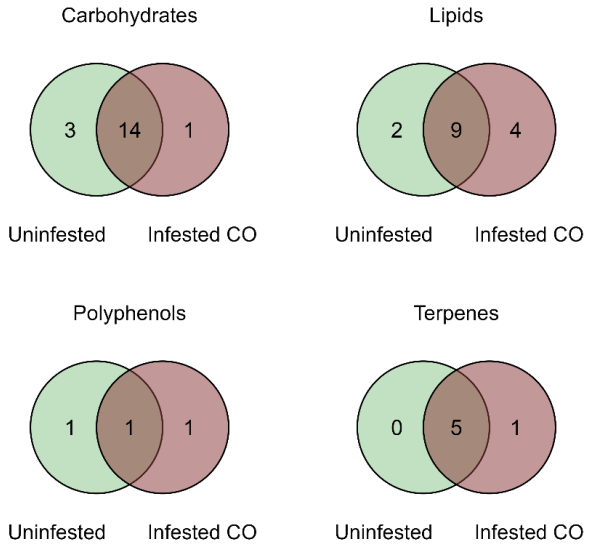

Fig. 2. Distribution of metabolites in uninfested and *Cameraria ohridella*-infested samples across four groups of metabolites: Venn diagrams show the overlap and uniqueness of metabolites within carbohydrates, lipids, polyphenols, and terpenes; green circles represent metabolites detected in uninfested samples, whereas brown circles represent those detected in infested samples; numbers indicate the number of unique and shared metabolites in each group

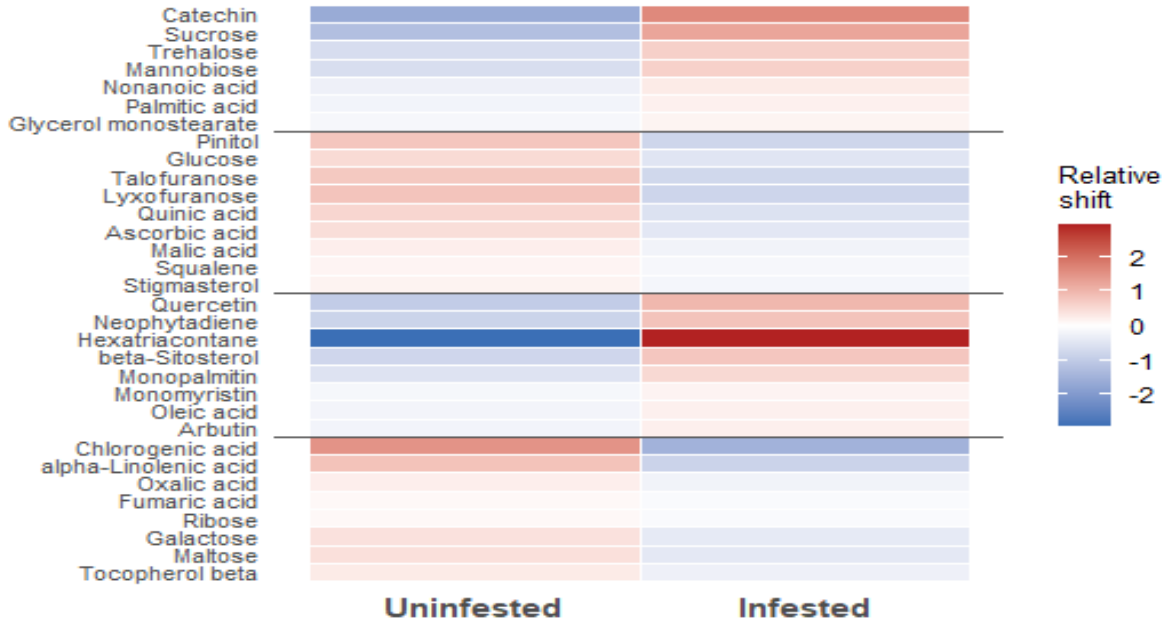

Fig. 3. Heatmap of relative shifts in metabolite abundance in *Aesculus glabra* leaves from uninfested and *Cameraria ohridella*-infested trees: colors indicate relative changes in metabolite levels: red, increase; blue, decrease; white, no change; metabolites are grouped according to their chemical class

The strongest increases were associated with catechin, sucrose, trehalose, mannobiose, hexatriacontane, quercetin, and neophytadiene, while marked decreases were recorded for chlorogenic acid, α-linolenic acid, glucose, and talofuranose.

Several metabolites, including myristic acid, stigmastanol, arabinose, α-tocopherol, γ-tocopherol, benzoic acid, and cyclohexaneacetic acid, exhibited minimal variation between infested and uninfested leaves. The chemical structures of selected metabolites associated with infestation-related changes in *A. glabra* leaves are shown in Figure 4. The illustrated compounds represent several major groups of metabolites identified by GC–MS analysis, including polyphenols, fatty acid derivatives, terpenoid-related compounds, steroids, and carbohydrates. Most of these metabolites were newly detected or exhibited increased relative abundance in *C. ohridella* infested leaves, highlighting the chemical diversity of metabolites associated with herbivory stress.

Discussion

Previous studies have described the diverse chemical composition of *A. glabra* tissues, including phenolic compounds, terpenoids,

and other specialized metabolites (Oszmiański et al., 2015; Velazquez Cruz et al., 2024). In particular, Oszmiański et al. (2015) reported 28 phenolic compounds in *A. glabra* leaves affected by *C. ohridella*, including changes in flavan-3-ol composition. In addition, phytochemical analyses of *A. glabra* bark extracts identified several specialized metabolites, including procyanidin, epicatechin, aesculin 6-rutinoside, isoscopoletin-β-D-glucoside, and eriocaffeate (Velazquez Cruz et al., 2024). These studies demonstrate that *A. glabra* contains a chemically diverse set of metabolites potentially involved in interactions with herbivores and plant stress responses.

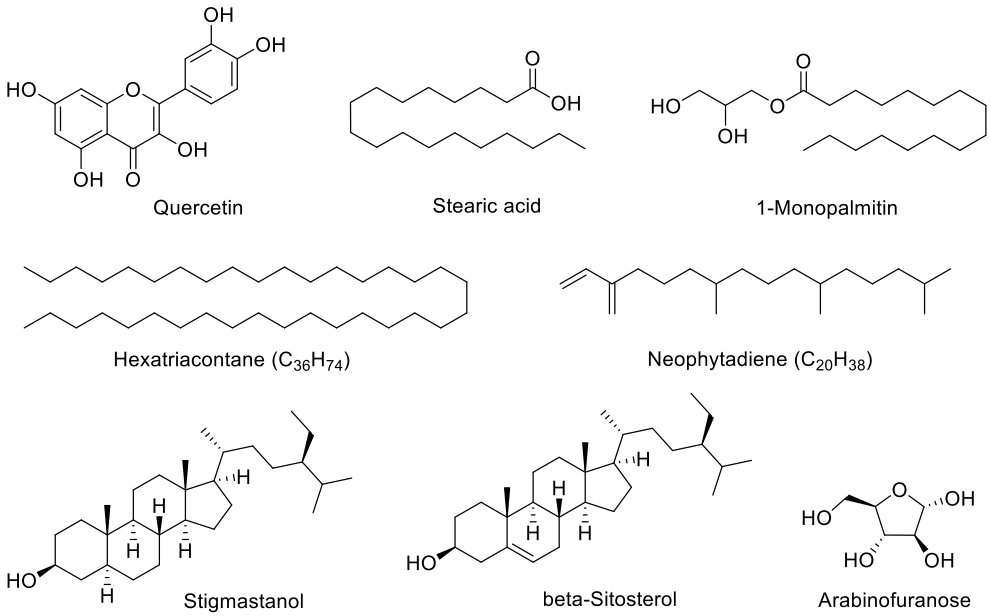

Fig. 4. Structures of major compounds found in *A. glabra* leaf extracts (drawn by the authors using ChemDraw 19.0)

The present study demonstrated pronounced changes in the metabolic profile of *A. glabra* leaves associated with *C. ohridella* infestation. A substantial reduction in the number of detected metabolites was observed in infested leaves, where the total number of identified compounds decreased from 114 to 62. Such a reduction in metabolite diversity may reflect stress-associated metabolic restructuring in assimilating tissues under herbivory pressure. Comparable metabolic alterations have previously been reported in woody plants exposed to insect herbivory and tissue damage (Kessler & Baldwin, 2002; Hartmann & Messier, 2008).

The most pronounced changes were observed among carbohydrate-related metabolites. Although the diversity of detected carbohydrates markedly declined in infested leaves, several soluble sugars, including sucrose, trehalose, and mannobiose, exhibited increased relative abundance. This pattern suggests selective reorganization rather than uniform suppression of carbohydrate metabolism. Soluble sugars are involved not only in carbon allocation and energy metabolism but also in osmotic regulation, reactive oxygen species balance, and stress signaling (Couée et al., 2006; Rolland et al., 2006). Similar herbivory-associated alterations in carbohydrate metabolism have been described in *Quercus* species, where insect damage affected soluble sugar composition and secondary metabolism (Schweitzer et al., 2012). In particular, the increased abundance of trehalose observed in infested *A. glabra* leaves may be associated with stress-related metabolic adjustment, as trehalose has been linked to stress tolerance and signaling processes in plants (Rolland et al., 2006).

Pronounced changes were also observed in the phenolic profile of infested leaves. The increased relative abundance of catechin together with the appearance of quercetin in infested tissues is consistent with previously described stress-associated accumulation of flavonoids in plants subjected to herbivory and oxidative stress (Harborne & Williams, 2000; Treutter, 2006; Agati et al., 2012). Flavonoids are known to participate in antioxidant protection and may influence insect feeding behavior, survival, and host recognition (Simmonds, 2001; Simmonds, 2003; Singh et al., 2021). Experimental studies demonstrated that flavonoids may negatively affect herbivore growth and nutrient assimilation (Diaz Napal & Palacios, 2015; Cui et al., 2019). According to Riddick (2024), flavonoids can act as feeding deterrents, repellents, or low-toxicity insecticidal compounds against certain groups of insects. In addition, herbivory-associated changes in catechin levels have previously been documented in *Quercus* species, where specific polyphenols were linked to plant defense responses (Moctezuma et al., 2014).

Changes in lipid- and terpenoid-related metabolites were also associated with *C. ohridella* infestation. Increased relative abundance of nonanoic acid and the appearance of compounds such as monopalmitin, monomyristin, and neophytadiene may reflect stress-associated modifications in lipid and terpenoid metabolism. Fatty acids are known to participate in plant signaling and defense-related responses (Heil & Ton, 2008; Kachroo & Kachroo, 2009). In addition, terpenoid-related metabolites are widely involved in plant interactions with herbivores and other environmental stressors (Dixon & Paiva, 1995; Erb & Kliebenstein, 2020; Divekar et al., 2022).

Conversely, several metabolites, including α-linolenic acid, chlorogenic acid, and β-tocopherol, were detected only in uninfested leaves, while reduced relative abundances were observed for squalene, β-amyrin, α-amyrin, lupeol, and stigmasterol in infested tissues. These changes may indicate alterations in secondary metabolism associated with herbivory stress. In particular, decreased squalene abundance may be associated with modified triterpenoid and sterol metabolism, as squalene represents an important precursor in the biosynthesis of multiple terpenoid-derived compounds (Moses et al., 2013; Tholl, 2015). Similar shifts in specialized metabolite composition under stress conditions have been described for various plant species (Wink, 2010). At the same time, several metabolites, including myristic acid, stigmastanol, arabinose, α-tocopherol, γ-tocopherol, benzoic acid, and cyclohexaneacetic acid, exhibited relatively stable abundance in both infested and uninfested leaves. The persistence of these compounds may indicate their involvement in constitutive metabolic functions associated with cellular stability under biotic stress.

Conclusion

Cameraria ohridella infestation was associated with substantial changes in the metabolite composition of *A. glabra* leaves, including reduced metabolite diversity and selective accumulation of stress-associated compounds. The most pronounced alterations were observed among carbohydrate-related metabolites, accompanied by changes in

phenolic, lipid-, and terpenoid-related compounds. The appearance of several metabolites exclusively in infested leaves together with reduced abundance or disappearance of others indicates extensive metabolic restructuring associated with herbivory stress. These findings highlight the potential role of specialized metabolites in the biochemical responses of *A. glabra* to insect infestation under urban environmental conditions.

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